ELSEVIER
ACADEMIC
PRESS

ENCYCLOPEDIA OF FOREST SCIENCES

EDITED BY

JEFFERY BURLEY
JULIAN EVANS
JOHN A YOUNGQUIST

ENCYCLOPEDIA OF
FOREST SCIENCES

ENCYCLOPEDIA OF FOREST SCIENCES

Editor-in-Chief
JEFFERY BURLEY

Editors
JULIAN EVANS
JOHN A YOUNGQUIST

ELSEVIER
ACADEMIC
PRESS

Amsterdam Boston Heidelberg London New York Oxford
Paris San Diego San Francisco Singapore Sydney Tokyo

Elsevier Ltd., The Boulevard, Langford Lane, Kidlington, Oxford, OX5 1GB, UK

Elsevier Inc., 525 B Street, Suite 1900, San Diego, CA 92101-4495, USA

First edition 2004

Library of Congress Control Number: 2003113256

A catalogue record for this book is available from the British Library

ISBN: 0-12-145160-7 (set)

This book is printed on acid-free paper

Printed in Spain

EDITORIAL ADVISORY BOARD

FOREWORD

This is a most timely publication because of the vast amount of new information on forest sciences that has been produced over the last few years and because of the growing realization of the vital importance of forests to the world. Fortunately for our future, the world is beginning to realize that forests are both vital for our survival and that they offer many benefits. These benefits vary from the more obvious ones such as timber and fibers for paper pulp, to the environmental aspects such as the sequestration of carbon, the protection of watersheds and the prevention of flooding in many areas. Also there is a growing emphasis on the production of non-timber forest products because of their role in sustainable management of forests.

Since forests are so crucial to our future their sustainable management is essential and this requires a great amount of expertise and information. As I look at the list of the authors and the advisory board of this Encyclopedia, it reads like a who's who of forest science. These experts have put together a collection of information and up-to-date contributions that will be an invaluable resource for anyone involved with forests in any way. I am sure that students at all levels, their teachers and lecturers, professional researchers, policy makers, and even the interested layman or amateur forester will find these volumes of great use.

As I look through the coverage I find it most comprehensive and contemporary. It includes such important modern topics as the molecular biology of forest trees, the role of forests in the carbon cycle, computer modeling and the use of recently developed methods such as geographic information systems. More traditional aspects such as forest biology and ecology, the processing of forest resources into a wide range of products, forestry management and practice and the economic and social aspects of forestry are brought up-to-date here. Not only are the contributions themselves useful, but they also direct the serious investigator to more in-depth or advanced material on each topic. It is also most useful that this fine work will be available in an electronic version that will facilitate cross-referencing to related topics and references.

I know that I will find these volumes most useful and frequently used and I am sure that they will be a standard reference work on forest sciences for at least the next decade. How timely at a period of human history when there is a desperate need to stop deforestation, re-forest many destroyed areas and develop better methods for sustainable use of forests and to conserve the many species of plants and animals which they hold.

Prof. Sir Ghillean Prance FRS
School of Plant Sciences, University of Reading,
Reading, UK

INTRODUCTION

At the start of the Third Millennium the levels of public and political attention to forests, their benefits to mankind, and their management are at their highest. National and international institutions, governmental and non-governmental organizations, all forms of media and representatives of civil society are searching for socially equitable methods of managing forests to obtain all their multiple benefits. Underlying this search is the need for precise and relevant information about the forests, their uses and management together with the political and social institutions that can best effect sustainable management.

Our audience for this reference work includes libraries, governmental and non-governmental organizations, universities and individuals involved in research on forests, forest products and services, and relevant topics, local, national and international decision-making authorities and administrations, forest land-owners and other forest-dependent individuals.

The ranges of biophysical and socio-economic aspects of forests, forestry, forest products and forest services are extremely large; correspondingly, past and current research cover large numbers of scientific disciplines and policy issues. Systematic research has been undertaken for over a century in some forest sciences such as silviculture and forest management; in other topics newly emerging techniques, such as those of molecular genetics, are being developed to aid understanding of physiological and environmental characteristics of trees and forests or to assist selective breeding of trees for plantations. An Encyclopedia of Forest Science therefore has to encompass a broad spectrum of pure and applied sciences, ancient and modern technologies, and old and recent knowledge.

In this Encyclopedia we have obtained outstanding contributions of some 200 specialists covering 250 topics that have wide implications for forest conservation, management and use worldwide. Of course, it is not possible to cover every possible subject of relevance to forests but the ones selected are generally of global interest; and even if they are of local, national or regional character, they are important to all those concerned with forest management, research, education, training, policy-making or public information.

Because of the great breadth of expected readership we have asked a wide range of contributing experts to produce up to approximately 4000 words summarizing current views of their topic. The contributions are not written in the traditional form of a scientific journal article with detailed bibliographic references for all major statements. Rather each is a continuous, highly readable description based on an author's personal view of the state of knowledge in her/his area of expertise. Selected major references are given at the end of each contribution to facilitate and encourage further reading on the subject. Wherever possible photographs, other graphical illustrations and tables are used to make the material more concise and visualized. Cross-referencing between contributions and the provision of dummy entries in the table of contents facilitate a full coverage of material relevant to each topic.

Some contributions are short because it proved difficult to identify an author with the appropriate experience and willingness to write full articles. However, these may be enlarged in future editions of the Encyclopedia and in the web-based version of it. The availability of modern information technology facilitates not only the preparation of such a work but also the maintenance of its timeliness, the spreading of its availability and the ease of searching and downloading selected material.

As Editors we thank the authors for their contributions, the editorial advisors for their specialist support, and the staff of Elsevier for their prompt and effective actions that have allowed the four volumes of the Encyclopedia to be published within two years of the initial commissioning of this reference work. We hope that the Encyclopedia will prove to be a valuable tool and source of information for many years to come. In particular we hope it will encourage a growing public and a dedicated profession to understand the facts and institutions necessary for wise management, use and conservation of the world's forest resources for the equitable benefit of all mankind.

Jeffery Burley
Julian Evans
John A. Youngquist

GUIDE TO USE OF THE ENCYCLOPEDIA

Structure of the Encyclopedia

The material in the Encyclopedia is arranged as a series of entries in alphabetical order. Most entries consist of several articles that deal with various aspects of a topic and are arranged in a logical sequence within an entry. Some entries comprise a single article.

To help you realize the full potential of the material in the Encyclopedia we have provided three features to help you find the topic of your choice: a Contents List, Cross-References and an Index.

1. Contents List

Your first point of reference will probably be the contents list. The complete contents list will provide you with both the volume number and the page number of the entry. On the opening page of an entry a contents list is provided so that the full details of the articles within the entry are immediately available.

Alternatively you may choose to browse through a volume using the alphabetical order of the entries as your guide. To assist you in identifying your location within the Encyclopedia a running headline indicates the current entry and the current article within that entry.

You will find 'dummy entries' where obvious synonyms exist for entries or where we have grouped together related topics. Dummy entries appear in both the contents list and the body of the text.

Example
If you were attempting to locate material on yield tables and forecasting via the contents list:

YIELD TABLES *see* MENSURATION: Forest Measurements; Growth and Yield; Timber and Tree Measurements; Yield Tables, Forecasting, Modeling and Simulation.

The dummy entry directs you to the Yield Tables, Forecasting and Simulation article, in the MENSURATION entry. At the appropriate location in the contents list, the page numbers for articles under Mensuration are given.

If you were trying to locate the material by browsing through the text and you looked up Yield Tables then the following information would be provided in the dummy entry:

Yield Tables *see* **Mensuration**: Forest Measurements; Growth and Yield; Timber and Tree Measurements; Yield Tables, Forecasting, Modeling and Simulation.

Alternatively, if you were looking up Mensuration the following information could be provided:

MENSURATION

Contents

Forest Measurements
Timber and Tree Measurements
Growth and Yield
Yield Tables, Forecasting, Modeling and Simulation
Tree-Ring Analysis

2. Cross-References

All of the articles in the Encyclopedia have been extensively cross-referenced.

The cross-references, which appear at the end of an article, serve three different functions. For example, at the end of the PATHOLOGY/Diseases of Forest Trees article, cross-references are used:

i. To indicate if a topic is discussed in greater detail elsewhere.

> PATHOLOGY/Diseases of Forest Trees.
> *See also*: **Ecology**: Plant–Animal Interactions in Forest Ecosystems. **Pathology**: Diseases Affecting Exotic Plantation Species; Heart Rot and Wood Decay; Insect Associated Tree Diseases; Leaf and Needle Diseases; *Phytophthora* Root Rot of Forest Trees; Pine Wilt and the Pine Wood Nematode; Root and Butt Rot Diseases; Rust Diseases; Stem Canker Diseases; Vascular Wilt Diseases. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

ii. To draw the reader's attention to parallel discussions in other articles.

> PATHOLOGY/Diseases of Forest Trees.
> *See also*: **Ecology**: Plant–Animal Interactions in Forest Ecosystems. **Pathology**: Diseases Affecting Exotic Plantation Species; Heart Rot and Wood Decay; Insect Associated Tree Diseases; Leaf and Needle Diseases; *Phytophthora* Root Rot of Forest Trees; Pine Wilt and the Pine Wood Nematode; Root and Butt Rot Diseases; Rust Diseases; Stem Canker Diseases; Vascular Wilt Diseases. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

iii. To indicate material that broadens the discussion.

> PATHOLOGY/Diseases of Forest Trees.
> *See also*: **Ecology**: Plant–Animal Interactions in Forest Ecosystems. **Pathology**: Diseases Affecting Exotic Plantation Species; Heart Rot and Wood Decay; Insect Associated Tree Diseases; Leaf and Needle Diseases; *Phytophthora* Root Rot of Forest Trees; Pine Wilt and the Pine Wood Nematode; Root and Butt Rot Diseases; Rust Diseases; Stem Canker Diseases; Vascular Wilt Diseases. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

3. Index

The index will provide you with the page number where the material is located, and the index entries differentiate between material that is a whole article, is part of an article or is data presented in a figure or table. Detailed notes are provided on the opening page of the index.

4. Glossary

A glossary of terms used within the Encyclopedia appears in Volume 4, before the index. This is organised alphabetically and features explanations of many of the specialist terms used throughout this publication.

5. Contributors

A full list of contributors appears at the begining of each volume.

CONTRIBUTORS

S AbuBakr
Western Michigan University
Kalamazoo, MI, USA

C M Achiam
University of British Columbia
Vancouver, BC, Canada

B J Aegerter
University of California
Davis, CA, USA

S N Aitken
University of British Columbia
Vancouver, Canada

A E Akay
Kahramanmaras Sutcu Imam University
Kahramanmaras, Turkey

W Alfaro
Corporación Nacional Forestal
Santiago, Chile

P W Allen
Harpenden, UK

A Alonso
Smithsonian Institution
Washington, DC, USA

E Apud
University of Concepción, Chile

R G Aravamuthan
Western Michigan University
Kalamazoo, MI, USA

N A Aravind
Ashoka Trust for Research in Ecology and the Environment
Hebbal, Bangalore, India

J E M Arnold
Oxford, UK

U Arzberger
Food and Agriculture Organization
Rome, Italy

R H Atalla
USDA
Madison, WI, USA

S Avramidis
University of British Columbia
Vancouver, Canada

A Baldini
Corporación Nacional Forestal
Santiago, Chile

N A Balliet
University of Northern British Columbia
Prince George, BC, Canada

J C G Banks
Australian National University
Canberra, Australia

J Barbour
US Department of Agriculture Forest Service
Portland, OR, USA

J Barlow
University of East Anglia
Norwich, UK

R D Barnes
University of Oxford
Oxford, UK

J R Barnett
University of Reading
Reading, UK

T M Barrett
USDA Forest Service PNW Research Station
Forest Inventory and Analysis
Portland, OR, USA

S Bass
Department for International Development
London, UK

C Beadle
CSIRO Forestry and Forest Products
Hobart, Tasmania, Australia

P Bebi
WSL Swiss Federal Institute for Snow and Avalanche Research
Davos, Switzerland

S Bell
Edinburgh College of Art
Edinburgh, UK

N Bhattarai
Government of Nepal
Kathmandu, Nepal

P P Bhojvaid
Forest Research Institute
Dehradun, India

A Blum
Wageningen University
Wageningen, The Netherlands

B Bonnell
Canadian Forest Service
Ottawa, Canada

T H Booth
CSIRO Forestry and Forest Products
Canberra, ACT, Australia

N M G Borralho
Forest and Paper Research Institute (RAIZ)
Alcoentre, Portugal

Ž Borzan
University of Zagreb
Zagreb, Croatia

J L Bowyer
University of Minnesota
St Paul, MN, USA

C L Brack
Australian National University
Canberra, Australia

P Brang
Swiss Federal Research Institute WSL
Birmensdorf, Switzerland

B V Bredenkamp
Department of Forest Science
University of Stellenbosch
South Africa

J L Brewbaker
University of Hawaii
Honolulu, Hawaii, USA

R D Briggs
State University of New York
Syracuse, NY, USA

N Brown
Oxford Forestry Institute
Oxford, UK

L A Bruijnzeel
Vrije Universiteit
Amsterdam, The Netherlands

E M Bruna
University of Florida
Gainesville, FL, USA

R D Burdon
New Zealand Forest Research Institute
Rotorua, New Zealand

J A Burger
Virginia Polytechnic Institute and State University
Blacksburg, VA, USA

J Burley
University of Oxford
Oxford, UK

D F R P Burslem
University of Aberdeen
Aberdeen, UK

Alexander Buttler
University of Franche-Comté
Besançon, France

T D Byram
Texas A&M University
College Station
TX, USA

N Bystriakova
International Network for Bamboo and Rattan
Beijing, China

I R Calder
University of Newcastle upon
Tyne, UK

J H Cameron
Western Michigan University
Kalamazoo, MI, USA

A E Camp
Yale University
New Haven, CT, USA

M G R Cannell
Centre for Ecology and Hydrology
Penicuik, Scotland, UK

R Ceulemans
University of Antwerp
Wilrijk, Belgium

J L Chamberlain
US Department of Agriculture Forest Service
Blacksburg, VA, USA

D C Chaudhari
Forest Research Institute, Dehradun
Uttaranchal, India

J P Cornelius
World Agroforestry Centre
Lima, Peru

J Croke
University of New South Wales
Canberra, Australia

B Dahlin
Swedish University of Agricultural Sciences
Alnarp, Sweden

F Dallmeier
Smithsonian Institution
Washington, DC, USA

C Danks
University of Vermont
Burlington, VT, USA

R K Didham
University of Canterbury
Christchurch, New Zealand

A F G Dixon
University of East Anglia
Norwich, UK

J R dos Santos
National Institute for Space Research
São José dos Campos, Brazil

M R Doshi
Progress in Paper Recycling
Appleton, WI, USA

A Ducousso
INRA, UMR Biodiversité Gènes et Ecosystèmes
Cestas, France

J M Dyer
Weyanwega, WI, USA

O Eckmüllner
Institute for Forest Growth and Yield Research
Vienna, Austria

T Elder
USDA – Forest Service
Pineville, LA, USA

H F Evans
Forestry Commission
Farnham, UK

J Evans
Imperial College London
Ascot, UK

B Fady
Institut National de la Recherche Agronomique
Avignon, France

L L Fagan
Landcare Research
Lincoln, New Zealand

W C Feist
Middleton, WI, USA

M Ferretti
LINNÆA ambiente
Florence, Italy

D Fjeld
Swedish University of Agricultural Sciences
Umeå, Sweden

P D Fleming III
Western Michigan University
Kalamazoo, MI, USA

E M Flores
Academia Nacional de Ciencias
San José, Costa Rica
US Department of Agriculture Forest Service
Starkville, MS, USA

L Fortmann
University of California–Berkeley
Berkeley, CA, USA

J K Francis
Jardín Botánico Sur, San Juan
Puerto Rico, USA

C E Frazier
Virginia Technical Institute
Blacksburg, VA, USA

J S Fried
USDA Forest Service PNW Research Station
Forest Inventory and Analysis
Portland, OR, USA

C J Friel
University of California
Davis, CA, USA

W S Fuller
FRM Consulting
Federal Way, WA, USA

K N Ganeshaiah
Ashoka Trust for Research in Ecology and the Environment
Hebbal, Bangalore, India

M Garbelotto
University of California – Berkeley
Berkeley, CA, USA

R García
St Louis, MO, USA

B Gardiner
Forest Research
Roslin, UK

J Ghazoul
Imperial College London
Ascot, UK

J N Gibbs
Aberyail, Llangynidr
Wales, UK

S Gillett
University of Oxford
Oxford, UK

D L Godbold
University of Wales
Bangor, UK

H Goldemund
GeoSyntec Consultants
Atlanta, GA, USA

I S Goldstein
North Carolina State University
Raleigh, NC, USA

T R Gordon
University of California
Davis, CA, USA

J Grace
Edinburgh University
Edinburgh, UK

J E Grogan
Yale University
New Haven, CT, USA

J B Hall
University of Wales
Bangor, UK

J E Hall
Canadian Forest Service
Ottawa, Canada

S W Hallgren
Oklahoma State University
Stillwater, OK, USA

A L Hammett
Virginia State University and Technical Institute
Blacksburg, VA, USA

W E Hammitt
Clemson University
Clemson, SC, USA

G E St J Hardy
Murdoch University
Murdoch, Western Australia

R Harmer
Forest Research
Farnham, UK

S Harris
University of Oxford
Oxford, UK

C D B Hawkins
University of Northern British Columbia
Prince George, BC, Canada

H R Heinimann
Swiss Federal Institute of Technology
Zurich, Switzerland

R Heinrich
Food and Agriculture Organization
Rome, Italy

R Helliwell
West End, Wirksworth
Derbyshire, UK

T L Highley
Henderson, NV, USA

T M Hinckley
University of Washington
Seattle, WA, USA

P Hogarth
University of York
York, UK

C J Houtman
USDA
Madison, WI, USA

M A Hubbe
North Carolina State University
Raleigh, NC, USA

I R Hunter
International Network for Bamboo and Rattan
Beijing, China

J Huss
University of Freiburg
Freiburg, Germany

P Hyttinen
Regional Council of North Karelia
Joensuu, Finland

P J Ince
USDA Forest Service
Madison, WI, USA

J L Innes
University of British Columbia
Vancouver, BC, Canada

G E Jackson
Edinburgh University
Edinburgh, UK

K Jacobs
University of Pretoria
Pretoria, South Africa

R James
Australian National University
Canberra, Australia

J P Janovec
Botanical Research Institute of Texas
Fort Worth, TX, USA

M K Joyce
Western Michigan University
Kalamazoo, MI, USA

M Jurvélius
Forestry Department, FAO
Rome, Italy

F A Kamke
Virginia Polytechnic Institute and State University
Blacksburg, VA, USA

A Kangas
University of Helsinki
Helsinki, Finland

J Kangas
Finnish Forest Research Institute
Joensuu, Finland

P J Kanowski
Australian National University
Canberra, Australia

M Kappelle
Utrecht University
Utrecht, The Netherlands

K Kärkkäinen
Finnish Forest Research Institute
Vantaa, Finland

M Karki
Medicinal and Aromatic Plants Program in Asia
New Delhi, India

D F Karnosky
Michigan Technological University
Houghton, MI, USA

B Kasal
North Carolina State University
Raleigh, NC, USA

S N Kee
University of California
Riverside, CA, USA

G Kerr
Forestry Commission Research Agency
Farnham, UK

B B Kinloch
Institute of Forest Genetics
Berkeley, CA, USA

E D Kjaer
The Royal Agriculture and Veterinary University
Hoersholm, Denmark

M Köhl
Dresden University of Technology
Dresden, Germany

C C Konijnendijk
Danish Forest and Landscape Research Institute
Hoersholm, Denmark

A V Korotkov
UN Economic Commission for Europe Timber Section
Geneva, Switzerland

V Koski
Vantaa, Finland

M V Kozlov
University of Turku
Turku, Finland

A Kremer
INRA, UMR Biodiversité Gènes et Ecosystèmes
Cestas, France

B Krishnapillay
Forest Research Institute Malaysia
Kepong, Malaysia

T Krug
National Institute for Space Research
São José dos Campos, Brazil

S A Laird
University College London
Ascot, UK

D Lamb
University of Queensland
Brisbane, Australia

A Lawrence
University of Oxford
Oxford, UK

R R B Leakey
James Cook University
Cairns, Queensland, Australia

S R Leather
Imperial College London
Ascot, UK

V LeMay
University of British Columbia
Vancouver, BC, Canada

W J Libby
University of California Forest Products Laboratory
Berkeley, CA, USA

K H Ludovici
US Department of Agriculture Forest Service
Research Triangle Park, USA

A E Lugo
US Department of Agriculture Forestry Service
Río Piedras, Puerto Rico, USA

H G Lund
Forest Information Services
Gainesville, VA, USA

E Mackie
Forest Research
Farnham, UK

P Maclaren
Piers Maclaren & Associates
Rangiora, New Zealand

P Maiteny
South Bank University
London, UK

K M Martin-Smith
University of Tasmania
Hobart, Tasmania, Australia

W L Mason
Northern Research Station
Roslin, UK

R Matthews
Forest Research
Farnham, UK

C Mátyás
University of West Hungary
Sopron, Hungary

D G McCullough
Michigan State University
East Lansing, MI, USA

J J McDonnell
Oregon State University
Corvallis, OR, USA

T J McDonough
Institute of Paper Science and Technology
Atlanta, GA, USA

C R McIntyre
McIntyre Associates
Walls, MS, USA

K McNabb
Auburn University
Auburn, AL, USA

R E McRoberts
US Department of Agriculture Forest Service
St Paul, MN, USA

F Médail
Université d'Aix–Marseille III
Aix-en-Provence, France

R Meilan
Oregon State University
Corvallis, OR, USA

M J Meitner
University of British Columbia
Vancouver, BC, Canada

F Meyer
University of Concepción
Chile

E Mikkonen
University of Helsinki
Helsinki, Finland

H G Miller
University of Aberdeen
Aberdeen, UK

M R Milota
Oregon State University
Corvallis, OR, USA

A J Moffat
Forest Research
Farnham, UK

S A Mori
New York Botanical Garden
New York, USA

L A Morris
University of Georgia
Athens, GA, USA

M A Murphy
Virginia State University and Technical Institute
Blacksburg, VA, USA

P G Murphy
Michigan State University
East Lansing, MI, USA

K K N Nair
Kerala Forest Research Institute
Peechi, Kerala State, India

G Newcombe
University of Idaho
Moscow, ID, USA

D D Nicholas
Mississippi State University
MS, USA

W L Nutter
Nutter & Associates, Inc.
Athens, GA, USA

T Nuutinen
Finnish Forest Research Institute
Joensuu Research Center
Joensuu, Finland

C D Oliver
Yale University
New Haven, CT, USA

P M O Owende
Institute of Technology Blanchardstown
Dublin, Ireland

P E Padgett
USDA Forest Service
Riverside, CA, USA

P Parker
Western Michigan University
Kalamazoo, MI, USA

D Parry
State University of New York
Syracuse, NY, USA

T Peck
European Forest Institute
Vaud, Switzerland

H Pereira
Instituto Superior de Agronomia
Lisbon, Portugal

C A Peres
University of East Anglia
Norwich, UK

D Peterson
Western Michigan University
Kalamazoo, MI, USA

B M Potts
University of Tasmania
Hobart, Tasmania, Australia

G T Prance
University of Reading
Reading, UK

M Predny
Virginia Polytechnic Institute and State University
Blacksburg, VA, USA

M L Putnam
Oregon State University
Corvallis, OR, USA

F E Putz
Center for International Forestry Research
Jakarta, Indonesia

A K Rai
Forest Research Institute
Dehradun, India

I V Ramanuja Rao
International Network for Bamboo and Rattan (INBAR)
Beijing, China

T B Randrup
Danish Forest and Landscape Research Institute
Hoersholm, Denmark

S Rani
North-Eastern Hill University
Shillong, India

R B S Rawat
National Medicinal Plants Board
New Delhi, India

M Rebetez
Swiss Federal Institute for Snow and Landscape Research
Lausanne, Switzerland

M L Reid
University of Calgary
Calgary, AB, Canada

R S Reiner
USDA
Madison, WI, USA

M Reinhard
Swiss Federal Institute for Snow and Landscape Research
Lausanne, Switzerland

D M Richardson
University of Cape Town
Cape Town, South Africa

G J F Ring
University of Wisconsin–Stevens Point
Stevens Point, WI, USA

A Robinson
University of Idaho
Moscow, ID, USA

R Rogers
University of Wisconsin–Stevens Point
Stevens Point, WI, USA

R M Rowell
University of Wisconsin–Madison
Madison, WI, USA

P W Rundel
University of California
Los Angeles, CA, USA

J D Salter
University of British Columbia
Vancouver, BC, Canada

R Sands
University of Canterbury
Christchurch, New Zealand

P S Savill
University of Oxford
Oxford, UK

O Savolainen
University of Oulu
Oulu, Finland

L G Saw
Forest Research Institute Malaysia
Kepong, Kuala Lumpur, Malaysia

H Schanz
Wageningen University
Wageningen, The Netherlands

S E Schlarbaum
University of Tennessee
Knoxville, TN, USA

M Schneebeli
WSL Swiss Federal Institute for Snow and Avalanche Research
Davos, Switzerland

S H Schoenholtz
Oregon State University
Corvallis, OR, USA

W Schönenberger
Swiss Federal Research Institute WSL
Birmensdorf, Switzerland

H T Schreuder
USDA Forest Service
Fort Collins, CO, USA

T P Schultz
Mississippi State University
MS, USA

F W M R Schwarze
EMPA, St. Gallen, Germany

D F Scott
Okanagan University College
Kelowna, Canada

G M Scott
State University of New York
Syracuse, NY, USA

W E Scott
Miami University
Oxford, OH, USA

R A Sedjo
Resources for the Future
Washington, DC, USA

E-H M Sène
Food and Agriculture Organization
Rome, Italy

J Sessions
Oregon State University
Corvallis, OR, USA

R Uma Shaanker
Ashoka Trust for Research in Ecology and the Environment
Hebbal, Bangalore, India

S R J Sheppard
University of British Columbia
Vancouver, BC, Canada

T Sievänen
Finnish Forest Research Institute
Helsinki, Finland

E A Simmons
National School of Forestry
University of Central Lancashire
Penrith, Cumbria, UK

F L Sinclair
University of Wales
Bangor, UK

J P Skovsgaard
Royal Veterinary and Agricultural University
Forest & Landscape Denmark
Coperhagen, Denmark

P Smethurst
CSIRO Forestry and Forest Products and Corperative
Research Centre for Sustainable Production
Hobart, Tasmania, Australia

I R Smith
University of Queensland
St Lucia, Australia

S Smulski
Wood Science Specialists Inc.
Shutesbury, MA, USA

M Spalding
UNEP World Conservation Monitoring Centre
Cambridge, UK

M R Speight
University of Oxford
Oxford, UK

R Spinelli
National Council for Research – Timber and Tree Institute
Florence, Italy

E L Springer
University of Wisconsin
Madison, WI, USA

B Stanton
GreenWood Resources
Clatskanie, OR, USA

J K Stone
Oregon State University
Corvallis, OR, USA

K Suzuki
The University of Tokyo
Tokyo, Japan

R Szymani
Wood Machining Institute
Berkeley, CA, USA

K ten Kate
Insight Investment
London, UK

R O Teskey
University of Georgia
Athens, GA, USA

R C Thakur
Michigan Technological University
Houghton, MI, USA

K Theron
Department of Forest Science
University of Stellenbosch
South Africa

J R Thompson
Talo Analytic International, Inc.
Duluth, GA 30096, USA

B K Tiwari
North-Eastern Hill University
Shillong, India

T Tokola
University of Helsinki
Helsinki, Finland

M Tomé
Instituto Superior de Agronomia
Lisbon, Portugal

E Tomppo
Finnish Forest Research Institute
Helsinki, Finland

M A Topa
Boyce Thompson Institute for Plant Research
Ithaca, NY, USA

S Torreano
The University of the South
Sewanee, TN, USA

H Tynsong
North-Eastern Hill University
Shillong, India

S J Van Bloem
Michigan State University
East Lansing, MI, USA

J P van Buijtenen
Texas A&M University
College Station, TX, USA

S Vedavathy
Herbal Folklore Research Centre
Tirupati, India

R A Vertessy
CSIRO Land and Water
Canberra, Australia

J A Vozzo
US Department of Agriculture Forest Service
Starkville, MS, USA

F G Wagner
University of Idaho
Moscow, ID, USA

C Ward Thompson
OPENspace Research Centre
Edinburgh, UK

S E Ward
Mahogany for the Future, Puerto Rico

R H Waring
Oregon State University
Corvallis, OR, USA

J Webber (Retired)
Ministry of Forests, Research Branch
Victoria, BC, Canada

J F Webber
Forestry Commission Research Agency
Farnham, UK

M Weiler
University of British Columbia
Vancouver, BC, Canada

L T West
University of Georgia
Athens, GA, USA

C J Weston
University of Melbourne
Creswick, Victoria, Australia

T L White
University of Florida
Gainesville, FL, USA

K L Whittaker
University of Melbourne
Creswick, Victoria, Australia

K F Wiersum
Wageningen University
Wageningen, The Netherlands

K E Wightman
Purdue University
West Lafayette, IN, USA

R J E Wiltshire
University of Tasmania
Tasmania, Australia

M J Wingfield
University of Pretoria
Pretoria, Republic of South Africa

H Wolf
State Board for Forestry (Saxony)
Pirna, Germany

J L G Wong
Wild Resources Ltd
Bangor, UK

P J Wood
Commonwealth Forestry Association
Oxford, UK

M Worbes
University of Göttingen
Göttingen, Germany

M A Wulder
Canadian Forest Service
Victoria, BC, Canada

L A Xu
Nanjing Forestry University
Nanjing, Jiangsu, China

A D Yanchuk
British Columbia Ministry of Forests
Victoria, BC, Canada

J A Youngquist
Forest Products Consultant
Verona, WI, USA

R L Youngs
Virginia Polytechnic Institute and State University
Blacksburg, VA, USA

J I Zerbe
USDA Forest Products Laboratory
Madison, WI, USA

A Zink-Sharp
Virginia Polytechnic Institute and State University
Blacksburg, VA, USA

B Zobel
North Carolina State University
Raleigh, NC, USA

CONTENTS

VOLUME 1

A

B

C

N

O

P

Q

R

VOLUME 3

S

VOLUME 4

A

AFFORESTATION

Contents

Species Choice

T H Booth, CSIRO Forestry and Forest Products, Canberra, ACT, Australia

Published by Elsevier Ltd., 2004

Introduction

Species choice is not a new problem. In 1665 John Evelyn wrote in his book *Sylva*:

> First it will be requisite to agree upon the species: as what species are likely to be of greatest use, and the fittest to be cultivated and then to consider how planting may be best effected.

When the Food and Agriculture Organization produced a book on *Choice of Tree Species* in 1958, the importance of first identifying the purpose of tree planting was still recognized. Over 130 pages of the book deal with ecological principles to assist selecting trees for use in different parts of the world. This includes descriptions of various climate, soil, and vegetation classifications. These systems are now mainly of historical interest. But before the widespread availability of computers, information on environmental conditions was often represented as classes, and areas suitable for particular species were frequently shown as zones on maps.

In terms of introducing exotic species, the work of Golfari was some of the most practically important. Golfari and his colleagues produced maps dividing Brazil into 26 regions on the basis of altitude, vegetation types, mean annual temperature, rainfall and its distribution, water deficit, and frost occurrence. They indicated species, mainly eucalypts and pines, suitable for particular regions.

Information of this sort is developed on the basis of knowledge of conditions within a species natural distribution, as well as its success or failure when evaluated in trials outside its natural distribution. For example, two volumes written by Poynton, published in 1979, describe the introduction of eucalypts and pines to southern Africa. These books provide some of the most detailed descriptions of tree species trials ever prepared. The volume on eucalypts includes information on the introduction of 134 species. Details of natural occurrence, characteristics and uses, silviculture, utilization, and potential are presented for each species and results from trials are summarized. Details for specific trial sites are also tabulated for each species. Information is provided on country, plantation name and plot number, silvicultural zone, altitude, annual rainfall, aspect, soil depth and texture, age, stocking, mean diameter at breast height (dbh), mean height, mean volume, and mean annual increment as well as general comments on health and form. Information on the latitude, longitude, and elevation of 271 sites is provided in an appendix along with mean maximum temperature of the warmest month, mean minimum temperature of the coldest month, and mean annual rainfall of each site where available. Another appendix includes recommendations for species suitable for particular climatic zones and a map is included showing these zones.

A Guide to Species Selection for Tropical and Sub-Tropical Plantations, produced at the Commonwealth Forestry Institute in 1980, marked a significant step away from the use of classifications and maps, and towards the use of computer-based methods. The characteristics of 125 species were described in terms of 40 factors grouped within headings, including taxonomy, natural occurrence, climate, soils, silviculture, production, protection planting, timber, utilization, nursery, principal pests and diseases, and principal references. For those users with access to a computer a program was provided to search these data. But as personal computers were not widely available in 1980, instructions were also provided on how to use punched cards to sort through the data manually and select suitable species for particular uses and environments.

Unlike the books prepared by Poynton, the *Guide to Species Selection* only provided summary information for particular species and not site-specific results. In the late 1980s the Commonwealth Scientific and Industrial Research Organization (CSIRO) Division of Forestry and Forest Products developed a computerized tree crop database called TREDAT. This was designed for the storage and selective retrieval of results from trials. It currently contains information for 411 species, mainly of Australian origin, and for 303 sites, mainly in Australia. It includes information on a total of 90 factors relating to site characteristics, management history, tree performance, botanical identity, and project description. Though this information is useful for assisting species selection, the system contains only raw data for specific sites. It does not contain summary information on the characteristics and requirements of particular species.

Over the years many articles and books have been written to assist species selection for particular countries or regions. These usually contain summary information on factors such as uses, natural occurrence, plantations outside the natural distribution, and environmental requirements. Sometimes these descriptions are complemented by tabular information, which makes it easier to check the uses and environmental requirements of many species quickly. As personal computers became more widely available several programs were developed that enabled tabular data to be searched more efficiently. When selecting tree species for a particular site it is well worth checking to see if a relevant article, book, or computer program exists to assist species choice in a particular region of interest.

Previous reviews have identified some key questions to consider when selecting species for planting. These are:

- What are the environmental characteristics of the site?
- What product or service is the tree species to provide?
- Which species will grow on the sites available?

Site Characterization

It is usually desirable to collate some basic information on site conditions before considering which species are suitable for planting. The location of sample sites can be accurately recorded using global positioning systems (GPS). The location of sites may also be recorded in terms of slope, aspect, and position in the landscape (e.g., hilltop, midslope, or valley bottom).

Minimum climatic information includes mean monthly values for maximum temperature, minimum temperature, and precipitation. Key factors such as mean annual temperature, mean maximum temperature of the hottest month, mean minimum temperature of the coldest month, rainfall seasonality, and dry-season length can be simply calculated from these monthly values. In frost-prone areas, information on absolute (i.e., record) minimum temperature is also useful. Monthly mean temperature and rainfall data are generally readily available from standard sources, such as summaries published by national meteorological agencies and the Food and Agriculture Organization or from the web. In some cases interpolation relationships may be available that allow more reliable estimates to be made for sites which are some distance from meteorological stations. Monthly mean values for solar radiation and evaporation may also be useful to run models that can estimate potential growth rates. However, they are not generally required for species selection.

Samples for assessing soil conditions can be obtained by using soil augers or digging pits. If large areas are to be sampled, mechanical drilling equipment or backhoes can speed up the sampling process. For species selection purposes only simple information on soil texture as well as reaction (pH) and drainage are usually required. More detailed physical and chemical information may be taken to estimate potential productivity. For example, measurements of soil depth as well as texture allow water-holding capacity to be estimated. Samples for chemical analysis are often taken from the topsoil layer (i.e., *A* horizon) and at a lower depth. Analyses may be carried out for major nutrients, such as nitrogen, phosphorus, and potassium, as well as for exchangeable cations of minor nutrients. If appropriate, other analyses such as soil salinity may also be required.

Information on natural vegetation was widely used to assist species selection in the past. Both overstory and understory species respond to the climatic and soil conditions of the site and can provide an indication of its potential for other species. However, as potential sites for plantations have often been previously disturbed, the value of natural vegetation as an indicator of site potential has declined.

The CAB International Forestry Compendium

Having collected information on site conditions, the questions of which species are suitable for particular uses and which species will grow on particular sites can be considered.

The Forestry Compendium developed by CAB International (CABI) is probably the most impressive tool that has been developed to assist tree species choice. The Forestry Compendium aims to provide global coverage and was prepared using contributions from hundreds of experts around the world. It includes a taxonomic database for 22 000 species, with detailed descriptions for 1200 species. The first CD-ROM version of the global module was released in 2000 and a revised version was issued in 2003. It is planned to release improved CD-ROM versions every 2–3 years and a version including the latest amendments can also be accessed via the internet (www.cabicompendium.org/fc).

A particular advantage of the CABI system over other tree selection systems is that it allows access to the research literature by providing over 50 000 references with abstracts. For example, the reference browser in the 2003 CD-ROM version provides access to abstracts of 67 references mentioning species choice and 128 references referring to species selection.

Though the Forestry Compendium has many potential applications, tree species selection is one of its main purposes and it includes a detailed species selection module, which can be entered from the main menu. The user can select from scores of options listed under four main headings: uses, distribution, environment, and silviculture.

Uses

Determining the ultimate use of trees is a vitally important step in species selection. Modern forest processing facilities generally require raw materials of consistent quality. So, if the aim is to grow trees to supply an existing processing plant then the species selection process may be easy. The existing plantations or forests supplying a particular facility may already indicate the only acceptable species.

However, if opportunities to use different species are more open, the Forestry Compendium can assist selection within three main usage categories: land/environment, wood, and nonwood, that together include a total of more than 110 subcategories (**Figure 1**).

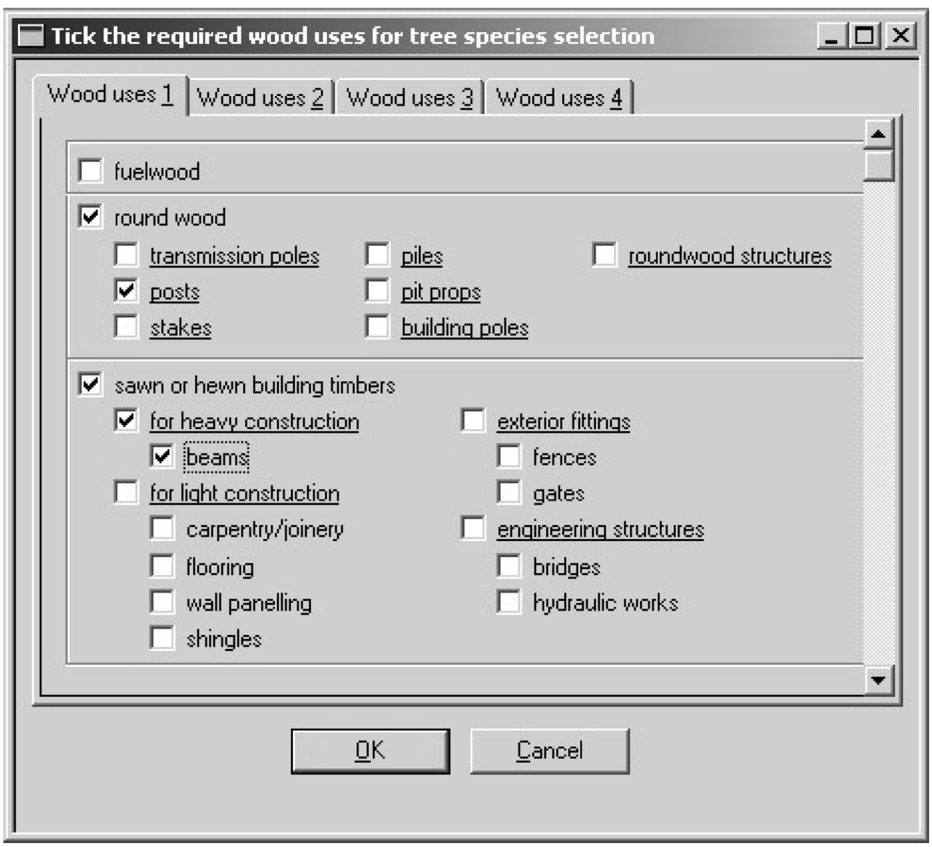


Figure 1 CABI *Forestry Compendium* – wood uses, menu 1 of 4. Reproduced with permission from CAB International (2003) *Forestry Compendium.* CAB International, Wallingford, UK. Available as CD-ROM or online at: www.cabicompendium.org/fc.

Distribution

The Forestry Compendium's Tree Species Selection Module provides the option to select a species on the basis of its country or region, or on latitudinal limits. It is possible to select species that are native or have been introduced to more than 650 countries or regions.

Environment

Altitude, rainfall, temperature, and soil properties are the main environmental categories used in the Tree Species Selection Module to determine which species can grow on particular sites. Altitude, rainfall, and temperature data can be entered as single numbers or ranges.

Soil properties can be selected under four main headings. Soil texture includes light (sands and sandy loams), medium (loams and sandy clay loams), and heavy (clays, clay loams, and sandy clays) options. Soil drainage includes free, impeded, and seasonally waterlogged. Soil reaction includes very acid (pH <4.0), acid (pH 4.0–6.0), neutral (pH 6.1–7.4), and alkaline (pH >7.4). Special soil tolerances include shallow, saline, sodic, and infertile.

Silviculture

Various silvicultural characteristics can be selected within the Tree Species Selection Module. For example, an ability to tolerate any or all of nine factors, including drought and termites, can be selected. Similarly, ability to coppice or fix nitrogen can be selected from six silvicultural characteristics. Options are also provided to select from three categories of seed storage, five categories of vegetative propagation, and five methods of stand establishment.

Species Selection

The user can select a wide variety of options within the four main headings of uses, distribution, environment, and silviculture. The database can then be searched for species that satisfy any or all of these characteristics. **Figure 2** shows the results of a simple search carried out using the Forestry Compendium.

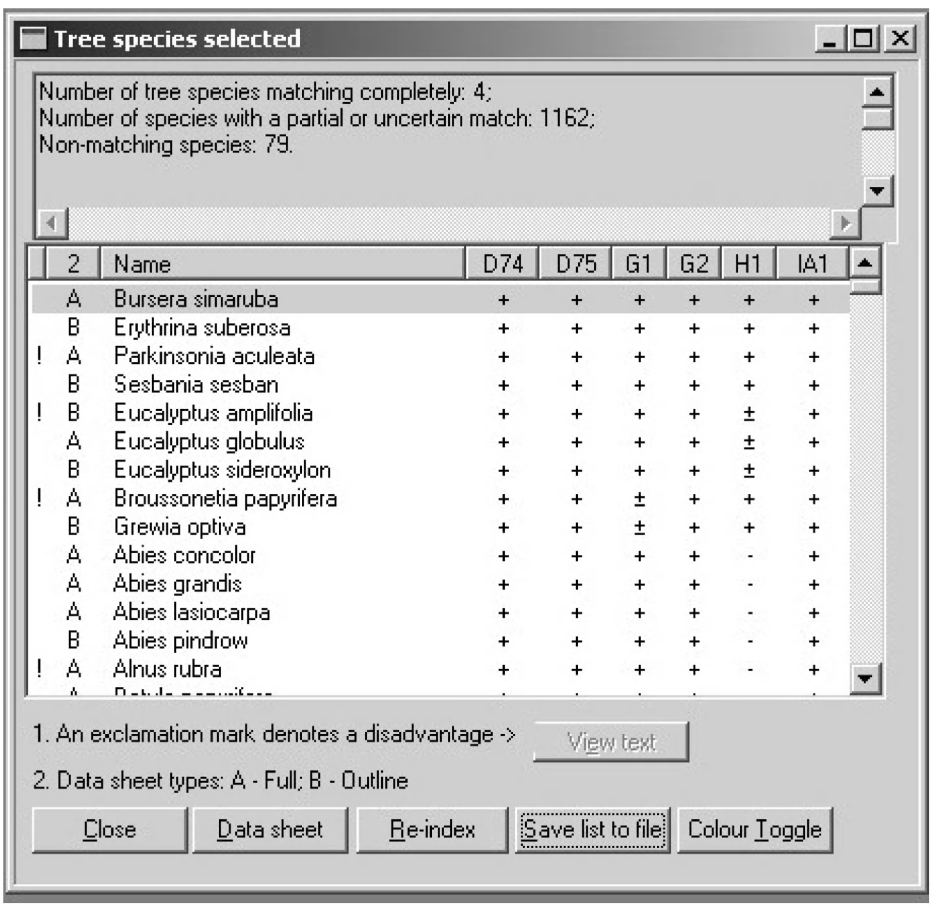


Figure 2 CABI *Forestry Compendium* – tree species selection output. Reproduced with permission from CAB International (2003) *Forestry Compendium*. CAB International, Wallingford, UK. Available as CD-ROM or online at: www.cabicompendium.org/fc.

The features requested were D74 wood pulp, D75 short fiber pulp, G1 mean annual rainfall 500–750 mm, G2 winter rainfall seasonality, H1 mean annual temperature 20–25°C, and IA1 light-texture soil (sands, sandy loams). The output indicates the number of species that completely satisfy the requirements, those that provide a partial match, and those that fail on all counts. Individual species are listed with those that satisfy most criteria at the top of the list.

Exclamation marks in the first column indicate potential problems, such as possible risk as weed species. There is increasing concern about species that can become established outside the areas where they are intended to grow. Particular care should be taken when introducing potentially invasive species, such as *Prosopis juliflora* and *Acacia* spp., into areas where they have not previously been grown.

The second column indicates if full (A) or outline (B) data sheets are available. Full data sheets include sections on name, importance, botanical features, geographic distribution, environmental amplitude, silviculture and management, protection, variation and breeding, uses, disadvantages, and references. The columns following the species name indicate whether it has fully satisfied (+), partially satisfied (+/−), or failed to satisfy (−) the particular criterion.

Checking the data sheets will indicate that some of the species shown in **Figure 2**, such as *Bursera simaruba* and *Erythrina suberosa*, have little current commercial use. Others, such as *Eucalyptus globulus*, have been successful in many countries. Information like this can help select species worth including in trials. However, if it is available, the most useful information may come from practical experience in local and nearby regions.

Pests and Diseases

The Forestry Compendium provides information on insect pests, diseases, and parasitic plants which may cause problems for particular trees within each species description. For example, *Lophodermium pinastri* causes needle cast problems for *Pinus sylvestris* (Scots pine) in nurseries and in young (2–5-year-old) high-density plantations. Highlighting the name of the disease and selecting a 'soft link' button brings information about the disease onto the screen. This often includes maps showing the countries where it has been observed. Where available, control methods for important pests and diseases are described within each tree species description.

Matching Species and Sites

The CABI *Forestry Compendium* can be very helpful in assisting the process of species choice, but there are other useful tools and critical considerations. For example, it may be important to know in more detail where a particular species will grow, how well it will grow, and whether there are any economic, social, or environmental problems with its use.

Climatic Mapping

Climatic factors are important in determining where particular species will grow. Great advances have been made since the mid-1980s in developing interpolation methods to assist estimating mean climatic conditions for any location around the world.

For example, CSIRO's Division of Forestry and Forest Products has used an interpolated climatic database prepared at the University of East Anglia's Climatic Research Unit to develop a world climatic mapping program. This can take in any of the 1200 descriptions of species climatic requirements included in the Forestry Compendium and map which of 67 477 locations in a half-degree grid satisfies the description. For example, **Figure 3** shows climatically suitable areas for *Tectona grandis* (teak) with the description of climatic requirements being used shown below the map.

Climatic mapping programs are very helpful in checking and improving descriptions of species climatic requirements. For example, the description shown in **Figure 3** should probably be slightly modified to include some wetter and warmer areas in India. It is very difficult to appreciate the implications of a written description of climatic requirements, but a map makes these immediately apparent.

Descriptions of species climatic profiles can be developed from analyses of their natural distributions as well as their performance in trials outside their natural distribution. Ideally, geocoded data (i.e., latitude, longitude, and elevation) are collated for both the natural distribution and successful trials and interpolation relationships are used to estimate mean climatic conditions for each location.

In addition to the world climatic mapping program, CSIRO has developed more detailed climatic mapping programs for a wide range of regions, including Africa, mainland South-East Asia, and Latin America, as well as for individual countries, including Australia, Cambodia, China, Indonesia, Laos, Thailand, Philippines, Vietnam, and Zimbabwe.

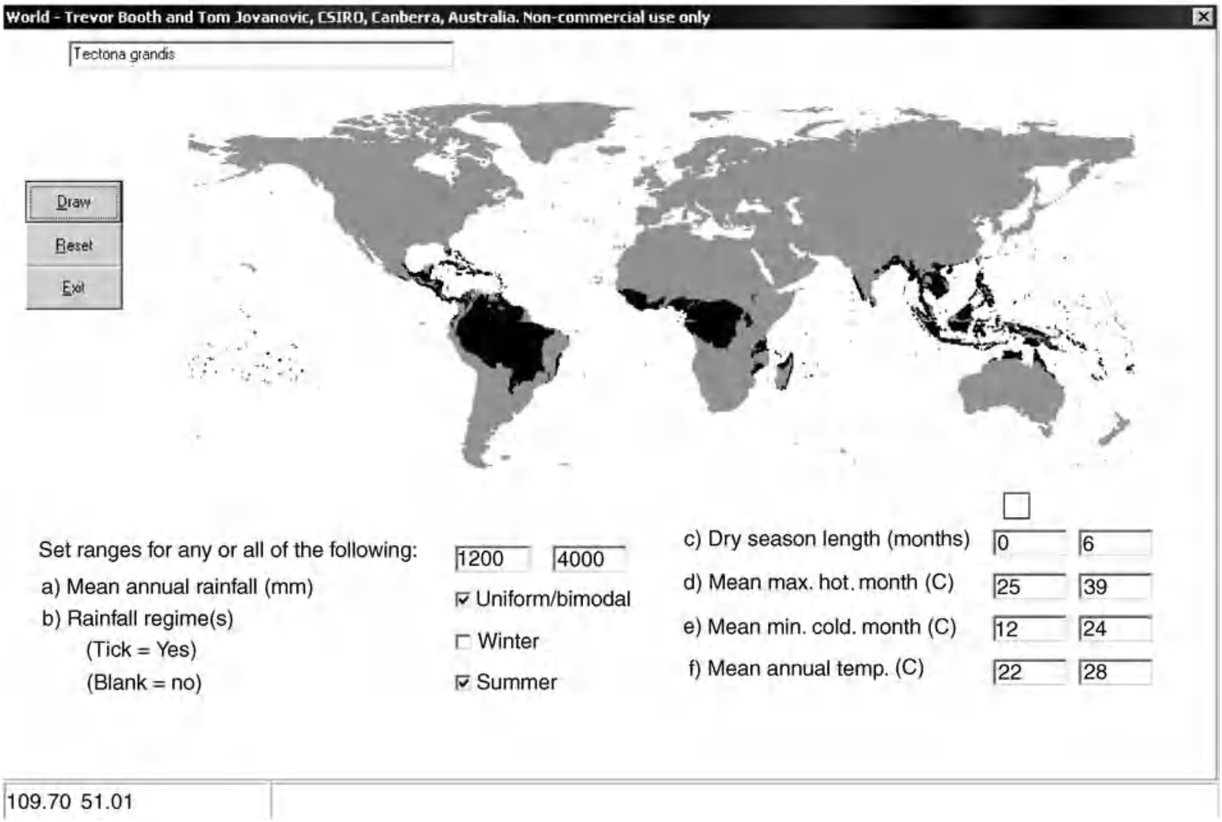


Figure 3 World climatic mapping program – black areas are climatically suitable for *Tectona grandis* according to description in CAB International (2003) *Forestry Compendium*. Wallingford, UK: CAB International. Available as CD-ROM or online at: www.cabicompendium.org/fc.

Tree Growth Models

When choosing species for planting it is useful to know not only where a particular species will grow, but also how well it is likely to grow at selected locations. Considerable progress has been made in recent years in developing simple tree growth models, such as 3-PG and ProMod. These take in simple information on climatic and soil conditions and predict likely growth rates for particular species. Models of this sort can be used to estimate potential productivity at individual sites or run for many hundreds or thousands of gridded sites to produce an indication of potential productivity across broad regions.

Economic, Social, and Environmental Suitability

In addition to local testing a consideration of the social and environmental implications of introductions should also be part of the tree selection process. This is particularly important if the species is an exotic. In the past, economic considerations have tended to dominate the choice of tree species. Economic considerations remain important, but social and environmental issues should also be assessed.

Social issues should involve a consideration of the likely impacts of tree species introductions into a particular region. Many social issues, such as the replacement of agricultural land by forestry plantations, may not be related to species choice, but visual impact is an example where species selection may be important.

Environmental issues include questions such as the decision whether to use native or exotic species. Biodiversity is an important environmental issue and use of native species may be preferred for this reason. However, use of highly productive plantations of exotic species may allow larger areas of native forest to be used as nature conservation reserves.

Water use is emerging as a major issue in many countries, so the efficiency with which different species use water may need consideration.

Opportunities for Future Developments

In the past the emphasis on tree selection has been at the species level. Some information about important hybrids and provenances is provided in the Forestry Compendium, but generally existing tree species selection systems provide little or no information at the provenance or clonal levels. In the future more information will be included in selection systems about requirements of particular genotypes, including provenances, hybrids, clones, and genetically modified material. For the present, field trials are essential before embarking on any large-scale afforestation program. Improved genetic material developed for another region may not necessarily perform any better than the best natural provenances when introduced into a different environment.

Improved genotype–site matching will require more detailed information on both tree growth and site conditions. Comparing the results of trials in many different countries and areas would be assisted by the development of an internationally agreed minimum dataset for evaluating tree growth and environmental conditions at trial sites. This dataset will need to include information about soil physical and chemical status to assist predictions of potential productivity and sustainability. If an agreed minimum dataset could be established it would be logical to develop an international database, similar to TREDAT, which contains information on observations from individual sites, as well as summary data of the type in the Forestry Compendium database. It would also be desirable to collect minimum dataset information on growth and environment for sample locations within existing plantations, so that production level performance could be more reliably compared with results from small-scale trials.

Improvements in remote sensing will allow more reliable growth predictions to be made for different genotypes over broad areas. Remote sensing is already beginning to provide some useful information on important soil properties such as water-holding capacity and nutrient conditions. However, validating remote sensing observations by selective on-ground sampling is likely to be required for the foreseeable future.

Though great improvements have been made in estimating mean climatic conditions over broad areas, more could be done to evaluate climatic variability. Improved climatic data are becoming available for factors such as rainfall variability and frost risk. Greater use of this information should be made in species selection systems.

In the past climatic databases have typically used monthly mean data. Data storage and transmission speeds have increased so greatly that access to actual time series data of hourly rainfall and temperature data for many years is now becoming practical. These datasets will allow factors such as insect development and leaf wetness to be estimated for potential planting sites. This will allow pest and disease risks to be more reliably estimated.

If predictions of climatic change are realized, this factor may also need to be considered in species selection. At present regional predictions of climatic change are not sufficiently accurate for forest managers to include this factor when selecting trees for planting.

Great progress has been made in developing methods to fulfill the need identified by John Evelyn in 1665 of identifying the fittest trees to be cultivated on any particular site. However, even better tree selection methods will be required to realize the full benefits of the improved genetic material that is becoming available for planting.

See also: **Mensuration**: Forest Measurements. **Resource Assessment**: GIS and Remote Sensing. **Silviculture**: Silvicultural Systems. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts.

Further Reading

Booth TH, Jovanovic T, and New M (2002) A new world climatic mapping program to assist species selection. *Forest Ecology and Management* 163: 111–117.

Brown AG, Wolf LJ, Ryan PA, and Voller P (1989) Tredat: a tree crop data base. *Australian Forestry* 52: 23–29.

CAB International (2003) *Forestry Compendium*. Wallingford, UK: CAB International. Available as CD-ROM or online at: www.cabicompendium.org/fc.

Evans J (1987) Site and species selection — changing perspectives. *Forest Ecology and Management* 21: 299–310.

Evans J (1992) What to plant? Chapter 8. In: *Plantation Forestry in the Tropics*, 2nd edn. Oxford: Oxford University Press.

FAO (1958) *Choice of Tree Species*. FAO forestry development paper no. 13. Rome, Italy: FAO.

Golfari L, Caser RL, and Moura VPG (1978) *Zoneamento Ecologico Esquematico para Reflorestamento no Brasil*. PNUD/FAO/IBDF/BRA-45 serie tecnica no. 11. Centro de Pesquisa Florestal da Região du Cerrado, Belo Horizonte.

Pan Zhigang and You Yintian (1994) *Growing Exotic Trees in China [in Chinese]*. Beijing: Bejing Science and Technology Press.

Poynton RJ (1979) *Tree Planting in Southern Africa*, vol. 1 — *The Pines*. Report to the Southern African Regional Commission for the Conservation and Utilization of the Soil (SARCCUS). South Africa: Department of Forestry.

Poynton RJ (1979) *Tree Planting in Southern Africa*, vol. 2 — *The Eucalypts*. Report to the Southern African Regional Commission for the Conservation and Utilization

of the Soil (SARCCUS). South Africa: Department of Forestry.
Savill P, Evans J, Auclair D, and Falk J (1997) *Plantation Silviculture in Europe*. Oxford: Oxford University Press.
Webb DB, Wood PJ, and Smith J (1980) *A Guide to Species Selection for Tropical and Sub-Tropical Plantations*. Tropical Forestry Papers no. 15. Oxford: Department of Forestry, Commonwealth Forestry Institute. (Revised 2nd edition published in 1984.)

Ground Preparation

A Baldini and W Alfaro, Corporación Nacional Forestal, Santiago, Chile

Introduction

Ground preparation is defined as the set of preliminary operations on soil that are required for effective establishment of tree seedlings. The main objective of ground preparation is to assure access to nutrients, air, and water for the seedlings to be planted.

Ground preparation is associated with site preparation. Ground preparation is more focused in soil treatment for plant establishment, considering the simple meaning of ground as 'solid surface of the earth' or 'the upper soil.' Site preparation may be understood as a wider concept referring to a modification of the surrounding environment for plant establishment. In this sense, site preparation may include operations prior to ground preparation.

Thus, site preparation includes clearing, soil cultivation, and also protection operations, such as management of pre-existing vegetation especially weeds, fencing and other animal control systems, protection of plants against frost and wind, etc. Conversely, ground preparation as a normal step leading to plant establishment is concerned with soil cultivation, including either drainage or water storage according to site conditions.

As a major operation for ground preparation in planting sites, soil cultivation frees ground and it facilitates a deeper penetration of water and air into the root zone and therefore, it allows root systems better access to soil nutrients and assists their correct placement, anchorage, and development. Also, draining facilitates aeration for roots in extremely wet and waterlogged fields. Furthermore, water harvesting increases soil water availability in dry zones.

Intensity of the operations for ground preparation may be defined in terms of work or power per unit area, which varies from site to site, depending on constraints of cost, plantation objectives, and site conditions. Ground preparation work may be classified as low intensity operations or high intensity operations. Low intensity operations include basically manual support and simple soil cultivation. High intensity ground preparation includes the use of agricultural machinery and mechanical support for soil cultivation.

Operations for ground preparation may be further classified according to their use of labor or machinery. Thus ground preparation may be implemented through a manual support system, a mechanical or machinery support system, or a combination of both systems. Ground preparation with manual support is normally preferred in low intensity ground preparation and small-scale operations such as the construction of furrows, mounds, bunds, ditches or trenches.

In general terms, field conditions such as slope, deepness, and stoniness are not limiting factors for manual ground preparation, which is performed by using hand tools such as shovels or spades, *azadas*, or a plow drawn by animals. Also, ground preparation with manual support may be used for smoothing and compaction of mounds and bunds, when combined with machinery or mechanical support operations.

Ground preparation with machinery or mechanical support is used for large-scale operations and it cannot be used on steep slopes because its application requires gentle to moderate slopes. Operations of ground preparation with mechanical support involves plowing, disking, or bedding, mounding, also scratch or spoil drain mounding, ditching, ripping, subsoiling or scarifying operations. However, disking and ripping are the most widely used operations of this type.

Machinery used for mechanical support operations consists of tractors or dozers with special attachments, especially blades, disks, rippers, rutters, or excavators, among other devices. Agricultural equipment may be used in most operations for soil cultivation in planting sites, where field conditions are not too rugged or stony. Heavy machinery should be used if there are relatively adverse conditions such as heavy clay soils, moderately steep slopes, or stoniness in the field.

Thus mechanical support to ground preparation can be classified into three categories of equipment: (1) machines for vegetation cutting and stump removal; (2) machines for vegetation cutting plus breaking up the ground up to certain depth; and (3) machinery that breaks ground structure to a deep level (**Table 1**).

For example, bulldozers may be used to remove remaining trees and stumps. A rotovator works over ground vegetation and it turns over the upper soil

Table 1 Equipment required for ground preparation, according to field conditions

Fields conditions	*Operation*	*Machinery recommended*
Deep soil; light soil density; flat to gentle slope	Cultivation without restriction	Low intensity work: agricultural disks on tractor
Deep soil; light soil density; flat to gentle slope	Ripping and mounding without restriction	Low intensity work: winged ripper on tractor; disk mounder on tractor
Deep soil; heavy soil density; moderate slope	Cultivation with restriction	Moderately high intensity work: heavy disks on tractor
Moderately deep soil; very heavy soil density; moderately steep slope	Ripping and mounding with restriction	Very high intensity work: ripper on bulldozer; 'Savannah' type mound plow; excavator on hauler
Shallow soil; steep slope	Machinery operation restricted	Manual support system recommended

layer. Rippers are typical devices for breaking up soil in depth. A mechanical excavator may be used for ground preparation in areas with heavy slash where stump and debris removal should be done prior to any plant establishment operation.

Appropriate operations for ground preparation depend on soil physic features, relief, water regime, and previous management. Field conditions requiring ground preparation are related to dense grass cover, detrimental field disturbance, compaction, heavy bulky soils, waterlogging, or dryness. Analysis of these conditions allows definition of needs for clearing, land reclamation, soil cultivation, drainage, or water harvesting.

Clearing

Clearing is an important preliminary matter in ground preparation and it is carried out to remove cover, specially shrubs and trees. Clearing allows effective soil cultivation, improving access for establishment operations. Clearing for plantation development may include the removal of posts from old fencing, stump and timber removal, and filling of holes.

Areas carrying a dense cover of grass require special attention because they put up competition with tree seedlings. First, grass needs to be eliminated with herbicides and allowed to decompose prior to working for complete breakdown of the sod. Then, soil cultivation may be required and appropriate cultivation might be considered, such as line cultivation with a heavy disk, mound plow, or ripper if necessary.

Soil cultivation is strongly recommended in sites carrying bracken (*Pteridium aquilinum*) or light scrub. Soil cultivation should be done twice in dense bracken or scrub cover: once in autumn; then again in the following summer. Over winter the sod and rhizomes break down and any new spring germination is removed in the second cultivation. In this case, the rhizomes mat of bracken has to be completely broken before plant establishment and seedlings planted into mineral soil.

Land Reclamation

Management conditions leading to soil cultivation for plant establishment are related to disturbance during harvesting. Site disturbance may be considered desirable for forest regeneration. However, site disturbance may occur under inappropriate conditions, e.g., a high risk of compaction, erosion, or soil mass movement, especially when soil is water saturated. Thus, land reclamation may be performed if disturbance becomes detrimental.

For example, compaction may occur due to machinery travel during harvesting operations, e.g., where conditions in soil water content are not appropriate for machinery operation such as skidders or feller buncher harvesters. Land reclamation is intended to return the site as closely as possible to its initial level of productivity in such a manner that the site will maintain that level of productivity without further management.

Land reclamation is often very expensive and does not guarantee that an area can be returned to its former level of productivity. Therefore, prevention is always the best way to deal with detrimental site disturbance. The first step in undertaking reclamation work is the development of the reclamation plan. The reclamation plan should include specific instructions and procedures for different treatments.

A reclamation plan must be based on specific site conditions, such as: moisture regime; soil texture; nutrient status; range and wildlife interests; possible negative consequences of the reclamation; locally available resources; and special concerns for the given site. Some of the options currently being explored i.e. the process of land reclamation are: recontouring of steep cuts; loosening the soil; revegetation; restoration of organic matter; fertilization; and, finally, monitoring.

As an example, soil can be loosened by a variety of methods, including a ripper, winged ripper, winged subsoiler, excavator with bucket, or excavator with fork. The winged subsoiler and ripper are usually more applicable to large areas of continuous disturbance, such as roads and landings.

Revegation is an important measure for land reclamation because vegetation plays an important role in maintaining soil structure, and when it is removed, exposed mineral soils are more susceptible to compaction damage. High root activity helps restore and maintain soil structure. Traditional approaches for revegetation have been to plant grass plus legume mixtures, which are useful in extreme situations where erosion control is necessary. However, there are circumstances where these types of mixtures may compete for moisture with seedlings or may increase the risk of frost damage.

Organic matter may be restored by moving forest floor or logging debris from slash piles or roads. The layer of organic material on the forest floor surface serves many important functions: it is often an important nutrient reservoir; it prevents soil erosion; and it protects soil from compaction after the removal of vegetation. Straw is a suitable mulch, because of its relative unpalatibility and low carbon/nitrogen ratio. Hydroseeding mulches may be used in certain cases, or plants such as rye grain, which generally do not survive in extreme conditions and die after 1 year, leaving a layer of organic matter on the ground.

Fertilization replaces nutrients lost from the site, stimulates biological activity to speed up the process of soil structure restoration, and accelerates ground-cover development. Nutrient application may also help to offset an anticipated decline in productivity when other means are not practical.

Compaction

The physical effect of compaction on soils is an increase in soil bulk density. Other effects of soil compaction are: reduction of porosity and thus aeration and useful water retention; loss of soil structure; reduced hydraulic, thermal, and gas conductivity; and increased dry strength or shear stress. Thus, soil compaction may affect root growth, limiting the roots' ability to explore the soil volume for nutrients and water moisture.

Other side effects of soil compaction include: increased risk of ponding of water; greater depth of soil freezing; and reduced growth of soil organisms. Any of these changes can contribute to short-term reductions in tree growth or long-term reductions in site productivity.

Cultivation

Cultivation is carried out to improve soil physical conditions, to allow improved root growth and therefore tree anchorage, to improve root access to soil nutrients and moisture, and to improve the quality of planting. Also, cultivation removes competing weeds, thereby improving moisture and nutrient availability to planted seedlings; and it provides a surface to which herbicides can be effectively applied.

It is important to determine the optimum technique for ground preparation in any particular field condition. A balance of cost to effectiveness must be achieved; on some sites, e.g. sites with heavy weed infestation such as blackberry (*Rubus fruticosus*) or gorse (*Ulex europaeus*), it will not be economically possible to establish plantations due to high costs of controlling this type of weeds. In addition, poor cultivation may increase erosion. Farmers should be aware that preparation equipment can be very specific where heavy work is required; in such a case special care must be taken to minimize erosion.

Soil cultivation should be contoured on all soils of high or very high erosion class such as silty or granitic soils, and on slopes greater that 15% for the moderate to high erosion class. All cultivation must avoid disturbing flowlines. In areas of very high rainfall cultivation may be undesirable for some moderate and moderate to high erosion class soils above 15% slope.

Soil cultivation lines oriented at right angles to the contour will facilitate machine access for subsequent establishment and harvesting operations on other than high and very high soil erosion classes and on slopes over 15% on moderate to high soil erosion class.

Soil cultivation must be done when the soil is friable, dry enough to crumble from cultivation but not so dry that it pulverizes. The soil should only be lifted enough to cause fracturing and then dropped back without any inversion of the soil profile. Soil cultivation is normally performed through disking.

Disking

Disking is an operation for ground preparation using disks as attachment devices on a tractor. Disking may be used to improve soil structure; to break down compacted surface horizons; to break up sods or bracken rhizomes; or to prepare a cultivated weed-free surface for herbicide application. Disking may be carried out on soils not requiring subsoil ripping.

Disk type will depend on the field conditions. Soil should be cultivated as deep as rocks and roots permit and to a minimum depth of 0.20 m. Heavy disks should be used, because smaller disks do not cultivate to sufficient depth. Mounding disks are used for drainage and water harvesting systems.

Disking is effective in soils with compacted surface and it promotes infiltration. Nevertheless, disking may reduce medium pore soil volume in dry areas and therefore it may affect water availability for plants. Also, disking may affect soil organic matter.

Ripping

Trees form shallow root systems where there is any impediment to root penetration. Shallow root systems make trees susceptible to windthrow, and to summer drought stress. Thus, ripping is required on compacted and heavy clay soils. Ripping breaks up subsoil, promoting root penetration to a reasonable depth. Grassland soils should benefit from ripping. In general, light density soils such as sandy soils do not require ripping.

Normally, ripping is carried out with a winged ripper. Ground preparation of planting sites by cultivation with a winged ripper will break up hard soil pans, increasing infiltration, and enhance early root development and subsequent tree growth. The wing on the ripper spreads the shattering effect of the ripper by lifting the soil as the ripper is pulled through and then dropping and shattering it behind the ripper.

Ripping should ideally be carried out to a depth of 1 m, or a minimum of 0.7 m for satisfactory results. Subsoil shattering occurs over most of the planting site when soils are relatively dry. Under this condition, subsoil shattering is obtained at a reasonable speed. Speed of ripping is important for shattering soil and large machines capable of reasonable speed should be used where possible.

Rippers shatter compact soils and provide easy access to the ripped profile for roots when fitted with a wing at least 0.40 m wide, mounted at the toe, and angled rear-upwards. Narrow boot rippers without wings produce very narrow shattering and can cause trenching in moist soils. Suitable rippers are commercially or locally made.

Subsoil plows are designed to provide full ground preparation treatment in hilly areas worldwide. Subsoil plows are designed for areas where the dozers available are lower in horsepower. More maneuverable than a heavy trailing unit, subsoil plows are very rugged machines designed for use with 225–350 HP dozers. The design may include a heavy-duty coulter and swept-back tine, and a choice of two or four disks. Subsoil plows may have the ripper shank and the disk body both in the swiveling frame, for high maneuverability on sloping ground. Also, some equipment includes a disk coulter ahead of the ripper shank.

High-performance plows may be used for bedding and soil structure improvement at higher speeds. They can use a four-point linkage lift kit, a 48-inch coulter, ripper shank and either two or four 36-inch cultivating discs. High-performance plows have a new design of hubs and spindles, which are massively stronger than previously. Bodies have been completely redesigned to allow up to 34-inch high-lift jump height. It is now very unlikely that a jump-arm would ever hit against the mechanical stop and it will be rare for the weight of the plow to be placed on the disk spindles, even in extremely high stump conditions. As an example, the action of the 'Savannah' jump arm raises the disk higher with a minor angle of cut and a greater rolling effect over a stump, eliminating stresses on the disk and spindle in straight-line plowing.

Effective depth of subsoiling has been a matter for debate around the world. Effectiveness is one criterion, but economy is a better approach for foresters to use. Generally, it may be much better to have a slightly shallower depth using a winged ripper tip, than to deep rip using only a standard ripper tip. The standard ripper tip will not create any fracture zone in plastic or wet soil condition. On the other hand, using a wide-winged tip and with plenty of longitudinal surface area, it is possible to break out plastic soils right to the surface. Thus, a subsoiling operation may be effective if it can produce additional growth in trees to justify expenses.

Mound Plowing

Mound plowing is an operation that raises the level of ground surface on planting spots. Mound plowing is often carried out on low-lying, flat areas, wet and poorly drained sites, and shallow infertile soils. It enables low, wet parts of generally better sites to be developed and planted. Mound plowing may be applied if 20% maximum of the field area is affected by waterlogging. Mounds can increase runoff on poorly drained sites and large mounds may provide a better rooting medium on wet or shallow soils. Mounds can be used in dry areas to retain runoff and therefore increase moisture content in soil.

Mounding is more effective on fine-textured soils. Soil is well aerated by mounding but it may need consolidation before planting. This can be achieved by rolling or by allowing the soil some time to settle, about 1–2 months before planting. Mounding delineates rows and it leaves an obvious planting line thereby reducing planting cost. Planting holes may be dug easily in loose soil. Seedling roots may be arranged neatly, minimizing shock or damage. These conditions allow seedlings to begin to grow earlier, increasing the length of the first growing season.

Mound plowing is often done in conjunction with ripping. Mound plowing allows planting directly over the ripped line. Mound plowing is best carried out when soils are moist but not wet. Plowing should be complete by early autumn to allow time for the mound to pack down before planting.

Various mound plows are available for use. Normally a set of tandem offset 600–800 mm diameter disks is attached to a tractor or dozer, which works well in easy conditions. Much heavier disks are available, and the recommended big disk for special operations is the 'Savannah' plow, which is mounted directly onto a large bulldozer.

Operational Impacts

Ground preparation has both positive and negative effects on soil properties. Use of proper equipment and correct timing of preparation will reduce any detrimental impact. **Table 2** describes the potential impact of ground preparation operations on soil properties.

Drainage

Draining is a special operation in waterlogged fields, and its objective is to promote aeration for root systems. Normally, draining is carried out by ditching, bedding, or mounding. Ditching allows water to be discharged towards lower areas. Bedding and mounding raises ground allowing a water-free zone on upper soil.

Spine drainage is a typical example for ditching drainage systems. In this system, a central trench is excavated in the slope direction. Lateral trenchs regularly spaced on both sides are connected to the central trench that receives their discharge. Spine drainage is a very efficient system for depleting local water table in planting sites; however, it has significant impacts on sediment yield and is therefore falling out of use.

Bedding and mounding are the preferred systems to address drainage in planting sites. These operations raise the ground to a position free of water, increasing available root depth and protecting seedling stems from low temperatures occurring during frost over the ground surface. Most of the better results in tree growth are obtained by placing seedlings over the top of the mound.

Bedding is an operation more appropriate for clear areas, because it is difficult to get a continuous line of plowing for bedding under conditions such as heavy slash or high stumps. Therefore, mounding should cope better with irregularities on the ground surface.

Table 2 Potential impact of ground preparation operations on soil properties

Soil factor	*Operation*		
	Disking	*Ripping*	*Mounding*
Compaction	+ SI (r–2-LT)	+ HI (r–1-LT)	+ SI (r–1-LT)
Soil moisture	+ SI (r–2-LT)	+ HI (r–1-LT)	+ HI (r–2-LT)
Soil organic matter	– LI (r–2-LT)	O	– LI (r–1-LT)

Impact sign: +, positive; –, negative.
Impact magnitude: O, no effect; LI, light effect; I, significant effect; HI, very significant effect.
Importance: 1, point; 2, local.
Reversibility; r, reversible effect; p, irreversible effect.
Duration: SD, short-term effect; LD, long-term effect.

Water Harvesting

In dry areas, water harvesting must be considered in order to supply water if it is deficient during establishment and early growth of plantation. Water harvesting should gain massive adoption in the near future because of the excellent results obtained in the afforestation of areas with rainfall as low as 80 mm year^{-1}. Most harvesting systems are designed for flat areas. Nevertheless, higher steep slopes also may be treated with the systems for water collection. There are many water harvesting systems that can be applied for improving forest plantations. For example, microcatchments or 'negarims,' contour bunds, contour stone bunds, semicircular bunds, individual terraces, 'limans,' 'kasukas,' permeable rock dams, subsurface dams, and others.

Water harvesting systems are ground preparation systems with a high cost and a considerable amount of ground disturbance. Nevertheless, water harvesting systems can make feasible afforestation in dry zones, achieving good success in tree growth. As an example, **Table 3** shows the earthworks required for three of the most popular water harvesting systems.

Water harvesting systems should be considered as soil and water conservation systems, because besides harvesting water for the trees, they simultaneously conserve soil. Dimensions of water harvesting systems are based on the catchment area size required to provide an additional supply of rainfall. Under extreme conditions of drought there must be a minimal runoff in the area. The design of water harvesting systems must also consider maximum discharge in order to avoid destruction of the structure. Larger structures may take more labor per unit volume of earthworks than smaller structures such as negarim microcatchments, because of the increased earthmoving required.

Negarim microcatchments are diamond-shaped basins surrounded by small earth bunds with an infiltration pit in the lowest corner. Runoff is collected from within the basin and stored in the infiltration pit. Microcatchments are mainly used for

Table 3 Minimum earthworks required by typical water harvesting systems

Additional rainfall supplied by water harvesting system (mm)	Runoff (mm)	Crop area to catchment ratio	Trees per hectare	Earthworks with a minimum cross section of 0.08 m^2 and a forest crop area of 4 m^2 ($m^3\,ha^{-1}$)		
				Microcatchments	Contour bunds	Semicircular bunds
200	10	1 : 20	125	208	48	80
150	20	1 : 7.5	330	288	128	211
100	30	1 : 3	850	464	200	326

growing trees or bushes. This technique is relatively easy to construct and appropriate for small-scale tree planting in areas with moisture deficit. A modified system is used in Latin America by a double plowing at right angles to get the diamond shape over the ground. Also, the soil in the pit is removed and placed in the top of the bund at the lowest corner of the diamond and one to three seedlings spaced at 0.4–0.6 m are planted at that point. This planting method is named the 'taba-ue' system from its original name in Japanese. The cluster of plants creates its own environment and the synergy effect can improve their survival and growth.

Contour bunds are a simplified form of microcatchments. Bunds follow the contour at regular spacing. Small earth ties perpendicular to contour prevent collapse of the system under high intensity rain events. Construction of bunds can be mechanized and the technique is therefore suitable for implementation on a larger scale. Bund construction is relatively economical particularly for large-scale implementation on even land. Contour bunds are suitable for trees and also for the cultivation of crops or fodder between the bunds.

Semicircular bunds are earth embankments in the shape of a semicircle with the tips of the bunds on the contour. Semicircular bunds are used mainly for rangeland rehabilitation or fodder production, with varying dimensions. This technique is also useful for growing trees and shrubs and, in some cases, has been used for growing crops. They may be placed as an *in situ* short slope catchment or an external long slope catchment, depending on the location and the chosen catchment to cultivated area ratio. Semicircular bunds, 'half moon' or 'demi-lune' in francophone Africa, are recommended as a quick and easy method of improving rangelands in semi-arid areas, and may be used in afforestation projects. Semicircular bunds are more efficient in terms of impounded area to bund volume than other equivalent structures such as trapezoidal bunds, for example.

Contour ridges, sometimes called contour furrows or microwatersheds, are used for crop production, and the technique may also be applied for afforestation purposes. This is a microcatchment technique where ridges follow the contour at a spacing of usually 1–2 m. Runoff is collected from the uncultivated strip between ridges and stored in a furrow just above the ridges. Crops are planted on both sides of the furrow. Contour ridges are simple to construct with manual or machinery support, and this can be even less labor intensive than the conventional tilling of a plot. The yield of runoff from microcatchment lengths in contour ridging is extremely efficient and when designed and constructed correctly there should be no discharge out of the system. Contour ridges provides even growth because each plant has a similar contributing catchment area. Contour ridges is a technique being tested for crop production in Africa.

Trapezoidal bunds have a layout with shape of a trapezoid, a base bund connected to two side bunds or lateral walls, which extend upslope at an angle of usually 135° or higher. Trapezoidal bunds are used to enclose larger areas up to 1 ha or more. In this system, runoff is harvested from an external catchment area. Crops such as trees are planted within the enclosed area. Overflow may discharge throughout a spillway constructed over the central bund or as a channel at the end of the lateral walls. The main advantages for this technique are simplicity of design and construction, and the minimum maintenance required.

Contour stone bunds are used to reduce runoff speed, thereby promoting infiltration and collecting sediment. The water and sediment harvested improve crop growth. Bunds construction is a traditional practice in many parts of the world and villagers may be trained effectively in its application. Stone bunds are well suited to small farmers because of their low cost and simplicity. Improved construction and alignment along the contour makes the technique considerably more effective. Stone bunding techniques are used for hillside terracing around the world, specially in the Andean zone. The supply of stones may be a constraint for application of this technique. The filtering effect of the semipermeable barrier along its full length spreads the runoff, avoiding concentration and resultant damage. Systems based on stone do not need spillways and they require much less maintenance.

Permeable rock dams are a floodwater farming technique where runoff waters are spread in valley bottoms for improved crop production. The structures are typically long and low dam walls across valleys. Rock dams have been developed mostly in West Africa, and the technique had grown substantially by the end of the 1980s. The technique is labor intensive and needs a group approach, as well as some assistance with transport of stone.

Water spreading bunds are often applied in situations where trapezoidal bunds are not suitable, usually where sudden runoff discharges may be extremely high and would damage trapezoidal bunds or where the crops to be grown are susceptible to the temporary waterlogging, which is a characteristic of trapezoidal bunds. Water spreading bunds are usually used to spread floodwater which has either been diverted from a watercourse or has naturally spilled onto the floodplain. The bunds, which are usually made of earth, slow down the flow of floodwater and spread it over the land to be cultivated, thus allowing it to infiltrate. Water spreading bunds may be combined with the construction of a ground dam, which is a long structure that retains subsurface flow.

Final Remarks

Several ground preparation operations and their uses have been described. Tree growth following different treatments for ground preparation should be monitored and integrated on information systems. Further progress in forestry may be supported by information systems about the results of different treatments for ground preparation under specific field conditions.

Further Reading

Anderson GG (1998) *Site Preparation for Farm Forestry.* Agriculture Note no. AG0770. Victoria, Australia: Australia Forest Growers.

Boden DI (1992) The relationship between soil water status, rainfall and the growth of *Eucalyptus Grandis*. *South African Journal of Forestry* 156: 49–55.

Cunningham L (1994) The effect of site preparation and tending on the growth of *Pinus radiata* in the Southern Cape: five year results. *South African Journal of Forestry* 176: 15–22.

Dharamraj NM, Gaum WG, and Hildebrand A (1900) An investigation into the establishment of indigenous trees on treated mine residue soils in South Africa. *South African Journal of Forestry* 186: 33–40.

FAO (1991) *Water Harvesting: A Manual for the Design and Construction of Water Harvesting Schemes for Plant Production*. Rome: Food and Agriculture Organization.

Mason WL (1999) *Cultivation of Soils for Forestry.* Forestry Commission. Bulletin no. 119. London: HMSO.

Neilson WA (ed.) (1990) *Plantation Handbook*. Tasmania, Australia: Forestry Commission Tasmania.

Schönau APG, Verloren Van Themaat R, and Boden DI (1990) The importance of complete site preparation and fertilising in the establishment of *Eucalyptus grandis*. *South African Journal of Forestry* 116: 1–10.

Schutz CJ (1900) Monitoring the long-term effects of management practices on site productivity in South African forestry. *South African Journal of Forestry* 120: 3–6.

Shumba EM, Mushaka A, and Muchichwa J (1998) A survey of tree-planting practices in the smallholder farming sector of Zimbabwe. *South African Journal of Forestry* 182: 67–74.

Wadsworth FH (1997) *Forest Production for Tropical America*. Agriculture Handbook no. 710. Washington, DC: US Department of Agriculture Forest Service.

Wenger K (ed.) (1984) *Forestry Handbook*. New York: John Wiley.

Zwolinski JB, Donald DGM, and Van Laar A (1992) Regeneration procedures of *Pinus radiata* in the Southern Cape Province. I: Modification of soil physical properties. *South African Journal of Forestry* 167: 1–8.

Zwolinski JB, Donald DGM, Van Laar A, and Groenewald WH (1992) Regeneration procedures of *Pinus radiata* in the Southern Cape Province. V: Post planting mortality and growth of trees in response to the experimental treatments and planting site environment. *South African Journal of Forestry* 168: 7–22.

Stand Establishment, Treatment and Promotion – European Experience

J Huss, University of Freiburg, Freiburg, Germany

Introduction and Definitions

There are many aspects to the establishment of forest stands, which are reflected in a number of definitions:

- Reestablishment of existing forests is possible by means of generative or vegetative renewal. Strictly speaking, stands are regenerated only when grown from seed. This may occur through natural or artificial regeneration:
  - Natural regeneration takes place when seed is dispersed without human interference.

Figure 1 High forest in different manifestations: (a) even-aged pure Norway spruce (*Picea abies*) plantation (Riedenburg, south-east Germany), (b) uneven-aged naturally regenerated silver fir (*Abies alba*) and Norway spruce selection forest (Rippoldsau-Sch., south-west Germany).

   - Artificial regeneration involves direct seeding, as well as planting.

Both natural and artificial forest regeneration using seed results in high forests (**Figure 1**).

Vegetative renewal is the result of resprouting from the stumps left behind following harvesting. Most broad leaves sprout freely, giving rise to coppice forests (**Figure 2**). Such forests were widespread throughout Europe for centuries, and were an important source of firewood. A tree's ability to resprout from its stump, or to produce root suckers, decreases with age. Coppice forests are normally harvested after two to four decades and form relatively low forests. Vegetative renewal from the stumps is, strictly speaking, not regeneration, as the root systems are not regenerated and continue to age and deteriorate.

A combination of vegetative and generative renewal takes place in coppice forests with standards ('middle forests') (**Figure 3**).

- Reestablishment of forests is often referred to as reforestation and takes place shortly after the previous stand has been harvested, at which point the soil still predominantly exhibits characteristic forest soil properties.

Figure 2 Beech (*Fagus orientalis*) coppice stand shortly before next harvesting (Akcakoca, north Turkey).

Figure 3 Coppice with standards (mainly *Quercus petraea*) shortly after harvesting of the coppice shoots (Neuf-Brisach, France).

Figure 4 Norway spruce (*Picea abies*) plantation following afforestation of an old meadow (Hinterzarten, south-west Germany).

- Afforestation, on the other hand, takes place when areas have been used for purposes other than forestry for more than 50 years, according to a Food and Agricultural Organization definition (**Figure 4**). From a less precisely defined ecological viewpoint, afforestation is the restocking of sites which have lost their forest soil characteristics. This may arise as a result of various land-use types, such as agriculture, or degradation caused by erosion, and may occur over much shorter periods, depending on the local climatic and soil conditions.
- Stand establishment – depending on silvicultural systems – may take place under the canopy of old trees (**Figure 5a**) alongside forest stands (**Figure 5b**) or on large open areas resulting from clearcuts or other land uses (**Figure 4**). One of the main objectives of each of the silvicultural systems is to create microclimatic conditions appropriate to the ecological demands of the young plants of the different tree species.

  The larger the open areas, the greater the climatic stress conditions may become and the more tolerant the young regenerated plants have to be of such stress, for example, drought, heat, and early and late frosts (**Figure 6**). Usually a sheltering effect can be observed extending a distance across the regenerated area equivalent to the height of the neighboring stand. Generally, bare land conditions develop in areas larger than 0.5–1 ha. Large open areas (clearcuts) may be >5 ha, and very large ones >50 ha.
- The regeneration period largely depends on the type of regeneration and the silvicultural system employed. At one extreme it may require only 1 day to plant a small clearcut area, provided no beating-up is necessary in the succeeding years. The other extreme can be found in selection forests, where regeneration is a continuous process.

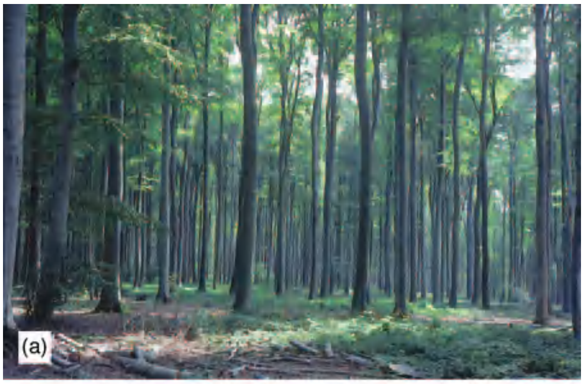


Figure 5 Natural regeneration with shelter for regrowth: (a) beech regeneration (*Fagus sylvatica*) under a shelterwood system (Bourbonnaies, France); (b) Norway spruce (*Picea abies*) regeneration under a strip-cutting system (Zeil, south-west Germany).

- The terms regeneration, planting, restocking, and afforestation denote processes, the results of which are seedlings, saplings, regrowth, plantations, and restocked forests, to mention but a few. In forestry practice, however, strict application of these definitions is seldom observed.

Figure 6 Norway spruce (*Picea abies*) although not very sensitive to frost, often suffers from late frost on large bare land areas (Pforzheim, south-west Germany).

Tree Species Selection

The tree species selected for restocking an area depends on several preconditions, such as the prevailing ecological conditions on the one hand, and the objectives of the forest owner and society on the other. These are illustrated in **Figure 7** and are explained in the following text.

Site Classification

The success of restocking an area is highly dependent on the site conditions. Sites are characterized by their climatic conditions and soil properties. Climate is the dominant site factor in mountainous as well as high mountain regions, and often negates the soil characteristics. Soil characteristics exert a greater influence on forest growth at lower elevations where the climatic conditions are relatively favorable.

Site classification systems, therefore, include two steps:

1. The demarcation of regional landscape units to characterize the predominant climatic influences.
2. The delineation and mapping of local forest site units within regional units, representing similar growing conditions for the tree species and including comparable risks.

Only a few Central European countries like Austria, Germany, and Switzerland currently possess area-wide maps providing elaborate site property

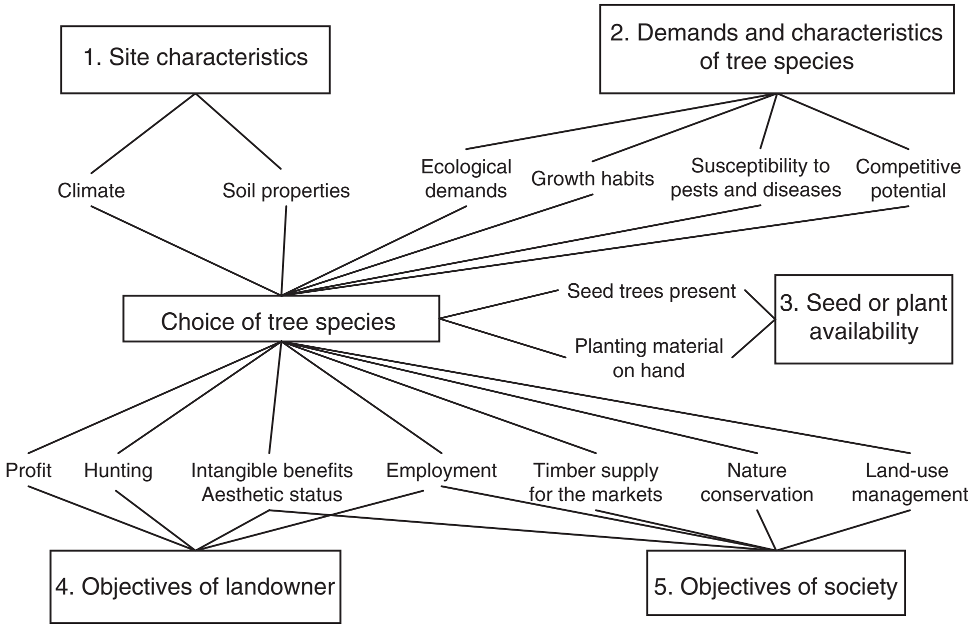


Figure 7 Preconditions and objectives influencing the choice of tree species when restocking forests.

information, enabling detailed planning of the optimum site-adapted stocking. Most European countries, however, possess maps indicating climatic or vegetational zones, which are of some help in the selection of site-adapted tree species.

As the majority of sites are located at lower altitudes and on soils mostly favorable to forest growth, the forest owners are free to select from many tree species for restocking. Other aspects may also be taken into consideration. The more extreme the sites become – high or very exposed elevations, very wet, dry or shallow soils – the fewer the options a landowner has in this regard.

Figure 8 Although clearcuts are diminishing in Scandinavia and Central Europe, an increasing area of bare ground has resulted from hurricanes over the last two decades (south-west Denmark).

Demands and Growth Characteristics of the Tree Species

The prevailing ecological conditions over an area to be restocked may also influence species choice. A large clear-cut or storm-damaged area (**Figure 8**) with a harsh climate, for instance, may be suitable for light-demanding yet stress-tolerant pioneers such as birch (*Betula verrucosa*, *B. pendula*), aspen (*Populus tremula*), or rowan (*Sorbus aucuparia*), whereas late successional species like beech (*Fagus sylvatica*) or silver fir (*Abies alba*) require the protection of a canopy of old trees against late frosts, drought, and high temperatures. Late successional tree species, therefore, cannot be regenerated on bare ground susceptible to the afore-mentioned stress factors unless a nurse crop is established to act in the same way as the old trees.

In order to reduce the microclimatic stress for young regrowth it proved effective to establish nurse crops through natural or artificial regeneration of pioneers (**Figure 9**).

All European forest tree species thrive best on relatively well drained soils, facilitating root growth, and with a sufficient nutrient supply in a moderately temperate climate. On these optimal sites, all species will exhibit their highest production rates. Which species dominates in the long run, however, is determined by the competitive strength of the tree species. Pioneer species, both long- and short-lived, are less competitive than the late successional species. Growing in mixtures, they usually have to be actively favored by management if they are to survive against the more competitive species.

Figure 9 Nurse crops as a means of overcoming adverse bare-ground conditions: birch (*Betula pendula*) planted in a storm-damaged forest acting as a nurse for young oak (*Quercus petraea*) planted shortly afterwards (Kirchberg, south-west Germany).

Seed or Plant Availability

The choice of tree species is highly dependent on the presence of seed trees, which may also provide shelter against microclimatic stress conditions, in the event that natural regeneration is desired, or on the availability of adequate plant material from nurseries.

Objectives of the Forest Owner

Only a minority of forest owners can use their forests exclusively for hunting or pleasure. Most regard their forests as major sources of income and employment, but may take into consideration other functions and objectives in the management of their properties. Therefore, they choose productive species promising good prices in the market. Additionally, the costs of establishing a new stand are of great importance. The greater the emphasis placed on calculating the return on their investment, the more likely they are to choose the species that are easiest to plant and clean.

In most parts of Ireland, for example, oak forests (*Quercus petraea*, *Q. robur*) would be natural and suitably site-adapted. Oak forests are expensive to establish and require intensive weeding, however, and ultimately produce relatively low volumes of timber over long rotations. Planting of Sitka spruce (*Picea sitchensis*), on the other hand, costs much less and the revenue from the fast-growing species is much higher. It is, therefore, easy to understand why most private owners plant Sitka spruce instead of oak.

Objectives of Society

Society is currently seeking to play an active role in influencing the production, appearance, and services provided by forests, as they are an important part of the landscape, and represent comparatively natural ecosystems.

Additionally, an increasing fascination for nature protection ideas to counterbalance modern urban life may favor the reestablishment of 'natural forests.' Employment for rural populations and the supply of a large variety of timber assortments for the markets, on the other hand, is a more general public issue.

Tree species choice is, therefore, a complex decision process and many interest groups may take part in it.

Types of Stand Establishment

Forest stands can be established by means of natural regeneration, direct seeding, or planting. The details, advantages, and risks of each procedure are discussed in the next section.

Natural regeneration is recommended where the following preconditions are met:

- Presence of seed-bearing trees on or in the vicinity of the area to be regenerated
- Existence of site-adapted tree species and provenances
- Seed production reasonably frequent. Some species, such as beech and oak, used to have good seed years at intervals of >5 years. Over the last three decades, however, the frequency of flowering has increased dramatically as a result of more frequent warm summers, which induce the formation of flower buds. Forest practitioners are, therefore, under less pressure to regenerate large areas immediately when the time comes to do so.

  Nevertheless, foresters can to a certain extent increase the intensity of flowering and seed production by promoting crown development of the final crop trees by means of consistent crown thinnings. Early and intensive thinnings ensure that the dominant trees will have developed large crowns decades before seed production becomes essential for regeneration. Some shade-tolerant tree species, however, such as beech, exhibit reactions to increased crown space even at advanced ages
- Soil conditions favorable to germination. Layers of litter, raw humus, and/or ground vegetation may seriously impede natural regeneration. The soil surface conditions may, therefore, require soil treatment in order to expose the mineral soil, thereby providing a favorable seed bed (**Figure 10**)
- Low risk for the development of seedlings. Mice (*Apodemus* spp.), voles (*Microtus* spp.), insects such as the pine weevil (*Hylobius abietis*), and deer (such as *Capreolus capreolus*, *Cervus elaphus*, *C. nippon*, *Dama dama*) may greatly endanger the young seedlings (**Figure 11**). Voles and beetles are less of a problem if the young plants are regenerated in the more moderate microclimate under the shelter of an old stand. Deer, however, can only be effectively excluded by fencing, which is very expensive.

Natural regeneration is only possible if old stands are remaining or have been rehabilitated through afforestation and allowed to reach seed-producing ages. This is the case in most Central and Eastern European, as well as Scandinavian, countries. Therefore, there is a growing tendency to make use of the opportunity to regenerate forests naturally. In these countries, the current aim is to reestablish at least half of the forest area naturally. In Eastern and southern European countries, however, most forests have only been established in the last decades and generally do not as yet produce sufficient seed numbers.

Direct seeding – though considered artificial regeneration – holds an intermediate position between both regeneration types. It combines the advantages of natural regeneration (low cost input; high number of plants per unit area, which is important in the case of broad leaves as it ensures a high rate of natural pruning, a precondition for valuable timber; and undisturbed root development) with those of planting (choice of tree species independent of the presence of seed-bearing trees;

Figure 10 Minor soil preparation to improve germination conditions. (a) Strip ploughing to encourage beech (*Fagus sylvatica*) nuts (Lembeck, west Germany); (b) strip ploughing to help Scots pine (*Pinus sylvestris*) seeds germinate (Bamberg, south-east Germany).

even tree cover over the whole area despite minor site differences caused by the site mosaic).

Direct seeding of acorns (mainly *Q. petraea*) has long been and still is important in forestry practice, as it is difficult to store them over winter. Therefore, the acorns are normally sown in ~5 cm deep furrows and covered with soil for protection (**Figure 12**).

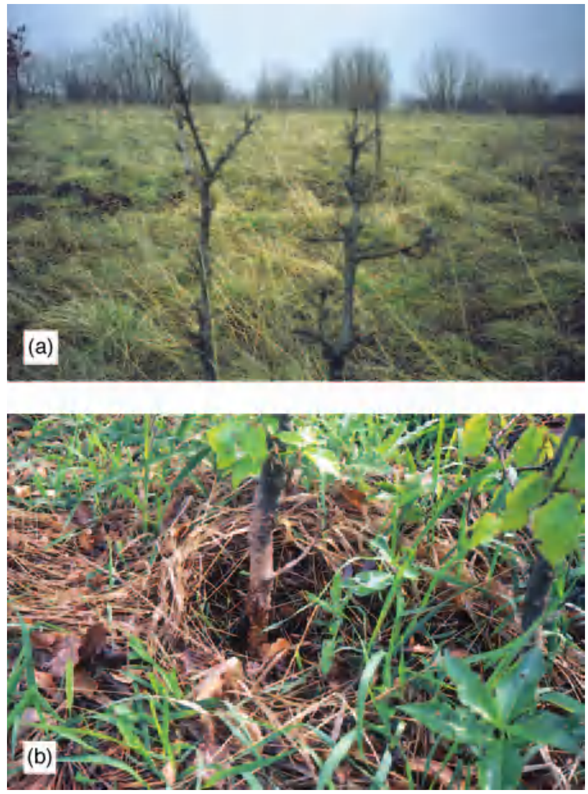


Figure 11 Damage caused by deer and voles. (a) Young oaks (*Quercus petraea*) heavily browsed by red and roe deer (*Cervus elaphus*, *Capreolus capreolus*; Hainich, east Germany); (b) young beech (*Fagus sylvatica*) ring-barked by voles (*Microtus agrestis*) (Zwiefalten, south-west Germany).

Direct seeding of birch (mainly *Betula pendula*) has recently received renewed attention as a means of restocking areas and establishing nurse crops after damage caused by hurricanes and SO_2 emissions (**Figure 13**).

Planting is the general alternative if the preconditions for natural regeneration are not met. The following are some of the advantages of planting over natural regeneration:

- independence with regard to tree species selection (from existing old growth)
- independent of mast years
- even, and calculable, stocking levels across the entire area
- reduction of the vulnerable period for young trees.

The possible objectives of planting are detailed in **Table 1**.

Planting can be carried out under the shelter of existing stands, as well on open areas, thereby resembling natural regeneration in some respects.

Figure 12 Successful direct seeding of acorns (*Quercus petraea*) (Rohrbrunn, south-east Germany).

Figure 13 Rehabilitation of forests following emissions. (a) Dead stand as a result of SO_2 emission (Ore Mountain, east Germany); (b) birch (*Betula pendula*) established by direct seeding on snow as a nurse crop. Beech (*Fagus sylvatica*) to be planted shortly afterwards under its shelter (east Germany).

Plant Types

A large variety of forests plants varying in their stage of development, size, sturdiness, source of origin, and type of production (bare-rooted or container plants) are available according to the different needs of the forester (**Table 2**).

Generally, small plants can be used when the subsoil texture is similar to that found in agriculture. In the past, soil preparation was commonly undertaken to reproduce similar conditions.

The increased vigor of ground vegetation species in the last three decades has meant an increase in the loss of young trees through competition. Additionally, deer browsing has become a serious problem regionally because of higher deer populations. Consequently, there has been a shift towards taller and sturdier plants (**Figure 16**).

Transplants and container plants are predominantly produced by large private nurseries (**Figure 18**).

In the EU the collection of seeds, plant production and distribution are organized according to legal regulations and special laws in several countries, in order to ensure that the origin of the seeds is documented through all stages of production down to the receipt by the consumer. In spite of these regulations, grave cases of willful deceit have occurred, resulting in the closure of several nursery enterprises.

The globalization of plant production in different countries has generated increased problems in ensuring

Table 1 Objectives of different planting types and planting procedure

Planting objective	*Procedure*
Production forest	Mainly planting across the entire area with one species only
Protection forest	Great differences according to the protection objectives, for instance: • erosion control • nature protection: reintroduction of rare species by planting single trees at varying distances or on special sites, increasing biological diversity
Recreation forest	Concentrating on forest edges: favoring esthetic values, avoiding straight lines, increasing visual diversity
Nurse crop	Planting of a pioneer species on large exposed open areas in order to create favorable ecological conditions under the shelter of which the final crop is later established
Underplanting	Planting shade-tolerant trees with a silvicultural function (shading the valuable trunks of dominant trees against epicormics, shading the forest floor to prevent the development of ground vegetation, an obstacle to later natural regeneration)
Enrichment planting	Introduction of additional tree species into incompletely regenerated regrowth (mainly after natural regeneration; **Figure 14**)
Filling-in	Stocking areas of unevenly developed naturally regenerated regrowth with plants of the same species
Beating-up	Replacement of dead plants 1 or 2 years after establishing the original plantation

Figure 14 Norway spruce (*Picea abies*) enrichment planting in a gap naturally regenerated by beech (*Fagus sylvatica*) (Donaueschingen, south-west Germany).

an appropriate control over the genetic quality of the plant material. Some forest enterprises, have, therefore, intensified natural regeneration and the collection of wildlings on their own property.

Planting Techniques

Although a great number of tools and machines have been developed during the last 200 years, hoes that produce narrow slits are still dominating (**Figure 19a**). New techniques even for steep terrain are under construction (**Figure 19b**).

Plant Density

The number of plants per unit area may vary between 6000 (beech) and 500 (poplar) plants per ha depending on the tree species and on several preconditions and characteristics of the plant material and the restocking area (**Table 3**).

Spacing

Row or quadrangular spacing is common on large areas. Common spacings are 3×1 m or 3×1.5 m and 2×2 m or 2.5×2.5 m. Row spacing involves lower planting costs, as well as savings later during tending operations, such as weeding, and has, therefore, increased importance.

Trials have recently been established to study the effect on saplings of planting in small groups (nest-planting, e.g., 100 nests per ha with 25 plants each, with 1×1 m spacings within the nests), with the spaces between groups left to natural succession, or else either sown or planted. The numbers of plants required, and as a consequence the costs, are lower than for traditional planting designs. Final results are not yet available, however.

Group Mixtures

There is an increasing tendency to establish forests with two or more species in the canopy. Unlike traditional plantings, these mixtures should always be established in groups of at least the size of the crown of a final crop tree (i.e., 50–150 m^2), thereby ensuring that the species which grow more slowly initially will not be overgrown by the faster ones.

Mixtures in rows have mostly proved unsuccessful because one species suppresses the other during a certain phase of development (**Figure 20**).

Plantation as a System

Plantations are in a certain sense a system, based on a combination of many preconditions and procedures. When establishing a new stand, on many sites the forest owner has the following options:

Table 2 Plant types used in forestry practice

Plant type	*Description/suitable for*
Seedlings	Seedlings spend 1 or 2 years in the seed bed; 10–30-cm tall seedlings are planted in the open if no humus layer is present. Litter and ground vegetation impede planting and seedling development. Although attractive for their low prices and planting costs, seedlings may be susceptible to high risks, for example, deer browsing (**Figure 15**)
Transplants	After 1–2 years in the seed bed, the seedlings are transplanted and left for 1–3 years in a new bed ($1+1$ to $2+3$), attaining heights of 30–80 cm. Transplanting reduces height growth, but favors the development of a compact root system with more fine roots, thereby simplifying the planting procedure and improving growth in the field. Undercutting plants in the seed bed also stimulates development of a compact root system. Due to the high costs of transplanting, undercutting has gained popularity. Transplants remain the most commonly used in practice, however (**Figure 15**)
Saplings	Plants of >1 m in height. Mainly broad leaves. Most common in horticulture. Important in earlier centuries for establishing standards in coppice stands and as solitary oaks. Increasing importance today because less susceptible to competition from ground vegetation and deer browsing. New planting techniques may lead to a reduction of the high planting costs (**Figure 16**)
Wildlings	Naturally regenerated young plants, 30–100 cm tall, extracted for the purposes of filling up incomplete young stands, for underplanting and for transplanting in a nursery. Wildlings have a proven site adaptation. A further great advantage is their availability. They often suffer from dieback if transplanted into open land, however, due to poor root development
Container plants	Seedlings grown in blocks of containers under semiindustrial conditions in plastic greenhouses for a few months. Low costs because of integrated lines from production to planting. Highly attractive to large-scale forest enterprises in the boreal zones. Of little importance in temperate zones because they are too small to withstand the intensive competition posed by the ground vegetation (**Figure 17**)

Figure 15 Beech (*Fagus sylvatica*) seedlings and transplants: $1+0$-year-old seedling only reach ~10 cm in height and normally cannot be used in the open; $2+2$-year-old transplants, however, reach ~80 cm in height and are able to withstand most of the dangers in the open.

- In order to save money in the first year the forest owner may choose small plants, which are cheap and easy to plant, but normally require intensive soil preparation. In the following years, however, several clearings of the competing ground vegetation may be necessary, as well as protection by fencing.
- As an alternative, the forest owner may buy saplings, which are much more expensive and difficult to plant, but do not require any further expenditure.

Upon reaching the thicket stage, the sum of the costs may be much lower using the second alternative and, additionally, the stand has reached this stage in a much shorter period of time. Apart from the differing growth rates and requirements of the young plants and the varying intensity of ecological influences, the economic aspects, such as the time of investment, as well as the interest rate, may strongly influence the owner's decision. Unfortunately, little experimental work has been carried out by forest research institutions and forest enterprises in order to obtain reliable data comparing the advantages and disadvantages of all of the factors and procedures influencing the establishment of young forest stands. In fact, this is a very complicated aspect of silvicultural research for the following reasons:

- Experiments of this type require long observation periods (10–20 years).
- There are many factors to be considered, not to mention their interactions.
- Some factors, such as weather conditions, browsing pressure, and ground vegetation competition, may vary from one year to the next.
- The conditions in forest practice are never stable over long periods of time.
- Finally, all these factors may have very long-lasting effects and even influence the final products.

Figure 16 Saplings do not need cleaning and fencing. (a) Beech (*Fagus sylvatica*) saplings planted in a gap caused by storm in a Norway spruce (*Picea abies*) stand (south-east Germany); (b) sycamore (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and wild cherry (*Prunus avium*) saplings planted in a wet area within a young beech stand (Ettenheim, south-west Germany).

Figure 17 Container types commonly used in Sweden. (a) Container with small root volume for Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Kopperfors multi-pots); (b) modern, much larger star pots for rough subsoil conditions.

Treatment and Promotion of the Regrowth

When young plants have reached an average height of ~50 cm, the differences between naturally and artificially established young stands tend to even out, except possibly for differences in density . Therefore, they can be discussed jointly.

Some of the following procedures may be essential in order to achieve the goals mentioned previously.

Regulating the Light Conditions

Young plants growing under the canopy of old trees increasingly need sufficient light, regardless of the type of establishment. A progressive opening of the canopy is an essential silvicultural procedure during the early phases of development. The speed at which the canopy is opened depends on the light requirements of the different tree species, and may take between 5 (oak) and 20 years (beech; **Figure 21**), or possibly even longer (silver fir).

Removal of Damaged Young Plants

The felling of canopy trees over existing regrowth often results in damage to some of the young plants during both harvesting and extraction procedures. These damaged saplings tend to become malformed, and should therefore be removed by cutting them down to the stump. Broad leaves tend to resprout

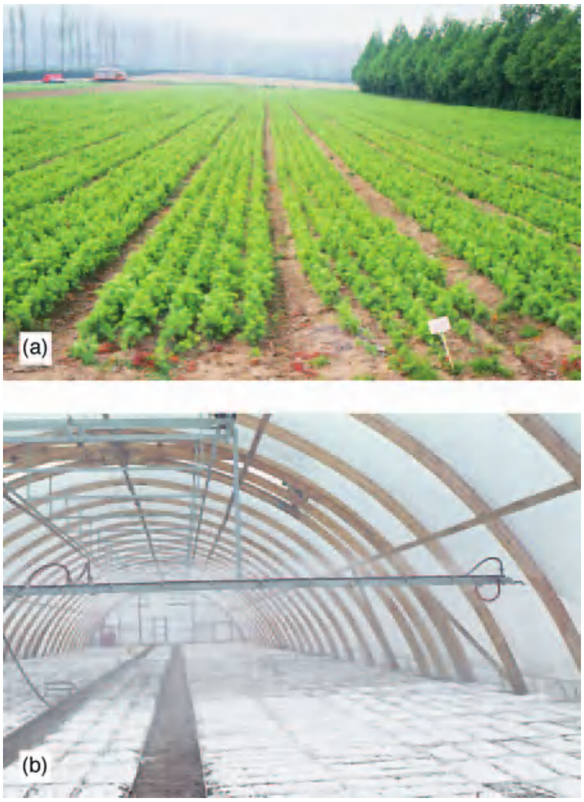


Figure 18 Private nursery (a) with long machine workable beds (west Germany) and (b) modern fully equipped, automatically managed greenhouse (Sweden).

Figure 19 (a) Various modern planting hoes; (b) modern sapling planting machine.

immediately, replacing the damaged individuals with straight and vigorous sprouts within a few years.

Regulation of Mixtures

Young naturally regenerated stands often contain more than one tree species. This species mixture has to be regulated prior to reaching the thicket stage (2–3 m in height). As has been mentioned already, the most common type of mixture is that of two or more final canopy species. If not planted in groups, the individuals of the different tree species should at this point be arranged into groups of at least the size of a grown crown. This ensures that none of the tree species will be entirely suppressed by the others because of diverging growth dynamics in particular development periods.

Regulation of Density

Naturally regenerated stands often exhibit very high tree densities. Plantations, too, are often naturally enriched by wild seedlings of pioneer species.

Very dense regrowth of certain species, for example, Norway spruce, often requires a long time to differentiate and to start developing. A systematic reduction of the plant numbers, e.g., in the form of line thinnings, or the selection of dominant individuals and the elimination of some of their competitors prior to reaching the thicket stage, therefore, helps to initiate differentiation within the young stand and improves its further development immediately.

Removal of Ground Vegetation and Climbers

Grasses especially may cause fire hazards in dry periods and may have to be cleaned even if they are no longer competitors for the saplings (**Figure 22**). In some areas, moreover, climbers such as *Rubus fruticosus* or *Clematis vitalba* may impede the development of the saplings even when they have already reached a height of some meters.

Negative Selection, Shaping, and Pruning of Saplings

There are several situations which may justify tending measures in the early stages of young stand development, i.e., before they have reached the thicket stage:

1. Some very dominant individuals already display poor form. These young trees will suppress their better-formed, but slightly less competitive

Table 3 Factors affecting the plant density of plantations

Factor	*Influence on plant density and the subsequent procedures*
Natural pruning ability of the tree species	Most broad leaves lose their branches easily when densely planted, thereby ensuring a high-quality lower stem. They are, therefore, maintained at close spacings in their youth. Poor self-pruners, including most conifers, poplars, and wild cherry must be pruned artificially if high-quality timber is desired
Quality of planting stock	Freshly harvested plant material exhibits higher survival rates. Therefore, the plant numbers can be reduced
Weather conditions at time of planting	Rainy weather with low temperatures at planting and for some days after improves successful establishment. The choice of an appropriate planting season will also allow for a reduction in the number of plants
Plant size	Seedlings and small transplants may experience higher losses after planting. Therefore, more plants are required than is the case with taller plant material
Type of restocked area	Young plants growing under the canopy of the old stand are less susceptible to climatic stress, and attacks by insects and mice, and will therefore survive better. Their stem form also benefits from the shade. Consequently, the number of plants can be reduced
Vigor of ground vegetation	Thick layers of grasses, brambles (*Rubus fruticosus*), and bracken (*Pteridium aquilinum*) result in high losses. Therefore, taller and more vigorous plants are necessary
Anticipated browsing pressure by mice and/or deer	Based on experience, damage by deer and mice has to be anticipated and compensated for with greater plant numbers

Figure 20 Line planting normally results in pure stands because one species will always dominate, and should, therefore, be avoided.

neighbors before they reach the thinning stage. Timely elimination of these individuals will raise the quality of the whole stand and improve the selection of potential crop trees at a later stage.

2. Removal of forks of dominant individuals (often called 'formative pruning') may improve their quality, where only a limited number exist.
3. Pruning of big side-branches in groups of naturally regenerated regrowth may also help to improve the quality of the whole stand.

Early tending normally significantly reduces the effort required during the thinning phase.

Figure 21 Final stage of beech (*Fagus sylvatica*) shelterwood system (Czech Republic).

Final Considerations

Stand establishment and early treatment procedures have a direct influence on the intensity of the subsequent measures. Carefully established and well-treated young stands will later need little input in terms of the regulation of mixtures, increasing the proportion of valuable timber or aesthetic

Figure 22 Dry grasses often cause fires in young plantations (Kelheim, south-east Germany).

improvements. Initial omissions, on the other hand, may later require a great deal of energy and financial input in order to achieve the original goals. Often it is not possible to compensate for a delay in tending in the early phases of stand development. The stand will never reach the possible optimum in terms of quality or fulfillment of its functions and services.

Apart from these direct interactions between early and later interventions, the intensity of stand establishment procedures has an effect over the whole life of a stand. The species distribution, horizontal texture, and even to some extent vertical structure are largely fixed and adaptation to suit new management concepts is limited – even more so with increased age.

All procedures necessary to establish and treat young stands are investments in a distant future. Many forest owners, and society as a whole, are not willing or able to spend much money and effort on forests which they will never harvest. Furthermore, it is almost impossible to predict the future needs of society with regard to production and services of the forests. For instance, is it possible that today's quality standards for the production of valuable timber will no longer be needed in the future?

Intensive and high-quality stand establishment and treatment, therefore, require a more ethical approach: how much should the current generation invest in the future of its children and their progeny?

See also: **Afforestation**: Species Choice. **Operations**: Nursery Operations. **Plantation Silviculture**: Forest Plantations; Stand Density and Stocking in Plantations; Tending; Coppice Silviculture Practiced in Temperate Regions.

Further Reading

Burschel P and Huss J (1997) *Grundriss des Waldbaus: Ein Leitfaden für Studium und Praxis*, p. 487. Berlin: Parey Buchverlag.

Joyce PM and OCarroll N (2002) *Sitka Spruce in Ireland*, p. 201. Dublin: COFORD.

Joyce PM (ed.) (1998) *Growing Broadleaves: Silvicultural Guidelines for Ash, Sycamore, Wild Cherry, Beech and Oak in Ireland*, p. 144. Dublin: COFORD.

Hunter ML (1990) *Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity*, p. 370. New Jersey: Prentice-Hall.

Piussi P (1994) *Selvicoltura Generale*, p. 421. Torino: UTET.

Savill P, Evans J, Auclair D, and Falck J (1997) *Plantation Silviculture in Europe*, p. 297. Oxford: Oxford University Press.

Schütz J-P (1990) *Silviculture 1: Principes déducation des forêts*, pp. 243. Lausanne: Presses polytechniques et universitaires romandes.

Smith DM (1986) *The Practice of Silviculture*, 8th edn, pp. 525. New York: John Wiley & Sons.

AGROFORESTRY

F L Sinclair, University of Wales, Bangor, UK

Introduction and Definition

Agroforestry is a term for practices where trees are combined with farming, as well as for the interdisciplinary subject area embracing land use systems, at a range of scales from that of the field to the planet, that involve interactions amongst trees, people, and agriculture. Put simply, agroforestry is where trees interact with agriculture. There is a long tradition of agroforestry practice in many parts of the world, but it has come to scientific prominence, and has emerged as a major focus in international development, only during the last quarter of a century. The term clearly derives from uniting two subject areas, forestry and agriculture, which for a long time, but not necessarily for good reasons, were institutionally separated the world over, in terms of education, research, policy development, and its implementation. As such, agroforestry has been at the forefront of much recent innovation in both farming and forestry. The principal forces driving this innovation have been the introduction of a more human perspective from the agricultural tradition into forestry, while emphasizing a more ecological as opposed to agronomic perspective in agriculture, including the longer time horizons and larger spatial scales that forestry has always embraced.

Why Agroforestry?

Interactions between trees and agriculture are clearly manifest at a range of scales from that of the field, the farm and the landscape, to that of the whole planet. Trees provide a range of valuable products such as food, fuel, fibers, fodder, and medicines that make important contributions to the rural economy, as well as influencing ecosystem services such as biodiversity conservation, water yield and quality, carbon storage, and soil conservation. Agroforestry research and development seek to improve rural livelihoods by producing more products of higher value from trees and associated crops or livestock, while conserving the resource base, in terms of ecosystem attributes like biodiversity and soil fertility, from which they are ultimately derived. Because of their large stature and longevity, trees often make important contributions to the sustainability of productive landscapes.

The Significance of Scale

At a field scale, trees may be grown in intimate mixtures with crops or grazed pasture, or cropping or grazing may occur in forests. At a farm scale, areas of farm woodland may interact biophysically and economically with crop or livestock enterprises on the farm. Biophysical interactions, for example, occur where woodland shelters an agricultural field or acts as a reservoir for crop or livestock pests or their predators. Economically, there are interactions through resource allocation of land, labor, and capital amongst competing activities in an integrated farm business.

At a landscape scale and beyond, the pattern of tree cover and agricultural land uses may combine to determine a range of productive and service functions. These include food and fuel production and their importance to the rural economy, water yield and quality across catchments, and regional biodiversity. Nutrient transfers across landscapes are often important. The soil fertility on privately owned crop land in the Nepalese mid-hills for example, is sustained by nutrient transfers via livestock from common property forest and grazing areas. Islands of fertility develop around trees in dry areas, as a result of tree litter inputs beneath the crown and animals congregating around trees and depositing nutrients there. In terms of biodiversity, farm trees in the landscape surrounding cloud forest reserves in central Costa Rica are vital for conservation of migratory birds like the resplendent quetzal. The birds are crucial to the burgeoning ecotourism industry in the country, but if they are to be retained in the reserves, then there has to be sufficient tree cover in the farming landscape for them to make their passage from the cloud forest to the coast and back.

On a continental scale, there are now attempts to manage tree cover to create a contiguous Mesoamerican corridor of tree cover connecting North and South America, and the shade trees in pastures and on coffee and cocoa farms in the region may be a vital component of this. At a global scale, it is clearly interactions amongst agricultural and forest land uses across the land surface that determine the terrestrial sink and emission of carbon and hence impact on global climate change.

Agroforestry Practices

Trees and Arable Crops (Silvoarable)

Agroforestry practices predominantly involving trees and crops are known as silvoarable or agrosilvicultural practices. These include ‘taungya,’ where farmers are allowed to cultivate crops amongst young trees during forest establishment, and various traditional and novel ways in which farmers retain or plant trees in crop fields. Important examples include extensive parkland systems that cover much of West Africa, as well as savannas more generally around the world, where farmers retain valuable and predominantly naturally regenerated native trees in their crop fields, in addition to the modern technology of hedgerow intercropping (also referred to as alley cropping), where fast-growing shrubs, that are often nitrogen fixing, are grown between strips of crops and periodically cut back to provide a nutrient-rich mulch to fertilize the crop. When practiced on slopes, as contour hedgerows, and specifically sited and spaced to reduce soil erosion, hedgerows are effective because the rate of water infiltration is increased thereby reducing runoff, and soil builds up behind the hedgerow creating biologically, as opposed to mechanically, constructed terraces.

Trees, Livestock, and Grazed Pasture (Silvopastoral)

Combinations of trees with grazed pasture are referred to as silvopastoral practices. These include various forms of forest grazing as well as trees retained in pasture to provide fodder and either shelter or shade, or both, for animals. Forest grazing may occur for predominantly productive or conservation purposes. In the UK for example, periodic grazing is now being used as a management tool to maintain open canopy woodland habitat and to retain understory ferns that would otherwise be outcompeted by grasses. In northern Europe, there has been a resurgence of interest in pasture woodland and parkland, both from a historical perspective as examples of a biocultural heritage, and for conservation of some rare lichens and fungi. Further south in the Mediterranean, the Spanish 'dehesas' that combine grazing and acorns from cork oak as fodder for pigs are of similar conservation interest, because they are the last remnants of habitat for the Iberian lynx. Dispersed trees in seasonally dry tropical pastures have recently been found to be far more important contributors to dry-season cattle diets than previously thought. In these and wetter tropical pastures, trees may also make important contributions to nutrient cycling and regional biodiversity conservation, and are an important tool for ecosystem rehabilitation in areas where forest conversion to pasture has been followed by ecosystem degradation.

Trees and Animals without Pasture

There are also agroforestry practices involving more direct interactions between trees and animals without a pasture component. These include fodder banks, where fast-growing trees in blocks provide a cut-and-carry fodder resource for livestock, and sericulture, which for 4500 years in China, has involved feeding mulberry (*Morus alba*) leaves to the domestic silkworm (*Bombyx mori*) and then harvesting silk by unraveling the cocoon. It takes over 4 tonnes of mulberry to produce a silk blouse!

Plantation Tree Crop Agroforestry and Multistrata Systems

Another important group of agroforestry practices involve combining plantation tree crops such as cocoa, coconut, coffee, oil palm, rubber, and tea either with shade trees or by intercropping between the tree crop rows. Intercropping is generally practiced amongst immature tree crops to provide short-term income before the tree crops yield, such as banana grown with rubber up to canopy closure in Sri Lanka, but there is scope for understory crops or pasture beneath mature stands of some tree crops with light canopies like coconut and rubber, or amongst cocoa bushes in extensive smallholder agroforests. For example, there is currently much interest in the understory herb *Thaumatococcus daniellii*, which grows well under mature rubber. This plant is the source of thaumatin, a substance 3000 times sweeter than sugar that is used as a natural sweetener and was selling on the London market in 2003 at over £4000 kg^{-1}, so could provide useful supplementary income for smallholder rubber growers in West Africa. Although coffee, cocoa, and tea can be grown in open conditions with high levels of inputs and intensive management, farmers often plant or allow regeneration of interspersed trees to reduce inputs required for the tree crop, modify the microclimate to control pests and diseases, or provide additional sources of income from fruit or timber. So, although often called shade trees, shade may not be their primary function. For example *Cordia alliodora* is commonly found in central American coffee plantations, as an important timber resource, whereas *Erythrina* spp. in the same plantations may be heavily pollarded and used to fix nitrogen and recycle nutrients. Income from some fruit trees such as *Dacyroides edulis* in Cameroon can be more valuable than the cocoa crop itself in smallholder multistrata cocoa agroforests.

There has been much recent interest in extensive areas of multistrata agroforests in Southeast Asia, Africa, and Latin America. Cocoa agroforests in West Africa and coffee and cocoa systems in Latin America have already been alluded to. In Southeast Asia, there are an estimated 3 million ha of jungle rubber in Indonesia, where a long rotation slash-and-burn cycle is used to produce secondary forest enriched with rubber. In northern Thailand, there are extensive areas of thinned hill evergreen forest enriched with tea that are now being considered for management as buffer areas around less disturbed forest. The forest functions provided by extensive and contiguous areas of these perennial agroforests, or land use mosaics of which they are a significant part, contrast sharply with intensive monocultural agricultural alternatives but the challenge is to ensure that they are also as productive for people whose livelihoods depend on them.

Forest Gardens and Gathering of Non-Timber Forest Products

There is a blurry distinction between these multistrata agroforests, predominantly enriched with a particular tree crop such as rubber, tea, or cocoa and more diverse forest gardens, usually close to settlements, that are used to derive a wide array of household subsistence items and some produce for sale. Often these are homegardens with a predominant tree component, as in the Kandy forest gardens on lower slopes in upcountry Sri Lanka. They are characterized by their species diversity and are usually supplementary to other field agriculture, such as paddy rice cultivation in valley bottoms in Kandy. Forest gardens appear in many forms throughout the world, with varying ratios of planted to naturally regenerated trees, from enriched forest to completely planted and manicured tree gardens, and so they vary in the extent to which their structure and species diversity is forestlike and hence their environmental significance over and above the direct benefits obtained from them by farmers. There is also a host of non-timber forest products (NTFPs) including products from undomesticated trees, herbs, and fungi, as well as insects and wild animals, that may be harvested from forest. Where people are making a regular harvest from forest resources, we see the first stages of agricultural use of forest resources, and hence an important form of agroforestry.

Reliance on Wild Trees in Agroforestry and Opportunities for Domestication

Despite their importance to local livelihoods and as foreign-exchange earners for some countries in their range, many valuable agroforestry trees remain essentially wild and hence threatened because their exploitation, without steps being taken to ensure conservation and regeneration, may be unsustainable. There is also a vast untapped potential to obtain higher value from these trees by more controlled production and marketing. Some well-known trees fall into this category, such as the shea butter in West Africa (*Vitellaria paradoxa*), from which comes a range of local foods, as well as expensive cosmetic products and a cocoa substitute sold in industrialized countries (in 2003 pure shea butter was selling in the UK for over £140 per liter as a skin cream). The baobab (*Adansonia digitata*) is a distinctive landscape feature in farmers' fields across much of Africa, from which fibers, fodder, and many other locally important products and cultural values are derived. Marula (*Sclerocarya birrea*) is a locally important fruit in southern Africa, high in vitamin C, used to flavor an internationally marketed liqueur, and is also the source of a high-quality oil derived from the kernel, which is now the basis of a new cosmetic range retailing in Europe. There are also some useful closed forest species, such as *Prunus africana* from which an effective cure for benign prostatic hyperplasia is derived. This is a condition affecting more than half the men over 60 in industrialized countries, and harvesting of bark of the tree has led to threats of local extinction in parts of its range around Mount Cameroon and in Madagascar.

While both shea and marula are marketed in Europe as sustainable tree products, from fair trade with African women in Burkina Faso and Namibia respectively, there are concerns about the age and sex ratios of some marula populations. Marula is dioecious, with different male and female trees, and it appears that there may be a tendency for people to remove male trees because they compete with crops but do not fruit. Once many males have been removed, the female trees are less likely to get pollinated by the bees that transfer the pollen from male to female trees, and so they too produce less fruit and hence become vulnerable to removal. Stopping such a spiral of decline requires research on pollination, to determine how many male trees need to be retained over what distances in the landscape; this should lead to the establishment of social structures that allow management of tree numbers at a landscape scale, involving groups of villages each comprising many individual farmers. Such links between ecological and social issues are characteristic of agroforestry. There are also a host of NTFPs including herbs and fungi that are presently harvested from the wild, from wild ginseng (*Panax quinquefolius*) in upstate New York in the USA to *Thaumatococcus daniellii* in the moist forests of Ghana and the Ivory Coast. The domestication and commercialization of these wild trees and other NTFPs to ensure sustainable production into the future is a main thrust of international agroforestry research and development.

Agroforestry as a Science and in Development

Recognition of the Importance of Agroforestry

In its short history as a scientific subject and an international development imperative, agroforestry has developed rapidly and it continues to do so. Recent trends in the focus of agroforestry research and extension are informative. We can chart its entry to the international stage, by the emergence of ICRAF, then the International Council for Research in Agroforestry, now the World Agroforestry Center, in 1978. This was 5 years after the Center for Tropical Agricultural Research and Higher Education (CATIE), which pioneered research, education, and extension on agroforestry with perennial tree crops in Latin America, had come into existence. For the first decade or so, the focus was on describing various traditional agroforestry practices around the world and developing methods for analyzing land use systems involving trees and their potential improvement paths, by drawing on contributing disciplines. These included ecology, anthropology, agronomy, soil science, and forestry. There was also intensive, predominantly agronomic, research on a few technologies, most notably alley cropping pioneered at the International Institute of Tropical Agriculture (IITA) and closely associated and sometimes confused with this, on contour hedgerows. This agronomic research was accompanied by conventional tree improvement of a few exotic, nitrogen-fixing, tree species, used in these technologies, principally *Leucaena leucocephala* and *Gliricidia sepium*. As a council, ICRAF did not have a remit to do research itself, but to coordinate research with national partners.

Changing Imperatives and Farmers' Priorities

In the early 1990s ICRAF joined the Consultative Group on International Agricultural Research (CGIAR) system and became a research center. This coincided with results emerging from well-funded and rigorous scientific research on tree crop interactions and a shift away from the centralized development of one or two technological interventions on research stations for widespread dissemination to farmers, towards encouraging local development of a wide range of tree species, in various productive and environmentally protective niches on farms and in farming landscapes. This more closely matched what farmers were doing and wanted. While contour hedgerows were a successful centrally developed and promoted technology, alley cropping with fast-growing exotic shrubs had been somewhat oversold as a panacea for replenishing and maintaining soil fertility. It was realized that it was only likely to be useful in a rather limited domain, where there was already sufficient soil fertility for fast growth of shrubs and not too much competition for water, and where land was scarce relative to labor. Improved fallow interventions, where fast-growing shrubs are grown sequentially between cropping phases rather than simultaneously with the crop, were found useful, especially in drier conditions.

There have also been a number of spectacular problems with widely used germplasm of some shrub species as, for example, the *Leucaena* psyllid that spread around the world devastating susceptible stands owing to their narrow gene base in Africa and Asia that had been selected in environments free from pest pressure. This was coupled with a realization that conventional tree improvement, involving selection for only a few traits under controlled conditions, led inevitably to trees suitable for monoculture rather than polyculture; and this spawned a move to encouraging local, village level domestication. This involved selection for improvement within, rather than outside, the farming system for which the trees were to be used. This had advantages of maintaining a broader genetic base and ensuring that people currently benefiting from exploiting the wild resource were involved and benefited from the domestication process. Emerging results of research on local knowledge revealed that farmers often already used sophisticated criteria to evaluate attributes of trees that affected both how the trees interacted with crops and soil, and how they were productive, in terms of understanding variability in fodder value and fruit quality.

In temperate regions, agroforestry gained considerable credence in the USA, Australia, and Europe as agricultural policy increasingly sought to balance environmental and productive goals.

Moving to Larger Scales and Trade-Offs Between Production and Ecosystem Services

Most recently, the scope of agroforestry research and development has on the one hand expanded to encompass landscape, regional, and global issues, while on the other it has concentrated on delivering impact locally. The landscape scale has emerged as a key focus of research and development, requiring explicit trade-offs to be made amongst stakeholders and between the productive, food, fuel, and income-enhancing functions and ecosystem services. This involves addressing natural resource management issues, involving complex interactions amongst disciplines, over large temporal and spatial scales and with groups of people with diverse interests. This has brought into sharp focus the need to develop appropriate policy environments in tandem with developing technical understanding. It is also imperative to find inclusive interdisciplinary and participatory methodologies that are rigorous enough to cope quantitatively with specific natural resource management issues, while remaining transparent enough to engage a broad enough range of stakeholders.

See also: **Silviculture**: Managing for Tropical Non-timber Forest Products. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Soil Development and Properties**: Nutrient Limitations and Fertilization.

Further Reading

Buck LE, Lassoie JP, and Fernandes ECM (eds) (1999) *Agroforestry in Sustainable Agricultural Systems*. Boca Raton, FL: CRC Press.

Garrett HE, Rietveld WJ, and Fisher RF (eds) (2000) *North American Agroforestry: An Integrated Science and Practice*. Madison, WI: American Society of Agronomy.

Gordon AM and Newman SM (eds) (1997) *Temperate Agroforestry Systems*. Wallingford, UK: CAB International.
Hislop M and Claridge J (eds) (2000) *Agroforestry in the UK*. Forestry Commission Bulletin no. 122. Edinburgh, UK: Forestry Commission.
Huxley PA (1999) *Tropical Agroforestry*. Oxford, UK: Blackwell Science.
Izac A-MN and Sanchez PA (2001) Towards a natural resource management paradigm for international agriculture: the example of agroforestry research. *Agricultural Systems* 69: 5–25.
Ong CK and Huxley P (eds) (1996) *Tree–Crop Interactions: A Physiological Approach*. Wallingford, UK: CAB International.
Sanchez PA (1995) Science in agroforestry. *Agroforestry Systems* 30: 5–55.
Schroth G and Sinclair FL (eds) (2003) *Trees, Crops and Soil Fertility: Concepts and Research Methods*. Wallingford, UK: CAB International.
Sinclair FL (1999) A general classification of agroforestry practice. *Agroforestry Systems* 46: 161–180.
van Noordwijk M, Cadisch G, and Ong CK (eds) (2004) *Below-Ground Interactions in Tropical Agroecosystems: Concepts and Models with Multiple Plant Components*. Wallingfood, UK: CAB International.
Young A (1997) *Agroforestry for Soil Management*. Wallingford, UK: CAB International.

Air Pollution *see* **Environment**: Carbon Cycle; Impacts of Air Pollution on Forest Ecosystems; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Health and Protection**: Diagnosis, Monitoring and Evaluation. **Site-Specific Silviculture**: Silviculture in Polluted Areas. **Soil Development and Properties**: Nutrient Cycling; Soil Contamination and Amelioration. **Tree Physiology**: Stress.

Arboriculture *see* **Urban Forestry**

B

BIODIVERSITY

Contents

Biodiversity in Forests

H G Lund, Forest Information Services, Gainesville, VA, USA
F Dallmeier and A Alonso, Smithsonian Institution, Washington, DC, USA

Introduction

Interest in biodiversity began in the mid-1980s with the Biodiversity Symposium, held in Washington, DC, sponsored by the National Academy of Science. Within increasing human populations and rising demands for resources and living space, the need to conserve biological diversity rose to the forefront with the development of the Convention of Biological Diversity (CBD) in 1992. The purpose of the Convention is to conserve biological diversity, promote the sustainable use of its components, and encourage equitable sharing of the benefits arising out of the utilization of genetic resources. Biodiversity inventories provide the building blocks upon which to carry out the intent of CBD and to meet local needs. Using inventories as the base, industry and other development opportunities should incorporate biodiversity within their management practices.

The concept of biological diversity is defined in Article 2 of the CBD as follows:

> 'Biological diversity' means the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.

It is widely recognized that the earth's biodiversity is poorly known. Although 1.75 million species have been discovered and described, the number will be much greater once we include bacteria, viruses, most of the marine species, and most of the arthropods. There is no doubt that we are now destroying this diversity at an alarming rate. No one knows exactly what the current extinction rate is, but recent calculations put it at between 1000 and 10 000 times greater than it would naturally be. The rate of extinction also appears to be increasing. Species are threatened in every habitat on every continent, though the severity of threat varies from place to place. A vital question is how badly this loss affects ecosystem functioning and our eventual well-being. Although current studies are impressive, they are tiny in comparison to the amount of unknown diversity and the urgency and importance of finding out what are available and taking steps to preserve and sustainably use the remaining.

The CBD obliges signatory nations to undertake an inventory of their biological diversity to provide basic information about the distribution and abundance of biodiversity. Such data are necessary for the long-term sustainable management, use, and conservation of biodiverse areas. Parties are to monitor the elements of biological diversity, determine the nature of the urgency required in the protection of each category, and sample them in terms of the risks to which they are exposed. They are to report on the biotic wealth and national capacity, the goals and gaps, strategic recommendations, and characteristics of the action. Specifically, under Article 7. Identification and Monitoring, nations are to:

- Identify components of biological diversity important for its conservation and sustainable use
- Monitor components of biological diversity, paying particular attention to those requiring urgent conservation measures or which offer the greatest potential for sustainable use

- Identify processes and categories of activities which have adverse impacts on the conservation and sustainable use of biological diversity, and monitor their effects
- Maintain and organize data derived from identification and monitoring activities.

Forest certification systems resulting from agreements in the United Nations Conference on Environment and Development (UNCED), Agenda 21, include criteria, indicators, or principles that address biodiversity as a critical component to sustainable development.

In order to meet the above requirements, parties need inventories of biological diversity. The objectives of biological diversity inventories may be to:

- Identify priority conservation areas
- Provide the necessary baseline data for monitoring the effects of anthropogenic disturbance or climate change on the biota
- Detect changes in ecological diversity that exceed the range of natural variation, across a range of spatial and temporal scales
- Provide an 'early warning' of impending irreversible changes
- Provide reports to the public on the status of ecological diversity in a timely and accessible manner
- Meet national and international commitments for monitoring biodiversity
- Provide data consistent with the requirements of forest certification programs.

Biodiversity Types

CBD addresses three types of diversity: genetic, species, and landscape or ecosystem. Each has special features and challenges for inventory.

Genetic Diversity

Genetic diversity is the degree of variability of the genetic material of an organism. Assessment of genetic diversity is time-consuming and prohibitively expensive, requiring modern laboratories and expensive chemicals. Species are defined by the differences in their genes. Therefore, one often uses species diversity to estimate genetic diversity.

Species Diversity

Species diversity encompasses the number, types, and distribution of organisms found in a given area. Species diversity is the standard unit of measurement in most biodiversity surveys. The advantage of inventorying species is the advantage of being natural biological divisions and that they are easily identifiable. Many people already know high-interest organisms such as flowers and birds so identification of these organisms is relatively easy.

However, there are a very large number of species. A high proportion of them, particularly invertebrates, are as yet undescribed. Moreover, the identification of described species often requires a high level of expertise. Identifying all species in even a limited area is generally impracticable.

A common solution is to select certain taxa as indicator groups to act as surrogates for the whole biological diversity. Using indicator species can reduce the cost of the survey. The following options for indicators are in order of preference.

1. Best estimates: using genealogy to predict genetic or character richness.
2. Popular estimates: using species richness.
3. Practical estimates: using higher taxa or environmental variables as surrogates.
4. Relationship among estimates: a scale of surrogacy for mapping more of biodiversity value at lower cost.

To be effective, indicators should be:

- readily quantifiable
- easily assessed in the field
- repeatable and subject to minimal observer bias, and cost-effective
- ecologically meaningful – that is, to be representative of the taxic variation, microhabitats, and trophic diversity in the area and in close association with, and identification of, the conditions and responses of other species.

Scarce and less familiar species with short mean generation times may respond most rapidly to environmental deterioration. Thus these may make better indicators for environmental monitoring than the larger, better-known organisms.

Landscape Diversity

Landscape diversity refers to the spatial heterogeneity of the various land uses and ecosystems within a larger area. Surveys of landscapes are useful for locating and prioritizing areas to protect. The natural environment is a highly variable continuum and is difficult to divide into a series of discrete, discontinuous units. Remote sensing and geographic information systems (GIS) obviate the need to develop the complex habitat and ecosystem classifications. Different, measurable attributes of the environment can be stored in separate layers within a GIS, such as soil characteristics, altitude, rainfall, percent canopy cover, mean height of dominant vegetation, and distributions of individual species. These can then be played back in any number of ways.

Inventory Challenges

When compared to traditional forest surveys, the challenges for biodiversity inventories include the number of species, their mobility and/or seasonality, and time and resources available.

There are between 10 and 20 million species on earth. This is about 10 times as many as have been formally described by taxonomists in the past 250 years or so. Most species occur in the tropics, where taxonomic resources are scarcest. When considering all the species that may be present in an area – from insects to mammals, and from fungi to trees – it is generally impossible to enumerate and count each and every species in a given area. Consequently, taxonomically complete inventories are rarely conducted unless the area is very small.

Because of the vast differences in goals and areas to be surveyed, there are no well-defined rules as to how to perform biodiversity surveys. Unlike trees, fauna are mobile. Some flora and fauna may only be found during certain times of the year. Selecting the time to do an inventory is a major challenge.

Lastly, inventories take time – for planning, execution, and analysis – and time is running out for many species. Any inventory is costly. Inventories involving biological diversity are exceptionally costly, primarily because of the expertise necessary to locate and identify species. Taxonomic resources available to undertake large-scale inventories are few and far between. Accurate inventory requires access to reference collections and literature. These resources are primarily concentrated in the large museums of a few temperate countries.

To be able to make judgments concerning status and changes we have to have methods of measurement. Information on the identity, location, population size, or community distribution of a resource is obtained initially by field inventory and frequently displayed as resource maps. Inventory and monitoring of biological resources provide baseline information on the presence and distribution of biological resources and biological information necessary to implement adaptive management.

Types of Biological Surveys

There are two general types of biological surveys – taxonomic and abundance. Taxonomic and abundance surveys may be scientifically designed, where the sampling is repeatable, or search-based inventories, where it is not. The limitations of search-type inventories include nonrepeatability due to lack of predetermined and documented sampling protocols. The advantage of searching is that it may provide the most taxonomically complete inventory.

Taxonomic Surveys

Taxonomic surveys are undertaken to locate and document occurrences of particular species, in other words, what species exist in forest A. The primary goal of surveying the flora and fauna is to develop a list of the different species that are present on the site and not necessarily their numbers and condition. The data gathered are used to identify new occurrences of sensitive species, monitoring endangered populations, evaluating conservation priorities of an area, and bioprospecting. Sampling should take place in both undisturbed and disturbed areas.

The sampling of vegetation is more or less straightforward – plots and transects. The survey of fauna – things that move – is slightly more difficult. As a result, we see more subjective and opportunistic methods being used.

Vegetation is frequently observed and measured using fixed-area nested plots. The size of the plot or subplots will depend on the vegetation being observed. Large plots, such as 5×20 m, may be used for recording trees where plots as small as 2×0.5 m may be used for herbaceous vegetation. A series of permanent nested plots may provide information on spatial patterns of species and allow for statistical comparisons and can be used to detect trends in richness over time.

Transects for noting both flora and fauna biological diversity often utilize gradient-directed sampling. Transects are selected to transverse the steepest environmental gradients present in the area, while taking into account access routes. This technique is appropriate for rapidly assessing species diversity, while minimizing costs, since gradient transects usually capture more biological information than randomly placed transects of similar length.

Arthropods are often sampled using pan traps or pit-fall traps placed in microhabitats. Microhabitats may be identified based upon soil particle sized, amount and type of litter, surface moisture, vegetation structure, dominant plant species, and degree of shade. Voucher specimens are also used to sample invertebrates since most species are poorly known and difficult to identify.

Amphibians and reptiles are sampled using a variety of methods, including visual and audible searches along transects and within quadrats, sticky traps, and pit-fall traps. Sites are often subjectively selected to ensure sampling of all habitats and to minimize the number of species encountered.

Birds are sampled using mist-netting, point counts, and transects. The advantages of mist-nets are that:

- relatively little training is necessary to set up the nets and collect the birds
- identification tools may be used with birds in hand
- the method does not require vocalization knowledge
- the repeatability and accuracy of the data collected are high
- data can be collected on the physical condition of the birds
- recapture provides demographic data
- secretive and inconspicuous species may be detected.

Vocalizations and observations are used in point counts and transects. They have the advantage that they are less labor-intensive than mist-netting, they sample a larger proportion of the bird community, and estimates of population density may be obtained. The main disadvantage is the significant training in recognizing the birds and their calls.

Trapping is often used to sample small mammals. The advantage of trapping is that it may also provide voucher specimens.

Large mammals are surveyed using direct observations, aural identification of animal vocalizations, scent-post surveys, use of mammalian signs, and trapping.

Abundance Surveys

Abundance surveys focus on the number of given species – in other words, how many gold finches are found in forest A? They are used for developing and evaluating management plans. These generally use remotely sensed data, GIS systems, preexisting cartographic maps and inventories and field sampling. One may collect either qualitative data (presence/absence, also known as binary) or quantitative data, in which the numbers of individuals for each species are counted.

Biodiversity Inventory Strategies

There are two strategies for conducting biodiversity inventories – those for rapid assessment and those for baseline. Both may be used as a base for monitoring.

Rapid Assessment

Rapid-assessment methods and sampling for indicator species are designed to identify and monitor selected biotopes of critical value. These surveys are often conducted on a regional or national basis to supply information necessary for the selection of conservation areas and other types of land-use planning. They may also be conducted locally where some type of land-use activity is planned. Speed is critical. Thus it is natural to focus on well-known and easily recognized organisms, such as mammals, birds, trees, and butterflies.

These assessments often employ a ‘top-down’ analysis that begins with an assessment of the natural communities present and their relative quality and condition. This information is subsequently used to determine where different species-oriented surveys should be conducted. This approach, commonly referred to as ‘coarse filter – fine filter,’ concentrates inventory efforts on those sites most likely to contain target species. These are very quick surveys that can be used to identify, with high spatial resolution, and within a short time frame, priority areas for the conservation and sustainable management of biodiversity.

Rapid assessments are carried out to identify areas quickly that need immediate protection. They usually consist of mapping out areas to be preserved. They are often conducted by teams of scientists and local experts aimed at identifying areas that have or are likely to have considerable diversity of species – especially those that may be considered rare or endangered.

Baseline Assessment

Once one has established conservation areas or areas of concern or importance, then there emerges the need for monitoring and for knowing what is present in order to manage the resource. This requires the second type of inventory – baseline assessment, which focuses species. Baseline assessments are designed to find out what is in a given area and may include taxonomic surveys or abundance surveys. They are used as a foundation for monitoring change.

Sources for baseline assessments include satellite data, aerial survey, existing maps, field survey, and expert advice. One can combine these disaggregated data sets in a GIS to generate maps according to need.

Monitoring and Evaluation

Monitoring is the act of observing something, especially on a regular or ongoing basis, and keeping a record of observations made. The main objective of monitoring is to reveal discrepancies between forecast and achievement in time for remedial actions to be taken. It also provides critical information to identify natural changes from human-induced changes.

Repeated surveys allow examination of time and spatial changes. Monitoring sites may consist of both permanent sites (visited one or more times each year) and nonpermanent sites. The permanent sites may be stratified across the different kinds of habitat/plant communities, replicated for each habitat/plant community monitored, and reflective of the different grades of habitat quality or condition. Landscape-level monitoring at the ecoregion level is often dependent on acquiring the appropriate GIS-based vegetation maps.

Monitoring can serve as a warning system, alerting managers that change in biodiversity may require changes in management regimes to ensure protection of scarce resources. Monitoring involves the repeated collection and analysis of observations and measurements to evaluate changes in populations of species and environmental conditions.

If there is the possibility that a sampling area may again be visited again, permanently mark the plots for remeasurement. Use care in remeasurement, take care to prevent an area from being overly disturbed. Permanent monitoring plots that collect reliable data can also act as standard reference points for the interpretation of changes observed by satellite.

Monitoring often occurs at the population (individual or multiple species) or ecosystem (individual or multiple habitats/plant communities) levels to facilitate tracking trends in resource size or distribution. Monitoring may also be conducted to obtain information on the condition of the resource and includes tracking characteristics such as contaminant concentrations, health of individuals, population vigor, and habitat quality. Lastly, monitoring can occur at regional scales that enable tracking changes in land use and fragmentation patterns.

For monitoring to be effective:

- Baseline (i.e., inventory) information must be collected or available.
- Monitoring objectives must be established.
- Monitoring actions must be repeated over time using consistent, standardized procedures.
- Monitoring results must be interpreted relative to the baseline information and the monitoring management objectives.

Quantitative data are more desirable for monitoring. They allow changes in the population to be measured instead of the population simply being recorded as present or absent.

Steps for Developing a Biodiversity Inventory

The steps are similar to those for developing most any other type of resource inventory and monitoring program:

1. Carry out a stakeholder consultation to identify the issues.
2. Gather known information.
3. Define assessment and baseline programs together with management objectives.
4. Define the issues and develop options throughout the process.
5. Implement assessment.
6. Implement adaptive management, assess and monitor.

Carry out a Stakeholders' Consultation to Identify the Issues

Develop and record the long-term rationale, objectives, and design of the monitoring program. Establish goals and objectives and the biodiversity endpoints that an agency, organization, or company wishes to assess and maintain.

Gather Known Information and Lay Necessary Groundwork

Make use of existing biodiversity-related data and analyze in a GIS-based format if possible. Existing information may consist of maps, reports, data, taxonomic specimens, personal knowledge, and remote sensing imagery. Information on areas similar to the one under study is also helpful.

Define Assessment and Baseline Programs Together with Management Objectives

The purpose may be to determine the extent, distribution, and condition of existing vegetation types, the probable distribution of species of concern, and the distribution (and intensity) of stressors (e.g., habitat fragmentation). Establishing baseline conditions may require the integration of monitoring programs and data-sharing among other landholders and resource agencies within the ecoregion.

- Delineate areas of high species richness and endemism, as well as areas and ecosystems at high risk of impoverishment because of their particular susceptibility to human-induced stressors. The preceding areas warrant more intensive monitoring.

- Identify indicators of structural, functional, and compositional biodiversity at several levels of the hierarchy that correspond to endpoints.
- For each major class of habitat (which may contain different plant communities), identify control areas (i.e., generally free from human-induced impacts) and areas subject to more intensive management or environmental stress.

Define the Issues and Develop Options Throughout the Process

Through the stakeholder workshops and consultation process, identify critical biodiversity issues related to the operation. Formulate specific questions to be answered by monitoring. Typical questions may include:

- Are populations of species of concern declining, stable, or increasing?
- What are the patterns of species diversity across habitats and plant communities?
- Is the diversity, at its different levels of organization, declining, stable, or increasing?
- How are the size, distribution, and condition of native habitats and plant communities changing? How does biodiversity differ between natural and artificial ecotones (i.e., transitional areas between ecosystems or plant community types)?

Specify thresholds for the biodiversity endpoints that will trigger the need for changes in management practices.

Identify resource needs Understanding the resource needs and ascertaining the level of support are essential to ensure success of the biodiversity inventory. Critical resources may include time, commitment, and funding allocated to the project, as well as a sufficient number of people trained to conduct biodiversity assessments, devise the monitoring strategies, and improve the sampling protocols. These elements need to be balanced with professional expertise, adequate technology to manage information and voucher collections, and an appropriate budget for field equipment, data management, and publications.

Define spatial and temporal scales The scale at which the survey is carried out depends upon the goals of the project and on the unit of biodiversity being used. The scale should be appropriate to the organisms being surveyed.

The frequency of monitoring depends largely upon the goals of the project and the life history of the species; population changes that may be the result of regular cyclical fluctuations may appear drastic if the cycle is not known. Consideration of such natural cycles is important to the monitoring of populations.

Design protocols The next step is to design a monitoring protocol to address issues such as sampling design, data management and analysis, interpretation of results, and reporting mechanisms. Design requires a balance between time and effort and interpretability of data.

For taxonomic surveys, sampling effort can be expressed in many ways: as search time per site, as search within a given distance of a reference point or line, or as total number of sites or replicates needed to find a pattern. Setting a definite time limit also allows the survey to be more standardized and results can be compared from year to year.

For a survey to be considered scientific, it should be random. Consider using a grid covering the entire area of interest. A systematic network of fixed sample points across the entire region is one approach that would sample most vegetation types proportional to their size and at the same time be low-cost.

Different data collection approaches may be used to meet the above objectives.

Respond to emerging lessons and reassess objectives Ask:

- Have the objectives been clearly stated and are they realistic?
- What monitoring protocols are required to achieve the biodiversity conservation objectives? What is the timeline for accomplishing the objectives?
- Will the information that is gathered assist managers in making informed decisions?
- Can the results of the management decisions be statistically analyzed?
- Has a cost – benefit analysis been completed?
- What is the scale of the monitoring program?
- What kinds of teams and organizations are required to achieve the objectives?

The monitoring strategy will continually evaluate the relevance of its biodiversity endpoints, the questions asked, the indicator variables selected for monitoring, and their relationships. Changes to the monitoring strategy and its in-the-field protocols will be made as necessary.

Implement adaptive management, assess, and monitor Assessment and monitoring protocols are essential to develop a solid scientific foundation for biodiversity monitoring. In recent years, there has been an increased emphasis on standardizing monitoring protocols to facilitate comparisons among different projects. The long-term data obtained from implementation of such protocols are helpful in detecting the magnitude and duration of change, how related taxa are changing, and early-warning indicators of ecosystem health. They serve as the basis for formulating additional research hypotheses, and most importantly, the data can be used to guide management decisions for biodiversity conservation.

The results of monitoring should be analyzable in a statistically rigorous manner. Also, the results should be capable of synthesis into an assessment that is relevant to policy-makers and that can be used to make positive changes in management direction.

Continually evaluate how well the selected indicators correspond to the biodiversity endpoints of concern. The results of the biodiversity monitoring effort should be used as an important component of adaptive management. If monitoring indicates an adverse change in the resources then the monitoring results should be used to formulate appropriate changes in management actions.

Linking with other Inventories

Biodiversity inventories, by design, are often limited to very specific sites. However, such inventories may overlook other sites that need protecting. Therefore some types of broad area inventories are desired. Where possible and feasible, these inventories should be incorporated within existing resource management inventories such as forest surveys by adding new variables to be collected in the field such as:

- characteristics of habitats (springs, moist land, land with a high biological value)
- characteristics of forest/vegetation margins (length, form, and structure)
- description of vegetation in the grass, shrub, and tree strata
- effects of other uses of the land (agriculture)
- geohydrological features: surface and subsurface water resources
- land-use history and changes over time (grazing, agriculture, special practices)
- quantities and dimensions of standing and fallen dead trees, and of rotten trees, and the extent of such rot
- soil and the land form/geological features, including variables subject to change over time
- remarkable vegetation from the viewpoint of their phenotype.

Such additions to ongoing natural resource inventories may effectively improve our knowledge of the biological resources with minimum effort.

See also: **Biodiversity**: Endangered Species of Trees; Plant Diversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife. **Environment**: Environmental Impacts. **Genetics and Genetic Resources**: Forest Management for Conservation. **Landscape and Planning**: Landscape Ecology, the Concepts. **Resource Assessment**: Forest Change; GIS and Remote Sensing.

Further Reading

Bernhardt T (1999) Part 4. Biological surveys. In: *Theory of biodiversity*. Available online at: http://www.redpath-museum.mcgill.ca/Qbp/2.About%20Biodiversity/surveys.htm.

COP (1996) Appraisal of the SBSTTA review of assessments of biological diversity and advice on methodologies for future assessments. Item 8.2 of the provisional agenda. In: *Conference of the Parties to the Convention on Biological Diversity*, 15 November 1996, Buenos Aires, Argentina.

Dallmeier F and Comiskey JA (eds) (1998a) *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies*. Man and the Biosphere Series, vol. 20. Paris: UNESCO.

Dallmeier F and Comiskey JA (eds) (1998b) *Forest Biodiversity in North, Central and South America, and the Caribbean: Research and Monitoring*. Man and the Biosphere Series, vol. 21. Paris: UNESCO.

Fabbro L (2000) *Assessment of Biodiversity Amazonia Biodiversity Estimation using Remote Sensing and Indigenous Taxonomy*. Project presented at the European Space Agency Symposium 2000, 16–21 October 2000, Gotheborg, Sweden. Available online at http://www.amazonia.org/Biodiversity/ABDE/ABDE/index.htm.

Gauld ID *Inventory and Monitoring Biodiversity: A Taxonomist's Perspective*. Theme 1: Biological inventory and monitoring. Available online at http://www.earthwatch.org/europe/limbe/imbiodiv.html#Heading4.

Hawksworth DL (ed.) (1995) *Biodiversity Measurement and Estimation*. London: Chapman & Hall.

Heywood VH and Watson RT (eds) (1995) *Global Biodiversity Assessment*. Cambridge, UK: Cambridge University Press.

Layton PA, Guynn ST, and Guynn DC (2002) *Wildlife and Biodiversity Metrics in Forest Certification Systems*. Final report. National Council for Air and Stream Improvement, Inc. Available online at http://www.biodiversitypartners.org/im/BiodiversityMetricsReport(08-08-02).pdf.

Noss RF (1990) Indicators for monitoring bio-diversity: a hierarchical approach. *Conservation and Biology* 4: 355–364.

Pelz DR and Luebbers P (1998) Quantifying biodiversity – the effect of sampling method and intensity on diversity indices. *Environmental Forest Science* 54: 373–378.
Taylor CM, Mayne JC, Kabel M, Rice R, and Dallmeier F (1992) *Long-Term Monitoring of Biological Diversity in Tropical Forest Areas: Methods for Establishment and Inventory of Permanent Plots*. MAB digest no. 11.
Wilson EO and Peter FM (1988) *Biodiversity*. Washington, DC: National Academy Press. Available online at http://bob.nap.edu/books/0309037395/html/.

Plant Diversity in Forests

D F R P Burslem, University of Aberdeen, Aberdeen, UK

Measurement of Diversity

Diversity can be measured either as species richness, the number of species per unit of land surface area or per unit number of individuals in a sample, or as a derived index that attempts to reflect the variation in relative abundance within a community as well as its richness. Commonly used indices of diversity are the Simpson's index (D) and the Shannon index (H), which are defined as follows:

$$\text{Simpson's index } D = \frac{1}{\sum_{i=1}^{S} P_i^2}$$

and

$$\text{Shannon index } H = -\sum_{i=1}^{S} P_i \ln P_i$$

where S is the total number of species in the community and P_i is the proportion of individuals represented by the ith species. These indices have the useful property that their values increase with greater evenness in the relative abundance of species for a given species richness.

Distribution of Diversity at Large Scales

At a global scale, the diversity of plants in forests, as in all plant communities, varies with climate and soil conditions, although there is also a pervasive imprint of history that disrupts large-scale relationships between plant diversity and biophysical conditions under some circumstances. The relationship between climate and plant distribution was promoted by the systematic collation of climate data by the German ecologist Heinrich Walter that allowed him to conduct a comparative analysis of the distribution of diversity at large spatial scales. By representing climates using a standardized format (referred to as a 'klimadiagram'), Walter proposed a hierarchical classification of world vegetation in which vegetation 'types' are nested within vegetation 'zones.' Four of Walter's vegetation zones possess vegetation types that can be described as forests: the tropical-cum-subtropical, warm temperate, cool temperate and cold temperate vegetation zones (the fifth, the Arctic vegetation zone, does not possess forests although dwarf trees are present in Arctic vegetation). Walter determined that the distinction between vegetation zones was determined on the basis of temperature, and that the series of vegetation types within each vegetation zone were differentiated on the basis of rainfall-related criteria.

Temperature

Classifying vegetation was the first step to obtaining a mechanistic understanding of the distribution of world vegetation. Subsequent work has refined our knowledge of the distribution of diversity, and robust generalizations are now possible. First, it is evident that forests lying closer to the equator possess a higher plant species richness and diversity than forests at higher and lower latitudes. This statement assumes that the comparison being made is of forests at the same altitude, subjected to equivalent rainfall regimes and excludes forests growing on soils that are deficient in their availability of plant nutrients, such as N, P, or K, or supply an extreme of potentially toxic elements such as Ni or Al. Thus a hypothetical transect starting on the equator in wet evergreen tropical lowland rainforest in Southeast Asia and running north through the warm temperate evergreen and cool temperate deciduous forests of eastern Asia and thence into the cold temperate (boreal) forest of eastern Siberia would encounter forests of decreasing plant diversity with increasing latitude. This gradient in plant diversity is expressed among the trees that form the forest canopy, but is also observed among other life-forms such as shrubs and herbs. Some life-forms (such lianas and epiphytes) are rare or absent outside the tropics. Similar transects running north from equatorial forests in Africa and South America would not encounter such a well-ordered sequence of vegetation zones. The southern hemisphere lacks cool temperate deciduous forests at low altitudes and lacks boreal forest entirely because the continental land-masses do not extend sufficiently far south. Diversity of plants in forests also declines with increasing altitude on mountains at all latitudes, although the precise nature of these changes varies as a function of local site conditions.

Rainfall

The second most important factor influencing the distribution of plant diversity at large spatial scales is the amount and seasonal distribution of rainfall. Walter recognized series of vegetation types related to such changes in moisture regimes within each of the five vegetation zones, and in climates that are capable of supporting forests, vegetation types are synonymous with forest types. Within the tropical-cum-subtropical vegetation zone, which lies at the lowest latitudes in South and Central America, Africa and Madagascar, South and Southeast Asia, and the Pacific, plant diversity in forests decreases along the series of vegetation types represented by tropical lowland evergreen rain forest, tropical semievergreen rainforest, tropical deciduous forest and Savanna. At these latitudes, plant diversity is lowest in semidesert and perennial plants are absent from true deserts, but these are not forests. Along this series, mean annual rainfall declines from approximately 1800–5000 mm in climates supporting evergreen tropical forest to approximately 250–700 mm in climates supporting Savanna vegetation, while the number of dry months per year (defined as months that receive <100 mm on average) increases from 0–4 to 7–11 for the same comparison. Both total annual rainfall and the seasonal distribution of rainfall have important influences on plant distribution and diversity in the tropics. At the wetter end of the gradient, the transition between vegetation types is driven by the number of dry months rather than the total annual rainfall, but the converse is true at the drier end of the main climatic gradient.

Series of vegetation types related to variation in moisture regimes can also be recognized in the warm, cool and cold temperate vegetation zones and in the (nonforested) arctic vegetation zone, and plant diversity in forests declines in successively drier climates at these cooler latitudes, as it does in the tropics. The warm temperate series possesses just two vegetation types that can be described as forests: warm temperate rainforests in wetter environments and Mediterranean-type forest (or Savanna or scrub) in sites that experience a winter maximum of rainfall and a distinct cool season. Warm temperate rain forests tend to occur on the eastern fringes of continental land-masses (for example in Japan, south-eastern Australia, and New Zealand) and are intermediate in species richness between evergreen tropical rainforests and temperate deciduous forests. Both the cool and cold temperate vegetation zones also contain two vegetation types that can be described as forests. Cool temperate rainforests occur in areas with a maritime climate that receive winter rains and no summer drought in both the northern hemisphere (in a coastal strip from northern California to Canada) and the southern hemisphere (coastal areas of southern Chile). The characteristics of these two blocks of cool temperate rainforest differ considerably: in the northern hemisphere the characteristic tree species are gymnosperms and include, for example, the redwood (*Sequoia sempervirens*), while the southern hemisphere equivalent is dominated by species of southern beech (*Nothofagus* spp.). In less distinctly maritime temperate climates the dominant forest trees are deciduous and these conditions give rise to the cool temperate deciduous forests of eastern North America and western Europe. There is no southern hemisphere equivalent of these cool temperate deciduous forests. At higher latitudes in the northern hemisphere there is a transition to forests in which gymnosperm trees become dominant across the landscape and in which plant diversity is markedly lower than in the cool temperate forest types just described. These are the cold temperate or boreal forests that circle the northern polar regions. In Europe these forests are referred to as 'taiga' and are dominated by just two species (*Pinus sylvestris* and *Picea abies*), while the North American and East Asian boreal forests are more species-rich. In the most continental climates (i.e., those that experience the lowest winter temperatures and the lowest annual rainfall) of the boreal forest region in eastern Siberia, the evergreen forest gives way to a species-poor forest of deciduous conifers such as larch (*Larix dahurica*). Larch forests clothe 2.5 million km^2 of eastern Siberia, but there is no equivalent climate or forest type in North America.

Soil Conditions

The third factor in the hierarchy of determinants of the distribution of plant diversity in forests is soil conditions. This term by itself obscures a variety of different factors that contribute to plant diversity, and global generalizations are unlikely to be satisfactory. Theoretical models of plant competition can be interpreted to predict either an increase or a decrease in plant diversity along a gradient of soil fertility, and empirical tests of these ideas are few in number. Part of the difficulty with testing these ideas is that changes in soil conditions rarely occur in isolation of changes in climate, in part because climatic conditions themselves influence physical and chemical processes in soils. However, two examples from tropical forests can be used to infer an influence of soil nutrient availability on forest plant diversity.

First, lowland forests in relatively aseasonal environments in the western part of the Amazon basin possess a higher diversity and richness of forest trees than forests in equivalent climates in the eastern Amazon. One potential cause of this difference is the greater nutrient availability in the relatively young volcanic soils in the western Amazon, although it may also be relevant that forests of the western Amazon are exposed to a higher frequency of disturbance by meandering rivers. Disturbance may influence plant diversity in a variety of ways as described below. The second example is less equivocal. Among the tropical lowland forests of both South America and Southeast Asia are patches of forest on highly nutrient-starved podzolic soils characterized by a thick organic layer and a bleached sand-rich mineral horizon. These forests are referred to as 'kerangas' in Southeast Asia and by a variety of labels, including 'caatinga,' in South America, and in both cases they are examples of heathland ecosystems. They are all characterized by a low richness of plant species, including trees, when compared to adjacent forests on richer soils. The mechanisms that determine the relatively low species diversity of tropical heath forests are unknown, but it is possible that the physiological and morphological trade-offs required to tolerate low nutrient conditions have evolved relatively infrequently in tropical lowland tree floras. Similarly, forests growing on soils that supply an excess of plant nutrients that are also potentially toxic at high concentrations (such as Ni in ultramaphic vegetation) are species-poor compared to adjacent forests growing on less extreme soils. Mangrove forests are also species-poor relative to dry-land forests in similar climates, presumably because the physiological adaptations required to tolerate high internal Na concentrations have evolved only rarely.

Other Determinants of Plant Diversity

Taken together, the interpretation presented above could be taken to imply that variation in plant diversity can be explained on the basis of deterministic processes that are driven by the biophysical environment. However, this would be an oversimplification of the origins of variation in forest plant diversity. At least three additional factors must be considered as important in any explanation of diversity: these factors are biogeographic history, the size of the local and regional species pools, and disturbance.

Biogeographic History

The effects of biogeographic history pervade the distribution of diversity, particularly at large spatial scales. Regional differences in diversity have arisen because the distribution of the continents has changed during the evolution of land plants, and because climate itself is not constant in time at any one locality. Thus the effects of tectonic drift and climate change are superimposed on contemporary climate and soil conditions as important determinants of present-day plant diversity. Two examples will be used to illustrate these processes. First, it is well known that the diversity of forest trees in the cold temperate deciduous forests of eastern North America is greater than in the equivalent forests of western Europe, despite the equivalence of the current climate of these regions. This difference has been explained by the difference in the ease of migration of forest trees in North America (where the mountains run north–south) and Europe (where the mountains run east–west) in response to Pleistocene glaciations. As mountains might represent a barrier to plant dispersal, it has been suggested that in Europe plants are prevented by the Alps and the Pyrenees from migrating into relatively warm climates during the onset of glacial conditions in north and west Europe. Similarly, recolonization of formerly glaciated landscapes in northern Europe from refugia in south and eastern Europe is slowed by these montane barriers to dispersal. These barriers to the movement of plants do not exist in eastern North America because the dominant mountain chain (the Appalachians) runs north–south, and dispersal can occur along lowland valley corridors.

The second example illustrating the importance of biogeography derives from the observation that the lowland tropical forests of Africa are less rich in species than forests of tropical South America and Southeast Asia, when sites with a similar contemporary climate are compared. Again, it is possible to interpret this difference as a reflection of changes in climate during the Pleistocene interacting with differences among the continents in the distribution of land at different altitudes. The cumulative frequency distribution of land surface area with increasing altitude rises much faster for Africa than for either of the two other continents, which suggests that average elevation of lowland tropical forest sites is greatest in Africa. Under current climates these differences are not sufficient to fragment lowland forests in Africa, but during drier and cooler phases of the Pleistocene the proportion of the landscape that would have provided climatic conditions suitable for the maintenance of a lowland tropical forest flora would have been much lower in Africa than in South America or Southeast Asia. Thus the African forests would have become more fragmented, and extinctions of forest trees would have been more prevalent. The differences we observe today are a reflection of these interactions between landscape structure and climate change.

Size of the Species Pool

The second major factor that might disrupt the relationship between biophysical conditions and forest plant diversity is the size of the local and regional species pools. As discussed above, historical explanations can account for some differences in the number of species available to colonize a site, but other factors are also involved. These ideas were brought together in MacArthur and Wilson's theory of island biogeography, which was originally formulated as a theoretical exploration of the effects of island size on species richness, but has now been applied to island-type ecosystems on nonislands. MacArthur and Wilson proposed that the number of species occupying an island could be explained in terms of a dynamic equilibrium between local immigration, emigration, and extinction events. Since the probability of colonization and extinction can be modeled as a function of factors such as island size and remoteness from a source population, it is possible to derive theoretical predictions for island species richness as a function of these factors. The most important of these functions is the species-area relationship, which takes the following form:

$$S = c.A^z$$

where S is species richness, A is island area, and c and z are constants. This function implies that the log of species number is a linear function of log island area.

There are many demonstrations of the effect of increasing area on species richness, including some for forest trees. However, there is also controversy in the ecological literature over whether the increase is driven by a pure 'area effect,' or whether larger areas of island or habitat-island are richer because they contain a greater diversity of habitats. Nonetheless the theory of island biogeography helps explain why remote oceanic islands, such as Hawaii and the Galápagos Islands, possess relatively species-poor floras for their climate and may help to explain why habitat fragmentation reduces forest plant diversity.

Disturbance

The final factor that must be considered in any consideration of the mechanisms driving forest plant diversity is disturbance. Disturbance is defined and described elsewhere in this volume (*see* **Ecology**: Natural Disturbance in Forest Environments). Forests are subjected to a variety of types and scales of natural disturbance processes, and are also heavily influenced by human activities. By definition, disturbance has short-term negative impacts on diversity at the scale at which the disturbance occurs, for example by removing individuals through tree mortality. However, the relationship between disturbance and diversity at larger and longer spatial scales is complex and not necessarily predictable. One of the most influential theoretical models of the relationship between disturbance and diversity is Connell's intermediate disturbance hypothesis (IDH), which proposes that diversity of plant communities is maximized at the mid-point of plant succession, and in communities that are subjected to intermediate intensities or frequencies of disturbance. According to the IDH, sites very early in succession or those that suffer a high frequency or intensity of disturbance have a low diversity because relatively few species possess the traits associated with colonizing unoccupied or heavily disturbed sites. Diversity initially rises through succession because site conditions are ameliorated by the earliest colonizers, and because species accumulate by random dispersal events, but declines in late succession because a small number of competitively superior species are able to co-opt the available resources and exclude the early colonizing species. However, in most communities the low diversity, late-successional communities rarely arise before a new disturbance event sets back succession to an earlier stage. Thus, diversity is maximized at the mid-point of succession when early-successional, disturbance-dependent species coexist with late-successional competitive dominants.

The IDH is a controversial concept and has rarely been tested adequately for forests. However, in one recent test in a lowland tropical forest in French Guiana it was found that tree species diversity was greater in lightly logged forest than in unlogged forest or forest that had been heavily logged, in support of the IDH. Other attempts to test the IDH in forest communities have either failed to find support for it, or have been flawed in their design or interpretation.

Disturbance to forests by anthropogenic activity can reduce plant diversity, particularly in the tropics. The principal drivers of disturbance are clearance for permanent agriculture and plantation forestry, shifting cultivation, and logging. Fragmentation has independent effects on forest plant diversity because fragmentation increases the amount and importance of edge habitats and brings forest edges close to species that inhabit the forest interior. Small forest fragments also reduce the effective population size of plants and thus increase their probability of extinction (*see* **Ecology**: Biological Impacts of Deforestation and Fragmentation).

Conclusions

Although patterns in forest plant diversity at large spatial scales are now well described, there are still substantial lacunae in the record that can only be resolved by additional botanical exploration. In some parts of world (for example, areas of the Philippines, Indonesia, and the Atlantic forest of Brazil), it is likely that deforestation and forest fragmentation have already eliminated any further scope for describing natural patterns of forest plant diversity at a more local scale. The mechanisms that determine the large-scale patterns in plant diversity remain poorly understood and are likely to vary substantially between regions and localities. Current theories suggest that the diversity of forest floras reflects a balance between biophysical, historical, and anthropogenic causes, but robust predictions of diversity at a local scale are not yet possible.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation; Natural Disturbance in Forest Environments. **Environment**: Impacts of Elevated CO_2 and Climate Change. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Tree Physiology**: Forests, Tree Physiology and Climate.

Further Reading

Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199: 1302–1310.

Currie DJ and Paquin V (1987) Large-scale biogeographical patterns of species richness in trees. *Nature* 29: 326–327.

Gaston KJ (ed.) (1996) *Biodiversity: A Biology of Number and Difference*. Oxford, UK: Blackwell Science.

Grubb PJ (1987) Global trends in species richness in terrestrial vegetation: a view from the Northern Hemisphere. In: Gee JHR and Giller PS (eds) *Organisation of Plant Communities Past and Present*, pp. 99–118. Oxford, UK: Blackwell Scientific Publications.

Hubbell SP (2001) *Unified Theory of Biodiversity and Biogeography*. Monographs in Population Biology no. 32. Princeton, NJ: Princeton University Press.

Huston MA (1994) *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge, UK: Cambridge University Press.

MacArthur RH and Wilson EO (1967) *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Molino J-F and Sabatier D (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294: 1702–1704.

O'Brien EM, Field R, and Whittaker RJ (2000) Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. *Oikos* 89: 588–600.

Ricklefs RE and Schluter D (eds) (1993) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago, IL: University of Chicago Press.

Ricklefs RE, Latham RE, and Qian H (1999) Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos* 86: 369–373.

Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge, UK: Cambridge University Press.

Tilman D (1982) *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.

Walter H (1984) *Vegetation of the Earth and Ecological Systems of the Geo-Biosphere*, 3rd revd edn, Trans. E. Ulmer. Berlin: Springer-Verlag.

Whittaker RJ, Bush MB, and Richard K (1989) Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. *Ecological Monographs* 59: 59–123.

Endangered Species of Trees

G T Prance, University of Reading, Reading, UK

Introduction

Unfortunately the topic of endangered species of trees is a vast one because of the extensive loss of their habitat in most parts of the world and in many cases because of overexploitation. The World Conservation Union's (IUCN) *Red List of Threatened Plants*, published in 1997, lists almost 34000 species of plants that are now threatened with extinction. That is just over 10% of the total number of plant species in the world. These lists include many species of trees. Red data lists exist for many countries and are catalogs of species where future survival in nature is uncertain. Most threatened species of trees are those of the tropical regions and on oceanic islands, in the tropics because of habitat destruction and because of the enormous diversity and often localized distribution of individual species, and on islands because they tend to have many unique endemic species, but also because of habitat destruction and the introduction of alien invasive species that take the place of the native flora. For example, about 85% of the Madagascan flora is endemic to that island nation and only 20% of the original vegetation remains. It is therefore inevitable that some species have gone extinct and others are under threat. A recent red data book for the ten countries of southern Africa cataloged 3900 taxa that are threatened with extinction and listed 33 that are recorded as being extinct.

Areas of the world such as Madagascar where wildlife and plants are richest and are most endangered have been termed 'hot spots' by ecologist Norman Myers. It is in these areas where most species of trees are also endangered. One particularly critical hot spot is the Atlantic Forest Region or *mata atlântica* of Brazil. This narrow strip of rainforest along the coast contains many endemic species of plants and animals. A study of a sample of tree species from that region carried out in 1981 showed that 53.8% of the sample of 127 tree species were endemic to the Atlantic forest and another 11.8% endemic to the coastal forest plus some part of the rapidly disappearing forests of the Planalto of Central Brazil, for example jequitibá (*Cariniana estrellensis*) (see **Figure 3**). It has been estimated that 6000 species of plants are endemic to the coastal forest hot spot. This region is classified as a hot spot because only about 7% of the original vegetation remains. The forest has been replaced by sugar cane, cattle pasture, and cacao plantations. Many species of trees that were collected and classified during the nineteenth century have not been re-collected in recent times. For example, *Roupala thomesiana* (a species of *Roupala*, a genus of trees whose wood is much used) was collected in the forests of Bahia state by Swiss botanist Jacques Samuel Blanchet in 1833. It has never been seen since the original collection and this is a common feature of Atlantic coastal forest species.

Another important hot spot for trees is the Guinean forests of West Africa that extend from Sierra Leone to Cameroon. The entire Guinean forest ecosystem has been reduced to a series of small fragments in each of the countries where it occurs. It is estimated that only 14.3% of the original closed canopy forest remains. This area too, like the coastal forests of Brazil, houses many endemic species of trees with at least 25% of the vascular plant species endemic to the hot spot.

The Wallacea hot spot includes the central islands of Indonesia from Sulawesi to Ceram and from Lombok to the Tanimbar Islands. This area named after the co-discoverer of evolution, Alfred Russel Wallace, contains many endemic species of animals and plants including many commercial timbers such as kawi (*Agathis* spp.) and the magnificent yellow-flowered legume *Pterocarpus indicus*. It is in many of the 27 areas defined as hot spots that the greatest number of tree species are endangered.

Here a selection of endangered tree species from different places and endangered for different reasons, have been chosen to illustrate the situation.

The Conifers or Softwood Species

The cone-bearing trees are some of our most ancient species that have survived through the ages and many changes in world climate. The data from the World Conservation Union estimate that 327 of the 586 species of Pinopsida (pines and their close relatives) are threatened. 133 species or 53% of the pine family (Pinaceae) are listed in the *Red Data Book*. Conifers include many magnificent trees such as the giant redwoods of California and are still one of the major sources of timber and so it is unfortunate that so many species are under threat of extinction.

The Wollemi Pine and the Dawn Redwood

The Wollemi pine is an Australian conifer that was only discovered in 1994 in a gorge only 150 km from Sydney. It belongs to an evolutionary line thought to have been extinct for many millions of years. Studies of fossil pollen showed that this genus was once widespread and abundant in Australia. Its population declined for natural reasons and one small population has survived in the Wollemi National Park. It is a member of the plant family Araucariaceae which include the much cultivated species the monkey-puzzle tree from Chile (*Araucaria araucana*) and the Norfolk Island pine (*Araucaria heterophylla*). Once it was discovered, the Wollemi pine soon became listed as rare and endangered and considerable efforts are being made by the Royal Botanic Gardens in Sydney to protect and propagate this species, of which fewer than 40 individuals exist in the wild.

A similar situation occurred for the dawn redwood (*Metasequoia glyptostroboides*) from China. This living fossil was discovered in the early 1940s. Since over 2000 trees of this species existed, seeds have been widely distributed to gardens around the world to ensure its survival as a species.

Alerce: The Patagonian Cypress

Alerce (*Fitzroya cupressoides*) is a magnificent tree of the forests of southern Chile and Argentina. The huge trees are slow-growing and take many hundred years to reach their full height of 50 meters and up to 2 meters diameter. Trees of 70 m × 4 m have even been recorded. The timber of alerce has been much used in house construction and for roof shingles and even for boat building. As a result of its valuable timber this species has become so rare that it is listed both in *Red Data Books* and in the Convention on Trade in Endangered Species (CITES). The pressure on this species is from overuse rather than rarity. Clandestine shipments of alerce wood are still occasionally apprehended by UK Customs. Many of the conifers that are endangered are so because of overuse of the timber and poor management of the resource.

Monterey Cypress

The Monterey cypress (*Cupressus macrocarpa*) is a small to medium-sized tree now confined to two small groves on the Pacific coast of central California. This picturesque tree has a small often contorted cone-shaped crown. It is not of importance as lumber, but is now often cultivated as an ornamental and in windbreaks and hedges. This is endangered in the wild because of the destruction of its native habitat, but is unlikely to become extinct because of its wide use in gardens around the world. Fortunately the entire wild population is protected within the Point Lobos Reserve and the Del Monte Forest and so it is unlikely to become extinct.

Bermuda Cedar

The Bermuda cedar (*Juniperus bermudiana*) is the last conifer discussed here. It is under threat for another reason. Approximately 90% of the trees died between 1944 and 1950 because of infestation by two accidentally introduced scale insects, the juniper scale (*Carulaspis visci*) and the oyster-shell scale (*Lepidosaphes newsteadi*). This tree, which dominated the forests of Bermuda, was a great loss and many exotic species were introduced to replace it. Some trees have survived but destruction of habitat for tourist resorts has reduced the possibility of reafforestation efforts. The species itself is unlikely to become extinct because it is now grown elsewhere and has become common on the island of Saint Helena. Many island species around the world have become endangered through the introduction of alien pests and diseases, or even other species of trees such as *Eucalyptus*, which take over at the expense of the native forest.

The Monocotyledons

The flowering plants have generally been divided into two major groups, the monocotyledons and the dicotyledons, based on the number of seed leaves in the embryo. Most of the monocots are narrow-leafed with parallel veins and are herbaceous, but one group, the palms, are secondarily woody and constitute one of the most important components of tropical rainforest. Since many palm species are critically endangered, a few examples are discussed here. Of the approximately 3000 species of palm, 869 (26%) are listed in the IUCN *Red Data Book*.

Madagascan Palms

There are about 170 species of palm in Madagascar and all but five are endemic. Many of the palms have very restricted distribution and are known from areas of less than 1 square kilometer in the wild. Since natural habitats are being destroyed so rapidly in Madagascar, a large number of the palm species are critically endangered. The species *Voaniola gerardii* was only described in 1989 in the Masoala Peninsula of northeastern Madagascar. Fewer than ten trees of the robust forest palm that is 15–20 m tall are known to exist. The fruit are a rich red-brown and seeds have been collected and germinated at Kew. *Voaniola* is also of interest because it has 596 chromosomes, the most ever recorded for a monocotyledon. Apparently this palm has been much harvested destructively to collect the palm cabbage or heart-of-palm for use as a salad vegetable. The ravimbe palm (*Marojejya darianii*) is another recent discovery that was named in 1984. This magnificent large-leafed palm reaches 15 m in height. It is only known from a single locality in swamp forest near Maroantsetra also in the northeastern part of the country. Unfortunately one of the threats to the existence of *Marojejya* has been the destructive collecting by palm fanatics, who often collect all the seed from a tree. A tree of the rare *Beccariophoenix madagascariensis* was actually cut down to obtain seed. At Mantaly where one of the two known populations of this tree occurs, in July 1992 nine mature trees had been felled for their palm-heart, leaving fewer than 20 mature trees alive. *Lemurophoenix halleuxii* (**Figure 1**) is probably the most majestic palm of the whole island. The 50 remaining trees are not regenerating well because the seeds are much sought after and regularly harvested for export to palm enthusiasts. The wonderful selection of palms from Madagascar are in a precarious state through destruction of habitat, harvesting for timber and palm-heart and collecting by palm fanatics and so it is probable that several species will soon be extinct in the wild (**Figure 2**).

New Caledonian and Other Island Palms

New Caledonia is another island territory where the majority of plant species are endemic. All 31 species of palm and all but one of the 17 genera are endemic and at least eight species are highly endangered. *Burretiokentia hapala* with its bright green trunk marked with pale rings of the leaf scars is an elegant palm that is known only from a few individuals in two localities. *Cyphophoenix nucele* is known from a single small population on the island of Lifou. The only other species of this genus, *C. elegans*, is also found in a very small population which is

Figure 1 The palm *Lemurophoenix halleuxii* from Madagascar. There are only about 30 individuals left of this majestic species. Photograph courtesy of H. Beentje.

Figure 2 The palm *Orania ravalea* from Madagascar was only described as new in 1995 and fewer than 500 individuals remain of this elegant tree. Photograph courtesy of H. Beentje.

endangered by frequent forest fires. Thus the whole genus *Cyphophoenix* is endangered, as is the case with many other genera of palms. Most tropical islands have listed species of palms and could be mentioned. There are several endangered species of palms in Hawaii in the genus *Pritchardia* and the once common vuleito palm of Fiji (*Neoveitchia storckii*) is reduced to a single population of about 150 trees. The only palm of Easter Island, *Paschalococcus disperta*, is extinct and was only described from subfossil fruit. The chonta palm (*Juania australis*) of Juan Fernández Islands or Robinson Crusoe Island is highly endangered from illegal felling and habitat destruction by grazing animals.

Continental Palms

It is not just island palms that are endangered, there are also many examples from continental areas. The IUCN *Red List* names three species of *Maxburretia* from Thailand and the Malay Peninsula. The most endangered is *M. rupicola* which is confined to three limestone hilltops all near to the city of Kuala Lumpur. One site is threatened by quarrying and another experiences frequent fires caused by careless climbers. The palm genus *Aiphanes* has 22 species most occurring along the Andes in Colombia, Peru, Ecuador, and Bolivia. Most of the species are narrow endemics in an area where much destruction of the natural vegetation has occurred. It is hardly surprising that 17 of the 22 species have found their way into the IUCN *Red Data Book*. For example, *Aiphanes duquei* is now restricted to two National Parks in the Cordillera Occidental of Colombia.

The urgoun or dalla palm (*Medemia arjun*) of Egypt and Sudan was abundant there in ancient times. The population has been decimated by exploitation of the leaves for making mats and by destruction of its habitat by irrigation schemes along the River Nile. It was known only from three localities in Egypt and one in the Sudan. Two of

Figure 3 This lone individual of the jequitibá tree, *Cariniana legalis* (Lecythidaceae) remains in the botanical garden in Rio de Janeiro. (It is believed that this same tree was once kissed by Einstein.) Because of its excellent timber it is becoming rarer even in the conserved remnant of Brazil's Atlantic coastal rainforest.

these localities have only a single tree left and it is dubious that any trees remain at the third.

These few examples serve to show that many palms around the world are severely threatened and some even extinct. Palms are one of the most useful of all groups of plants and it is tragic that so many are being lost forever.

The Dicotyledons

This vast group includes all other trees that are not either conifers or palms. There are many endangered species of dicots (**Figure 3**) and a few are highlighted here to illustrate what is happening to trees around the world.

South American Mahogany

This species (*Swietenia macrophylla*) grows in Central America and in Mexico and in an arc around the western and southern fringes of the Amazon basin. It is severely threatened due to overexploitation for its much sought-after timber and because of habitat loss. Mahogany is the most valuable timber of the American tropics. The area where it grows in southern Amazonia is also one of the major areas of deforestation. Mahogany, due to its high value, has been logged illegally from parks, reserves, and indigenous areas. For several years efforts to have this species listed in the CITES treaty was resisted by the principal exporting countries such as Brazil and Colombia, but in 2002 it was finally included in Appendix II which means that companies will have to alter the way in which they harvest the species and prove that it was obtained legally from a sustainable source. This was a major step forward because mahogany logging companies opened many roads to reach the scattered populations of wild mahogany which gave farmers access to remote areas. This process will now be slowed down by the listing of mahogany and will help to spare other trees. Mahogany has largely been harvested from wild trees because it has not done well in plantations due to attack from the shoot-boring insect *Hypsipyla grandella*.

Brazilian Rosewood

Rosewood (*Aniba rosaeodora*) contains the essential oil linalol which has become much used by the perfume industry. To harvest linalol, trees are felled and the wood chipped and steam distilled. Local distilleries have been built in many parts of Amazonia and teams sent out to harvest all the trees within range. This means that this species is now rare and as a consequence the level of harvesting has also decreased considerably, but not before the species has become threatened.

Saint Helena Ebony and the Toromiro

The ebony (*Trochetiopsis melanoxylon*) was the major timber of the island of Saint Helena in the South Atlantic (**Figure 4**). It was much sought after by trading ships for its wood and was believed extinct from the beginning of the nineteenth century. However two depauperate trees were discovered on a cliff in 1970 and cuttings taken from them have been successfully propagated in efforts to reintroduce the species. Like many island endemics it quickly suffered from both overuse and habitat destruction. It is notable that many of the most endangered species of trees are also those of most use. Another example of this is the toromiro tree (*Sophora toromiro*) from Easter Island in the South Pacific. The toromiro was also a useful timber that was much used by the natives for their elegant wood carvings. By 1917 only

Figure 4 *Trochetiopsis melanoxylon*, the Saint Helena ebony, was reduced to two impoverished individuals in the wild which were growing on a cliff face. Propagation and reintroduction programs of several institutions have assured the survival of this species that was on the brink of extinction.

one tree remained and fortunately explorer Thor Heyerdahl collected seeds before it was exterminated by grazing in 1972. The toromiro has survived in botanic gardens from the seeds collected by Heyerdahl and also in a few private gardens in Chile. From this genetically small population efforts are now being made to reintroduce to Easter Island what was once its most useful species of tree.

Brazil Wood

Brazil is the only country named after a wood. The Brazil wood (*Caesalpinia echinata*) is native to the Atlantic coastal forest hot spot and is listed as vulnerable in the IUCN *Red Data Book*. Within Brazil it is listed as endangered in five eastern coastal states. This wood was much sought after for the purple dye that was mainly exported to Portugal, often in exchange for enormous numbers of cattle. The heartwood is still much sought after for violin and cello bows. The species was almost eliminated by overuse, but since it is a national symbol, widespread replanting is taking place and this is a species that is unlikely to become extinct.

Meranti and Balan Woods

There are 357 species of the meranti and balan genus (*Shorea*) of the Dipterocarpaceae family of the Asian tropics. *Shorea* is the most important timber genus in tropical Asia and species grow in Sri Lanka, to South China, Malaysia and throughout Indonesia. Many species of this genus have localized distributions on one or only a few islands and so are particularly vulnerable to over exploitation. It is sad to see that 72 species of *Shorea* are listed in the IUCN *Red Data Book* as well as seven species of the related timber genus *Parashorea*. *Shorea fulcata* from Vietnam is listed as recently thought to have become extinct. The cause of endangerment of species of *Shorea* are mainly from habitat destruction. Many of the more commercially important species are now in managed forests and plantations, but all the wild species could be of importance to future breeding programs and would be a serious loss to forestry if they should become extinct.

Sapele

The sapele (*Entandophragma cylindricum*) is a mahogany relative that occurs in West Africa from the Ivory Coast to Nigeria in the Guinea hot spot. The wood is much exploited and is sought after for veneer, doors, and furniture. Over harvesting is occurring and it has been listed as a priority for genetic resource conservation before all the best timber trees are removed. The IUCN stated in 1996 that 'harvest and milling of the current species mix based on sapelli and sipo (*Entandophragma utile*) is clearly not sustainable ecologically or economically.' This is unfortunately true for many timber species of the tropics in America, Africa and Asia.

Endangered Trees Mean Endangered Wildlife

Many species of animals are dependent on trees for their existence and so the endangerment of trees also means the endangerment of animals that feed on their leaves, nectar, or fruit, or depend on trees for shelter. In 1992 entomologist Terry Erwin showed that rainforest canopy contains an incredible amount of insect diversity and that much of this is specific to individual species of tree. Therefore to lose a species of tree is also a threat to the many species of insects and other organisms that depend upon it for their existence. Likewise trees are dependent upon animals for their pollination and the dispersal of their diaspores. Pollinator extinction is becoming an increasing threat to many species of plant. For example Hawaii's native screwpine (*Freycinetia arborea*) was once pollinated by four bird species that are now either extinct or endangered: the Hawaiian crow (*Corvus tropicus*), the o'u parrot (*Psittirostra psittacea*), the Kona grosbeak (*Ehloridops kona*), and the palila (*Loxioides japonica*). The screwpine might have become extinct had not the introduced Japanese white-eye (*Zosteropsis japonica*) become a substitute effective pollinator.

Fruit bats play an important role as pollinators and seed dispersers of many species of trees in the Old World tropics and many oceanic islands. The Rodrigues flying fox (*Pteropus rodricensis*) once

Figure 5 This maçaranduba tree (*Manilkara huberi*) was felled to collect a few dollars worth of latex and illustrates the wanton destruction of many forest trees for little gain.

Figure 6 This rare treelet, *Rhabdodendron macrophyllum*, grows only in white sand areas around the city of Manaus, Brazil. Most of its habitat has been destroyed as the building industry mines the sand for house construction in the city.

occurred on both the islands of Rodrigues and Mauritius in the Indian ocean. It was exterminated from Mauritius many years ago but remained abundant on Rodrigues until, by the mid-1990s, its population was reduced to fewer than 100 animals through a combination of habitat destruction, hunting, and cyclone damage. Reforestation and protection of the bats has now increased the population to almost 2000 individuals, so there is renewed hope for the bat and for the plants that depend on it for their pollination and dispersal.

Selective logging often removes trees that provide important resources for forest fauna, such as timber species that provide fleshy fruits eaten by birds and frugivore mammals. The maçarandaba tree of Amazonia (*Manilkara huberi*) is an important timber tree (**Figure 5**) that is being logged but its fruit are eaten by parrots, monkeys, coati, deer, and tortoises. The populations of some vertebrate frugivores and seed predators can markedly decline in logged forests.

The important Brazil nut tree of the Amazon forest depends upon two species of bee to pollinate its flowers and the agouti to disperse its seeds. Many such interdependencies between trees and animals exist and to avoid extinction it is vital to maintain habitat that allows this web of biological interaction to continue.

Conclusions

The examples of threatened species of trees chosen here are just a few of the many that are now listed, but they show that wherever humans are active in a forested region of the world, often the most useful species of trees are becoming rare through over-exploitation and loss of habitat (**Figure 6**). From the Amazon to Asia, from Africa to Australia important tree species are under threat of extinction. Particularly susceptible are those on islands such as Saint Helena, Hawaii, New Caledonia, and Madagascar where endemism is high but habitat destruction and introduced alien species are both also rife. Trees are vital to the survival of many other organisms and each tree species has many other species that depend upon it for survival. Much more still needs to be done before it is too late to ensure that some of the most useful species of trees are not lost forever. We also need the large variety of trees that exist to sustain climate and ecological balance and perhaps even the future of all life on earth.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife. **Environment**: Environmental Impacts; Impacts of Air Pollution on Forest Ecosystems; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Forest Management for Conservation; Population, Conservation and Ecological Genetics. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Tropical Ecosystems**: Bamboos, Palms and Rattans; Swietenia (American mahogany); Lecythidaceae.

Further Reading

Farjon A, Page CN, and the IUCN/SSC Conifer Specialist Group (1999) *Conifers: Status Survey and Conservation Action Plan*. Gland, Switzerland: IUCN.

Dransfield J and Beentje H (1995) *The Palms of Madagascar*. Kew, UK: Royal Botanic Gardens.

FAO (2001) *State of the World's Forests 2001*. Rome: Food and Agricultural Organization of the United Nations.

Golding J (ed.) (2002) *Southern African Plant Red Data Lists*. Pretoria, South Africa: Southern Africa Botanical Diversity Network.

Groombridge B (ed.) (1992) *Global Biodiversity: Status of the Earth's Living Resources*. London: Chapman & Hall.

Hilton-Taylor C (ed.) (2000) *2000 IUCN Red List of Threatened Species*. Gland, Switzerland: IUCN.

Hunt D (1996) *Temperate Trees under Threat*. Morpeth, UK: International Dendrology Society.

IUCN (2001) *The Red Book: The Extinction Crisis Face to Face*. Mexico City: CEMEX.

Mittermeier R, Myers N, and Mittermeier CG (1999) *Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. Mexico City: CEMEX and Conservation International.

Oldfield S, Lusty C, and MacKinver A (eds) (1998) *The World List of Threatened Trees*. Cambridge, UK: World Conservation Press.

Walter KS and Gillett HJ (eds) (1997) *The IUCN Red List of Threatened Plants*. Cambridge, UK: World Conservation Monitoring Centre.

C

CANOPIES *see* ECOLOGY: Forest Canopies. ENTOMOLOGY: Foliage Feeders in Temperate and Boreal Forests. ENVIRONMENT: Impacts of Air Pollution on Forest Ecosystems. HYDROLOGY: Hydrological Cycle. MEDICINAL, FOOD AND AROMATIC PLANTS: Forest Biodiversity Prospecting. TREE PHYSIOLOGY: Canopy Processes; Shoot Growth and Canopy Development.

CLIMATE CHANGE *see* ENVIRONMENT: Carbon Cycle; Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. GENETICS AND GENETIC RESOURCES: Genetic Aspects of Air Pollution and Climate Change. TREE PHYSIOLOGY: Forests, Tree Physiology and Climate; Stress. WOOD USE AND TRADE: Environmental Benefits of Wood as a Building Material.

CONSERVATIONS *see* BIODIVERSITY: Biodiversity in Forests; Endangered Species of Trees; Plant Diversity in Forests. GENETICS AND GENETIC RESOURCES: Forest Management for Conservation; Population, Conservation and Ecological Genetics. MEDICINAL, FOOD AND AROMATIC PLANTS: Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. TREE BREEDING, PRINCIPLES: A Historical Overview of Forest Tree Improvement.

COPPICING *see* PLANTATION SILVICULTURE: Short Rotation Forestry for Biomass Production. SILVICULTURE: Coppice Silviculture Practiced in Temperate Regions; Natural Regeneration of Tropical Rain Forests; Silvicultural Systems.

CRITERIA AND INDICATORS *see* SUSTAINABLE FOREST MANAGEMENT: Certification; Definitions, Good Practices and Certification; Overview.

D

DEFORESTATION *see* ECOLOGY: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife; Natural Disturbance in Forest Environments. RESOURCE ASSESSMENT: Forest Change; Regional and Global Forest Resource Assessments. SILVICULTURE: Treatments in Tropical Silviculture. SUSTAINABLE FOREST MANAGEMENT: Causes of Deforestation and Forest Fragmentation.

DISEASES *see* HEALTH AND PROTECTION: Biochemical and Physiological Aspects; Diagnosis, Monitoring and Evaluation. PATHOLOGY: Diseases Affecting Exotic Plantation Species; Diseases of Forest Trees; Heart Rot and Wood Decay; Insect Associated Tree Diseases; Leaf and Needle Diseases; *Phytophthora* Root Rot of Forest Trees; Pine Wilt and the Pine Wood Nematode; Root and Butt Rot Diseases; Rust Diseases; Stem Canker Diseases; Vascular Wilt Diseases. TREE BREEDING, PRACTICES: Breeding for Diseases and Insect Resistance.

DISTURBANCE *see* ECOLOGY: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife; Natural Disturbance in Forest Environments. SILVICULTURE: Forest Dynamics; Natural Stand Regeneration. SUSTAINABLE FOREST MANAGEMENT: Causes of Deforestation and Forest Fragmentation.

E

ECOLOGY

Contents

Plant–Animal Interactions in Forest Ecosystems

J Ghazoul, Imperial College London, Ascot, UK

Introduction

Flowering plants, being sedentary, have co-opted animal partners for purposes of gene exchange and propagule dispersal, through pollination and seed dispersal. To secure these services plants provide a variety of flower or fruit rewards creating some of the most common and obvious mutualistic interactions in the natural world. However, plants are also eaten by animals which graze on leaves, bore through stems, or predate seeds. Plants have therefore evolved mechanisms to promote the efficiency of mutualistic interactions and protect against herbivores and seed predators. This article describes the range of ecologically significant plant–animal interactions that commonly occur in temperate and tropical forest systems.

Mutualistic Interactions

Pollination

Most flowering plants are animal pollinated, and indeed the function of flowers is to attract animal vectors for pollen dispersal. Most flowers offer a reward to pollinators which is usually nectar or pollen, but can also include resins (e.g. Clusiaceae), waxes, or oils (orchids). Pollinators attracted to flowers collect the resources and in the process pick up pollen through contact with the anthers and deposit pollen they are carrying onto the stigma where pollen germinates and ultimately fertilizes the ovules. Not all flower visitors act as pollinators, however, and there is widespread ‘theft’ of floral resources where animals benefit from the floral resources but fail to pollinate the plant, either because they are the wrong size or shape to contact the anthers or stigma, or because they obtain nectar by piercing the sides of the corolla thereby bypassing the reproductive tissues.

Pollinators vary in their degree of effectiveness, and the extent to which they are specialized to pollinate one or a few flowering species. Pollination can be passive, where pollen is picked up and deposited inadvertently by the pollinating vector, or it can be active where pollinators seek out pollen. Active pollinators often have specialized morphological traits, such as the pollen combs and baskets on the hind legs of honeybees, used to collect and store pollen.

Some plants have developed alternative and deceptive ways of securing pollination services by temporarily trapping pollinators or by attracting them with floral displays that offer no reward. Other plants, including some large dipterocarp trees in Southeast Asia offer only pollen as a reward which, although consumed by the pollinators, is also carried by them to neighboring plants.

Pollinators range in size and diversity from tiny fig wasps and thrips to large fruit bats and terrestrial mammals, although by far the most important pollinators are bees. Honeybees pollinate many forest trees in tropical regions including many large canopy species, but solitary or semisocial species are also widespread pollinators occurring in forest canopy and understory. Although honeybees are very effective pollinators they are generalist in their foraging behavior and forage preferentially on species occurring at highest frequency or density. Such frequency-dependent foraging behavior does not, therefore, favor rare or highly dispersed plants which become more dependent on pollinators that may be more specialist in their floral resource requirements. Many anthropogenically altered forest habitats have suffered a decline in the richness of pollinator communities and introduced honeybees may to some extent ameliorate these impacts. Plants with generalist pollination systems may be resistant to such changes but plants pollinated by insects and animals other than common bees could potentially suffer a decline in reproductive output through pollination failure.

Other invertebrate pollinators include beetles, flies, butterflies, moths and thrips. Flowers pollinated by each of these groups have, evolved morphological structures and phenological patterns to increase the probability of successful pollination and to limit access to the flowers by other flower visitors that are relatively ineffective as pollinators. Tropical forests contain many invertebrate-pollinated species, while in temperate forests wind pollination is more widespread.

Vertebrate pollinators primarily include birds and bats, but a variety of terrestrial mammals also act as pollinators, including possums and shrews. Even lizards have been noted to pollinate some plant species but such examples are notable by their rarity.

One of the best known highly specific interactions among plants and animals is the fig pollination system. Fig species (*Ficus*) have evolved to be entirely dependent on specialized fig wasps for pollination. The tiny wasps live as adults for only a few days and spend almost their entire life within figs. Figs are actually clusters of flowers enclosed within a spherical or cylindrical structure termed a syconium. Female wasps enter the syconium through a narrow hole to seek out the tiny flowers upon which they lay their eggs. Wasp larvae feed on floral tissue destroying ovules in the process. Larvae develop into adult wasps that emerge into the central chamber of the syconium where they mate, after which the males die. During this time pollen either adheres to female wasps passively or is actively collected by them prior to their emergence from the syconium in search of another fig tree. Pollination occurs when the wasps enter another syconium to lay eggs. Although many flowers are destroyed, sufficient remain to produce pollen and seed. This highly coevolved system is all the more remarkable in that each *Ficus* species is exclusively pollinated by a single, or rarely two, fig wasp species. Despite the potential vulnerability of such highly specialized mutualisms to the loss of one of the partners, the fig–fig wasp mutualism seems very resistant to anthropogenic impacts on forested landscapes.

Seed Dispersal

A second mutualism associated with plant reproductive processes is that of dispersal of seed by animals. In the immediate vicinity of the parent plant competition for resources is intense and the risk of death from pathogens or seed predators is disproportionately high (see below). Thus if seed production is to be translated into seedling recruitment dispersal of seeds away from the parent into uninhabited sites suitable for growth is necessary. Plants achieve this by a variety of biotic and abiotic mechanisms. In tropical moist forests transportation by biotic mechanisms is much more important than it is in temperate or tropical dry forests where wind is an effective dispersal agent.

Plants that use animal agents to disperse seeds may offer inducements in the form of a nutritious reward to attract dispersal agents. Many tropical plants, as well as temperate ones, surround their seeds with fleshy fruit that is sought by animals that consume the fruit and in so doing disperse the seed. The seeds are spat out or may be swallowed along with the fruit, only to be ejected with the feces having passed through the digestive tract unharmed. Indeed, many seeds require exposure to digestive acids in vertebrate guts before they are able to germinate. Dispersal of internally transported seed is a function of animal movement and the duration of passage through the gut. Asian rhinoceroses and elephants both consume and defecate seeds, but while elephants defecate at more or less random locations, rhinoceroses repeatedly visit latrines that can accumulate tens of thousands of seeds.

Animal foraging behavior also dictates the pattern of dispersal. Many forest rodents ‘scatterhoard’ seed, that is they store a little food in each of numerous caches which results in widely dispersed small seedling clumps. Burial of oak seeds by squirrels, for example, results in seedling distribution that is not unlike dispersal by wind, where most of the seeds are within a few meters of the parent tree with a much smaller proportion distributed further away. Such behavior is contrasted with ‘larderhoarding’ in which all food is stored in one or very few locations, resulting in a much higher density of seedlings per clump. Seed hoarding by animals can be a highly effective means of dispersal. Jays that hoard pine nuts in North America can disperse seed 20 km from the trees at which the seed were collected.

Other plants offer a small amount of fleshy tissue that is attached to the end of the seed and serves the same function as fruit. In the case of the cashew nut trees (*Anacardium* spp.), the fleshy aril is consumed by bats usually some distance from where they were collected and the seed is discarded. Thousands of other plants offer a similar reward, termed an elaiosome, that is collected by ants. Elaiosomes contain chemicals that attract ants and stimulate them to carry the seeds back to the nest where the elaiosome is consumed leaving the seed to germinate in the environmentally nutritious and safe surroundings of the ant nest. Ant-dispersed seeds occur in a wide variety of plant families, notably the Fabaceae, Mimosaceae (acacias) and Sterculiaceae, and in several forest habitats including tropical rain, savanna, and sclerophyll forests.

Seed dispersal mutualisms are usually fairly generalist with a wide variety of animal seed dispersal vectors being attracted to the fruit of any particular tree. The fruit of bird dispersed seed tend to be smaller than those of mammal dispersed seed though there are few specialized plant-seed disperser mutualisms. One exception is the Australian mistletoe bird (*Dicaeum livuninaceum*) which specializes on mistletoes.

It is estimated that around 10% of flowering plants have fruits that bear hooks, barbs, claws or a sticky surface by which they become attached to the hair or feathers of passing animals. These seeds are passively carried by the animal until they fall off or are brushed off. Such dispersal does not constitute a mutualistic plant–animal interaction as the seeds or fruit can be an irritation to the animal concerned.

Seeds may be moved to their ultimate location in several stages, with different agents responsible for each stage. Thus a fruit that is initially dropped from a tree into a stream may be later picked up by a rodent that only partially consumes the fleshy tissue before dropping it to be harvested by ants that drag the seed into the nest. Seed dispersal can therefore consist of a complex array of sequential events involving a suite of dispersal agents.

Plant Protection by Ants

Ants are important mutualistic partners to a variety of plant species in tropical forests, protecting plants from herbivores, providing plants with essential nutrients and, as has already been described above, dispersing seeds and fruits. In most ant–plant mutualisms plants provide ants with accommodation, in the form of hollow stems, roots or thorns, or swollen petioles or leaf pouches, and food such as extrafloral nectar or food packages that are rich in protein and lipids. In return ants provide protection from herbivores by attacking any insect or vertebrate that contacts the plants. In the most famous plant–ant mutualism in central America *Pseudomyrmex* ants not only provide protection from herbivores but also clear competing seedlings from around the base of the host *Acacia* trees. Ant protection from herbivory has been observed in a wide variety of plant families common in tropical or subtropical forests. These include bamboos, fast growing pioneer species (*Macaranga* and *Cecropia*), rattan palms, and understory woody plants (*Cordia alliodora*). The mutualism is also geographically widespread and has evolved independently at least twice among *Acacia* trees in Central American dry forests and African savanna forests, and the ferocity of weaver ants (*Oecophylla*) which construct nests from freshly woven leaves of a variety of trees is familiar to forest workers throughout Southeast Asia.

In some cases (as for the plants *Hydnophytum formicarium* and *Myrmecodia tuberosa*) ants provide food for the plants by depositing their refuse in absorptive chambers that house the ants. Such specialized myrmecotrophic plants are in the main tropical epiphytes in open forests and savannas growing on nitrogen-deficient soils, thus acquisition of nitrogen from ant waste is the principle benefit to the plants. A far greater number and diversity of plants that house ants for protective purposes may additionally benefit nutritionally, though to a lesser degree, from ant waste products and discarded prey that accumulate in nesting cavities.

Ants are well known for their habit of maintaining colonies of sap-sucking homopteran insects on plants. Homopterans take sap directly from the plant phloem and excrete unwanted organic acids and sugars in the form of honeydew that is harvested by ants. The ants tend and protect the homopterans from parasites and predators, hence this interaction could be construed as being antagonistic as far as the plant is concerned. However, some evidence suggests that ants regulate homopteran populations and prevent outbreaks that might be highly detrimental to plants, and the presence of ants can also provide protection against herbivory. Currently there is little conclusive information on the balance of costs or benefits to plants of homopteran-tending ants, although in one study the presence of homopteran-tending ants on birch in Finland greatly reduced damage by leaf feeding caterpillars.

Antagonistic Interactions

Animals cause damage to plants by consuming vegetative tissue or propagules, or by mechanical destruction such as trampling. Plants tolerate a certain amount of tissue loss but such damage may make them susceptible to secondary infestation by pests and pathogens or place them at a disadvantage relative to unscathed neighboring competitors. In response to the onslaught of primary consumers plants have evolved a variety of physical, chemical, and biological defenses, albeit at some cost of production.

Herbivory and Plant Defenses

Animals that feed on plant tissue are varied and abundant. Vertebrates graze and browse leaves and gnaw at roots and tubers. Insects chew, mine, or gall leaves, as well as suck sap and bore stems, and even an entire tree may be defoliated by a single caterpillar outbreak (**Figures 1–3**). Plants can usually recover from such damage as only a portion of the plant is consumed and, owing to their repeating modular construction, lost parts can be readily renewed (although continued intensive attack will eventually kill a plant).

Despite the huge abundance of leaves in forests there are few canopy mammals that are able to effectively digest cellulose, the main component of leaves. Those that do, such as sloths and howler monkeys in the Neotropics, and orangutans, proboscis monkeys, and chimpanzees in the Old World tropics, rely on a suite of symbiotic gut microorganisms to digest cellulose in their large stomachs. Among birds, the large stomach required to digest leaf material has limited such a widespread food to only a single species, the hoatzin of South America.

Figure 1 *Alcidodes ramezii* (Curculionidae) recently emerged from the fruit of *Dipterocarpus obtusifolius* (Dipterocarpaceae). Weevils are important seed predators of many tropical trees and in some cases can destroy over 90% of the entire seed produced in a particular fruiting event. Photograph courtesy of Richard Davies.

Vertebrate grazers and browsers are, however, abundant on the ground and ruminants such as deer, giraffes, and oxen as well as other forest mammals such as elephants, consume large amounts of leaf material. Their impacts on forest composition and succession can be dramatic as they may preferentially feed on seedlings and saplings thereby preventing tree regeneration and succession to mature forest. Overstocking of deer in Scotland, for example, has a severe impact on the regeneration of native pine woods. In African savannas the balance between grazers which feed on grasses and browsers which attack trees can have long-term effects on the extent of trees in the landscape.

Figure 2 The caterpillar of the emperor moth *Imbrasia belina* (Saturniidae), commonly called the mopane worm, feeding on the leaves of its host plant the mopane tree *Colophospermum mopane* (Colophospermaceae). Mopane woodlands are dominated by this one tree species, and because few other herbivorous species find the leaves of the mopane tree palatable, *I. belina* often achieves very high population densities in sporadic outbreaks. Widespread defoliation of mopane woodlands occur during such outbreaks.

Figure 3 An unpalatable caterpillar on *Shorea leprosula* (Dipterocarpaceae). Many caterpillars sequester the toxic secondary compounds produced by leaves for their own defense against predators.

The most important herbivores in tropical forest habitats in terms of the amount of plant biomass consumed are insects, in both adult and larval forms. Grasshoppers, katydids, some beetles and ants, and the larvae of moths, butterflies, and many flies and sawflies consume vast quantities of leaf material. Many other insect grazers, such as springtails, feed on root tissues. A large number of insects belonging to the orders Coleoptera (beetles), Lepidoptera (moths), Diptera (flies), and Hymenoptera (sawflies) consume tissue between the epidermal layers of leaves creating conspicuous mines or blotches. Leaf-mining insects lay their eggs on the leaf surface or directly into the leaf. Larvae may feed on leaf tissue or just on sap exuded from damaged tissue.

In Neotropical forests leaf-cutting ants (*Atta* spp.) are the dominant herbivores consuming more vegetation than any other group of animals, and it has been estimated that 12–17% of all leaf material produced in Neotropical forests is harvested by *Atta* ants. Species selection appears indiscriminate and leaf-cutting ants will even harvest agricultural crops. Consequently, leaf-cutting ants contribute greatly to nutrient cycling in tropical forests with each colony using about 50–250 kg of dry matter each year. The underground nests of *Atta cephalotes* can cover several tens of square meters and contain up to 5 million workers. In these huge nests leaf material is used to culture specialized fungi on which the ants feed.

Gall-forming invertebrates induce plants to form abnormal growths within which the insect gains both shelter and food. Gall formers include species of mites, gall-wasps, flies, weevils and aphids and are abundant on both temperate and tropical trees, the tree families most heavily galled in Europe being Fagaceae (oaks and beech) and Salicaceae (willows and poplars). All parts of a plant may harbour gall formers, with leaves being most commonly attacked, though nematodes are unusual in attacking roots. Each galling species produces a characteristic gall structure the formation of which is usually induced by egg laying into the plant tissues. The larvae feed inside the gall where they are relatively protected from predators and desiccation. Gall-forming insects appear to increase in relative abundance with increasing aridity, presumably due to the protection a gall affords the developing larvae from desiccation.

Wood-boring beetles can cause extensive damage to trees particularly as they can also be a means of spread of pathogenic fungi. Bark beetles, for example, bore into tree trunks and excavate the wood just beneath the bark causing extensive damage. Trees often respond by flooding bore holes with sap but bark beetles may recruit to injured trees ultimately overcoming the trees' defenses.

Another important mode of consumption is to use strawlike mouthparts to suck fluids from plant vascular tissues, the phloem and xylem, which transport water, nutrients, and photosynthate. The most common sap feeders are aphids and other hemipteran bugs, although spider mites also follow this strategy.

Plants have, in turn, evolved a wide array of defensive compounds or physical structures that impede insect or vertebrate attack. Chemical defenses can reduce the digestibility of leaf tissue, or may have a toxic or repellent function. Tannins are large carbon-rich compounds that bind proteins making them difficult to digest. Toxic compounds include phenolics and alkaloids and these may poison or kill animals that consume them. Some plants have responded to attack by leaf miners by secreting latex which impedes or kills larvae. Mechanical defenses include the obvious spines and thorns to defend plants against vertebrate herbivores, and the less obvious silica structures that render grass and nettle leaves less palatable to vertebrates and invertebrates alike. Leaf hairs, called trichomes, sticky surfaces and often a combination of the two also limit herbivory, while structural tissue such as cellulose and lignin lining leaf veins is not easily digestible constraining herbivores to limited leaf areas. Plant chemical repellents may also deter insects from laying their eggs on plant tissues causing the insects to look elsewhere.

Many animals and insects have evolved mechanisms to overcome or tolerate plant defenses leading to a high degree of specialization on the host plants they infest. Insect larvae may even assimilate poisons rendering themselves unpalatable to predators. Repellents, on the other hand, do not kill herbivores so there is much weaker selection to develop counteractive mechanisms and, consequently, much less herbivore specialization.

Seed Predation

Seeds are highly nutritious packets of carbohydrates, proteins, and lipids that are readily consumed by vertebrates and invertebrates, but are only briefly available and less predictable than other plant tissues. Broadly, two groups of seed predators are recognized, those that consume seeds prior to their dispersal, and those that attack seeds that have already dispersed. Predispersal seed predators are mostly specialist sedentary feeders belonging to the insect orders Diptera, Lepidoptera, Coleoptera, and

Hymenoptera. Postdispersal seed predators are larger, more mobile, and generalist herbivores like ants and vertebrates, particularly rodents and birds. Predation rates are highly variable but can be as high as 100% of seeds produced. Although seed predation is an antagonistic interaction, some seeds that escape predation may be benefited by being dispersed into favorable microhabitats. Squirrels and other rodents cache large numbers of seeds a few of which will escape predation by being forgotten (see above). Nevertheless the vast majority of seeds encountered by seed predators are killed.

High rates of seed predation are thought to have led to the evolution of mast seeding among many tree species. Masting is the periodic synchronous production of seed that leads to such an abundance of seed that seed predators are satiated. As a result there is a greater probability of seedling recruitment following mast years. In nonmast years the dearth of seed resources may limit seed predator populations making them less able to exploit effectively periods of resource abundance. In Europe oak and beech trees produce mast crops once every two to ten years, while dipterocarp trees in Southeast Asia are well known for supra-annual mast fruiting events in which species belonging to several genera participate over areas extending to hundreds of square kilometers.

Mechanical Damage

Physical disturbance by large vertebrates is an important structuring component of forest systems. Large herbivores such as elephants can open up the canopy and disturb the soil by digging and scraping, creating opportunities for seedling recruitment especially for fast growing pioneers. In the tropical dry forest of Mudumalai Wildlife Sanctuary, southern India, very high tree mortality, largely a result of elephant damage, has been documented. Elephants are also known to play an important role in determining the abundance of trees in African savanna forests. In North America dam building by beavers can dramatically alter forest riparian habitats and, because they feed preferentially on deciduous species beavers cause an increase in the relative proportion of conifers. Animals that cause long-term and dramatic physical modification of habitats have been termed ecosystem engineers and may be important for maintaining high species and structural diversity by increasing habitat heterogeneity. At smaller scales and in temperate forests squirrels and deer cause damage to young beech and other trees by stripping bark. Such damage can cause considerable financial loss to plantation owners. Rodents attack tree roots even below ground, though such impacts are most significant in arid rather than forested environments.

Conclusion

There is a multitude of plant–animal interactions ranging from the antagonistic to the mutually beneficial. Both antagonistic and mutualistic interactions have enormous importance for the structure, composition, and functioning of forests as well as all other natural habitats. Often it is not easy to separate apparently antagonist behavior, such as seed predation, from mutualistic behavior such as seed dispersal, as the same animals often perform both functions. Furthermore, while antagonistic interactions such as herbivory, seed predation, or mechanical damage, are certainly detrimental to the individual plants affected, such behaviors may raise habitat diversity and richness by increasing heterogeneity and preventing dominance by fast-growing or competitively superior species. Additionally, many ecosystem functions are dependent on the interactions between plants and animals. Nutrient cycling and decomposition, for example, are functions of herbivory and the breakdown of organic matter by numerous soil-living invertebrates. The reproduction of flowering plants, particularly in the tropics, is dependent on the availability of pollinators. Humans are, of course, dependent on the continued functioning of these plant–animal interactions for crop production and soil fertility and the continued existence of viable diverse forests and their natural renewable resources.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife; Natural Disturbance in Forest Environments; Reproductive Ecology of Forest Trees. **Entomology**: Bark Beetles; Foliage Feeders in Temperate and Boreal Forests; Population Dynamics of Forest Insects; Sapsuckers. **Environment**: Impacts of Elevated CO_2 and Climate Change. **Silviculture**: Natural Stand Regeneration.

Further Reading

Crawley MJ (1997) Plant–herbivore dynamics. In: Crawley MJ (ed.) *Plant Ecology*, pp. 401–474. Oxford: Blackwell Science.

Proctor M, Yeo P, and Lack A (1996) *The Natural History of Pollination*. London: HarperCollins.

Wirth R, Herz H, Ryel RY, Beyschlag W, and Holldobler B (2003) *Herbivory of Leaf-Cutting Ants: A Case Study on* Atta Colombica *in the Tropical Rainforest of Panama*. Berlin: Springer-Verlag.

Reproductive Ecology of Forest Trees

J Ghazoul, Imperial College London, Ascot, UK

Introduction

Plant reproductive processes encompass biotic interactions, such as pollination and seed predation and dispersal, and abiotic elements, notably disturbance that creates differential reproductive opportunities for plant groups and thereby maintains diverse forest formations.

There are several important stages in the regeneration of trees, the first of which is the allocation of resources to reproductive structures as opposed to vegetative growth. Among flowering plants, that comprise the majority of tree species, allocation to reproductive structures such as flowers, seeds, and fruit may vary enormously and may comprise a substantial portion of photosynthate. Even within plant families some trees (e.g., some dipterocarps of the genus *Shorea*) produce several million tiny flowers, while others (e.g., *Dipterocarpus*) produce only a few hundred relatively large flowers. Flower number and morphology reflect pollinator syndromes while the trade-off between seed size and number has also generated a huge variety of options for reproductive success. Beyond being a crucial step in seed production, pollination is the first of two stages by which gene flow is effected, by gamete dispersal within populations. Seed dispersal represents a second opportunity for gene flow as seeds are transported to new locations by a variety of dispersal vectors. Dispersed seed may enter a variable period of dormancy before germination and growth to seedling stages. Biotic agents of mortality acting at each of these life stages can reduce enormously the probability of ovule survival to maturity. Thus the diversity of reproductive strategies observed among trees reflects physical, competitive, and coevolutionary interactions among plants and their biotic and abiotic environments at each of these life history stages. This article describes the diversity of tree reproductive strategies in temperate and tropical forests, emphasizing flower and seed life stages.

General Reproductive Strategies

Vegetative Reproduction

Plants as sessile organisms reproduce by means of their modular architecture and their capacity for reiterative growth – indeed, all plants are potentially clonal in that each module contains both reproductive and somatic tissue. However, production of independent offspring by means of vegetative growth is rare among trees, although detached branches of willows and poplars can sprout if maintained in moist conditions. Most broadleaves can produce new stems from cut or burned stumps even when the rootstock is hundreds of years old. Trees cut specifically for this purpose are referred to as coppice and are an important management feature of many European woodlands. Some conifers can also coppice (e.g., redwoods), or sprout from burned trunks (e.g., pitch pine), but most regenerate from seed.

Fallen trees that retain some connection to the soil through roots may develop new stems from epicormic shoot production. Indeed, small-leaved lime in the UK has been referred to as practically immortal for both this reason and for its vigorous coppicing response. Similarly, broken crowns can regenerate through epicormic stem proliferation.

Some plants are able to produce seeds in the absence of fertilization by partial or total suppression of meiosis and fusion of gametes. Such a process is termed apomixis and may be widespread among tropical trees.

Sexual Reproduction

All trees, excepting tree ferns, are seed-bearing and reproduce sexually by wind or insect-mediated transfer of male gametophytes, as pollen, to ovules. The gametophytes of all seed plants are enclosed within sporophyte tissues and, unlike ferns or nonvascular plants, are no longer free-living at any stage of their life history. Fertilization occurs when male nuclei are transferred to an ovule by way of a pollen grain that has been received on a compatible and receptive stigmatic surface.

Seed plants are taxonomically separated into two primary lineages, the gymnosperms (about 770 species) and the angiosperms (some 235 000 species). The gymnosperms consist of four phyla that include conifers, cycads, gnetophytes, and Ginkgophyta (solely represented by the maidenhair tree *Ginkgo biloba*), of which only the conifers form forest trees. The angiosperms differ from the gymnosperms in that they have their reproductive structures contained within flowers. Pollen transfer in almost all gymnosperms is effected by wind (some gnetophytes and cycads may be beetle-pollinated) while the flowers of angiosperms evolved to attract insect and animal pollinators, although many angiosperms have secondarily evolved to be wind- or water-pollinated.

Coniferous gymnosperms Almost all trees within the gymnosperms are conifers and it is these that dominate the boreal forests of Eurasia and North America. Conifers have their reproductive parts aggregated in unisexual cones which may be borne on the same tree (monoecious) or on different trees (dioecious). Cones consist of numerous scales, each of which bears either two pollen sacs (males) or ovules (females). All conifers are wind-pollinated and, given the inefficiency of wind pollination, often produce huge amounts of pollen. Pollen grains consist of a reproductive sperm cell and a tube cell, and have two wings or air-filled bladders that aid transport by wind. Pollen grains landing near an ovule are drawn towards it by a drop of liquid that is absorbed into the female scale. Pollination occurs when the pollen grain penetrates the micropyle, a small opening in the integument of the ovule. Following pollination, the cone is sealed by a thickening of the scales. One of the two cells that comprise the pollen grain elongates into a pollen tube that, over a period of several months or more, eventually reaches the egg cell. Fertilization follows when the sperm cell migrates through the pollen tube to fuse with the egg. The embryo develops within a naked seed and, after a further year, the cones ripen, dry, and open to release the winged seeds. Most conifers differ only slightly from this general pattern of reproduction, although yew *Taxus* sp. is notable in that its ovules are solitary, its pollen grains lack the 'wings' of most other conifers, and its large seed develops in a fleshy red aril which ripens within a year.

Angiosperms Apart from the obvious presence of a flower, angiosperms differ morphologically from gymnosperms in that the female gametophytes are greatly reduced in size. Consequently, the process of development is much faster and more efficient. Unlike gymnosperms, the seed food store only develops after fertilization and is therefore not wasted if fertilization fails to occur. Increased reproductive efficiency is thought to have contributed substantially to the flexibility of reproductive strategies and to the current dominance and diversity of the angiosperms.

The ovules of angiosperms are completely enclosed within the carpel (hence angiosperm, meaning hidden seed), a development that may have arisen to protect the ovules and pollen from insects. A pollen grain landing on the stigmatic surface germinates and extends a pollen tube through the style to fertilize the ovule. The fertilized embryo develops within a seed that may be enclosed in a nut or fruit to attract animal dispersal agents, or may be formed so as to facilitate dispersal by wind, water, or passive animal transport. In many species seed germination is delayed as seeds enter a period of dormancy until such time as environmental conditions trigger release from dormancy. Some seeds can persist in a dormant stage for decades or even centuries and collectively form the soil seed bank. Other seeds (e.g., of the dipterocarps) are recalcitrant and germinate very soon after dispersal, though the seedlings may persist for many years in deep forest shade to form a seedling bank until a canopy gap forms, allowing renewed vigorous growth.

Pollination of Angiosperms

Pollination is effected by a variety of biotic and abiotic pollination vectors, with biotic pollinating agents predominating in tropical zones and wind being relatively more significant in temperate regions. About 98% of all flowering trees in tropical rain forests are animal-pollinated; bees are by far the most important pollinators (**Table 1**). Pollination by beetles, hummingbirds, and small bees is more common among subcanopy trees but even here medium to large bees form the dominant pollinator group. Wind pollination is rare and confined to very few canopy and understory trees.

Pollination by Vertebrates

Pollination by vertebrates in north temperate forests is virtually nonexistent, but it is relatively common in tropical forests, and is also important in south temperate zones in Australia and South Africa. Among vertebrates, bats and birds are the principal pollinators, although some trees may also be

Table 1 Frequencies of different pollination systems among canopy trees at La Selva, a lowland tropical rainforest in Costa Rica

Pollination vector	*Percentage of tree species*	
	Canopy (n = 52)	*Subcanopy (n = 112)*
Medium-large bees	44.2	19.6
Small diverse insects	23.1	12.5
Moths	13.5	16.9
Small bees	7.7	17.0
Bat	3.8	2.7
Wasp	3.8	4.5
Hummingbirds	1.9	5.4
Butterflies	1.9	6.2
Beetle	0	10.7
Wind	0	3.6

Data from Bawa KS, Bullook SH, Perry DR, Coville RE, and Grayum MH (1985) Reproductive biology of tropical lowland rainforest trees. II. Pollination systems. *American Journal of Botany* 72: 346–356 and Bawa KS (1990) Plant–pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21: 399–422.

pollinated by various nonflying mammals. Pollination by bats is particularly common among the Bombacaceae, and the genera *Parkia* (Mimosaceae) and *Bauhinia* (Caesalpiniaceae). Flowers of bat-pollinated trees open at dusk or soon after and are typically large, white or pale, have a musky odor, and produce copious amounts of nectar. While this is energetically costly, gene flow by bat-dispersed pollen is potentially very great.

In the neotropics hummingbirds are the main avian pollinators and feed exclusively on nectar, although they primarily visit understory shrubs rather than trees. Their Old World counterparts are sunbirds which visit a wide variety of trees but also feed on insects. Bird-pollinated flowers are typically red and contain plentiful but dilute nectar, so much so that showers of nectar are brought down when shaking the branches of the coral tree *Erythrina* spp.

Pollination by Invertebrates

Bees and wasps Bee pollination is particularly important among canopy trees in tropical forests. Two groups of bees may be distinguished as pollinators: medium to large bees, including honeybees and a variety of solitary or semisocial bees; and small, mostly social bees of the Apidae family, notably the sweat bees. Large bees appear to predominate in forest canopies while small bees tend to visit understory trees (**Table 1**), though this pattern breaks down in more open dry forest formations. A diverse array of wasps and other hymenopteran insects visit generalized flowers on trees in taxa such as Anacardiaceae and Burseraceae, but their role is minor relative to other insect pollinator groups, the exception being agaonid wasps that are specialist pollinators of fig trees (*Ficus*, Moraceae).

Moths and butterflies Moth pollination, particularly by sphinx moths, is prevalent across the tropics and includes trees within the genera *Dipterocarpus* (Dipterocarpaceae) and *Plumeria* (Apocynacea). Moth-pollinated flowers typically open at dusk and are usually pale with deep corolla tubes that emit strong sweet scents. Moths can carry substantial amounts of pollen and cover great distances between successively visited plants, making them good pollinators of widely spaced trees. Butterflies, by contrast, are rare pollinators of trees, although they do pollinate certain species-rich genera, e.g., *Eugenia* (Myrtaceae).

Beetles Beetle pollination is common among Annonaceae, Lauraceae, Myrtaceae, and Palmae. A range of beetles visit a wide variety of floral morphological forms, although most beetle-pollinated flowers open at dusk and emit strong odors. Beetles generally consume pollen and flower parts rather than nectar. In Australian rainforests up to one-quarter of all plants may be pollinated by beetles, and such plants are found in all forest strata and include trees, shrubs, and epiphytes.

Flies Flies certainly contribute to the pollination of understory forest shrubs but are probably of minor importance in the pollination of forest trees. Exceptions include cacao (*Theobroma cacao*), pollinated by midges.

Thrips The synchronously flowering dipterocarps in Asian rainforests are thought to be primarily pollinated by thrips, tiny insects that can undergo massive population increases within a very short time in response to the sudden availability of floral resources generated by a mass flowering event. Dispersal of thrips is likely to be facilitated by winds above the forest canopy. Thrips also pollinate many species of Myristicaceae.

Wind Pollination

Other angiosperms have reverted to wind pollination and consequently have much reduced flowers, as visually attractive flowers are no longer necessary for pollinator attraction. While wind is ever-present, it is not a selective pollinator and is consequently inefficient over large distances. Wind pollination is therefore favored in species-poor forests where conspecifics are closely spaced. Wind-pollinated plants are associated with abundant pollen production and synchronous mass flowering events to ensure successful pollen transfer. To maximize the probability of catching randomly drifting airborne pollen, flowers are placed at the outermost edges of the crown or in pendant catkins to maximize exposure to wind, and stigmas are usually well exposed and have large surface areas.

Wind pollination is associated with temperate forests and dry, or seasonally dry, habitats where animal pollination vectors are comparatively rare and where rainfall rarely hinders pollen dispersal. The temperate forests of northern mid-high latitudes are dominated by species such as oak, beech, and birch, that rely on wind pollination. In the temperate rainforests of Chile, New Zealand, and the Pacific Northwest of America, wind pollination is again common, despite the wet climate. Open forests and savannas are particularly well represented by wind-pollinated trees. In the dense vegetation of a rainforest wind pollination is usually restricted to emergent coniferous trees (e.g., *Araucaria* and *Agathis*) and to trees occurring on ridge tops (*Balanops australiana, Nothofagus*). Wind pollination does, very rarely, occur in the rainforest understory among more specialized angiosperm groups, including Euphorbiaceae, Pandanaceae, and Palmaceae.

Breeding Systems and Incompatibility

Individuals of most tree species bear both male and female reproductive organs, and often within the same flower. Consequently there is a high risk of self-fertilization that would restrict genetic mixing and seed viability through inbreeding. Breeding systems have therefore evolved to limit or prevent self-fertilization. Plant breeding systems range from obligate outcrossing to predominantly selfing. This range of systems is not distributed randomly among species, as woody plants are usually associated with outcrossing and annual herbs with selfing. Outcrossing can be achieved or enhanced by spatial separation of male and female flowers, either on different trees (dioecy) or within individual trees (monoeicy), or by temporal separation of male and female reproductive organs by nonoverlapping maturation times (dichogamy). Where male and female reproductive parts are not separated, physiological self-incompatibility mechanisms that block pollen tube development may exist. Other strategies include selective abortion of selfed seed. There may be considerable variation in the reliability of self-incompatibility across and within species, and the proportion of selfed seed can be highly variable among individuals within a population.

Trees in both tropical and temperate systems are mostly outcrossed, although the mechanisms by which this is achieved vary between these regions. Temperate trees are mostly self-compatible, possibly an evolutionary response to unpredictable effectiveness of the pollination vector, and selfing is limited by the spatial separation of male and female flowers. Many conifers, for example, are monoecious and seed is mostly outcrossed. Tropical trees generally have hermaphroditic flowers but are mostly incapable of self-fertilization due to physiological self-incompatibility mechanisms. Spatial separation of flowers by dioecy is also common among tropical species. In tropical lowland forests of Guanacaste in Costa Rica, for example, 22% of trees are dioecious and a further 54% are physiologically self-incompatible.

Seed Morphology and Dispersal

Seed Size

Seed size varies among flowering plants from less than 10^{-6} g in orchids to more than 10^{4} g in coco-de-mer. Small seeds can be produced in greater numbers but have less chance of establishing successfully, owing to fewer stored reserves, and size is largely a trade-off between these two selection pressures. This trade-off is subject to variation in response to physiological, ecological, and environmental conditions acting on seed and seedlings. Heavy predation of seeds, for example, near parent trees favors dispersal, which may increase or decrease seed size depending on the dispersal agent involved. The requirement for light for early seedling growth can also be mediated by seed size – large seed size confers an advantage to seedlings in low light owing to the greater reserves available to them, though this advantage is only apparent during the earliest stages of growth. Nevertheless, larger seeds are generally found among trees whose seedlings establish in shaded environments, as for tropical canopy trees.

Seeds that are mammal- or gravity-dispersed tend to be large while bird- and wind-dispersed seeds are relatively small. Thus in successional forest habitats there is increasing abundance of large-seeded species with age from the initial disturbance. This is associated with the increasing size and slower growth rates of the colonizing plants with time, and a shift from wind or bird dispersal, typical of many pioneer species, to mammal or gravity dispersal associated with canopy and emergent trees. Despite these generalizations, much variation in seed size remains unexplained and other variables, such as antiherbivore strategies, mycorrhizal associations, or soil type, might also affect seed size among forest tree species.

Seed Dispersal

Seeds are designed to be dispersed away from the parent plant to escape predation and seedling mortality near the parent, to colonize spatially and temporally ephemeral habitats, or to locate microsites suitable for establishment and growth. However, most seeds are not dispersed far from the parent. As such, seeds have evolved a variety of morphological forms to maximize dispersal efficiency by way of biotic dispersal vectors, including vertebrates (bats, rodents, and other mammals, birds, and fish), invertebrates (ants and beetles), and abiotic vectors such as wind and water.

Understory herbaceous plants in temperate and tropical forests often have barbed or sticky fruit that adhere to the coats of passing animals. Most animal-dispersed seed rely on active dispersal by offering animals a food reward in the form of a fleshy fruit. Such fruits have developed traits, such as color or odor, that increase their attractiveness to the appropriate dispersers. In tropical forest communities 50–75% or more of tree species produce fleshy fruits adapted for dispersal by birds or mammals. Many temperate forest trees are also vertebrate-dispersed, although some, such as oak, lack obvious adaptations to attract dispersers. Plant–animal dispersal interactions, as for plant–pollinator interactions, tend to be generalized, with few being highly species-specific.

Abiotic dispersal mechanisms include gravity, wind, and water. Gravity-dispersed seeds simply fall beneath the parent tree, though the fruit may be adapted to drift laterally as it falls (as for dipterocarp trees). Wind-dispersed plants are relatively more common in dry, exposed, and open habitats. In tropical moist forests where wind dispersal is relatively rare, it is generally found among canopy trees or vines rather than understory plants. Dispersal by water is common among gallery forests and seasonally inundated floodplain habitats. Seeds of some coastal trees, notably coconut, are even dispersed on ocean currents.

Seed and Seedling Banks

The seeds of many plants undergo a period of dormancy which may be very short (on the order of a few days) or prolonged (several decades or more). The advantage of dormancy is that it allows a plant population to escape from certain environmental disturbances or temporally adverse conditions. Early successional and pioneer plants tend to have delayed seed germination until such time that light or water conditions become favorable for growth. The seeds remain in the soil, forming a soil seed bank, and only germinate when an appropriate environmental cue, such as increased light brought about by a tree fall, is received. Dormancy is also an effective strategy to avoid seedling desiccation during the dry season. Dormancy can be imposed by other traits, as in seeds carried by wind that are typically desiccated to facilitate dispersal and therefore need rehydration prior to germination. Similarly, dormancy of seeds dispersed by vertebrate consumption may be necessary to survive passage through animal digestive tracts.

In the deep shade environment of a tropical forest understory, intense competition for light favors seeds that germinate immediately, leading to the establishment of seedling banks. Although these seedlings have very slow growth, they are also best placed to take maximum advantage of light upon the formation of a canopy gap.

Natural Disturbance

Disturbance is a natural feature of all forest environments. Natural disturbances vary greatly in size and frequency, and they shape forest structure and composition. Disturbance creates new opportunities for propagules to establish and grow, from vertebrates turning over soil and leaves to expose a germinating seed to light, through tropical canopy gap formation following treefalls that release seedlings from light inhibition, to extensive windthrows of balsam fir forests that initiate regeneration waves of saplings. Regeneration of many forest trees is usually confined to gaps, and composition of the regenerating community is a function of gap size, shape, and location, and the coincidence between gap formation and a fruiting event. The establishment of some tropical trees, such as mahogany, is entirely dependent on large clearings created by high winds and subsequent fires, while seedlings of other species simply need canopy openings for further growth. Yet other species, such as beech and hemlock, are shade-tolerant and regenerate under closed canopies.

Natural fires occur in almost all forest systems, although coniferous and dry deciduous forests are more fire-prone. Conifers usually burn readily and, although some are well protected by thick bark, intolerant species survive by producing many widely dispersed seeds that germinate and grow rapidly following a fire. Some species, such as lodgepole pine, even need fire to stimulate the release of seeds, which then fall on to soil fertilized by ash and which is free from other competing species. Fire is an important ecological factor in many north temperate forests and serves to maintain forests in a non-equilibrium state. Fire-prone coniferous woodland, for example, develops a broad-leaved understory which, in the absence of fire, will eventually replace the conifers.

Recruitment to seedling cohorts is frequently episodic as seed production, dispersal, and the breaking of dormancy are often facilitated by unusual or periodic climatic and disturbance events. Mast seed production is widespread among tropical and temperate trees and may be initiated by El Niño climatic events (e.g., dipterocarps in Southeast Asia) or fire (e.g., ponderosa pine in the Rocky Mountains of North America). Irregular heavy seed production may satiate seed predators, allowing for at least some seed survival, or may simply be a response to conditions that are optimal for germination. Alternatively, an episodic pattern of regeneration may be imposed at a later regeneration stage should, for example, a pest or disease outbreak cause the mortality of all young saplings.

Conclusion

Successful reproduction of trees is a function of several sequential ecological processes, pollination and fertilization, seed development and maturation, seed predation, dispersal and germination, and seedling growth, many of which are mediated by mutualistic and antagonistic interactions with animals acting as pollinators, dispersers, seed predators, and leaf herbivores. These processes unfold in the context of the disturbance regime, which creates differential opportunities for propagules and seedlings. Quite different reproductive strategies exist among forest trees within and among communities. The most obvious is the overwhelming dependence of tropical trees on animal interactors for pollination and seed dispersal, compared to temperate species, for which abiotic agents are comparatively more important. Such differences in pollination and seed dispersal vectors are reflected in the efficiency of gene transfer and patterns of gene flow, and information about seed production and gene flow is critical for the design of forest management plans and strategies for the conservation of plant genetic resources.

Currently, there is little information about the pollinators and seed dispersers of many forest trees, or indeed about the importance of flower and fruit resources to animal communities. Even basic knowledge about factors that regulate seed production, viability, dormancy, and germination for many tree species remains to be discovered, and only recently have we begun to understand the importance of natural disturbance in shaping plant communities through differential reproductive success. Our ability to rehabilitate, conserve, and manage existing forests will continue to be improved by continued research on tree reproductive ecology within the context of the natural disturbance regime.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation; Natural Disturbance in Forest Environments; Plant-Animal Interactions in Forest Ecosystems. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Tree Physiology**: Physiology of Sexual Reproduction in Trees.

Further Reading

Bawa KS and Hadley M (eds) (1990) *Reproductive Ecology of Tropical Forest Plants*. UNESCO Man and the Biosphere Series.

Bawa KS, Perry DR, and Beach JH (1985) Reproductive biology of tropical lowland rainforest trees. I. Sexual systems and incompatibility mechanisms. *American Journal of Botany* 72: 331–345.

Peterken GF (1996) *Ecology and Conservation in Northern Temperate Regions*. Cambridge, UK: Cambridge University Press.

Forest Canopies

R K Didham, University of Canterbury, Christchurch, New Zealand
L L Fagan, Landcare Research, Lincoln, New Zealand

Importance

The word canopy is derived from the Latin *conopeum*, describing a mosquito net over a bed. For canopy researchers in many tropical and temperate forests, this derivation is all too fitting. Forest canopies are home to perhaps 50% of all living organisms, many of which are uniquely specialized for life in the treetops and seldom, if ever, venture to the ground below. The canopy is the photosynthetic powerhouse of forest productivity which fuels this spectacular diversity of species. Over 90% of photosynthesis occurs in just the upper 20% of tree crowns. Here, over 60% of the total organic carbon in forests is fixed and stored, forming an important buffer in the global carbon cycle. Other ecophysiological processes within tree crowns mediate the flow of nutrients through soil, regulate nutrient cycling processes that affect site productivity and the biomass distributions of plants and animals, as well as moderate the rates of transpiration and CO_2 exchange to the atmosphere that are crucial components of regional climatic circulation. In a very real sense, forest canopies form the substrate, the buffer, and the catalyst for interactions between the soil and the atmosphere. In this article, we highlight many aspects of forest ecosystem dynamics that are controlled directly by canopy processes. More importantly, however, detailed understanding of the structural and functional complexities of forest canopies has advantages beyond the scale of ecosystem functioning of local forest stands. Forest canopy dynamics are now incorporated as vital variables when modeling forest responses to the three most pressing issues in global change biology: the maintenance of biodiversity, the sustainability of forest production, and the stability of global climate.

Definition

For much of the early development of canopy biology, the nature and limits of forest canopies have been poorly defined. In a functional sense, the forest canopy includes all aboveground plant structures and the interstitial spaces between them, which collectively form the interface between the soil and the atmosphere. Historically, there was a tendency to use more subjective definitions of the canopy that only included arbitrary portions of the upper foliage of the tallest trees. In practice, however, it has always proven difficult to objectively define vertical substrata within forests, from either a structural or functional point of view. There is now clear recognition that most forest processes vary continuously from the soil to the atmosphere and there is little utility in considering the canopy out of context from forest dynamics as a whole. After all, tree crown physiology, resource allocation, growth and reproductive fitness are all critically dependent on belowground conditions experienced by tree roots, as much as they are on aboveground processes.

Discovery and Exploration

More than 85 years ago the naturalist and explorer William Beebe wrote that

> another continent of life remains to be discovered, not upon the earth, but one to two hundred feet above it.

It would be another decade before the first intrepid biologists ventured into the tropical forest canopy in Guyana, South America, using rudimentary line-throwing catapults and local Indian tribesmen as climbers. Scientific exploration did not really begin in earnest until the 1960s with a proliferation of simple observation towers built in various parts of the world, including the Democratic Republic of Congo, Malaysia, Panama, and Uganda, site of the famous Haddow Tower. Overwhelming numbers of new species, mostly insects, have since been discovered and critical observations made on the behavior and life history of rare birds, reptiles, amphibians, and mammals in their natural habitats. However, these descriptive accounts of canopy life amounted to no more than a drop in the ocean compared to the vast expanses of unexplored forest canopies in the world. Rigorous, comparative studies of canopy communities were set back for years by the logistical difficulties of conducting treetop investigations.

The scope and extent of canopy studies expanded greatly through the late 1970s and early 1980s, with a number of research groups working largely independently of each other. Without a doubt, this period of canopy science was more tool-driven (developing new techniques) than question-driven (developing new scientific hypotheses). As a result, even after intensive forest canopy studies became commonplace in the late 1980s, the wider scientific community still viewed the emerging discipline with mild disdain – a poorer anecdotal or descriptive cousin of terrestrial biology. Today, major new developments in canopy access systems, and a changing mind-set among canopy researchers, have all but allayed these criticisms. Forest canopy studies, today, address all manner of hypotheses using rigorous, replicated experimental designs that are the equal of any scientific investigation. Liberated from the constraints of three-dimensional movement within canopies, scientists are finally appreciating that answers to many of their questions about forest ecology and the interactions between the atmosphere and the soil can only be found by incorporating within-canopy processes. Once called the last great biotic frontier, forest canopies are now better understood than ever before and better appreciated and valued for the critical roles they play in forest ecosystem dynamics.

Modern Canopy Access Systems

Advances in canopy access systems have allowed canopy biologists to address an increasing diversity and complexity of issues. The advantages and limitations of each method for addressing differing ecological questions are outlined in **Table 1**.

Methods of Access

Ground-based methods It is not always necessary to climb into the forest canopy to complete a canopy study. For example, taking advantage of a ridge-top, hill, or bridge may provide a direct view into adjacent tree crowns. Technology such as radio-telemetry, hemispherical photography, telephoto lenses, and binoculars allow similar visual access to the canopy from the ground below. Most often, however, researchers want to collect samples or specimens from the canopy as well. One of the earliest methods for ground-based observers to retrieve samples from the canopy was the use of trained monkeys tethered to ropes. This method works extremely well for intensive botanical inventories of large areas over short periods of time. Other widely used methods for collecting plants include bending branches down, using a net or pole-pruner and ‘harvesting’ foliage with a shotgun or rifle. Canopy arthropods are frequently captured from the ground using insecticidal knockdown (canopy fogging or canopy misting), light traps, and a variety of baited interception traps. Canopy birds and bats are sampled using modified mist-net systems.

Ground-based methods are popular because of their ease of sampling targeted organisms, but the scope of such studies is limited because they do not incorporate *in situ* sampling in the canopy. Disregarding *in situ* canopy sampling can lead to biased results and hinder attempts to answer larger-scale questions in forest ecology. Some of the methods

Table 1 Modern canopy access systems and criteria for the selection of an appropriate method

Method of access	*Biology of organism*			*Spatial access*			*Replication and randomization*	*Long-term monitoring*	*Impact on ecosystem*	*Logistical constraints*				*Research applications*
	Sessile	*2-D mobility*	*3-D mobility*	*Horizontal extent*	*Vertical extent*	*Access to canopy–atmosphere interface*				*Cost*	*Ease of use*	*Major constraints*	*Major advantages*	
Ground-based methods														
Trained animals	X			Wide	Excellent	Not usually	Good replication and randomization	Difficult	Negligible	Moderate	Easy; one person	Locating and training	Rapid, high replication	Botanical surveys; plant phenology
Mechanical extension samplers (e.g., shotgun, nets)	X	X		Narrow	Narrow	No; unless SRT employed	Moderately good	Yes	Low–moderate; branch and foliage damage	Low	Easy; one person	Permits; skill; reach	Large sample area; flexible	Plant–insect interactions; leaf chemistry; vegetation dynamics
Intercept traps, mist-nets		X	X	Narrow	Wide	Not usually; can be attached to towers or poles above canopy	Good	Yes	Low; rope burn on branches	Low–moderate	Easy; one person	Activity-based	Standardized; quantitative	Arthropod, bird, and bat surveys; quantitative monitoring
Insecticide knockdown			X	Narrow	Moderate–wide	No	Low replication; good randomization	No	High; kills most arthropods	Moderate	Moderate; two people	Selective sampling difficult; wind	Comparative studies; surveys of large areas	Taxonomy; arthropod diversity; community composition
Climbing and mechanical methods														
Single rope technique (SRT)	X	X		Excellent; restricted to adjacent trees at each site though	Very good	Not usually; addition of mechanical extension samplers increases access	High level of replication and repeatability; limited full randomization	Difficult	Low; rope burn; snaps branches; damages epiphytes	Low–moderate	Easy; one person; stamina required	Branch availability; restricted reach; mobility	Flexible; lightweight; portable; versatile	Varied, e.g., phenology; canopy–soil interactions; arthropod community composition; herbivory
Ladders, booms, cherry-pickers	X	X		Moderate–very good	Moderate	Not usually; depends on canopy height	Moderate–good	No	Moderate; nails; vehicle access	Moderate–high	Easy; one or two people	Limited to sites near roads or on large trees	Stable platform; good horizontal reach	Herbivory; pollination; ecophysiology; vegetation dynamics

Towers and cranes														
Meteorological towers	X			Narrow	Excellent	Yes	Poor	Yes	Site construction	High	Difficult to build; easy use	Limited replication	Stable platform for instruments	Ecophysiology; photosynthesis; gas exchange; hydrology; canopy architecture; phenology; vertical stratification
Canopy crane	X	X		Moderate	Excellent	Yes	Low	Yes	Site construction; noise	High–very high	Difficult to build; easy use	Limited to fixed site; crane driver required	Long-term collaborative studies; stable platform	Varied, e.g., phenology; plant–insect interactions; vegetation dynamics; epiphyte communities; canopy architecture
Walkways, platforms, and cable cars														
Walkways, platforms	X		X	Narrow–moderate	Narrow–moderate	No	Moderate	Yes	Initial construction	Moderate–very high	Difficult to build; easy use	Limited to fixed site	Comfortable; useful for large groups; stable	Vertebrate behavior; monitoring forest dynamics
Cable cars, trams, ski lifts	X		X	Wide	Narrow; upper canopy	Yes	Moderate	Yes	Site construction; noise	High–very high	Difficult to build; easy use	Limited to fixed site	Long horizontal transects	Animal diversity; vertebrate behavior; seasonality
Balloons and rafts														
Canopy raft and sled	X	X	X	Excellent	Moderate–wide	Yes	Limited	No	Crushes foliage and branches	Very high	Moderate; climbing skills	Limited time at one site; wind	Stable platform above canopy	Varied, e.g., herbivory; arthropod community structure
Remote sensing														
Satellite data	X			Excellent	Narrow	Yes	Excellent	Yes	No	Very high	Access to data difficult	Available technology; computer processing	Landscape-level data	Landscape-level analyses of canopy architecture, leaf chemistry, productivity

mentioned above can be modified to collect samples directly in the canopy using line and pulley systems.

Climbing techniques and mechanical methods Brazilian Indians traditionally climbed tree trunks up to 40 cm in diameter using a loop of woven vines or cloth called a 'peconha', but this method is dangerous and cannot be used on trees of a larger diameter. Safety is a high priority for canopy biologists and modern climbing techniques incorporate rigorous safety measures. There are two climbing methods in practice today. The single rope technique (SRT) uses a relatively long (up to two times canopy height) fixed static rope, anchored to the ground at one end and climbed from the other end using mechanical 'jumar' ascendors. Alternatively, the arborist method involves the climber using a relatively short (e.g., 15 m) movable rope (lanyard pulley system) and is useful for climbing very tall trees or trees with few branches, and for transferring between adjacent trees within the canopy. Together, the two methods give almost total access to the canopy, including the outer foliage.

Arborist methods and SRT are often used to set up rigging lines in the canopy which enable a variety of instrumentation and collecting equipment to be hauled up and down from the ground. Line insertion techniques vary widely depending on the tools available. For example, ropes can be thrown by hand using throw bags, hand catapults, pole catapults, line-throwing guns, crossbows, or longbows (the best option for high canopies). Ropes, together with flexible ladders lashed to the tree, can allow rapid, repeated access into the canopy. Horizontal reach can be extended by using telescoping booms, consisting of lengths of aluminum piping that slide into one another, a steel cable, bosun's chair and manual lifting gear.

A more mechanized, but still highly mobile, access technique is the use of a hydraulic cherry-picker. Of course, roads are generally required in order to drive the cherry-picker to study sites, and trees along the forest edge tend to be the only ones accessible by this method. Booms and cherry-pickers provide stable working platforms and increased access to the outer foliage than climbing methods.

Towers and cranes Towers were first utilized to study vertical gradients in solar radiation, temperature, humidity, and wind speed in the late 1960s. Towers are costly to erect, but permit a range of investigations not possible from the ground. Towers can also be combined with horizontal access systems. The planned Canopy Operation Permanent Access System (COPAS) in French Guiana has multiple towers and a connecting cable system which will give access to 1.5 ha of forest canopy and will likely provide more detailed information than a single tower alone.

Canopy cranes provide even greater vertical and horizontal access than COPAS. The use of large construction cranes in forest canopies was pioneered in Panama at the Smithsonian Tropical Research Institute. Cranes provide permanent access to a finite number of trees, limited only by the length of the crane arm. Researchers are housed inside a gondola and maneuvered to specific sites within the canopy by ascending above the canopy and then descending back down into it. There are now 11 canopy cranes in place worldwide and an expanded network of cranes is planned as part of the Global Canopy Programme initiative.

Aerial walkways, platforms, and cable cars Aerial walkways and platforms have been used extensively to allow long-term observation within the canopy. They offer a good place to observe, educate, and study in large groups for long periods of time and they can become an integral part of the landscape, allowing researchers to study animal behavior or collect samples on a regular basis. Trams (or cable cars) supported by steel towers have also been suspended in or above the treetops in many parts of the world.

Balloons and rafts The canopy sky raft ('radeau des cimes') and sled were developed by Francis Hallé of Operation Canopéé in France. The large, inflatable raft is lowered onto the forest canopy surface by a dirigible balloon and is supported by several large canopy trees. The raft only remains in place for a few days or weeks to avoid permanent damage to trees or the risk of slipping. The sled is towed underneath the dirigible and can be flown just above the top of the canopy to sample many different tree crowns over a short period of time. Both the sled and raft have stable internal platforms from which to suspend climbing ropes, thereby increasing the vertical range of sampling. Another method of balloon access is a one-man helium balloon tethered to cables across the forest canopy, giving access to the outer edges of the canopy.

Remote sensing Forest canopy structure can be measured remotely using a wide range of sensors fitted to weather balloons, planes, or satellites. Three broad classes of sensors are available: (1) optical, (2) laser, and (3) radar. Aerial photographs can be taken that measure the outlines of individual tree crowns and the spatial extent of canopy gaps. Canopy height can be estimated crudely using stereo-pairs of air-photos. Optical satellite data (such as the LandSat multispectral scanner) can be used to estimate structural properties of canopies much more accurately, and even some aspects of leaf physiology and chemistry, including photosynthesis, transpiration, nitrogen, lignin, and pigment concentrations in leaves. Laser devices, particularly light detection and ranging (LIDAR) instruments, precisely measure vertical height from the ground to the canopy (in forests with fairly open structure). For dense forests, radar images (e.g., synthetic aperture radar (SAR)) provide an excellent means for penetrating foliage and estimating canopy structure. Both LIDAR and SAR can approximate vegetational biomass from signal reflection and scatter. Combinations of these methods have proven useful in monitoring forest responses to environmental change, such as in the use of the Scanning LIDAR Imager of Canopies by Echo Recovery (SLICER) to validate SAR data in North American forest ecosystems.

Selecting an Appropriate Method

Simply getting into the forest canopy is often the easy part – choosing the most *appropriate* method of access and deciding how to collect data once you are there is much more difficult. It relies on a clear evaluation of the research objectives and the tools and skills available to implement them. There are six major considerations when selecting an appropriate canopy access system (**Table 1**).

1. Life history and biology of the organism. A recurrent problem in forest canopy studies is how to sample efficiently and adequately document the life history of canopy inhabitants. The appropriateness of sampling techniques and methods of access will depend on the species or canopy properties under study. Some ground-based methods and towers, for instance, may be well suited to studying sessile organisms or organisms with limited mobility that perceive branches as two-dimensional planes, but are not as good for highly mobile organisms.
2. Spatial extent. From a research perspective, the most crucial attributes of a climbing method are the volume and shape of the space that can be accessed. Towers limit canopy access to a vertical transect line at one location, whereas walkways and trams permit good horizontal access at one vertical height. Other methods, such as canopy cranes, provide much better access to a fixed volume of canopy space, but suffer from limited ability to relocate to a new sampling location, as can easily be done with SRT, cherry-pickers, or other techniques.
3. Replication and randomization. Spatial and temporal replication are key considerations for any canopy study. There is a clear trade-off between ease of repeated access to a single point (e.g., towers, platforms, and so on) and access to multiple replicate locations in space (e.g., SRT, canopy raft, sled, and so on). Because of safety considerations for all canopy access techniques, true three-dimensional randomization is rarely achieved.
4. Long-term monitoring, in particular, is largely restricted to permanent structures such as towers, walkways, and cranes because of the need to have fixed, stable access over long periods of time, without the risk of cumulative damaging effects on the canopies under study.
5. Impact on the ecosystem is increasingly important when selecting a canopy access system. The technique used to access the canopy should avoid any damage that may affect the variables being measured, or the health of the tree being climbed. Regular checks on permanent structures and branches that are climbed on a regular basis are essential.
6. Lastly, logistical constraints play a central role in determining which method of access to choose. However, problems caused by the physical environment, costs, or available time should not be allowed to dictate the level of replication, randomization, or spatial access appropriate to the research question being addressed.

Canopies as the Substrate, Buffer, and Catalyst for Forest Dynamics

Canopy Architecture

Canopies provide the dominant structural influence on the movement of organisms, the availability of habitat, and the interactions between species and their abiotic environment in forests. Although the importance of canopy structure is still not fully appreciated, there is a burgeoning interest in the quantitative measurement of canopy architecture – the sizes, shapes, angles, distribution, and development of tree crown elements, such as leaves, twigs, and branches, within a three-dimensional medium. The most comprehensive, qualitative system for describing the growth patterns of trees is the Hallé–Oldeman system. Architectural development of trees is viewed in terms of a genetically programmed model in which individual architectural units are reiterated throughout the growth and development of the tree (**Figure 1**). Architectural models differ in terms of the presence of vegetative branching, orientation of vegetative axes, continuous or rhythmic growth, and varying developmental patterns of terminal buds and sexual tissues. Although numerous combinations of these characteristics are theoretically possible, the growth forms of trees are remarkably restricted. It appears that only about 30 architectural models occur in plants. Even trees that are totally unrelated may share the same architectural models. The Hallé–Oldeman system provides an elegant conceptual model to unite the common features of plant growth form among species. However, variation in the expression of architectural units during development, or asymmetrical growth and damage, can cause large variation in the quantitative outcome of canopy morphology. No two trees are ever structurally identical. A more precise description of canopy structure would have to emphasize branch order, leaf arrangement, length and diameter, longevity, share in total photosynthetic activity, and reproductive output.

Most commonly, quantitative variation in canopy structure is measured using surrogate estimates of the vertical distribution of leaf area index (LAI, the ratio of the total one-sided leaf area to the projected ground surface area below, in $m^2 m^{-2}$) (**Figure 2**) or leaf area density (LAD, the mean one-sided leaf area per unit volume of canopy space, in $m^2 m^{-3}$). The utility of these measures is evident in the highly contentious issue of vertical stratification in forests. From simple observational studies, strong vertical layering of canopies was thought to be a characteristic of tropical forests, but in cases where LAI or LAD have actually been quantified, vertical stratification has been found to be indistinct or nonexistent. The problem remains, though, that a wide range of measures exists for quantifying canopy structure and each may give a different perspective on stratification. For example, silviculturists may focus on the distribution of tree heights, ecologists may focus on the distribution of tree species within the forest, and tree physiologists or atmospheric chemists may focus on the distribution of leaf surface area.

At least part of the difficulty in extrapolating forest function from forest structure is that different organisms and different abiotic variables respond to canopy architecture in differing ways. For example, LAI may be a good predictor of photosynthetic activity in the canopy, whereas leaf optical properties, leaf angles, and LAI may be required to understand light transmittance to the forest floor. Conversely, LAI may bear no relation to colonization and diversity of epiphytic plants within tree crowns, which are more dependent upon structural attributes of branches and twigs. More generally, some organisms ‘perceive’ the canopy as a true three-dimensional volume, whereas others may perceive the canopy as a set of highly convoluted, two-dimensional surfaces. For example, mites and other wingless arthropods may view canopies, for all intents and purposes, as flat surfaces, because dispersal through air is highly limited. Other organisms, such as birds or bats, clearly view the canopy as a volume. This can have important functional implications for the effect of canopy structure on the distribution and abundance of organisms (or nutrients or chemicals, for that matter). Recognition of this difference has led to some astounding developments in the quantification of canopy structure. Recent studies have reversed the

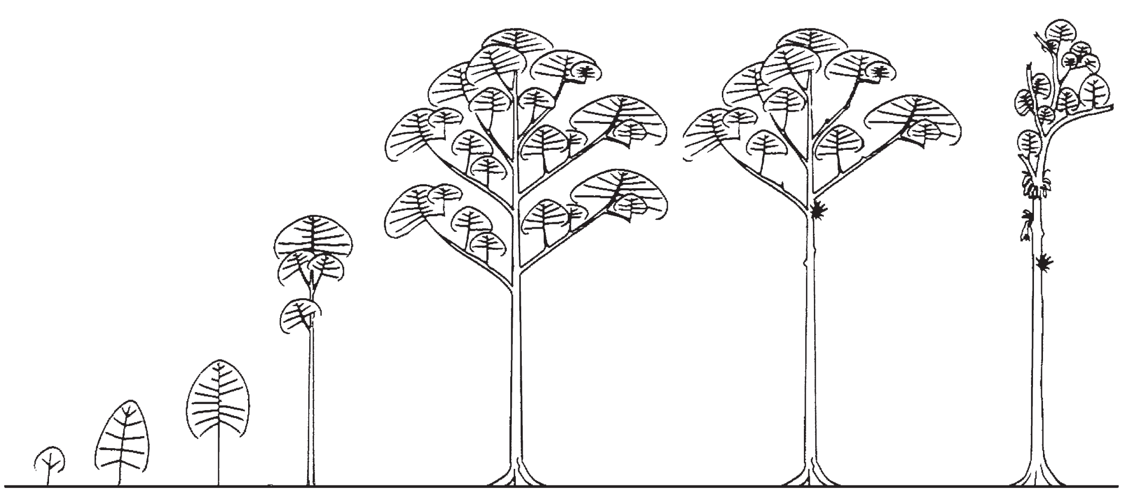


Figure 1 Schematic representation of the reiteration of architectural units during growth and development of a tropical tree. Although there are relatively few ‘ground-plans’ for crown architecture among species, every individual tree exhibits unique canopy structure due to asymmetrical growth and damage.

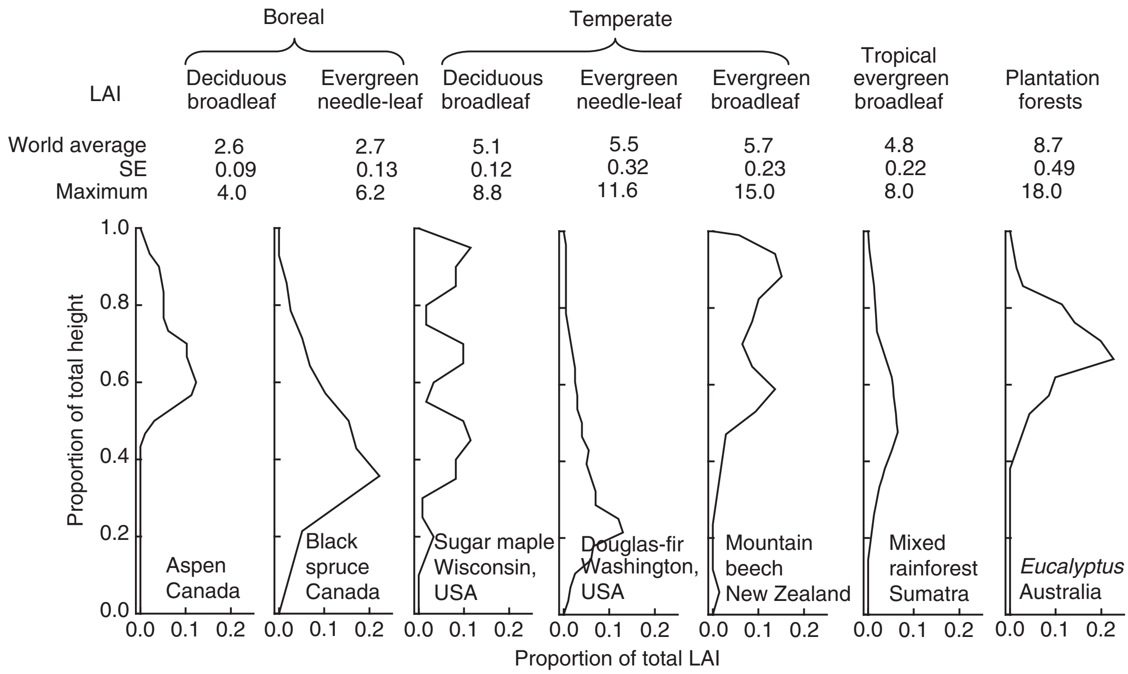


Figure 2 Summary of leaf area index (LAI) for major forest types of the world, showing the global average (in $m^2 m^{-2}$), standard error of the mean of multiple studies (SE) and maximum recorded value for each forest type. One example of vertical variation in canopy architecture is presented for each forest type. Aspen forest, Canada: canopy height (H_{max}) = 30 m, total LAI = 2.02. Black spruce forest, Canada: H_{max} = 14 m, LAI = 2.35. Sugar maple forest, Wisconsin, USA: H_{max} = 16 m, LAI = 6.10. Douglas-fir/western hemlock forest, Washington, USA: H_{max} = 56 m, LAI = 6.28. Mountain beech forest, New Zealand: H_{max} = 17 m, LAI = 6.95. Mixed broadleaf tropical rainforest, central Sumatra: H_{max} = 42 m, LAI = 7.50. *Eucalyptus nitens* plantation forest, Tasmania, Australia: H_{max} = 21 m, LAI = 7.00.

emphasis on quantitative structural elements in the canopy and measured the vertical distribution of empty space (gap size and frequency) in forests. Measurements produce a characteristic S-shaped distribution of open space with increasing height from the ground to the atmosphere above the forest.

Opportunities to integrate differing perspectives on canopy structure are expanding with the advent of remote sensing tools to more rapidly and accurately measure forest structure across large areas, and sophisticated computer software that can manipulate complex three-dimensional spatial models. The recent development of the Vertical Canopy LIDAR (VCL) has created new opportunities to remotely characterize the three-dimensional structure of the earth's surface by satellite and measure the vertical and horizontal distributions of plant structures across vast swathes of the planet. The VCL uses near-infrared wavelength laser pulses fired at regular intervals at the earth's surface. The time displacement of the reflected laser signal to the VCL determines the height above ground, with an incredible 30 cm vertical resolution, while the magnitude of signal scatter determines the absolute volume of canopy biomass intercepted by the laser. Already the VCL has produced revolutionary new views of forest canopies that would have taken several lifetimes of ground-based measurements to compile.

The measurement of canopy architecture has direct applications in a wide range of disciplines. For example, variation in forest canopy structure exerts strong regulation of radiation transfer to the ground surface, altering the extent of snow cover in forested regions of the boreal zone. Canopy removal by clear-cut harvesting slows snowmelt and markedly alters local climate compared to regions with intact canopy structure. In coniferous forests in Chile, forest canopy structure is also an important determinant of precipitation infiltration into soils, with dense canopies decreasing erosion and increasing the return time for landslide-forming events by over 20%. In other fields, quantitative models of three-dimensional canopy structures are being utilized to predict (and optimize) the dispersal pattern of pheromones released in forests to control insect pests, and drag coefficients and turbulence around canopy elements are being utilized to parameterize within-canopy atmospheric exchange models. The structural detail now being provided by high-resolution VCL remote sensing of forest canopies promises a revolution in our understanding of the relationships between (1) canopy architecture and habitat for plants and animals, (2) architecture and ecosystem functioning, and (3) architecture and carbon, water, and energy exchange.

Aboveground–Belowground Dynamics

Aboveground and belowground ecosystem processes are integrally linked by material transport between roots and crowns of individual plants and the plasticity of resource allocation among components of foliage, reproductive structures, branches, stems, defensive chemicals, roots, mycorrhizae, and root exudates. Although a full understanding of resource allocation in plants is limited by difficulties in measuring belowground processes, there is growing awareness that soil and root dynamics are critically dependent on forest canopy dynamics. Tree roots represent a major pool of stored nutrients and contribute a significant amount to total soil surface respiration in forests. For example, studies in pine forest in Oregon, USA, have shown that 18% of annual ecosystem respiration typically originates from foliage, 6% from woody debris and the remaining 76% from soil, with root respiration accounting for a massive 53% of total soil respiration. Most early studies concluded that root growth and respiration were limited by abiotic factors such as soil water content or soil temperatures, leading to concern over the effect of global warming on carbon balance within soils and possible atmospheric CO_2 emissions. However, new data suggest that root production is regulated instead by concurrent radiation interception and photosynthetic production in the canopy. Photosynthetic products are transferred below ground much more rapidly than ever previously imagined. In a remarkable experimental test of the importance of current photosynthesis to belowground respiration, researchers in northern Sweden girdled (stripped the bark from) mature pine trees over a large area to inhibit carbon allocation to the roots. Inhibition of root respiration virtually eliminated mycorrhizal fungi and reduced overall soil surface respiration by 54%, in striking concordance with findings on the importance of root respiration in Oregon.

Forest canopies also affect belowground processes by storing nutrients in foliage and regulating the input of available carbon, nitrogen, and other elements to the soil through litter fall. Despite the long-standing belief that nutrient availability in forests depends on species-specific characteristics of the chemistry and decay rates of litter on the ground, recent studies show that soil nutrient cycling is better predicted simply by the total mass of litter produced from the canopy and total nutrient content of leaves. Given that 90% of net primary productivity is channeled directly into the detrital pathway (largely via litter fall), belowground nutrient recycling, site fertility, and soil surface respiration are primarily regulated by within-canopy processes that affect foliar litter production.

Much of forest ecosystem research and global change biology is focused on understanding net ecosystem productivity – the balance between photosynthesis and ecosystem respiration – and it appears that canopy processes are not only the critical drivers of photosynthetic production in forests, but they are also important catalysts for soil surface respiration rates.

The Canopy–Atmosphere Interface

Forest canopies form an important buffer between the soil and the atmosphere, regulating the exchange of carbon, water, and energy that affects atmospheric chemistry. Forest canopies interact with the atmosphere in two important ways. First, through structural interference of airflow that creates turbulence. Second, through the interception of solar radiation and exchange of CO_2 and water vapor during photosynthesis, respiration, and transpiration.

Boundary-layer dynamics around leaves and branches are crucial to understanding atmospheric processes. This is not surprising when a single tree crown spanning just 20 m across can have 10 000 m^2 of foliage surface area. As a result, canopy leaves can filter 20–30% of bulk precipitation and intercept and concentrate even greater amounts of airborne nutrients and pollutants from the atmosphere. Lowered air velocity around canopy elements partially isolates the upper canopy from airflow in the surrounding understorey and atmosphere, creating a zone of contrasting internal dynamics. This buffering effect is explicitly recognized in the measurement of atmospheric gas exchange. Partitioning net ecosystem CO_2 exchange (NEE) between the soil, canopy, and atmosphere is a major objective for scientists studying gas exchange using the eddy covariance technique (measurement of the turbulent fluctuations of vertical air movement in conjunction with temperature, water vapor, CO_2, and other gases, calculating flux rates as the covariance of wind and one of the other variables). This has been achieved in a number of ways, including simple comparisons of below-canopy and above-canopy eddy systems, or the compartmentalized measurement of gas exchange from individual ecosystem components, such as soil, roots, wood, and foliage, using experimental chamber techniques. Results from chamber measurements are then scaled up to the ecosystem level to calculate NEE from days to several years. Another method to partition and integrate the role of forest canopies in NEE at the ecosystem level is to analyze the stable isotope ratios of carbon and oxygen in CO_2, as these vary according to the source of CO_2 exchange from different ecosystem compartments (for example, autotrophic versus heterotrophic respiration). However, canopy structure can influence the composition of stable isotopes in belowground and above-canopy compartments by modifying radiation interception and photosynthetic activity of ground vegetation, and by reducing turbulent upwelling of air from the ground and thus inhibiting the mixing of respired CO_2 from the soil. These processes make modeling and prediction of NEE heavily dependent on measurement of the characteristics of canopy structure and an understanding of within-canopy dynamics.

The Functional Importance of Forest Canopies in Global Change

Globally, forests cover over 25% of the land surface and store almost 50% of terrestrial carbon. Conversion and management of forests are altering global stability on three central fronts: (1) the ability of forest ecosystems to support a large proportion of global biodiversity, (2) the global sustainability of fiber production from forests and the maintenance of site productivity, and (3) the stability of global carbon balance, atmospheric chemistry, and atmospheric circulation patterns. Forest canopy processes are central to understanding the importance of forests in all three aspects of global change (**Figure 3**).

Maintenance of Biodiversity

Individual tree crowns often harbor rich microcosms of epiphytic life, complete with fully functioning aerial soil communities and complex food web dynamics analogous to the more extensive soil communities below ground. Over 10% of all vascular plants in the world are canopy epiphytes, often with a restricted resident fauna of vertebrates and invertebrates associated with them. The

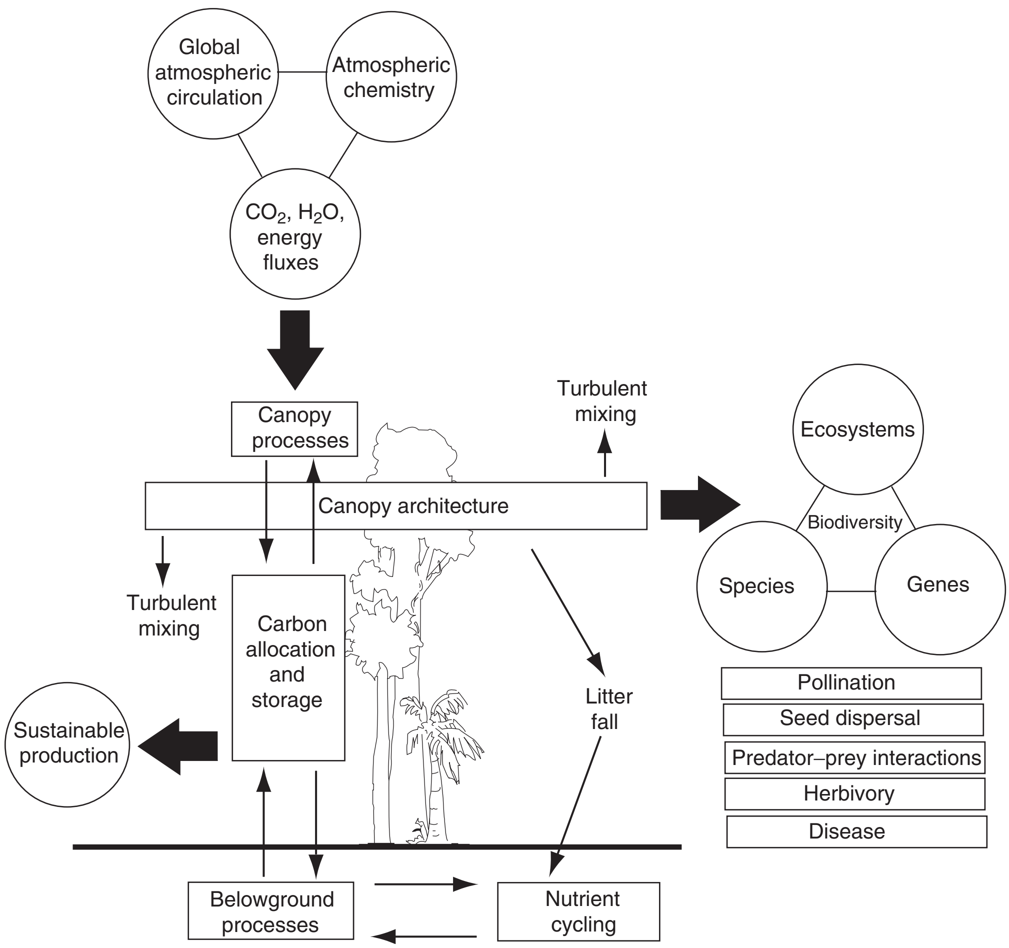


Figure 3 Conceptual diagram showing the key roles of forest canopies as the substrate, buffer, and catalyst for forest dynamics. The structural and functional attributes of forest canopies are central to the maintenance of global biodiversity, the sustainability of forest production, and the stability of global climate.

importance of canopy epiphyte communities is not trivial in terms of forest dynamics. Epiphyte biomass in some wet tropical forests is four times greater than that of host tree foliage, stored nutrients within epiphyte leaves may represent 50% of total canopy foliar nutrients, and dead leaves decay almost twice as fast in canopy soils than in ground soils. Incredibly, canopy soil biomass can be equivalent to the total biomass and available nutrient pools of terrestrial leaf litter in many forests. As a consequence, canopy epiphyte communities can have a large effect on primary production and nutrient cycling rates in forests.

The surface area, biomass, and productivity of tree crowns and associated epiphytic plants provide a diverse range of niches that are exploited by canopy organisms. Notable, in terms of their diversity and contribution to total global biodiversity, are the arthropods of tropical forest canopies. Large numbers of undescribed species in forest canopies have spurred intense speculation on the magnitude of total global biodiversity, with estimates ranging as high as 30–80 million species. With the availability of better data on species turnover rates between geographic regions, host specificity, species coexistence, and coevolutionary relationships among animals and plants in tropical forests, estimates have been revised downwards to 3–5 million species. This still represents a threefold increase in the total number of recognized species in the world – most of them thought to be in the canopies of tropical forests. However, there has been no rigorous assessment of whether a large proportion (42–66%) or a relatively small proportion (10–20%) of forest species are canopy specialists. It may well be that many forest canopy species utilize belowground habitats, or nonforest ecosystems, during larval life history stages of which we are not yet aware.

Nevertheless, it is the overwhelming superabundance and diversity of canopy organisms that perhaps best exemplifies the structural complexities of forest canopies, and is a cause for concern in the face of habitat modification. Variation in canopy architecture, changes in resource availability, and an increase in microclimatic extremes due to changing land use management all influence biodiversity in forest canopies. It is precisely the accelerating rates of forest loss and conversion since the 1950s, combined with recognition of the magnitude of forest canopy diversity in the 1980s, which have prompted fears of an extinction crisis. If even 10% of species in the world are solely restricted to forest canopies, and a further 50% of all forest species depend critically on the canopy for some aspect of their resource requirements, then preservation of intact forest canopy structure and function is clearly key to the long-term maintenance of global biodiversity.

Sustainability of Forest Production

Management of forests for fiber production uses conventional empirical, or statistical, approaches to estimating growth and yield based on accumulated experience of site quality, stand structure, or tree species traits in the area being harvested. However, the future of sustainable forest production lies in the application of process-based models for ecosystem management – models that define the actual mechanisms of net photosynthate assimilation, carbon allocation, and storage in aboveground structures, tree respiration, and long-term stand viability that is affected by processes such as nutrient recycling and maintenance of predator–prey interactions, pollination, and seed dispersal services. Forest canopies play a central role in all of these ecological and physiological processes and in the maintenance of ecosystem services in forests.

Process-based models have only recently begun to be implemented at an operational level in forest management. Not surprisingly, the initial focus has been on improving predictions of growth rates and enhancing total yield at the stand level. Several carbon balance models have been developed for this purpose, which treat the acquisition and distribution of photosynthetic products as central to understanding forest production. Gross primary productivity in this sense is driven almost entirely by canopy processes. Canopy architecture also affects the distribution of organisms and flux of abiotic variables that influence tree respiration. The dynamic balance between these effects of the canopy on assimilation and respiration of carbon determine the total amount and distribution of new growth. For example, Norway spruce trees with narrower geometrical crown shapes have a higher LAI, greater stemwood production per unit crown area and higher harvest index due to greater allocation of carbon to stems, rather than roots or foliage. This variation in allocation is determined both genetically and environmentally, but a radical new perspective on the importance of canopy architecture to forest production is that trees could be more intensively selected and 'domesticated' for improved carbon allocation performance. It should be recognized, however, that predictions of overall stand performance must incorporate not only the net carbon balance of individual trees, but also aboveground and belowground competition for resources between trees (whether of the same or different species) and the dynamics of stand structure in response to biotic and abiotic disturbances. For example, herbivory directly affects the amount of leaf material available for photosynthesis, carbon allocation to defensive chemicals, new foliage growth and stem increment, and ultimately forest production.

Other tree physiological processes, such as water balance or nutrient cycling, have received considerably less attention than carbon balance, but are nonetheless critical to forest production. For example, tree canopies on more fertile sites produce greater leaf biomass, which increases foliar litter inputs to the soil, reinforcing differences in site fertility, nutrient availability to roots and overall soil heterogeneity. This can be exacerbated in harvesting situations because forest removal eliminates the buffering influence of the forest canopy on soil microclimate and removes litter inputs. Without foliar litter inputs, it is thought that microbes become carbon-limited (instead of nitrogen-limited), leading to reduced assimilation rates of nitrates and contributing to a pulse of nitrogen availability in clearcut areas. This change in nutrient cycling even occurs in small gaps of just a few trees and in natural windfall gaps, but not following single-tree removals in which canopy cover is not greatly compromised.

Beyond physiological models of growth and yield, production can be limited by biological factors that limit growth (such as herbivory), increase mortality (such as disease), and reduce seed or seedling establishment (such as pollination limitation or seed predation). Many animals that live in forest canopies play important functional roles in the provision of ecosystem services, like pollination and predation, in forests. Maintenance of intact structure and functioning of forest canopies is likely to facilitate preservation of species that may have beneficial roles in the sustainability of future forest production. These roles may be as simple as pollinating flowers that ensure a continued seed supply for reforestation, or as important as dampening the oscillatory dynamics of pest insect populations.

Stability of Global Climate

Forest canopies account for at least 50% of global CO_2 exchange between terrestrial ecosystems and the atmosphere, as well as a significant proportion of global net primary productivity. Compelling evidence suggests that tropical forest canopies may be net carbon sinks, mitigating the rate of increase in atmospheric CO_2 concentration from anthropogenic sources. Increased deforestation and burning threatens to alter this balance by directly liberating vast amounts of carbon (and other elements) into the atmosphere, and indirectly limiting the net assimilation rate of carbon by disturbance to the remaining forest canopies. Synergistic interactions between deforestation, increased fire frequency, and drought in the Amazon Basin, the world's largest remaining expanse of tropical forest, are enhancing a positive feedback cycle in altered climatic circulation patterns and increased forest degradation. Experimental exclusion of rainfall from large areas of undisturbed tropical forest in eastern Amazonia has simulated the effects of increasing drought. A 40% reduction in precipitation throughfall to the soil significantly reduced tree growth and reproductive output, lowered net primary productivity and increased leaf loss and tree mortality, all of which resulted in the forest becoming a net source of CO_2 to the atmosphere rather than a net sink. Correlated drought and tree mortality effects have been detected at distances of up to 2–3 km inside 'intact' nature reserves, leading to concern over receding edges and the long-term viability of fragmented forest remnants. Because of the magnitude of change in disturbance regimes and climatic conditions in the wet tropics, vegetation dynamics in some areas are shifting away from high-diversity rainforest to low-diversity, fire-adapted sclerophyll vegetation.

The study of ecophysiological processes in forest canopies is not only critical for predicting forest responses to global change, but also for modeling how canopy structure and functioning mitigates future atmospheric CO_2 increase and climate change. Through diverse roles in carbon, water, and energy cycling, structural integrity of forest communities, nutrient cycling dynamics, and maintenance of forest productivity and biodiversity, forest canopies will shape the direction and magnitude of global change that human populations experience over the next millennium. We can either use this knowledge to advantage in conserving forests, or face a more extreme and more uncertain future.

See also: **Biodiversity**: Biodiversity in Forests. **Environment**: Carbon Cycle. **Hydrology**: Hydrological Cycle; Impacts of Forest Plantations on Streamflow. **Soil Development and Properties**: Nutrient Cycling. **Tree Physiology**: Canopy Processes; Forests, Tree Physiology and Climate; Shoot Growth and Canopy Development.

Further Reading

Basset Y, Novotny V, Miller SE, and Kitching RL (eds) (2003) *Arthropods of Tropical Forests: spatio-temporal dynamics and resource use in the canopy.* Cambridge, UK: Cambridge University Press.

Benzing DH (1990) *Vascular Epiphytes: General Biology and Related Biota*. Cambridge, UK: Cambridge University Press.

Carroll GL (1990) Forest canopies: complex and independent subsystems. In: Waring RH (ed.) *Forests: Fresh Perspectives from Ecosystem Analysis*, pp. 87–107. Corvallis, OR: Oregon State University Press.

Linsenmair KE, Davis JJ, Fiala B, Speight MR, and Davis AJ (eds) (2001) *Tropical Forest Canopies: Ecology and Management*, Proceedings of the European Science Foundation Conference, 12–16 December 1998, Oxford, UK.

Lowman MD and Nadkarni NM (eds) (1995) *Forest Canopies*. San Diego, CA: Academic Press.

Lowman MD and Wittman PK (1996) Forest canopies: methods, hypotheses, and future directions. *Annual Review of Ecology and Systematics* 27: 55–81.

Mitchell AW (1986) *The Enchanted Canopy: Secrets from the Rainforest Roof*. London: Collins.

Mitchell AW, Secoy K, and Jackson T (eds) (2002) *The Global Canopy Handbook: techniques of access and study in the forest roof*. Oxford, UK: Global Canopy Programme.

Moffett MW (1993) *The High Frontier: Exploring the Tropical Rainforest Canopy.* Cambridge, MA: Harvard University Press.

Perry DR (1986) *Life Above the Jungle Floor.* New York: Simon & Schuster.

Prescott CE (2002) The influence of the forest canopy on nutrient cycling. *Tree Physiology* 22: 1193–1200.

Russell G, Marshall B, and Jarvis P (eds) (1989) *Plant Canopies: their growth, form and function*. Cambridge, UK: Cambridge University Press.

Ryan MG (2002) Canopy processes research. *Tree Physiology* 22: 1035–1043.

Stork NE, Adis J, and Didham RK (eds) (1997) *Canopy Arthropods*. London: Chapman & Hall.

Natural Disturbance in Forest Environments

D F R P Burslem, University of Aberdeen, Aberdeen, UK

Introduction

Disturbance in plant communities has been defined as consisting of ‘the mechanisms which limit the plant biomass by causing its partial or total destruction.’ In forests, disturbance arises from the agencies of tree damage or death. At small spatial scales, individual trees die standing or fall over, but in both cases a gap in the canopy is created and this initiates a successional process known as the forest growth cycle. The agencies of natural disturbance at larger spatial scales include windstorms, fire, and landslides and these factors vary in their impacts on forests and the ensuing mechanisms of forest recovery. Natural disturbance regimes in forests are important because they impact on tree population dynamics, the relative abundance of different species and functional groups, the biomass and carbon content of vegetation, and interactions with other components of the biotic community. Community ecologists have highlighted the importance of disturbance among mechanisms proposed for the maintenance of tree species richness, particularly in species-rich tropical forest communities.

Small-Scale Disturbance: Gap Phase Dynamics

Small-scale natural disturbances are an inherent component of all plant communities because plants have a finite lifespan. In forests, the size of the individual tree at the time of its death and the mode of death determine the scale of the disturbance created. The death of individual small understory trees and shrubs that live their entire life in the shade, and of the suppressed juveniles of canopy trees, may have limited impact on forest stand structure. However, the death of canopy-level or emergent trees has significant potential for localized modifications of canopy structure, resource availability, and microclimates. Some large trees die standing, perhaps following lightning strike or the synergistic effects of old age and wood decay fungi. Many trees lose large branches or parts of their crown long before the entire tree has died, and these events may lead to partial opening of the canopy and to some damage of surrounding smaller trees and other plants. However, the threshold for a natural disturbance event is usually regarded as the death of an individual large canopy or emergent tree, which results in the creation of a hole through all layers of the forest down to 2 m above the ground surface (a canopy gap). The size of a canopy gap varies according to the height of the tree that died, its architecture (height : canopy width), and its neighborhood. The fall of a large tree will inevitably lead to damage or death of surrounding trees, particularly if their crowns are connected by lianas. Thus canopy gaps arising from small-scale tree death can vary from a lower limit of 25–50 m^2 up to about 1000 m^2 for a large multiple tree-fall gap. Gaps can be further divided into zones influenced by the fallen crown (crown zone), the bole (bole zone), and the site where the fallen tree had been rooted (root zone). In addition, when trees fall over, particularly during severe windstorms, they frequently create an elevated mound of consolidated soil and roots known as a tip-up mound and an associated pit with exposed subsoil on its base and sides. Microclimatic conditions and availability of some resources for plant growth are known to vary between zones within a gap and on tip-up mounds. This variation within canopy gaps and between gaps of different size is thought to be one factor contributing to the maintenance of tree species richness in forests.

Changes in Microclimate and Resource Availability Following Gap Creation

Solar radiation reaching the forest floor increases following creation of a canopy gap because canopy leaves absorb a high proportion of radiation that falls within the range of wavelengths absorbed by photosynthetic pigments (440–770 nm) and reflect radiation of all wavelengths. Thus the proportion of total irradiance that reaches the forest floor increases from about 1% beneath a mature closed canopy site to 10–25% in the centers of large canopy gaps. Solar radiation is important because it affects directly other aspects of the aerial microclimate, it contributes to modifications to the belowground environment, and it impacts on plant growth and development in gaps both directly (via photosynthesis) and indirectly (for example via temperature-mediated effects).

Measurements have demonstrated that canopy gaps have higher mean and maximum air and ground surface temperatures, lower mean relative humidity, and greater wind speeds than sites beneath a closed forest canopy. This combination of conditions drives greater evaporation from exposed surface soils and thus a reduced water content at the top of the soil profile. Water availability lower down the soil profile, however, varies according to the density of live fine roots that survive gap creation, and can be either greater or no different to conditions beneath closed canopy forest.

After a tree dies its tissues decompose and contribute to fluxes of carbon and nutrients from plant biomass into microbial biomass and soil compartments. Leaves are the most readily decomposable aboveground plant tissues because they have the highest concentrations of nutrients and the lowest concentrations of lignin and fiber. Therefore the crown zone of canopy gaps receives the highest quantities of dead organic material and a transient increase in available nutrients in soil has been detected. Organic matter decomposition rates are enhanced by the relatively high temperatures in gaps, and the lower density of live roots in soil results in reduced competition for nutrients. Woody material decomposes much more slowly than leaves, particularly the bole and other material of large dimension. In tropical forests, termites and other components of the soil mesofauna initiate and hasten the process of wood decomposition, although it is common to observe large boles surviving semi-intact long after the gap created by the fall of the tree has closed over the fallen bole.

Forest Regeneration in Gaps

The changes in microclimate and resource availability that are induced by gap creation contribute to the mechanisms of forest regeneration, which describes the processes of recovery following disturbance. Regeneration proceeds via processes of both sexual and vegetative modes of reproduction. It is initiated by the germination of seeds, which either emerge from the buried soil seed bank or arrive in the gap after it has been created, or by the release of seedlings and saplings that were present at the time of gap creation (advanced regeneration). In addition, saplings and small trees of some species that are damaged during gap creation have the capacity to produce epicormic resprouts that grow rapidly in height and can contribute significantly to the regenerating tree community. Gap creation also stimulates enhanced growth of tree canopies surrounding the opening, which contributes to canopy closure and influences the development of vegetation growing up in the gap.

Some trees possess mechanisms that increase the likelihood that they germinate and grow rapidly in response to the environmental conditions that are stimulated by gap creation. Some of the species that adopt this strategy are termed 'pioneers' because they represent a distinctive functional group among all forest floras and share a suite of life-history characteristics that predisposes them to establish and grow in canopy gaps. Species of birch (*Betula* spp.) are characteristic pioneers of the cool temperate deciduous forests of Western Europe and North America, while *Cecropia* (neotropics), *Musanga* (tropical Africa), and *Macaranga* (tropical Southeast Asia) are the classic genera of pioneers in lowland tropical evergreen rainforests. All forest floras possess pioneer species, but their abundance and richness vary according to the characteristic disturbance regime manifested at a particular site.

Many (but not all) pioneer species possess seeds that are small and widely dispersed by animals or wind. Small seeds have few resources with which to grow a shoot and therefore cannot establish when deeply buried beneath soil or litter. For this reason, many species have evolved photoblastic germination, that is, they only germinate when the seeds are illuminated by light rich in wavelengths in the far-red range of the electromagnetic spectrum (centered on 720 nm) relative to wavelengths in the red light range (centered on 660 nm). Thus species with photoblastic germination are described as being responsive to the red to far-red ratio of light. The function of this response is to prevent germination when the seed is located in an inappropriate microsite for successful emergence (i.e., buried beneath a layer of soil or litter), or establishment (i.e., beneath a closed forest canopy).

Photoblastic germination in pioneers is concentrated among species with the smallest seeds (e.g., in neotropical pioneers, seeds with a fresh mass <1.5 mg). However, pioneer species with larger seeds have evolved alternative mechanisms to target germination in well-lit canopy gap sites, such as germination in response to an increased magnitude of diel temperature fluctuation. Surface soil temperature rises higher during the day in canopy gaps than beneath a closed forest canopy and at night falls either to the same or to a lower minimum value because of enhanced radiative cooling. Thus the magnitude of diel temperature fluctuation is an index of canopy gap size and a number of species have been shown to germinate poorly in the absence of a fluctuating temperature regime. One example from semideciduous tropical forest in Panama is provided by balsa (*Ochroma pyramidale*).

Germination in gaps is important for pioneer tree species because they lack an ability to survive and grow in the shaded conditions of the forest understory. For example, their photosynthetic physiology is adapted to rapid carbon assimilation at high light rather than persistence for long periods in the shade. To achieve this, they produce short-lived leaves containing high concentrations of nitrogen (required for the enzymes involved in photosynthesis) that tend to be poorly defended against herbivores and pathogens. In addition, the high respiration rates required to maintain the enzymatic machinery involved in photosynthesis and carbon assimilation precludes long-term survival of pioneers in the shade.

The trade-off between survival in shade and growth response at high light is resolved in different ways by different tree species, so that a continuum of response to heterogeneity in light conditions will exist among any group of coexisting species. This shade-tolerance continuum has important consequences for the changes in community structure that occur during tree regeneration in gaps. As described above, pioneer species are well represented among the community of seedlings that establish early following gap creation, particularly in large gaps or the centers of small gaps. However, over time species with more shade-tolerant seedlings will become established beneath the developing canopy of the early-colonizing pioneers. The shade-tolerant species grow more slowly in height than the pioneers, but they survive for longer. Therefore as the cohort of pioneers matures and dies their canopies begin to receive more light and their growth rates increase. Ultimately, the saplings and pole-sized trees of these attain dominance in the gap, and the forest growth cycle is said to be in the 'building phase.' The cycle is closed by the growth of poles to canopy trees and the recreation of forest understory light and microclimatic conditions in the former gap site.

Importance of Chance Effects

The description of forest regeneration provided above implies that the changes that take place after small-scale disturbance are entirely deterministic, such that disturbances of a similar scale in sites sharing the same species pool would proceed through a predictable sequence to an end point that is identical in terms of species composition and structure to its status prior to the death of the original canopy tree. However, it must be recognized that this description is an oversimplified caricature of many highly complex processes that collectively reduce the predictability of forest regeneration pathways in a particular site. For example, it is highly unlikely that all species that have the ecological potential for regeneration in any particular site will actually get there, because of constraints on dispersal.

Forest Growth Cycle

The processes of tree death and regeneration described above are intrinsic to all natural forest communities. They provide examples of internal secondary successions that arise because of the uneven-aged structure of most natural forest communities. The heterogeneous nature of forest composition and history creates a mosaic of patches at different stages in the forest growth cycle. Experienced foresters and ecologists have attempted to map the distribution of patches at different stages using species composition and forest structure as indicators of patch status, although these efforts are inherently limited by the low degree of spatial coverage relative to inherent spatial heterogeneity. However, in one well-replicated study of a semideciduous forest in Panama, approximately 0.1% of the ground surface area was covered by canopy gaps (defined as contiguous areas of at least 25 m^2 in which the height of the canopy is <5 m).

Large-Scale Disturbances

In addition to the small-scale internal dynamics inherent to all forests, most forests also show evidence of perturbation by agencies operating over larger spatial and temporal scales. These factors can be divided into those that destroy all vegetation and *in situ* sources of regeneration (such as landslides, volcanoes, and earthquakes), and those that do not (for example, windstorms, lightning strikes, drought, and fire). This distinction is important because loss or burial of seeds and stumps means that forest recovery can occur only via a primary succession. By contrast, those factors that leave components of the vegetation or a buried soil seed bank intact will undergo secondary succession and a more rapid recovery of structure and floristic composition. There is a third category of disturbance factor that arises from gradual processes occurring over longer timescales, such as climate change and plate tectonics. Although these processes might fall under some definitions of disturbance, their impacts extend over such long intervals that short-term effects on community biomass (as opposed to species composition) are likely to be minimal.

Disturbances that Result in Primary Succession

Landslides occur wherever steeply dissected terrain occurs in a wet climate. They occur most often after earthquakes or periods of very heavy rainfall, and are therefore most frequent in mountainous, tectonically active regions of the world. In New Guinea, for example, 8–16% of the land surface area is affected by landslides per century. Landslides often result in the exposure of nutrient-poor subsoils and parent rock at the surface and plant recolonization of these sites tends to be limited by the low nutrient status and instability of the soil. The plant community that re-establishes may differ in composition from the surrounding vegetation for a long period because of the slow pace of succession on these substrates. Studies of forest regeneration on landslides in the Caribbean have suggested that old landslides provide a habitat for some species that do not occur elsewhere in the surrounding forest matrix.

Active volcanoes have the potential to destroy forests over a large area by the direct effects of lava and ashfall and indirect effects caused by tsunamis and changes to atmospheric conditions. For example, the 1883 and subsequent eruptions of Krakatau, in the Sunda Straits between Java and Sumatra, are still evident in the contemporary flora of the Krakatau island group, which is dominated by a small group of well-dispersed tree species. Differences in the species composition of the islands in the Krakatau archipelago demonstrate the vagaries of chance colonization events and the patchy effects of historic and contemporary volcanic activity. The long-distance effects of the eruption of Krakatau are also illustrated by impacts on forest structure and composition on Ujong Kulon, west Java, located 70 km from the island group.

Rivers that migrate across the landscape on decadal timescales can cause disturbance to natural forest communities and stimulate primary successions on newly deposited substrates. In the Amazon floodplain of Peru, rivers can move by as much as 180 m during the annual floods, with resultant dramatic impacts on forest structure and composition. The communities that develop on land exposed by lateral river movement are initially species-poor and dominated by early-successional pioneers, but these forests are gradually replaced by richer communities that are more similar to the surrounding matrix of terra firme forest. It is sometimes possible to identify zonation in forest structure and composition that reflects species accumulation over time and the nature of the underlying substrate as the river moves across the landscape.

Disturbances that Result in Secondary Succession or Recovery

Cyclones and hurricanes impact forests in two belts between 10° and 20° either side of the equator, although their frequency and intensity vary greatly. Severe windstorms also occur occasionally at higher and lower latitudes. Typhoons also have localized impacts on forests in their path and occur over a broad range of latitudes. In the Caribbean, forests are impacted by hurricanes once every 15–20 years on average, and the forests are, therefore, permanently in a state of recovery. Severe windstorms cause trees to be snapped, uprooted, and defoliated, but only a minority is actually killed instantaneously. Studies in the Solomon Islands and the Caribbean have shown in both cases that about 7% of trees were killed outright by severe windstorms, although a larger number were damaged. Recovery occurs by a combination of resprouting of surviving damaged stems, release of seedlings that had been previously growing in the shaded forest understory, and germination of pioneer species in response to canopy opening. The pioneer trees soon grow up, reproduce, and die, so that within a relatively short period the species composition of the forest community may differ little from that of the forest that existed prior to the storm. There are three caveats that must be considered in response to this statement. First, if a second or subsequent disturbance intervenes before recovery is complete, the structure and composition of the forest may become permanently affected, particularly if the windstorm is followed by fire. Second, forests that contain a mixture of species or species groups that are differentially susceptible to wind (e.g., susceptible conifers vs. tolerant angiosperms) may exhibit a higher dominance of the tolerant group after a severe windstorm, particularly in areas where severe windstorms are relatively infrequent. Third, forests that are most frequently impacted by severe windstorms may develop a modified structure, such as a low and even stature (as in the forests of the eastern Sierra Madre mountains of Luzon, Philippines), or an open structure with a low density of large trees and many lianas (for example in east-facing slopes of the north Queensland rainforests).

Windstorms and volcanic activity may be associated with lightning strikes that can cause death of trees in large numbers. Even if only one tree is struck by lightning, others surrounding it can be damaged or killed if they are connected by lianas or roots. In New Guinea, mangrove forests may have patches of up to 50 m in diameter in which all trees have been killed by lightning strike, and *Nothofagus* forests may possess circular holes with a similar origin.

Lightning strike may also give rise to natural fires that impact much beyond the original source of ignition. Fires are a natural and inherent component of the disturbance regime in most natural forests, including those in the wet tropics that were formerly considered not to burn. However, recent evidence derived from dating of charcoal fragments extracted from soil profiles in tropical rainforest areas of South America and Africa have demonstrated a history of recurrent fires on millennial timescales even in sites that are currently very wet. Fires are an even more important feature of the disturbance regime for dry tropical forests and woodland, Mediterranean vegetation, and boreal forest, for which frequent and intense fires may be an important component of ecosystem functioning. The importance of fires in these forests is demonstrated by the occurrence of species that are either tolerant of fire, or possess mechanisms that facilitate their regeneration after fire. Fire tolerance is conferred by shielding living tissue beneath a thick bark or in underground storage organs, while regeneration after fire is enhanced by fruit or seed structures that are stimulated by high temperatures. Although fires have the potential to destroy living plant tissues, they can also have an important role in releasing nutrients from recalcitrant pools in the ecosystem and reducing species dominance. These effects depend on the intensity, timing, and frequency of fire and interactions with other disturbance agents.

Severe fires may be associated with periods of low rainfall, either naturally because they are concentrated in the dry season, or at supra-annual scales because they follow climatic droughts. Droughts may themselves directly increase rates of tree mortality, particularly when they occur in forests that are not normally associated with water shortage. For tropical rainforests, there is evidence that large trees are relatively more likely to be killed during a drought than small trees, and that droughts contribute to increased susceptibility to disturbance by fire. Both drought and fire are therefore more common in years when the El Niño-Southern Oscillation (ENSO) phenomenon is impacting global climates. In one or more regions of the world, severe ENSO events may be associated with increased rates of forest perturbation from either drought, fire, flooding, windstorms, lightning, landslides, or combinations of these factors. As a dramatic illustration of this phenomenon the 1982/83 ENSO caused a reduction to one-third of average rainfall across some parts of Southeast Asia and destruction of 3 millions ha of rainforest in Borneo by drought and fire. In Panama, the same ENSO event caused increased mortality rates of 70% of woody plant species represented as individuals ≥ 1 cm diameter at breast height on a large forest plot, from about 2% year^{-1} in a nondrought period to about 3% year^{-1} in the interval spanning the ENSO-related drought. This 50% increase in mortality rate has been associated with dramatic changes in species composition on the plot, because not all species were affected equally.

Conclusions

This discussion has demonstrated that disturbance to natural forests varies greatly in scale and effect in different forest types and for different disturbance agencies, such that robust generalizations are difficult to construct. A disturbance regime has components describing the intensity, frequency, and extent of its effects, although these are rarely quantified. These properties are important because they may influence emergent properties of the forest community, such as species composition and tree diversity. For example Connell's intermediate disturbance hypothesis, relates the intensity, frequency, or timing of disturbance to community diversity and has recently been tested in forests (*see* **Biodiversity**: Plant Diversity in Forests). Although disturbance and its impacts are difficult to quantify, the evidence from historical and ecological analyses of forest communities is highlighting the importance of natural disturbance regimes to forest community structure and ecosystem functioning. It is self-evident that all forests experience the small-scale disturbances associated with individual tree death and mortality. However, it is now clear that most well-studied forests also exhibit the imprint of one or more of the large-scale disturbance factors discussed above. This consideration highlights the importance of disturbance history in any attempt to understand contemporary forest ecology.

Further Reading

Brokaw N and Busing RT (2000) Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* 15: 183–188.

Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199: 1302–1310.

Everham EM III and Brokaw NVL (1996) Forest damage and recovery from catastrophic wind. *Botanical Review* 62: 113–185.

Garwood NC, Janos DP, and Brokaw N (1979) Earthquake-caused landslides: a major disturbance to tropical forests. *Science* 205: 997–999.

Grime JP (1979) *Plant Strategies and Vegetation Processes*. Chichester, UK: John Wiley.

Hubbell SP (2001) *Unified Theory of Biodiversity and Biogeography*. Monographs in Population Biology no. 32. Princeton, NJ: Princeton University Press.

Hubbell SP, Foster RB, O'Brien ST, *et al.* (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554–557.

Johns RJ (1986) The instability of the tropical ecosystem in New Guinea. *Blumea* 31: 341–371.

Nelson BW (1994) Natural forest disturbance and change in the Brazilian Amazon. *Remote Sensing Reviews* 10: 105–125.

Sheil D and Burslem DFRP (2003) Disturbing hypotheses in tropical forests. *Trends in Ecology and Evolution* 18: 18–26.

Shugart HH (1984) *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. New York: Springer-Verlag.

Watt AS (1947) Pattern and process in the plant community. *Journal of Ecology* 35: 1–22.

White PS and Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62: 399–450.

Whitmore TC (1982) On pattern and process in forests. In: Newman EI (ed.) *The Plant Community as a Working Mechanism*, pp. 45–59. Oxford, UK: Blackwell Scientific Publications.

Whitmore TC and Burslem DFRP (1998) Major disturbances in tropical rain forests. In: Newbery DM, Prins HHT, and Brown N (eds) *Dynamics of Tropical Communities*, pp. 549–565. Oxford, UK: Blackwell Science.

Biological Impacts of Deforestation and Fragmentation

E M Bruna, University of Florida, Gainesville, FL, USA

Introduction

In addition to housing the majority of the planet's biodiversity, forest ecosystems are the basis for trillions of dollars in global revenue. They are homes to indigenous groups, sources of food, medicines, and raw materials for industry, and they provide opportunities for recreation and tourism. They are also being logged, cleared, or otherwise altered by humans at alarming rates. Consequently, understanding the physical and biological consequences of deforestation has become one of the leading areas of research in forest ecology.

This review aims to describe the physical and biological consequences of deforestation on four levels of ecosystem organization: individuals, populations, communities, and ecosystems. In addition, I will also highlight some of the major gaps in our understanding of how fragmented forests function.

Physical Consequences of Deforestation

Habitat Loss and Insularization

The most dramatic and immediately obvious consequence of deforestation is the loss of native habitat in newly cleared areas. However not all deforestation results in the denuded landscapes one typically associates with clear-cut logging or industrial cattle ranching. In many cases deforestation proceeds unevenly, leaving behind a patchwork of forest fragments that are isolated at varying degrees from one another. These fragments of forest are embedded in an intervening habitat, referred to as the 'matrix habitat,' whose use varies in intensity from regenerating forest, to cattle pasture, to human settlements. The study of the physical and biological consequences of this now widespread phenomenon, known as habitat fragmentation, has become one of the principal areas of research in conservation biology. While these consequences can vary substantially by location and forest type, some general patterns have begun to emerge. As a result, we now have a greater understanding not only of how individual species are influenced by fragmentation, but also of what some of the consequences of fragmentation are at community and even continental scales.

Abiotic Changes in Forest Fragments

The abiotic conditions in forest fragments change dramatically once fragments are isolated, and these alterations are thought to drive many of the biological changes observed in fragmented landscapes. Sunlight penetrates forest fragments from above as well as laterally at the fragment's margins. Consequently, there is an increase in the amount of photosynthetically active radiation (PAR) at the forest understory. There is also an increase in understory air temperatures, frequently by as much as 8°C, and fragments become drier since the elevated temperatures and wind turbulence near fragment edges act synergistically to reduce relative humidity. Increased exposure of trees to wind results in wind throws and snapped crowns, leaving the canopy ragged and allowing additional sunlight to reach the understory. The temperature of the soil can increase markedly, and surface soil moisture can be diminished or even depleted.

These changes are not felt uniformly throughout the fragment. The intensity of these changes is spatially variable, and diminishes rapidly with increasing distance from the fragment's edge (**Figure 1**). As a result, these changes are frequently referred to as 'edge effects.' The extent to which fragments are influenced by edge effects will vary depending on fragment size, with small fragments more susceptible to environmental changes than large ones. It also depends on fragment shape, or more specifically the ratio of fragment perimeter to area. Fragments with high perimeter to area ratios, such as linear strips along roadsides, have much of their forest near edges and therefore have a greater amount exposed to harsh environmental conditions. In contrast fragments with lower ratios of perimeter to area have a greater amount of the fragment in the more buffered fragment interiors (**Figure 2**).

Abiotic changes in fragments can be ameliorated over time if vegetation outside the fragment regenerates and 'seals off' the fragment edge. Fragments surrounded by activities that maintain sharp fragment borders, such as cattle ranching or wheat farming, remain continually exposed to altered environmental conditions. Conditions in fragments can eventually return to levels similar to those found prior to fragment isolation, if cleared areas are allowed to regenerate or if agroforestry and other less intense forms of land use are adopted.

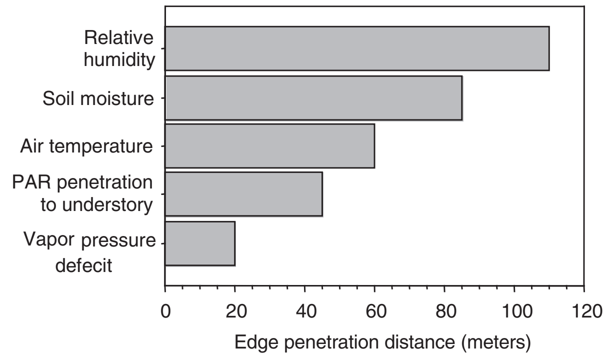


Figure 1 Edge penetration distances of abiotic changes in forest fragments. The *x*-axis indicates the distance (in meters) into forest fragments at which changes in abiotic parameters could be detected. PAR, photosynthetically active radiation. Adapted from Figure 32.1 in Laurance WF, Bierregaard RO (1997) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. Chicago, IL: University of Chicago Press with permission from the University of Chicago Press.

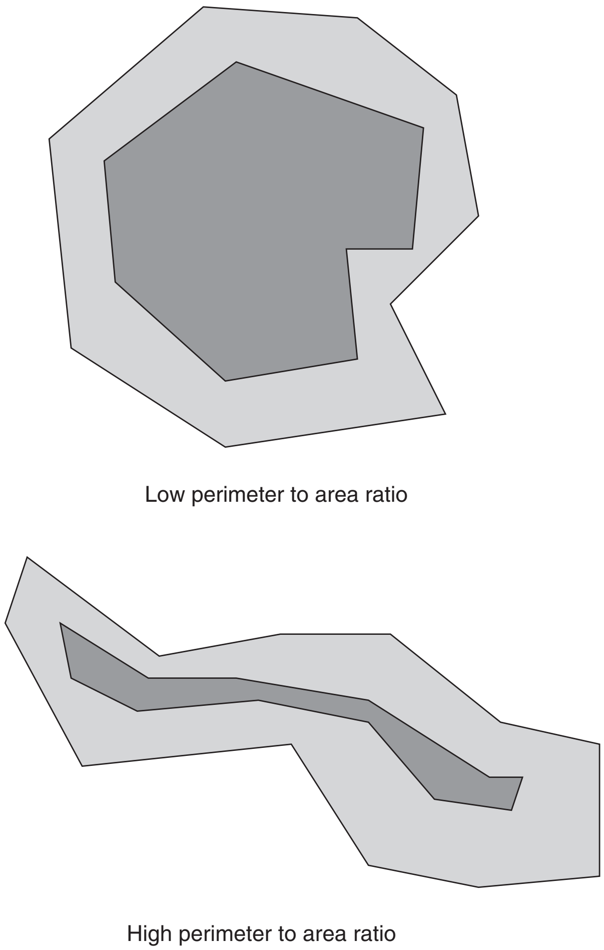


Figure 2 Influence of fragment shape on edge to perimeter ratio. The two fragments shown have approximately the same area, however the top one has a lower perimeter to area ratio. As a result, a greater proportion of the fragment is in the central core area that is buffered from edge effects (dark gray region).

Biological Consequences of Fragmentation

Changes in Individual Physiology and Behavior

As might be expected, the dramatic environmental changes in fragments can have serious consequences for the physiological condition of individuals that live there. For instance lizards in Australian rainforest fragments (*Gnypetoscincus queenslandiae*) have been found to be smaller than those in continuous forest, which could result from increased thermal variance during gestation or perhaps the reduced abundance of temperature-sensitive prey items. Similarly, temperature-related reductions in the abundance of insects could be responsible for the lower feather growth rates of the insectivorous birds *Glyphorynchus spirurus* and *Pipra pipra* in Amazonian forest fragments, though they could also have resulted from higher rates of evaporative water loss.

Plants surviving in fragments also appear susceptible to physiological changes. Some understory herbs, such as *Heliconia acuminata* (Heliconiaceae), shrink in response to the droughtlike conditions in fragments, and their leaves show signs of solar damage to the photosynthetic system. Their seeds also germinate less frequently in fragments than in continuous forest, which could be because they become buried under the leaf litter created by water-stressed trees or the light and temperature levels they use as cues to induce germination have changed. Plant mortality can also be sharply elevated in fragments, especially for the seedlings of shade-tolerant tropical trees such as *Pouteria caimito*, *Chrysophyllum pomiferum*, and *Micropholis venulosa*. Large adults of these species are also susceptible to increased mortality, since the inflexible trunks can be snapped by the gusts of wind that buffet fragment edges. Although the consequences of these changes for the long-term persistence of plant populations are unclear, they could be substantial – body size and physical condition are frequently correlated with reproductive success. It is worth noting, however, that the effects of fragmentation are not detrimental for individual physiology in all cases. For instance, individuals of *Pachira quinata*, an important timber species found in the dry forests of Central and South America, were found to develop crowns with more reproductive branches when isolated by fragmentation than when in continuous forest. This increased reproductive effort can probably be attributed to a lack of competitors in disturbed areas.

Perhaps less intuitive is the fact that forest fragmentation can also influence the behavior of individuals. An increasing number of studies have found that animals, even highly mobile ones such as migratory birds, are frequently averse to traversing roads, pastures, and the other types of clearings made by humans in forest landscapes. For example, mixed flocks of birds led by *Thamnomanes* antshrikes avoid crossing dirt roads through tropical rainforests if the vegetation along roadsides is regularly cleared. This aversion to clearing in the forest may lead to altered territory shapes and sizes, which can in turn increase the frequency of aggressive encounters between conspecifics. As might be expected, the birds will readily cross the roads again if the vegetation is allowed to regenerate.

Changes in Population Size and Genetic Structure

Ecological theory predicts that small or isolated populations are most likely to decline and become extinct, due in part to the effects of environmental and demographic stochasticity. It has therefore been hypothesized that populations in fragments will decline as well, particularly those that are in smaller or more isolated remnants. Empirical results partially support these conclusions, and the abundance of some organisms does decrease dramatically in forest fragments.

Species highly susceptible to population declines include large-bodied animals, which frequently require large areas in which to establish feeding or mating territories. Many of these species, such as the Florida panther (*Puma concolor coryi*) and black bear (*Ursus americanus floridanus*), can actually survive in a landscape that is only partially forested. However, the reduced amount of forest cover puts them in frequent contact with human populations, particularly when the cause of fragmentation is increased urbanization. As a result, they often have elevated rates of mortality due to poaching, collisions with automobiles, or exposure to pollutants and agricultural runoff.

Populations of species specializing on particular host-plants for oviposition or with highly specialized diets may also decline precipitously in fragmented landscapes. This is particularly true in tropical forests, where host plants and preferred food items are often patchily distributed and at extremely low densities. For example, the tropical butterfly *Hamadryas februa* utilizes the vine *Dalechampia scandens* for oviposition and larval development. Recent studies have found that butterfly populations in small fragments were not limited by their colonization ability or environmental conditions. Instead, it was the lack of host plants and high rates of emigration from fragments that constrained butterfly populations. While the 'fragments' in which these studies were conducted were a set of forested islands recently created by a hydroelectric project, they nonetheless demonstrate the importance of considering resource utilization in addition to habitat heterogeneity when evaluating the consequences of forest fragmentation.

Finally, populations of species with limited tolerance to abiotic changes may also be susceptible to declines in forest fragments. The increase in temperature and decrease in relative humidity that often accompany fragmentation are thought to be particularly detrimental to animals such as amphibians and invertebrates, which do not have the capacity to thermoregulate. One such example is of the Amazonian leaf-litter frog *Colostethus stepheni*, which has been found to have lower abundance in forest fragments than in continuous forest up to 19 years after fragment isolation. While a number of mechanisms could explain these reductions, one intriguing possibility is that altered abiotic conditions in fragments have delayed the sexual maturation of females. This delayed breeding would result in reduced per capita reproductive rates, ultimately driving the declines in growth rates of isolated populations.

As with individual physiology, however, the effects of fragmentation on population size are not uniformly negative. Populations of generalist invertebrates can increase dramatically in forest fragments, as can those of lianas, vines, rattans, and other pioneer plant species commonly found in natural forest gaps. The increased amount of edge habitat may also favor nest parasites such as cowbirds (*Molothrus ater*) or nest predators such as ravens (*Corvus corax*) and skunks (*Mephitis mephitis*), though the effects can vary considerably between species and locations. Still other populations show no change in density at all, although it is unclear if this is because the species under consideration are tolerant to fragmentation's consequences or because the studies have not continued long enough for changes in density to be detected.

The extent to which population size declines or increases in fragments may depend in part on how well individuals of each plant or animal species disperse across the intervening matrix habitat. This may be especially important for species that act as metapopulations, in which several subpopulations are linked to each other by dispersal. Unfortunately, detailed information regarding the movements of plants and animals between populations found in different forest fragments is rare, and the efficacy of habitat corridors connecting remnants of habitat to promote dispersal between isolated reserves remains the subject of ongoing debate. There is some indication that corridors may be useful in promoting the dispersal of at least some species, such as frogs, moths, small mammals, bush-crickets, and some birds. However there is little empirical evidence that dispersal alone will reduce the risk of population declines resulting from local changes in environmental conditions.

Isolated populations have been shown to suffer from increased rates of inbreeding depression, genetic drift, and reduced genetic diversity. These changes, which could result from reductions in population size following fragment isolation or because the movement of individuals between different forest fragments is limited, can have both short- and long-term consequences. In the short-term, populations of plants and animals may show an increase in fluctuating asymmetry (departures from bilateral symmetry) and other developmental problems due to reduced genetic diversity, as well have reduced fecundity. In the long term, genetic erosion could restrict evolutionary responses to changing environmental conditions and the potential for speciation, since genetic diversity provides the raw material upon which natural selection operates.

Changes in Community Composition and their Consequences

Using as a model MacArthur and Wilson's theory of island biogeography, researchers studying islands of forest have predicted that smaller fragments would support lower numbers of species than large fragments. This prediction has held true in a broad variety of temperate and tropical sites, with fragments often containing only a limited subset of a region's biota. These reductions in diversity have shown to affect disparate groups of plants and animals, including birds (e.g., insectivores, frugivores, cavity nesters), insects (e.g., beetles, fruit flies, ants), and plants (e.g., herbs, forbs, shade-tolerant trees).

Two different mechanisms have been invoked to explain this general pattern. First, populations in fragments could have become locally extinct following fragment isolation. Alternatively, lower diversity in fragments could also result from differences in the initial species composition of the patches that were isolated. This may be especially common in tropical forests, where regional species diversity is very high but many species are locally rare or patchily distributed. In this case a species may be missing from a fragment not because it went locally extinct, but because it was absent when the fragment was originally isolated.

Species diversity is not always lower in fragments, however, and there are numerous cases in which it has actually been found to increase following fragmentation. Many amphibians, insects, small mammals, and plants are habitat generalists tolerant of a broad range of habitat types. In some cases species diversity even increases despite the loss of forest-interior species, because their absence is compensated by an influx of generalists from the surrounding matrix. Perhaps one of the best examples of this phenomenon is tropical pool-breeding frogs, of which disturbed-habitat specialists (e.g., *Scinax rubra, Adenomera hylaedactyla*) can be found in recently isolated forest fragments and on the edges of continuous forest. Similar results have also been documented for small terrestrial mammals (e.g., *Oecomys* spp.), perhaps due to their preference for foraging in sites with abundant leaf litter and fallen branches.

Shifts in community structure may also depend on what trophic level a species occupies. Top predators such jaguars (*Panthera onca*) and gray wolves (*Canis lupus*) are hypothesized to be particularly vulnerable to extinction because they are found at lower population densities, forage in large territories, or are dependent on prey that can also be detrimentally affected by fragmentation. When these species become locally extinct, medium-sized predators (also known as mesopredators) such as coyotes (*Canis latrans*) and opossum (*Didelphis virginiana*) may increase in abundance. As a result, the abundance of the species preyed upon by the mesopredators will in turn decrease.

One of the defining features of forest habitats is the myriad interactions in which resident species are involved. Predation, herbivory, competition, and mutualisms all play an important role in structuring forest communities and promoting evolutionary change. As a result, it is widely believed that the disruption of these interactions in fragmented landscapes, particularly mutualistic ones related to plant reproductions and establishment, could have major repercussions for ecosystem functioning. In fact some authors have gone so far as to suggest that fragmentation-related reductions of these interactions will lead to 'ecological meltdown' or 'cascades' of further extinctions in forest fragments.

Some interactions relating to plant recruitment can be substantially modified in fragmented areas. For instance, the pollination of plants can decrease in fragments, either because pollinators are less abundant, they visit plants less frequently, or because they transfer less pollen per visit. Interestingly, a number of studies have also documented the opposite effect – dramatic increases in pollination in both fragments and the intervening matrix. The increase in these cases is usually due to a superabundance in the disturbed areas of exotic pollinators, such as the African honeybee (*Apis mellifera scutellata*). Seed dispersal and predation can be modified as well, although results to date have been somewhat contradictory. The quantity and composition of the seed rain has been shown to vary in disturbed habitats, due to changes in the abundance, diversity, or diet of dispersing animals such as monkeys, bats, birds, and dung beetles. Once these seeds are successfully dispersed, an influx of predators from the habitat surrounding fragments, particularly rodents and insects, can rapidly depress the seed numbers. This may be why the abundance of seedlings of understory plants is frequently much lower in fragments than in continuous forest. However, seedling numbers can also be lower if herbivory is higher in fragments and near edges, as might be expected given the larger populations of generalist browsers such as white-tailed deer (*Odocoileus virginianus*) or meadow voles (*Microtus pennsylvanicus*) in these areas.

Changes in Ecosystem Dynamics

Deforestation and fragmentation can also influence ecosystem processes at fragment, landscape, or continental scales. Within fragments, nutrient cycling can be substantially altered, since there is an increase in the amount of leaf litter on the forest floor and this litter often takes longer to decompose. At the regional scale, fragmentation can influence temperature and rainfall patterns. It is estimated that as much as 50% of rainfall in the parts of the Amazon is produced by the respiration of trees, and that by removing half the forest and replacing it with pastures total rainfall could be reduced by as much as 25%. Since forests are major reservoirs of the earth's terrestrial carbon, deforestation can also contribute significantly to global warming. As downed wood decomposes, it releases greenhouse gases such as carbon dioxide and methane. In fact it is hypothesized that as a result of this decomposition, deforestation alone contributes approximately one-fourth of all greenhouse gas emissions. Since tree mortality is elevated in fragments, this carbon is released by decomposing trees long after the original process of deforestation has been completed. These dead and downed trees, coupled with an increased accumulation of litter in fragments, also make fragments more susceptible to fires, which further alters the cycling of carbon and other nutrients. All of these changes in ecosystem processes can have major direct and indirect consequences for biodiversity. Increased fire frequency, for example, may directly cause the mortality of plants and animals in fragments. It may also indirectly drive reduced rates of individual growth and survivorship by altering the distribution of resources on which these individuals depend.

Future Directions

In this brief review I have attempted to summarize how deforestation and fragmentation can influence biological systems. However the field of fragmentation biology remains a dynamic and exciting one, and there is still much to learn regarding the structure and functioning of fragmented forests. For instance the precise ecological mechanisms responsible for most local extinctions from fragments are still unknown, as are the details regarding the dispersal of plants and animals between the remaining patches of forest. Finally, while the populations of plants and animals surviving in fragments continue to be the subject of considerable research, one cannot understate the importance of the matrix habitat in which these fragments are embedded. Some types of matrix habitat are better at mediating the impact of abiotic changes, while others have a higher diversity of species regenerating in them. Perhaps most importantly, matrix habitat influences the movement of plants and animals in fragmented landscapes. These movements are critical, since they may be sufficient to ameliorate population declines or inbreeding depression in fragments. All of these differences are dependent on how the land was managed immediately following forest clearing, therefore understanding the biological dynamics of forest fragments will require not only a greater understanding of what happens inside them, but also of what goes on in the habitat that surrounds them.

See also: **Biodiversity**: Endangered Species of Trees; Plant Diversity in Forests. **Ecology**: Human Influences on Tropical Forest Wildlife; Plant-Animal Interactions in Forest Ecosystems; Reproductive Ecology of Forest Trees. **Environment**: Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Forest Management for Conservation. **Landscape and Planning**: Landscape Ecology, the Concepts. **Soil Development and Properties**: The Forest Floor. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation.

Further Reading

Aizen MA and Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine 'Chaco Serrano'. *Ecological Applications* 4: 378–392.

Anciaes M and Marini MA (2000) The effects of fragmentation on fluctuating asymmetry in passerine birds of Brazilian tropical forests. *Journal of Applied Ecology* 37: 1013–1028.

Andresen E (2003) Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography* 26: 87–97.

Bierregaard RO, Gascon C, Lovejoy TE, and Mesquita R (eds) (2002) *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. New Haven, CT: Yale University Press.

Cunningham SA (2000) Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society Biological Sciences Series B* 267: 1149–1152.

Debinski DM and Holt RD (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14: 342–355.

Develey PF and Stouffer PC (2001) Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology* 15: 1416–1422.

Harrison S and Bruna E (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225–232.

Laurance WF and Bierregaard RO (1997) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. Chicago, IL: University of Chicago Press.

Laurance WF, Lovejoy TE, Vasconcelos HL, *et al.* (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16: 605–618.

Terborgh J, Lopez L, Nunez VP, *et al.* (2001) Ecological meltdown in predator-free forest fragments. *Science* 294: 1923–1926.

Human Influences on Tropical Forest Wildlife

C A Peres and J Barlow, University of East Anglia, Norwich, UK

Introduction

Different patterns of anthropogenic forest disturbance can affect forest wildlife in both tropical and temperate regions in many ways. The overall impact of different sources of structural and nonstructural disturbance may depend on: (1) the groups of organisms considered; (2) the evolutionary history of analogous forms of natural disturbance; and (3) whether forest ecosystems are left to recover over sufficiently long intervals following a disturbance event. The wide range of human-induced disturbance events are widely variable in intensity, duration and periodicity and are often mediated by numerous economic activities including timber and nontimber resource extraction, other causes of forest degradation, forest fragmentation, and forest conversion to other forms of land use. Examples of human enterprises that can severely affect wildlife may include hunting, selective logging at varying degrees of intensity, slash-and-burn agriculture, plantation forestry, selective removal of the understory to produce shade-tolerant crops, and outright deforestation for large-scale livestock operations. The resulting faunal assemblages can be drastically disfigured in highly modified forest landscapes compared to those in truly undisturbed forest lands containing a full complement of plant and animal species, which are being rapidly confined to the best-guarded strictly protected areas or the remote, roadless wildlands in the last remaining pristine forests.

In this article, we focus on tropical forests rather than their temperate counterparts because tropical forests arguably present the greatest challenge to global biodiversity conservation. We also focus on forest vertebrates because the effects of human disturbance on tropical forest invertebrates remain poorly known. Within the terrestrial vertebrates, most of our examples come from bird and mammal studies because effects of disturbance on reptile and amphibian assemblages remain poorly understood. We illustrate this discussion and review the evidence from the literature and our own field studies on the basis of three increasingly ubiquitous types of human disturbance in forest lands with severe consequences to the vertebrate fauna – hunting, selective logging, and wildfires.

Hunting

Hunting is perhaps the most geographically widespread form of human disturbance in tropical forests, although the total extent of this form of nontimber resource extraction cannot be easily mapped using conventional remote sensing techniques. Many parts of west Africa, Southeast Asia, and the neotropics are becoming chronically overhunted, partly as a result of burgeoning human populations that often escape to and become marginalized in frontier regions. Exploitation of wild meat (the meat from wild animals often referred to as bushmeat) by tropical forest-dwellers has also increased due to changes in hunting technology, scarcity of alternative protein sources, and because it is often a preferred food. Large-bodied game birds and mammals providing highly desirable meat packages and hunted for either subsistence or commercial purposes are particularly affected, because they are the main target species and tend to be associated with low reproductive rates, thus recovering slowly from persistent hunting pressure (**Figure 1**).

Estimates of Wild Meat Harvest

Studies of wild meat harvest tend to be approached at the level of subsistence communities, where wild animals can be intercepted, or market and restaurant surveys. These studies tend to severely underestimate the true mortality because many of the animals intentionally or incidentally killed in the forest are not retrieved, thus not translating into meat consumed at the level of villages, markets, or informal sales. The species most threatened by hunting may also be rarely seen in markets, because they were already at very low population densities.

Figure 1 A young Kaxinawa Indian hunter showing a recently killed howler monkey (*Alouatta seniculus*) and a white-faced capuchin (*Cebus albifrons*), which are unsustainably harvested at his indigenous reserve in western Acre, Brazilian Amazonia.

Subsistence Hunting

Subsistence game hunting can often have profound negative effects on the species diversity, standing biomass, and size structure of vertebrate assemblages in tropical forests that otherwise remain structurally undisturbed. This occurs mainly through local population declines, if not extirpation, of large-bodied vertebrate taxa which make a disproportionately large contribution to nonhunted forests in terms of their aggregate biomass and role in ecosystem functioning. Overharvested forest sites where large game species have been depleted thus tend to be dominated by small-bodied species that are either bypassed or ignored by hunters. Regardless of the nature of density compensation by small-bodied species following the local extinction of large vertebrates, important species interactions or ecosystem functions associated with large body size such as dispersal of large-seed plant species and herbivory of tree seedlings may no longer take place.

Overhunting

Overhunting of wildlife for meat consumption has reached an unprecedented scale across the humid tropics, causing local extinction of many vulnerable species. Yet productivity of tropical forests for wild meat is at least an order of magnitude lower than that of tropical savannas, and can only support fewer than 1 person per square kilometer if they depend entirely on wild meat for their protein. Reasons why the scale and spatial extent of hunting activities have increased so greatly in recent years include human population growth and migration; severe reduction in forest cover and nonhunted source areas; increased access via logging roads and paved highways into remote forest areas allowing hunters to harvest wild meat for subsistence or cash; the use of efficient modern hunting technologies especially firearms and wire snares; and, in some regions, greatly increased trade in wild meat. Forest defaunation driven by wild meat hunters has therefore become one of the most difficult challenges for tropical forest wildlife conservation.

In addition to drivers of the bushmeat harvest, wildlife depletion in tropical forests can be driven by extractive activities targeted to other desirable animal parts or products, including skins, feathers, ivory, horns, bones, fat deposits, eggs and nestlings, as well as live-captures of juveniles or adults for aviaries, aquaria, and the pet trade. These activities are often poorly regulated in the humid tropics, and have been responsible for wholesale extinctions of many target species.

Aggravating Effects

In frontier tropical forest regions, hunting and other forms of offtakes often co-occurs with different patterns of forest disturbance that can either aggravate or buffer the detrimental effects of faunal exploitation. For instance, effects of hunting are likely to be considerably aggravated by isolated forest fragmentation because fragments are more accessible to hunters, allow no (or very low rates of) recolonization from nonharvested source populations, and may provide a lower-quality resource base for the frugivore–granivore vertebrate fauna. On the other hand, selective logging may actually boost the local densities of large terrestrial browsers by puncturing and opening up the canopy, thus enhancing the understory productivity through a more favorable light environment. Likewise, slash-and-burn agriculture associated with long-term rotation of a successional mosaic can generate attractive foraging areas for populations of large herbivorous rodents and ungulates, as well as species preferring second-growth. We therefore turn to other important forms of anthropogenic disturbance involving structural changes to wildlife habitats in tropical forests.

Selective Logging

Selective logging is a major anthropogenic disturbance event in tropical forests, affecting around 15 000 km^2 a year of forest in the Brazilian Amazon alone. As only a small proportion of the remaining tropical forests is expected to be strictly protected within reserves, there is much debate over whether timber production can be reconciled with biodiversity conservation. For wildlife, the crucial issues are whether populations of species of conservation importance can be maintained within a matrix dominated by logged forests. However, despite the growing amount of literature documenting the effects of selective logging on the abundance and distribution of forest wildlife, the lack of agreement between studies means that few conclusions can be drawn. The disparity is highlighted by a recent review. In eight studies on the effects of logging on the forest avifauna, frugivorous birds were found to increase, decrease and to remain unaffected, whilst the same range of responses were demonstrated in different studies on forest chimpanzees (*Pan troglodytes*).

There are four major reasons why these studies have failed to find consistent results. Firstly, the effects of logging can be strongly influenced by the time elapsed since logging occurred, the number of recurrent logging events, the severity of the logging operation and extraction methods used, and the composition of the surrounding landscape. Secondly, sampling techniques are rarely standardized between studies. Effects may differ across different spatial and temporal scales, and by whether sampling focuses on understory species, canopy species, or species from all forest levels. Studies also differ depending on whether they examined tree fall gaps, or the entire logged forest matrix, in the latter case capturing many disturbance-intolerant species that are able to persist in unlogged refugia. Thirdly, some of the differences may be explained by geographic and historical factors. Production forests occur throughout the tropics, capturing many faunas that are unlikely to be equally adapted to disturbance. In the neotropics alone, logging appears to have greater impacts on the Amazonian avifauna than that in the Atlantic forest or in Belize, a difference that can be attributed to the more intensive history of natural disturbance events in those areas. Finally, few studies have incorporated the synergistic effects of other forms of disturbance that co-occurs with logging, including fires, edge effects, and area effects resulting from forest fragmentation (**Figure 2**).

Patterns of Adaptation

Despite these problems, some general patterns have become apparent. By opening up the canopy, and shifting much of the primary production to the understory, logging tends to simplify the vertical stratification of forest species. Both bird and butterflies typical of the canopy layer may begin to forage at lower levels, replacing many of the highly specialized shaded understory species that are adapted to foraging within the dark forest interior of undisturbed primary forest. This shift in productivity may also favor many large terrestrial browsers, and may boost the abundance of elephants, okapis, and duikers in African forests, or pacas, brocket-deer and tapirs in neotropical forests. The same may be true for highly folivorous arboreal mammals such as colobine primates and howler monkeys in African and neotropical forests, respectively. Across all taxa, specialists with narrow niches tend to decline whilst generalists that are able to switch between resources tend to increase. This is illustrated in primate populations; unripe seed and ripe fruit specialists such as bearded sakis (*Chiropotes* spp.) and spider monkeys (*Ateles* spp.), respectively, tend to decline in highly selectively logged forests, whilst generalists such as brown capuchins (*Cebus apella*) may increase.

Effect of Logging Method

One crucial factor in the overall impact of a logging operation is the method used for timber harvest and extraction, which will determine the proportion of the forest area affected by canopy gaps where the understory light environment is significantly different.

Figure 2 A roundlog loading bay and logging road in the Brazilian Amazon.

Selective logging operations targeting commercially valuable species accounting for considerably less than 1% of the forest basal area can result in as little as 5% and as much as 40% of collateral damage to nontarget species in the remaining stand. The level of collateral damage is context-dependent in terms of the size of trees, abundance of woody lianas spreading over adjacent tree crowns, terrain topography, and hydrology, but tends to increase with heavy mechanized machinery such as operations in which roundlogs are dragged out over long distance by bulldozers. Collateral damage is lowest where the extracted roundlogs can be floated out in the case of seasonally inundated forests, or removed by a system of steel cables or even cargo helicopters, or where the timber can be sawed *in situ* and removed by less destructive methods. Another important factor is whether the timber species targeted by loggers are important food sources for forest wildlife, and how crucial these are for a particular vertebrate assemblage when these food resources become available. For instance, the systematic offtake of important fruiting species may have a far greater impact on highly frugivorous species, particularly if these fruit crops would otherwise become available during annual periods of food scarcity.

Although changes in species abundance and distributions are common, the complete extirpation of species from logged forest has been rarely recorded. Most primary forest specialists merely exist at low population densities, utilizing small unlogged patches until the forest becomes suitable for recolonization. As a result, timber production has been promoted as a means of biodiversity conservation, as it is seen to provide an economic justification for large tracts of tropical forest outside protected areas. Management of the logging methods can substantially reduce their impact on forest structure (actually increasing long-term yields), whilst careful planning of unlogged refugia and corridors may ensure the survival and recolonization of disturbance-sensitive species. Despite these mitigation measures, timber production cannot be seen as a panacea to the problems of forest wildlife conservation in the tropics. Reduced impact methods are rarely used, and still account for a very small proportion of the logging concessions in the tropics. Furthermore, very little data exist on the effects of repeated timber harvests at variable intervals, a necessary component if production forests are to remain economically viable. Indeed, this may lead to structurally homogeneous forests unlikely to maintain the full array of biodiversity found in primary forest. Logging may also disrupt many of the complex interactions between species, the effects of which may not be noticeable in the short term.

Finally, logging cannot be examined in isolation from other forms of forest disturbance. The creation of logging camps, logging roads, and skidding trails generates greater demand for bushmeat and access to previously undisturbed forest, which greatly increases local hunting pressure. The logging access matrix also accelerates the rate of forest clearance for agriculture, and the associated effects of forest edges and fragmentation, which combined with the higher density of tree-fall gaps can greatly enhance both the risk and potential severity of wildfires in seasonally dry forest. These secondary effects are not restricted to conventional selective logging, but can also result from reduced-impact logging operations associated with lower levels of canopy damage. Without appropriate and enforceable postlogging restrictions, the role of timber production in conserving forest wildlife will be diminished well beyond the immediate impact of logging itself.

Forest Wildfires

Historically, fire events in tropical forests have been rare and largely associated with the mega El-Niño Southern Oscillation (ENSO) events of the past 7000 years. However, within recent years understory wildfires have become increasingly common events in tropical forests: in the 1997–1998 ENSO year fires burned around 17 million ha of lands in Indonesia and Latin America alone, much of which was tropical forest. Three factors explain this unprecedented increase of tropical forest fires, all of which can be related to anthropogenic activity:

1. Human-induced climate change exacerbates wildfire hazards by increasing the frequency and intensity of ENSO events, which cause abnormally long droughts in the dry season and allow normally fire-resistant forests to become flammable.
2. Selective logging lowers the flammability threshold of forests by reducing canopy cover and understory humidity, whilst increasing the amount and continuity of fine and coarse fuel loads on the forest floor.
3. Tropical agricultural practices are often heavily reliant on fire, ensuring that seasonally flammable forests are never far from ignition sources.

The consequences of these fires to forest structure and composition will depend on their severity, as well as the history of fires in a given forest ecosystem. Initially, low-intensity surface fires move slowly through the leaf litter, burning the fine and coarse fuel layer. Under normal fuel loads and humidity conditions, flame heights rarely exceed 10–30 cm. However, these fires serve to increase greatly the fuel load and open up the canopy, so that recurrent burns will become much more intense, scorching the canopy layer, and killing many of the surviving trees that remain after the first burn. Because of their recent historical rarity, very few studies have documented the effects of accidental fires on forest wildlife; the following is based on information from a small number of studies conducted in Amazonia and Southeast Asia, and outlines the effects of fires in their immediate aftermath, up to 1 month, and 1 to 3 years thereafter. However, considering that this is a recent phenomenon and the possible range of postburn responses, these conclusions cannot be generalized to all contexts.

Fire-Induced Mortality

Reports of the initial fire-induced mortality appear to be inconclusive. In Sumatra, the lack of animal carcasses following the fire was taken as evidence that most birds and mammals were able to escape the fire. However, in the Brazilian Amazon there is evidence of substantial mortality in several groups of terrestrial vertebrates including tortoises, tinamous, armadillos, and caviomorph rodents, whilst even more mobile arboreal species such as toucans, parrots, and some primate species can succumb to the fires, presumably through smoke asphyxiation. In high-intensity fires in forests burning for the second time, even large, highly mobile mammals, such as the collared peccary (*Tayassu tacaju*) and brocket deer (*Mazama* spp.), can be killed by the fires.

Many understory birds and forest lizards appear to be absent 1 month after the fires, perhaps reflecting the conspicuous lack of foraging opportunities in the scorched understory. Some canopy frugivores are also less abundant. In Sumatra, two hornbill and two primate species had either declined or become absent from burned forest, whilst in Amazonian forests many surviving canopy trees shed or aborted their fruit crops, leading to declines in the abundance of frugivorous primate species. These declines may have been exacerbated by hunting, as the open understory rendered many game species as easy targets for subsistence hunters.

Post-Burn Survival

Up to 1 to 3 years after the fires, many primary forest specialists appear able to persist in lightly burned forest, though most are found at much lower densities than in adjacent unburned forest. Considering the understory avifauna, highly specialized insectivores such as the dead-leaf gleaning and ant-following species, which often contain many regionally endemic species, appear to be the most vulnerable, and often disappear from burned forest. However, species richness at small spatial scales may actually increase in burned forest, as many gap specialists and edge species invade from more disturbed areas. As with logging, fires open up the canopy and shift primary productivity to the understory. This dense postburn regeneration, often spearheaded by bamboo and some pioneer tree and liana species, appears to cause an increase in the abundance of many terrestrial browsers in an Amazonian forest, most notably collared peccaries and both species of brocket deer. It also provides these species with a temporary refuge from hunting. Frugivorous primates appear to be far more susceptible than their folivorous counterparts, although most primates species manage to persist in forests succumbing to a single fire event, and may also benefit from reduced hunting pressure.

Where fire severity increases, either because of a recurrent fire, or a high level of preburn logging activity, the effects on wildlife is considerably greater. Most primary forest species, and even many gap and specialist species, are extirpated from the dense early-successional regeneration that follows these fires, and are replaced by species typical of young second-growth. The understory avifauna in twice-burned forest is almost entirely dissimilar with that found in the unburned forest, and becomes dominated by the second-growth specialists such as the wren *Thryothorus genibarbus*. Most primate species are also absent in this highly modified habitat, and only small-bodied species typical of young second-growth such as marmosets (*Callithrix* spp.) and titi monkeys (*Callicebus* spp.) are particularly abundant.

Overall, initial low-intensity fires appear to act in a similar manner to logging, puncturing the canopy, severely altering the understory light environment, and changing the abundance of many species. This, however, only rarely results in the local extinction of disturbance-intolerant species. In contrast, recurrent fire events from as early as a second burn appear to have a much greater effect in substantially disfiguring forest structure, and represent a serious threat to forest wildlife. While no information is available on the recovery of these forests it appears that the potential for the establishment of a recurrent burn regime in many tropical forests represents one of the largest contemporary threats to wildlife, as it can lead to the conversion of extensive closed-canopy forest lands into scrub savannas. This occurs concomitantly with the local extinction of almost all the forest wildlife typical of undisturbed forest. To a large degree wildfires in the humid tropics can represent an irreversible transition into replacement fire-climax ecosystems that provide considerably lower value both in terms of wildlife habitat and key ecosystem services.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation. **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Landscape and Planning**: Landscape Ecology, the Concepts.

Further Reading

Barlow J, Haugaasen T, and Peres CA (2002) Effects of surface wildfires on understorey bird assemblages in Amazonian forests. *Biological Conservation* 105: 157–169.

Bawa K and Seidler R (1998) Natural forest management and conservation of biodiversity in tropical forests. *Conservation Biology* 12: 46–55.

Fa JE and Peres CA (2001) Game vertebrate extraction in African and Neotropical forests: an intercontinental comparison. In: Reynolds JD, Mace GM, Redford KH, and Robinson JG (eds) *Conservation of Exploited Species*, pp. 203–241. Cambridge, UK: Cambridge University Press.

Johns AG (1997) *Timber Production and Biodiversity Conservation in Tropical Rain Forests*. Cambridge, UK: Cambridge University Press.

Kinnaird MF and O'Brien TG (1998) Ecological effects of wildfire on lowland rainforest in Sumatra. *Conservation Biology* 12: 954–956.

Nepstad DC, Moreira AG, and Alencar AA (1999) *Flames in the Rain Forest: Origins, Impacts and Alternatives to Amazonian Fire*. Brasília: Pilot Program to Preserve the Brazilian Rainforest, World Bank.

Peres CA (1999) Ground fires as agents of mortality in a Central Amazonian forest. *Journal of Tropical Ecology* 15: 535–541.

Peres CA (2001) Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology* 15: 1490–1505.

Peres CA, Barlow J, and Haugaasen T (2003) Vertebrate responses to surface fires in a central Amazonian forest. *Oryx* 37(1): 97–109.

Putz FE, Redford KH, Fimbel R, Robinson J, and Blate GM (2000) *Biodiversity Conservation in the Context of Tropical Forest Management*. Environment Paper no. 75. Washington, DC: World Bank.

Putz FE, Blate GM, Redford KH, Fimbel R, and Robinson JG (2001) Tropical forest management and conservation of biodiversity: an overview. *Conservation Biology* 15: 7–20.

Robinson JG and Bennett EL (eds) (2000) *Hunting for Sustainability in Tropical Forests*. New York: Columbia University Press.

Aquatic Habitats in Forest Ecosystems

K M Martin-Smith, University of Tasmania, Hobart, Tasmania, Australia

Introduction

There is a wide variety of aquatic habitats found in forested areas ranging from water-filled tree holes through to large rivers, lakes, and inundated forests. This article initially reviews the classification of aquatic habitats and some of their important geomorphological, physicochemical, and biological parameters. Following this, different classes of aquatic habitats in forests are presented in outline with consideration of their global distributions, defining abiotic characteristics and aquatic biota. A broad distinction has been made between aquatic habitats where the forest itself forms part of the habitat matrix (forested wetlands) and those where the forest is only on the periphery (water bodies in forests). Four subdivisions of forested wetlands are discussed: (1) peat bog forests, (2) swamp forests, (3) floodplain forests, and (4) mangrove forests, and three types of water bodies in forests: (1) container habitats (phytotelmata), (2) ponds and lakes, and (3) streams and rivers. For the latter groups, emphasis has been placed on the differences in characteristics when compared to nonforested ecosystems. Finally human interactions with aquatic systems are discussed, including both dependency on aquatic resources and anthropogenic threats.

There have been many attempts to classify aquatic habitat types based on combinations of geomorphological, physical, chemical, or biological characteristics. Some of the most important and frequently used classification variables are given in **Table 1**. Whilst providing an excellent framework for rationalizing our understanding of aquatic systems, there are inevitably exceptions to all classifications. Usually, this is because the habitat characteristics exist as continuous variables rather than distinct states and thus the criteria for inclusion in a particular category will be, to some extent, subjective. For example, some rivers will dry up to a series of pools, thus transforming a flowing water (lotic) habitat into a still water (lentic) one. Similarly, many of the habitat variables covary – nutrient levels are generally strongly correlated with organic production, for example. Despite these caveats, it is possible to identify a number of types of aquatic habitat in forested ecosystems.

At the highest hierarchical level, there is a broad distinction between aquatic habitats where the forest itself is an integral part of the habitat and those where the forest is only on the edges of the water body. There is no standard terminology for either group and there are a huge variety of local names for subdivisions within each. In this article, 'forested wetlands' is used for aquatic habitats where there are inundated live trees found throughout the water mass whereas 'water bodies in forests' is used where live trees surround or line the water and do not extend throughout the habitat.

Table 1 Some common continuous variables used to classify aquatic habitats

Type of variable[a]	*Example variables*	*End points of continuum*	
Geographical or geomorphological	Size of water body	Small	Large
	Depth of water	Shallow	Deep
	Permanence of water (hydroperiod)	Ephemeral	Permanent
	Stability	Fluctuating	Stable
	Degree of water flow	Lentic	Lotic
	Gradient	Steep	Shallow
	Latitude	Tropical	Temperate
Physicochemical	Temperature	Low	High
	Light	Fully shaded	Open
	Degree of mixing	Amictic	Polymictic
	pH	Acid	Alkaline
	Oxygen levels	Anoxic	Oxygenated
	Nutrient levels (N, P)	Low	High
	Suspended sediment	Clear	Turbid
Biological	Organic production	Oligotrophic	Eutrophic
	Source of production	Autochthonous	Allochthonous
	Organic debris	None	Plentiful
	Dominant trophic group	Shredders	Filter-feeders

[a] Some variables will only apply to a subset of aquatic habitats discussed in the text; for example, degree of mixing is generally only used for standing water bodies.

Forested Wetlands

The total extent of forested wetlands in the world has been estimated at 3.4 million km^2 but there are considerable uncertainties in this figure. Furthermore, there are very large variations in degree and period of inundation and thus the actual extent of forested wetlands at any point in time is difficult to determine. The local hydrological balance between inputs (rainfall, surface runoff, and groundwater seepage), storage, and outputs (evapotranspiration, infiltration, and runoff) determines the formation, maintenance, and hydroperiod (the amount of time that the forest is inundated) of forested wetlands.

Important characteristics shared by all forested wetlands are submerged physical habitat structure (tree trunks and branches) and wide distribution of terrestrially derived organic input over the entire water surface. Tree trunks and branches play a very important role in modifying hydrological parameters, including slowing of water flow and precipitation of suspended material. Furthermore, they provide surfaces for colonization by aquatic biota. Terrestrial input of material may be from the trees themselves (leaves, fruit, and seeds) or plants or animals living on the trees.

Four major categories of forested wetlands are described below, although the categories grade into one another, swamp forests often receiving river floodwater for example.

Peat Bog Forests

These are forests growing on peat-rich soils that are permanently waterlogged. They are formed where there are large inputs of fresh water and low levels of organic decomposition. Aquatic habitats in peat bog forests may be sporadic, seasonal, or permanent.

Distribution The vast majority of inundated forests on peat bogs are in boreal areas – extensively in Canada, Alaska, Scandinavia, Russia, and China. The coast of the southeast USA (Florida to North Carolina) also has considerable amounts, whilst in the tropics substantial peat bog forests are found in Borneo, Sumatra, and Papua New Guinea.

Physicochemical characteristics Peat bog forests that receive water input solely from rain (ombrotrophic) have a low pH and are low in inorganic nutrients. Where there are groundwater inputs in addition to rain, pH is near neutral and there are higher levels of nutrients. Water in all peat bog forests is often darkly colored from the presence of dissolved tannins which reduce light penetration. Water depth is shallow to moderate. Water movement is slight, thus turnover and flushing rates are low. Combined with high levels of organic materials, this leads to anoxic conditions particularly near the benthos.

Aquatic biota Few or no macrophytes are present because of low light levels and/or low pH. Similarly, algal production is low. Invertebrates appear to be specialists with adaptations to deal with low oxygen levels. Trophic food webs are based on detritus. In boreal areas fish are absent or restricted to a very few species. In the tropics there may be considerable fish diversity from families specialized to deal with low oxygen levels with adaptations including air-gulping and labyrinthine organs. There may be considerably greater fish diversity than is presently recognized because sampling effort has been low in these habitats. Other vertebrates such as turtles and snakes may spend time in these habitats but there are few or no obligate species.

Swamp Forests

Swamp forests are found on peat-poor soils that are permanently waterlogged. They may be created and maintained by land topography (basin swamps), hydrological barriers, and/or high water tables. Aquatic habitats in swamp forests may be sporadic, seasonal, or permanent. Palms are a prominent group in tropical swamp forests.

Distribution Swamp forests are distributed widely, but are more common in tropical rather than temperate zones. The largest areas of swamp forest are to be found throughout Central America, Brazil, Argentina, tropical Africa, and Southeast Asia (particularly Borneo, the island of New Guinea, Laos, and Cambodia). There are also substantial swamp forests in central Asia and the southern USA.

Physicochemical characteristics As there is a wide variety of mechanisms that create swamp forests physicochemical characteristics also vary widely. There is generally little or no water movement for most of the hydroperiod, particularly in basin swamp forests, and water depth is shallow to moderate. However, flushing may occur during seasonal or episodic flooding from rivers. Oxygen and nutrient concentration of the water varies considerably depending on source of input, soil, and vegetation type.

Aquatic biota Considerable diversity of aquatic biota may be found in swamp forests. Where there is not a closed canopy some development of rooted or floating macrophytes may occur. Invertebrates from a wide range of taxonomic groups (particularly insects, crustaceans, and gastropods) are present and trophic webs may be based on autochthonous production, terrestrial input from trees, or detritus. Vertebrates including fish, amphibians, and reptiles are present. Fish diversity may be moderately high with specialists on detritus and benthic or terrestrial invertebrates. Caimans, crocodiles, or alligators are often the top predators in the system.

Floodplain (Alluvial) Forests

These are forests that are seasonally or irregularly flooded by changes in river level. In temperate areas flooding is often associated with snowmelt in the upper reaches of catchments, whilst in the tropics monsoonal rainfall is the major contributor.

Distribution Floodplain forests are found throughout the world. The most extensive are associated with very large rivers such as the Amazon, Mississippi, Orinoco, Congo, and Mekong, although they are associated with almost all unregulated rivers. Estimates of the extent of floodplain forests have been generated by satellite imagery during periods of maximum inundation and include 300 000 km^2 for the central Amazon and 70 000 km^2 for the Mekong.

Physicochemical characteristics The predictability of flooding and hydroperiod depends on the gradient and water storage capacity of the rivers and streams. Forests associated with smaller, high-gradient streams and rivers have rapid changes in water level and irregular and short hydroperiods, whereas those through which large, lowland rivers flow have more predictable hydrological regimes. Water depth may be considerable (>12 m), although shallow depths are more common. Rising water levels transport sediment which is deposited in the floodplain and levels of inorganic nutrients are high. Waters are usually oxygen-rich during initial phases of inundation, although thermal stratification, anoxic conditions, and pH changes can develop over time. River regulation often changes the areas inundated and the hydroperiod substantially.

Aquatic biota Invertebrates, fish, amphibians, and other mobile riverine animals rapidly move into newly created floodplain habitats. This movement can be to escape high-flow conditions in the main stem of the river but is more often related to exploitation of the floodplain habitat for food, reproduction, or avoidance of predators. Where the hydroperiod is of sufficient duration, algae and aquatic macrophytes will become established and may add additional habitat and trophic complexity. Floating mats of vegetation may develop if the light environment is suitable. Aquatic insects, crustaceans, gastropods, and many other groups may reach high abundance levels and complex food webs based on autochthonous production, terrestrial input, detrital material and fruits and seeds develop. In the tropics, high diversity of fish, amphibians, and reptiles are found. These form the basis for well-known fisheries in the Amazon and Southeast Asia. The Amazon basin is home to more than 3000 species of fish, the majority of which spend at least some period of their life history in floodplain forests. It has been suggested that some of this extraordinary diversity is related to additional habitat and trophic interactions that occur during flooding of the forest. Similarly, there are at least 1200 species in the Mekong basin and 700 in the Congo basin, many of which are dependent on floodplain forests.

Mangrove Forests

Mangrove forests are found on the coastal fringes of land on sheltered shores. They are characterized by regular inundation by salt water during the tidal cycle and are composed of a specialized group of trees with adaptations to cope with this. Aquatic habitats in mangrove forests fluctuate in extent over short time periods.

Distribution Mangrove forests are exclusively coastal and predominantly found in the tropics. They are particularly abundant in Australia and Southeast Asia, the Indian subcontinent, Mexico, Central America and Brazil, and equatorial Africa.

Physicochemical characteristics The dominant abiotic factors in mangrove forests are tidal fluctuations in water level and salinity gradients related to proximity to the coast. Water levels change regularly on short timescales following tidal inundation with saline, marine water. Salinity decreases moving inland from the mangrove margin, dependent on levels of freshwater input. Soils are anoxic with large amounts of organic material present (primarily mangrove-derived).

Aquatic biota Plant and animal life in mangroves has to withstand large daily changes in abiotic conditions. Almost all species are of marine origin rather than freshwater origin and may undergo daily migrations or retreat to refugia in response to these variations. Distinct zonation in communities is seen with boundaries orientated parallel to the coast. There are few aquatic macrophytes although marine algae may be found on submerged parts of mangroves. Invertebrates (mostly gastropods and crustaceans) are abundant, with their production based on detritus. Marine fishes move into inundated mangrove areas on the rising tide to feed on invertebrates or detritus. However, there are few species that are restricted solely to mangrove areas, mudskippers being an exception. Crocodiles are characteristic top-level predators. Mangrove areas are very productive, exporting large amounts of carbon and contributing to substantial coastal fisheries through energy transfer or acting as 'nursery habitats' for exploited fishes.

Water Bodies in Forests

These aquatic habitats are found in virtually all forest ecosystems throughout the world, thus no distributional information is given. For ponds, lakes, rivers, and streams the forest is restricted to a fringe around or along the edges and the influence of the forest (shading, chemical, and biological inputs) is restricted to these areas. Obviously, the relative effect of the forest on the water body is dependent on the latter's size relative to the height and extent of the forest. Thus, smaller water bodies or those surrounded by large areas of forest may be profoundly influenced whereas large lakes and rivers may be similar to those in unforested areas. Three types of water bodies in forest are described on the basis of their origin and water movement.

Container Habitats (Phytotelmata)

Phytotelmata are water-retaining structures formed by hollows in plant materials. These containers may be holes in tree stems or branches, the leaf axils of plants (particularly epiphytic bromeliads), leaves of pitcher plants, or fruit husks. They are generally ephemeral although some 'tank' bromeliads may have water in them for their entire lives ($>$20 years).

Physicochemical characteristics The volumes of phytotelmata are small (up to 1300 cm^3) and the water contained within them shows no movement. Water quality is strongly influenced by the surrounding plant material. Most contain decaying plant material – leaves, wood, or fruit – and drowned animals. Leachates from this material and the forest canopy make the water acid and rich in organic nutrients. Oxygen concentrations are low because of decaying organic material.

Aquatic biota Algae may be found in phytotelmata that are in bromeliads located in the forest canopy. Aquatic insect larvae are often the dominant animal forms in phytotelmata, particularly flies and mosquitoes. Many of these are specific to particular phytotelm habitats and are not found elsewhere. Microcrustaceans (such as ostracods), gastropods, and aquatic mites are also found. In tropical areas, juvenile and/or adult frogs may be present. Food webs can be based on algae, detritus, or drowned animals.

Ponds and Lakes (Lentic Habitats)

Lakes and ponds are habitats that are enclosed by land with outflows small in comparison to their volume. They also have water movement that is not unidirectional. In the smallest ponds there may be little or no water movement, but in larger lakes wind and/or convection currents create water movement. Lentic habitats may be created by depressions in bedrock and sediment or by barriers and they are fed by a combination of one or more of the following water sources: streams and rivers, groundwater, and rain. Water depth in lakes in forested areas can be far greater than the other aquatic habitats considered in this article, reaching over 700 m for Lake Mjösen in Norway. There is a large range in surface area from tens of square meters to hundreds of square kilometers. Lentic habitats, particularly larger ones, share a number of similarities with marine habitats such as thermal stratification. Lakes can be sporadic, seasonal, or permanent.

Physicochemical characteristics The dominant abiotic factor in all but the shallowest lentic water bodies is stratification. Heating of the surface water (epilimnion) makes it less dense and it floats on top of cooler water underneath (hypolimnion). Mixing depth is dependent mainly on wind action. Stratification affects not only temperature but also oxygen and nutrient levels across the thermocline. Deep lakes are often anoxic below the thermocline. Turnover, where all of the water in the lake mixes, is strongly influenced by latitude. Cold temperate lakes may turn over twice a year, warm temperate lakes once, and tropical lakes daily or occasionally. In deeper lakes light may be rapidly absorbed. The influence of surrounding forests on ponds and lakes is greatest on the water quality entering through groundwater or rivers. Nutrient levels, pH, and organic input are dependent on the type of forest and soil. Effects on shading and temperature are minimal in comparison with streams and rivers.

Aquatic biota An important component of the flora of lakes is plankton. Autochthonous production by phytoplankton is the major source of organic material in large and/or deep lakes. Macrophytes may be found in shallow zones around the edge of the lake and occasionally may be an important source of organic material. There is a clear distinction in many lakes between benthic and pelagic animal communities. Benthic invertebrates include aquatic insects, crustaceans, and gastropods. These latter two groups may be of greater abundance, diversity, and importance than in lotic habitats. Where the hypolimnion is anoxic there are few benthic invertebrates. Benthic food webs are dependent on detrital input. Pelagic invertebrates include high abundance of zooplankton, particularly crustaceans (cladocerans and copepods) and rotifers, dependent on autochthonous phytoplankton. Aquatic insects – water beetles and water bugs – are also found in the pelagic zones. Fish are found in both the pelagic and benthic zones where there is sufficient oxygen. They may be specialized planktivores or generalist detritivores or omnivores. Reptiles, particularly turtles, are common in shallow areas. Wading and piscivorous birds are also conspicuous aspects of the fauna. There appear to be few generalizations possible about differences between lotic water bodies in forested and unforested ecosystems. Small ponds and the fringes of larger lakes may have faunal elements specialized to take advantage of terrestrial input (fruit, leaves, flowers, invertebrates), but these influences rapidly decrease in importance moving away from the shoreline.

Figure 1 Stream in primary forest, Sabah, Malaysia. Photograph courtesy of Keith Martin-Smith.

Streams and Rivers (Lotic Habitats)

These aquatic habitats are characterized by an overall unidirectional movement of water. However, there is considerable heterogeneity within most rivers and streams with areas of fast unidirectional flow (such as cascades, riffles, and runs), slow unidirectional flow (glides and reaches), and multidirectional flow or gyres (eddies, slacks, and pools) (**Figure 1**). These latter habitats may behave as lentic environments. Streams may be ephemeral, only flowing at certain times of year or after heavy rains, or permanent. There is a large size range from a few centimeters in width to a few kilometers for the biggest rivers such as the Amazon. Patterns in physicochemical and biotic characteristics are strongly related to position along the river course (river continuum concept) as well as temperate–tropical differences.

Physicochemical characteristics These parameters vary widely between different types of river. Depending on the geology, morphology, and forest cover of the catchment, there can be large differences in levels of suspended sediment, dissolved nutrients, oxygen, and pH. However, when compared to rivers running through nonforested areas, there are a number of generalities that can be made. Forests intercept and store water so that flows are moderated. Light levels are lower and the spectral composition is different because the forest intercepts much of the incident light. This effect is more pronounced in smaller rivers which may have completely closed forest canopies. Water temperatures are lower for the same reason. Inputs of dissolved, particulate, and large organic matter are greater than in nonforested catchments and have a different elemental composition. In deciduous forests there is a pulse of organic input with leaf fall, either seasonally or related to drought conditions. Thick layers of leaf litter can build up in temperate and tropical rivers providing an additional habitat for animals. Large woody debris is a significant structural aspect of forested rivers with important effects on hydrology (debris dams), nutrient retention and cycling, and animal microhabitat. Large woody debris is introduced into rivers by physical disturbance such as storms or floods and activity of animals, particularly the actions of beavers in northern temperate areas. Forestry activities have pronounced effects on water quantity, quality, sediment, and debris input.

Aquatic biota The aquatic biota of forested streams has been well studied around the world, particularly in temperate areas. Algae and aquatic plants may be present where current velocity is sufficiently low and there is adequate light penetration. Autochthonous production may peak in intermediate-size rivers where there is open canopy and shallow water depth while larger rivers often have floating mats of vegetation. Invertebrates from a wide range of taxonomic groups (insects, crustaceans, molluscs, and annelids in particular) are present although diversity tends to increase with decreasing latitude. Mayflies, stoneflies, caddis flies, dragonflies, beetles, and true flies are the dominant invertebrates in terms of numbers and biomass in many systems. Invertebrate production is dependent on leaf litter input in small streams, although grazing on autochthonous production may contribute in larger streams and rivers. The fauna in the streambed (hyporheic zone) is also an important component of the ecosystem, responsible for nutrient processing among other functions.

Fish and amphibians are generally present in all but the smallest and most ephemeral streams, again exhibiting distinct longitudinal zonation. Diversity increases moving from headwaters downstream and taxonomic composition changes through both species additions and replacements. The trophic structure of the fish community also changes with greater dependence on invertebrates and herbivory in upland streams while omnivory and piscivory are more important in lowland rivers. Additional food sources are available to fishes in forested streams, particularly terrestrial insects and fruit and leaves from trees. In north temperate streams migratory salmonid fishes may provide a large additional trophic subsidy, transferring production from the marine to the freshwater environment.

Reptiles, birds, and mammals may also be present either obligately or facultatively. Many snakes and most turtles spend large amounts of time in watercourses while crocodiles, alligators, and caiman are important predators in subtropical and tropical areas. Beavers are a conspicuous feature of north temperature forested streams with a profound influence on the structure of water bodies through their dam-building activities while otters may be found in temperature and tropical areas. River dolphins are a feature of large tropical rivers as are manatees in Central and South America.

Human Interactions with Aquatic Habitats in Forested Ecosystems

In many parts of the world there are intimate connections between human populations and the aquatic habitats described above. A large proportion of the annual protein intake may be derived from aquatic organisms, mainly fish. In the Amazon and Southeast Asia, floodplain forests support very large artisanal fisheries and human activities are synchronized with particular phases of the hydrological cycle. Very sophisticated methods of capture and exploitation exist to ensure maximum use of resources. For example, in the flooded forest system of Danau Sentarum, Kalimantan, only two of more than two hundred recorded species of fish are not used in some way by the several thousand people dependent on the system (**Figure 2**). Dozens of different fishing gears are used from lift and cast nets through gill nets and seines to large, semipermanent fish traps. Fry of certain large species (catfish and snakeheads) are captured and raised in floating cages where they are fed on smaller species. Highest catches are taken during the falling phase of the hydrological cycle and these fishes are preserved for use during the remainder of the year. Similarly, in northern temperate areas, salmonids from streams and rivers in forests are a vital part of the diet of native peoples.

Figure 2 Human use of aquatic resources in flooded forest, Kalimantan, Indonesia. Photograph courtesy of Keith Martin-Smith.

Conversely, many human activities threaten the integrity of aquatic habitats in forested ecosystems and individual species within them. The most prominent of these are resource overexploitation, habitat degradation from land-based activities (primarily logging), and the introduction of exotic species. Overexploitation of fishes has been documented as human populations increase and/or greater access to water bodies is created. The giant Mekong catfish and the Asian bonytongue are both considered threatened from overfishing. Logging, both selective and clear-cut, alters water quantity, timing, physicochemical parameters, and the aquatic biota. Sedimentation increases dramatically following logging and profoundly alters the ecosystem. Exotic species can also cause major, irreversible changes, with infamous examples including the water hyacinth and Nile tilapia.

While these threats are serious and immediate, they can be overcome if appropriate, sustainable solutions are developed. This will require adequate funding, political will and the application of multidisciplinary approaches.

Further Reading

Brönmark C and Hansson L-A (1998) *The Biology of Lakes and Ponds*. Oxford, UK: Oxford University Press.

Cushing CE, Cummins KW, and Minshall GW (eds) (1995) *Ecosystems of the World*, Vol. 22, *River and Stream Ecosystems*. New York: Elsevier.

Dobson M and Frid C (1998) *Ecology of Aquatic Systems*. Harlow, UK: Longman.

Dudgeon D (1999) *Tropical Asian Streams: Zoobenthos, Ecology and Conservation*. Hong Kong: University of Hong Kong Press.

Ewel KC and Odum HT (eds) (1985) *Cypress Swamps*. Gainesville, FL: University of Florida Press.

Giller PS and Malmqvist B (1998) *The Biology of Streams and Rivers*. Oxford, UK: Oxford University Press.

Goulding M and Barthem R (1997) *The Catfish Connection: Ecology, Migration and Conservation of Amazon Giants*. New York: Columbia University Press.

Goulding M, Smith NJH, and Mahar DJ (1995) *Floods of Fortune. Ecology and Economy along the Amazon*. New York: Columbia University Press.

Junk WJ (ed.) (1997) *The Central Amazon Floodplain: Ecology of a Pulsing System*. Berlin: Springer-Verlag.

Kalff J (2002) *Limnology*. Upper Saddle River, NJ: Prentice Hall.

Kitching RL (2000) *Food Webs and Container Habitats: The Natural History and Ecology of Phytotelmata*. Cambridge, UK: Cambridge University Press.

Lugo AE, Brown S, and Brinson M. (eds) (1990) *Ecosystems of the World*, Vol. 15, *Forested Wetlands*. New York: Elsevier.

Talling JF and Lemoalle J (1998) *Ecological Dynamics of Tropical Inland Waters*. Cambridge, UK: Cambridge University Press.

Taub FB (ed.) (1994) *Ecosystems of the World*, Vol. 23, *Lakes and Reservoirs*. New York: Elsevier.

Williams DD (1987) *The Ecology of Temporary Waters*. Caldwell, NJ: Blackburn Press.

ENTOMOLOGY

Contents

Population Dynamics of Forest Insects

S R Leather, Imperial College London, Ascot, UK

Population dynamics is the study of changes in the number of organisms in populations and the factors influencing these changes. It thus, by necessity, includes the study of the rates of loss and replacement of individuals and of those regulatory processes that can prevent excessive changes in those numbers.

A wide variety of factors can affect the population dynamics of a particular species. These can be divided roughly into two categories. First, the extrinsic or environmental influences on populations, such as temperature, weather, food supply, competitors, natural enemies, diseases, and all possible combinations of the preceding; and second, the interactions between members of the same populations, be these direct or indirect, e.g., intraspecific

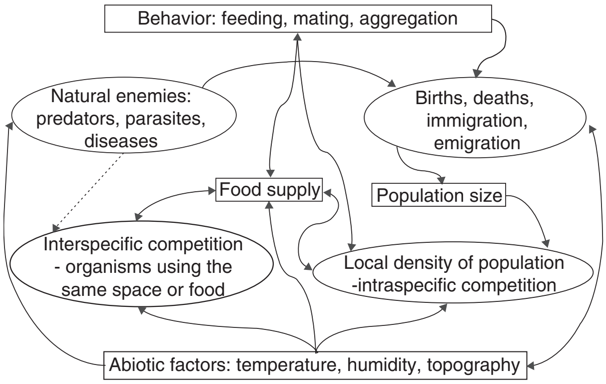


Figure 1 Factors influencing the population dynamics of a forest insect.

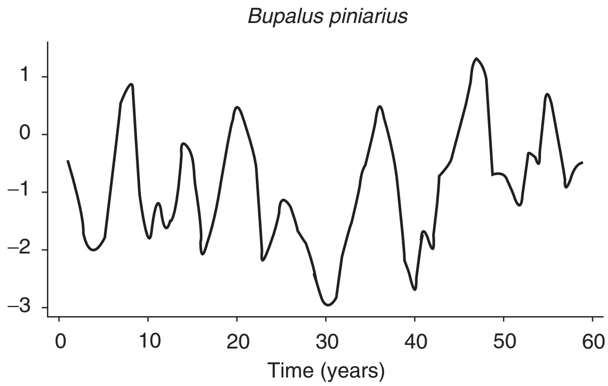


Figure 2 Populations of the pine looper moth, *Bupalus piniarius* (data from the Centre for Population Biology database).

competition, behavioral processes, and aggregation (**Figure 1**).

This article gives an overview of the main factors affecting the population dynamics of forest insects and explains how population cycles arise and are maintained.

Detecting Patterns and Identifying Processes

Perhaps the fundamental rationale behind the many published studies on population dynamics is the desire that population ecologists have for detecting and explaining patterns. The question that they are really trying to address, should they be honest, is why some species of insect are relatively scarce whilst others are extremely abundant and why some of the abundant species show cycles of abundance and relative scarcity. Cyclical fluctuations in population size are commonly seen in animal populations, with classic examples from mammals and birds, but the most dramatic examples are, without doubt, those shown by the invertebrates, and in particular, forest insects. The spectacular effects of defoliating forest Lepidoptera with their ability totally to defoliate hundreds of hectares of trees and their equally graphic population cycles have resulted in them becoming textbook examples (**Figure 2**). One of the most controversial debates of the past was whether population cycles were driven by abiotic factors or biotic interactions. At the moment the general consensus is that biotic factors, in particular density-dependent processes, are the major forces driving insect populations. The fact that the jury has voted for density-dependence does not, however, mean that the mechanisms that drive these population cycles are either fully understood or agreed upon.

As forest insects are of general and economic interest and generally occur in long-lived environments, there has been a tendency for field data to be collected over many years. The resulting time series (**Figure 2**) are often analyzed using sophisticated mathematical techniques. For example, autocorrelation analysis is used to describe the effects of a lagged population density and can also provide an indication of the periodicity of the time series. Partial autocorrelation, on the other hand, can provide an indication of the respective roles of direct and delayed density-dependent processes within a population. Whichever analysis is undertaken, the usual outcome is that the majority of forest insects, in particular the Lepidoptera, show periodic cyclical dynamics oscillating around a 6–11-year period, with delayed density-dependent effects being the most common driving variable. Although these mathematical and statistical approaches to exploring long-term data series are useful in providing an overview of the ecological processes and revealing hidden patterns, the mechanisms that drive the patterns are what most ecologists are really interested in discovering.

Although abiotic factors such as weather, plant stress, and site factors have all been implicated as contributing to, if not driving, the oscillatory behavior of forest insects, it is generally agreed that biotic factors, in particular natural enemies and the insect's host plants, are the major factors causing the population cycles. Weather and other abiotic factors undoubtedly play a major supporting role in modifying the peaks and troughs of the populations, if not in their timing and frequency.

Top-down versus Bottom-up

During the latter part of the twentieth century the acrimonious nature of debate over the factors enabling the regulation of herbivorous insect populations derived from the peculiar and partisan views of the importance of the host plant versus the natural enemies of the herbivore, i.e., whether the population was driven from the bottom up by the effects of the plant or from the top down by the impact of the natural enemies. These positions were at one time deeply entrenched and I remember as a postgraduate student being deeply sceptical about the relevance of natural enemies in agroecosystems and crop protection, despite the undoubted success of some biological control operations. Ecologists tended to study only one part of the system and ignore the other as being largely irrelevant – the emphasis was on ditrophic rather than on multitrophic interactions. Fortunately, most ecologists now agree that there is room for both top-down and bottom-up forces to act together to influence the populations of insect herbivores. There is, however, still much debate as to which is the most important and whether the relative importance of one over the other is fixed in a particular system or varies according to environmental conditions.

Insect population biologists working in forest ecosystems could perhaps be excused for espousing the top-down view, as it is well known that forest Lepidoptera are attacked by a large number of natural enemies, in particular Hymenopteran and Dipteran parasitoids. Parasitoids are distinguished from parasites in that their host usually dies as a result of their attack and that some parasitoids also directly predate their hosts as well as laying their eggs inside or next to them. Parasitoids do have an important role in the population dynamics of forest insects and, in many cases, as in small ermine moths, appear to be the major cause of the cyclical crashes in population seen in these insects.

The role of predators is less well supported. There is good evidence that predators have an effect on the population dynamics of forest insects, e.g., outbreaks of the pine beauty moth, *Panolis flammea*, in northern Scotland are associated with a lack of generalist predators such as carabid beetles and spiders; other forest Lepidoptera, notably the Douglas-fir tussock moth and the spruce budworm in North America, are subject to substantial predation by these agents. Evidence for the action of predators as a causal mechanism for cyclical population fluctuations is in shorter supply. The predation of pine sawfly cocoons by small mammals (*Sorex* spp.) has been postulated to influence the cyclical population dynamics of Diprionid sawflies in northern Europe and predators are claimed to be the driving mechanism causing the oscillatory behavior of southern pine beetle populations in the USA.

An important natural enemy complex that may be responsible for the maintenance of population cycles in forest insects are the insect pathogens: viruses, bacteria, protozoa, and fungi. For example, nuclear polyhedrosis viruses (NPVs) and the granulosis viruses have dramatic physical effects on forest Lepidoptera and Hymenoptera and appear to be responsible for sudden population crashes in these organisms. In addition, they have been used worldwide in attempts to control forest insect pests. Until recently, however, it was difficult to prove that they had a major role to play in the induction of population cycles. New developments supported by simulation modeling indicate that if pathogens act at the same time as resource competition then population cycles are more likely to be generated.

All of the preceding are so-called 'top-down agents.' What about those operating from the bottom up? It may appear that the plant can have little influence on the generation of population cycles. It seems intuitively obvious that plants are inherently more or less susceptible/suitable to attack by a particular herbivore species. Plant breeders have used this knowledge for a long time when seeking to breed insect- and disease-resistant crop plants as part of pest management systems. There are, however, ways in which the host plant can influence the development of population cycles in forest insects. First, even if the nutritional quality of the host plant remained unchanged, the build-up of the herbivore population on the host plant can result in competition for resources, either through depletion of the food source or by the increase in the number of larvae feeding on a finite host plant. Second, the physiological state of trees (and other plants) is not static, and their susceptibility/suitability as food plants both within and between years can be changed. Insect feeding, for example, can in some cases induce rapid changes in plant physiology and biochemistry (rapid induced responses). The biochemistry of the leaves can change detrimentally for the insect and leave the equivalent of a nasty taste in the insect's mouth, resulting in its either ceasing feeding altogether or moving to a new leaf or site on the same leaf. Although this phenomenon has been demonstrated on many occasions, it is not likely to influence cyclical population behavior. A more likely candidate is the so-called delayed induced responses where attacked trees become more resistant or less palatable to the insect herbivores the following year. The effect is mediated through the mother, in that the changes in food quality and an increase in the degree of larval crowding cause reductions in growth and developmental rates, resulting in smaller, less fecund adults. A reduction in the fitness of individual adults can markedly affect the population dynamics. In other words, the population cycles are driven by long time lags by the action of density-dependent factors, i.e., larval quality is impaired by insect-induced changes to the host plant, the insect population decreases, and the quality of the host plant slowly improves or returns to normal, at which point individuals within the insect population become fitter (faster-growing, larger and more fecund) and the cycle starts anew.

The classic example of this phenomenon is the larch bud moth, *Zeiraphera diniana*, the larvae of which defoliate *Larix decidua* and *Pinus cembrae* in the European Alps. Outbreaks of the larch bud moth occur at regular 9-year intervals in the Engadine valley. The cycles are hypothesized to be caused by host-induced changes in the quality of the larvae. When defoliated by the moth larvae, the raw fiber content of the new larch needles increases considerably; this has a strong negative effect on larval survival and female fecundity. It can take several years for the raw fiber content to return to normal and this in itself constitutes a delayed negative-feedback mechanism which in theory could be sufficient to generate regular population cycles. Mathematical modeling and many years of observation appear to support this hypothesis. Gypsy moth, western tent moth, and autumnal moth populations also show similar responses to the quality of their host plant in that host-mediated maternal effects affect the quality of their offspring and may generate cyclical population dynamics. There is, however, some debate as to the generality of these results and evidence of whether the maternal carry-over effects can generate the cycles on their own is equivocal.

Multitrophic Interactions

The situation becomes more complex when the top-down forces meet those operating from the bottom up: the tritrophic or multitrophic interactions, between the predators, parasites, and other natural enemies, the herbivores and their host plants. This can be expressed in a number of ways, but perhaps one of the best known is the sublethal plant defenses paradox. The paradox resides in the fact that the host plant gains more by being partially resistant to the insect herbivore than by being immune. To possess total immunity against an insect herbivore requires a large investment in defenses, be this through antibiosis, antixenosis, or architectural attributes such as spines, thick cuticles, and resin flow. Any resources invested in defense are of course not available for growth and reproduction and this imposes a fitness cost. If, on the other hand, the plant reduces its investment in defenses, it has more reproductive currency to spend. By being partially resistant (i.e., partially susceptible), however, the insect herbivore is able to consume it, thus reducing reserves available for growth and reproduction. On the face of it this is potentially reducing the fitness of the plant. If there was a simple trade-off between the plant's investment in defenses (carbon-based) and the amount likely to be eaten by the herbivore (nitrogen-based), there would be no paradox. Put simply, the insect herbivore requires x amount of nitrogen to complete development and any reduction in plant nutritional quality implies that the insect needs to eat more plant to obtain the required amount of nitrogen to complete its development. As the insect is not killed or repelled by the plant, it remains on the plant and continues to feed until it reaches adulthood or its own reproductive threshold. Hence the paradox. By being less suitable as a food source, the plant appears to be encouraging the insect to eat more of it. This does not appear to be the best form of defense. Bear in mind, however, that the general effect of sublethal plant defenses is either to slow down the growth of the insect or, for example as in the case of rapidly induced defenses, to cause the insect to change feeding site more often. These effects have the same net outcome. The insect herbivore becomes more vulnerable to its natural enemies. In the case of reduced insect growth rates, it remains in a vulnerable (less developed) stage for longer and thus has more chance of encountering a predator or parasitoid. In the case of the rapid-induced defense scenario, where the leaf becomes less palatable, the insect moves from one feeding site to another more often and spends more time exposed on the leaf (caterpillars often feed in bouts, coming out from sites within the inner parts of the plant foliage to feed, and then returning to the relative safety of the area near the main stem). The overall result is more journeys back and forth and thus more chance of encountering a predator or parasitoid. In addition, by changing feeding sites more often, the insect makes more holes in the leaves and this acts as a 'supercue' for vision-dependent predators such as birds.

Yet another effect of sublethal plant defenses is that the insect herbivore, feeding as it does on a suboptimal diet, is more likely to become stressed and more susceptible to infection by pathogens, e.g., fungal and viral diseases, although in some cases it is possible that the insect is able to sequester plant chemicals that inhibit virus infection.

Population Cycles

So how do these top-down and bottom-up forces interact with the insect herbivore to produce the population cycles seen in so many forest Lepidoptera? Populations that cycle are characterized by highs (peaks) and lows (troughs) in abundance. As foresters usually first become aware of defoliating insects when they outbreak, it is appropriate to start our consideration on a peak, when the population is at its maximum.

The herbivore population is at its peak, and the trees are likely to be showing marked signs of defoliation, either totally stripped or at least half their foliage removed. The nutritional quality of the plants for the insect is at its lowest, either because of a scarcity of foliage and/or because of induced defenses. Interspecific competition between the insects is markedly higher than before and the caterpillars are small and stressed. Their growth rates will be low and this will make them susceptible to natural enemies. Natural enemy populations are now increasing rapidly and parasitism and disease rates are now extremely high. Any caterpillars that survive to pupate will be small and, if they survive the winter, will produce even smaller and less fecund adults than before. The herbivore population now begins to decline steeply. The natural enemy populations are now at their highest levels and competing amongst themselves. The nutritional quality of the trees is still very low, although consumption of the foliage is lower than before as there are now fewer caterpillars. The caterpillars, although likely to be growing and developing slightly faster than the season before, are now greatly outnumbered by their natural enemies. The herbivore population crashes and they virtually disappear from the forest. The following season caterpillar numbers are extremely low indeed. New foliage will be available and the nutritional quality will be improving. Food is thus in relatively plentiful supply. Most of the natural enemies will fail to find suitable hosts or prey as the herbivore population is so low.

The natural enemy populations now crash. The following year, the few emerging herbivore adults are able to exploit an underutilized food resource and pick egg-laying sites likely to maximize offspring fitness. The emerging caterpillars thus find themselves with a plentiful and relatively defenseless source of nutrition. Their environment is relatively competition-free and consequently they are able to grow and develop rapidly, attaining relatively large sizes and hence, after pupation, producing large and fecund adults. Natural enemy populations are almost nonexistent and, as the herbivores are likely to be widely dispersed and uncommon, predation, parasitism, and disease are also likely to be very low. The herbivore population will thus start to increase. However, as the herbivore population increases, the nutritional quality of the host plant begins to decrease, first perhaps by the induction of plant resistance but also by depletion of the resource as more and more foliage is removed by the feeding caterpillars. Interspecific competition is also likely to influence the quality of the herbivore. As a result the larvae will be smaller and less well defended, and will grow and develop more slowly. After pupation, the emerging adults will be smaller and less fecund. The effects of the levels of natural enemies (predation, parasitism, and disease) will also be more marked. The herbivore population, although composed of poorer-quality individuals, will continue to increase, but at a slower rate and the herbivore population reaches its peak as the combined effects of natural enemies, host quality, and insect quality have their greatest effect and then the cycle starts again.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Bark Beetles; Defoliators; Foliage Feeders in Temperate and Boreal Forests; Sapsuckers. **Health and Protection**: Integrated Pest Management Principles. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Bonsall MB, Godfray HCJ, Briggs CJ, and Hassell MP (1999) Does host self regulation increase the likelihood of insect–pathogen population cycles?. *American Naturalist* 128: 228–235.

Dempster J and McLean IFG (eds) (2000) Insect Populations in Theory and Practice. Dordrecht, The Netherlands: Kluwer Academic.

Dwyer G, Dushoff J, Elkinton JS, and Levin SA (2000) Pathogen-driven outbreaks in forest defoliators revisited: building models from experimental data. *American Naturalist* 156: 105–120.

Ginzburg LR and Taneyhill DE (1994) Population cycles of forest Lepidoptera: a maternal effect hypothesis. *Journal of Animal Ecology* 63: 79–92.

Hanski I (1987) Pine sawfly population dynamics – patterns, processes, problems. *Oikos* 50: 327–335.

Haukioja E (1991) Induction of defenses in trees. *Annual Review of Entomology* 36: 25–42.

Herms DA and Mattson WJ (1992) The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67: 283–335.

Hunter MD, Varley GC, and Gradwell GR (1997) Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Sciences USA* 94: 9176–9181.

Mason RR, Jennings DT, Paul HG, and Wickman BE (1997) Patterns of spider (Araneae) abundance during an outbreak of western spruce budworm (Lepidoptera: Tortricidae). *Environmental Entomology* 26: 507–518.

Myers JH (1990) Population cycles of western tent caterpillars: experimental introductions and synchrony of fluctuations. *Ecology* 71: 986–995.

Price PW, Bouton CE, Gross P, *et al.* (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* 11: 41–65.

Solomon M (1969) *Population Dynamics*. London: Edward Arnold.

Speight MR, Hunter MD, and Watt AD (1999) *Ecology of Insects: Concepts and Applications*. Oxford, UK: Blackwell Science.

Turchin P, Taylor AD, and Reeve JD (1999) Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* 285: 1068–1071.

Watt AD, Leather SR, Hunter MD, and Kidd NAC (1990) *Population Dynamics of Forest Insects*. Andover, UK: Intercept.

Foliage Feeders in Temperate and Boreal Forests

D Parry, State University of New York, Syracuse, NY, USA

D G McCullough, Michigan State University, East Lansing, MI, USA

Introduction

Insect consumers of tree foliage comprise one of the most abundant and diverse feeding guilds in forest ecosystems. Known as folivores, this guild is integral to the structure and functioning of forests. Folivores influence vital ecosystem processes in forests, including nutrient turnover, competition among plants, and stand structure. In addition, these insects are critical sources of food for many invertebrate and vertebrate predators. In this article, we will address foliage-feeding insects that affect trees in temperate and boreal forests. In these ecosystems, an estimated 10–30% of the total leaf area is annually removed by leaf-chewing forest insects. In some forest types, defoliating insects strongly influence productivity and the long-term dynamics of the ecosystem. Foliage-feeding insect species have little effect on tree health in most years. During outbreaks of some insect defoliators, however, the entire canopy can be consumed, sometimes for several years in succession. While outbreaks may cause significant economic harm by accelerating tree mortality, reducing productivity and increasing fire risk, they may also play an important long-term role in maintaining healthy forests.

Diversity

In this section, we focus on folivores with chewing mouthparts, which represent the vast majority of insects feeding on the leaves of hardwood trees (deciduous angiosperms) and the needles of conifers (gymnosperms). The forest defoliator guild is comprised of insects from several different orders. The greatest diversity of species is found within the order Lepidoptera. Nearly all larval Lepidoptera are herbivorous whereas the adults may imbibe fluids such as nectar or, as in many economically important species, may not feed at all. The sawflies (Symphyta), a relatively primitive group of Hymenoptera, are also important foliage feeders. Like the Lepidoptera, larval sawflies are herbivorous while adults generally do not feed. In addition to sawflies, leaf-cutting ants (family Formicidae) are another group of Hymenoptera that feed on foliage. While not important or diverse in temperate regions, leaf-cutter ants are the dominant herbivore in many tropical forests. Among the beetles (order Coleoptera), the diversity of leaf-feeders is richest in the large families Chrysomelidae and Curculionidae. Both adults and larvae in these families feed on foliage. Several other insect orders also contain species that can function as forest defoliators. These include grasshoppers, crickets, and walking-sticks from the order Orthoptera, and several families of flies (order Diptera). Other guilds of tree-feeding insects, such as sap-feeders and shoot borers, can also cause defoliation but will be described in other articles (*see* **Entomology**: Defoliators; Sapsuckers).

Feeding Ecology

Folivores with chewing mouthparts can be partitioned based on their general feeding type. Three types are generally recognized: free-feeding, shelter-feeding, and leaf-mining. Insects that free-feed consume leaf tissue openly. Species utilizing this type of feeding may consume all parts of the leaf (many caterpillars, sawflies, and orthopterans) or may avoid veins and other structural tissue (shot-hole, window-feeding, or skeletonizing). Skeletonizing is characteristic of chrysomelid beetles as well as some caterpillars and sawflies. Because free-feeding species are exposed to predators as they forage, many have adaptations, that may reduce their risk of mortality from these natural enemies. These include high mobility, nocturnal feeding, cryptic coloration, sequestration of toxins, physical defenses such as urticating or stinging hairs, or stereotyped defensive behaviors like regurgitation, head flicking, or dropping immediately to the ground upon sensing danger.

Another common feeding strategy is shelter-feeding. Shelter-feeding species may enclose and feed on foliage within a silk structure, or may use silk to roll leaves or to tie leaves or needles together. Enclosures are often used by gregarious species including fall webworm (*Hyphantria cunea*) and ugly-nest caterpillar (*Archips cerasivorana*). Many solitary species of Lepidoptera, as well as some sawflies, create tubes or shelters by leaf-rolling or tying. These structures provide a concealed place for the larva to rest and feed. Leaf-rollers and leaf-tiers tend to have lower mobility than free-feeders and fewer species have evolved physical or chemical defenses. Instead they rely on reduced visibility to escape natural enemies. Some species have evolved behaviors thought to lower the risk of detection by parasitoids that rely on chemical signals to find their hosts. For example, a number of lepidopteran leaf-rollers eject their frass (feces) from the feeding tube, often for considerable distances, which reduces the scent profile of the caterpillar.

Leaf-mining represents another type of folivory. Insects that mine leaves or needles are usually small and dorsoventrally compressed, an adaptation for feeding between the upper and lower layers of the leaf epidermis. Leaf-mining requires a more intimate association with the host plant and specific behaviors may be required to avoid host defensive responses such as leaf-shedding, withdrawal of nutrients, or increased concentrations of secondary chemicals. These behaviors can be critical as many leaf-miners utilize only a single leaf over their lifespan and cannot mitigate unfavorable conditions by moving. Several families of Lepidoptera, sawflies (Tenthredinidae), the dipteran families Agromyzidae and Anthomyiidae, and the beetle families Chrysomelidae, Buprestidae, and Curculionidae have all adopted this life-history strategy. Folivores may utilize one feeding method when small, while switching to another feeding strategy in later larval stages. For example, spruce budworm (*Choristoneura fumiferana*) larvae may mine needles in the early larval stages, but utilize a needle-tying feeding strategy as they become larger.

Population Dynamics

The population dynamics of forest-defoliating insects have long been of particular interest to ecologists. The vast majority of this research has focused on a relatively small group of species characterized by explosive changes in population density known as outbreaks. This bias is primarily due to the spectacular nature of outbreaks and the potential of these species to cause economic harm. Because factors important in the dynamics of outbreak species may not necessarily be the same for the vast majority of leaf-feeding forest insects that never outbreak, we must be cautious in generalizing from studies of outbreak species. In outbreaking species, populations increase from virtually undetectable levels to densities that defoliate entire forests, often in only a few generations. While outbreaks occur at irregular intervals in some species, there are a fascinating subset of species whose populations rise and fall at regular intervals, known as cycles. A number of our most economically damaging species fit this profile.

Life-History Traits

Several studies have attempted to assess whether or not outbreaks are a property of particular life-history attributes found in some forest insects. Among Lepidoptera, for example, gregariousness, flightlessness, egg-clustering, low host plant specificity, and nonfeeding adults are all found in greater frequency in species known to have outbreaks. However, there does not appear to be either a single trait or a suite of overarching traits that are uniformly associated with species that outbreak. All of the above traits can be found in species which do not outbreak. In addition, species such as the forest tent caterpillar (*Malacosoma disstria*), larch budmoth (*Zieraphera diniana*), autumnal moth (*Epirrita autumnata*), budworms (*Choristoneura* spp.), and gypsy moth (*Lymantria dispar*) outbreak in only portions of their ranges, suggesting that alone, life-history characteristics are insufficient to explain outbreak dynamics.

Population Regulation

Regardless of whether a species is prone to outbreak or not, there are three forces that influence the density and dynamics of populations: (1) top-down, driven by organisms in trophic (feeding) levels above the folivore; (2) bottom-up, the influence of species in trophic levels below the folivore; and (3) horizontal, competitive interactions with other herbivores. The relative importance of these factors is likely species-specific. Historically, top-down and bottom-up factors were considered separately, but there is increasing recognition that they function in tandem to influence population dynamics. Communities of leaf-feeding insects were also thought not to be structured by competition, a view that is less tenable when indirect competitive interactions such as those mediated through changes in host plant quality or through shared natural enemies are considered.

Top-down regulation of herbivorous insect populations is driven by a suite of organisms collectively called 'natural enemies.' Natural enemies of forest insects include invertebrate and vertebrate predators, parasitoids, and pathogens. Important invertebrate predators include pentatomid bugs (Hemiptera), ants and wasps (Hymenoptera), spiders (Arachnida), and carabid beetles (Coleoptera). Insectivorous birds and small mammals such as mice and shrews are examples of important groups of vertebrate predators. Foliage-feeding insects are susceptible to many pathogenic organisms, including viruses, bacteria, fungi, and protozoans. In addition, they are attacked by a staggering diversity of parasitoids. The vast majority of parasitoids are found within two superfamilies of Hymenoptera, the Ichneumonoidea and Chalcidoidea, and a large and diverse family of Diptera, the Tachinidae. In general, the larvae of parasitoids develop within or sometimes on the body of a host species. Parasitoids often possess remarkable adaptations for locating hosts and for circumventing the immune system of their insect victims. Once the developing parasitoid completes larval development, the host is usually killed.

The relative importance of natural enemies varies among folivores and may also vary within a species in different parts of its range, or at different population densities. For example, in the gypsy moth, vertebrate predation on pupae and large larvae by white-footed mice is important at low population densities whereas a nuclear polyhedrosis virus (NPV), a pathogen, dominates mortality in many outbreak populations. In other species, such as tent caterpillars and budworms, specialist parasitoids may play an integral role in the cyclical rise and fall of population densities.

For leaf-feeding insects, the host plant is the primary bottom-up factor influencing their populations. Trees are not passive recipients of herbivory. Indeed, millions of years of evolution have led to numerous physical and biochemical traits that confer some degree of resistance to folivores. Concentrations of primary compounds important to insects such as water and nitrogen, secondary compounds such as tannins and terpinoids, and physical properties such as toughness vary among leaves on an individual tree, among trees, and across entire forested landscapes. Foliage quality for herbivores also changes seasonally and is generally highest in the spring. As current-year needles or new leaves fully expand, the concentration of indigestible fiber and lignin increases. New growth on conifers is of much higher quality for many foliage-feeding insects than needles retained on the tree from previous years. Thus, folivorous insects encounter great temporal and spatial variation in the quality of leaves on which they feed. To counter this, insects have evolved detoxification mechanisms, feeding behaviors, and/or restrict their feeding to specific times of the season such as early spring.

Trees may respond actively or passively to insect feeding or may simply be tolerant to some level of leaf loss. Active responses occur rapidly following damage and these wounding responses often involve the production of compounds such as proteinase inhibitors or polyphenol oxidases that deter feeding or reduce the nutritional value of the leaf to subsequent herbivores. Such responses can be site-specific or can be rapidly propagated throughout the plant. The production of these compounds may involve complex biochemical signaling pathways that are only just beginning to be understood.

Trees also exhibit passive responses that result in deterioration of the nutritional value of a leaf following defoliation. While not as rapid as the wounding responses above, these effects may last for a year or more. Water and nitrogen are often reduced in damaged leaves or in trees that were severely defoliated in the previous year. In addition, levels of some carbon-based secondary compounds such as tannins may be elevated in the same trees. The combination of lower concentrations of primary nutrients and higher concentrations of secondary compounds may reduce the performance of folivorous insects on these trees. These long-term responses can reduce insect fecundity and growth for several years. These effects have been well documented for autumnal moth on mountain birch, forest tent caterpillar on aspen, and black-marked spear moth (*Rheumaptera hastata)* on paper birch.

Phenology is the seasonal timing of specific growth, developmental, and reproductive processes. In trees, the phenology of budbreak, flowering, or leaf drop, is recognized as being critical in determining the density of some foliage-feeding insect populations. For example, jack pine budworm (*Choristoneura pinus*) larvae survive by feeding in pollen cones in the spring until new needles, their preferred food, begin to expand. Many other spring-feeding folivores must time their hatch to coincide with budbreak, when primary nutrients such as water and nitrogen are high, many secondary compounds are low, and physical properties such as toughness are at their seasonal minima. Hatching earlier than budbreak may lead to starvation, whereas hatching late may lead to lowered fecundity, longer development times, and higher mortality.

Intra- and interspecific differences among trees in phenology and phytochemistry can shape foliage-feeding insect communities in both time and space. For example, the population density of folivores feeding on white and black oaks varies across the landscape with greater diversity and abundance on trees with lower tannin levels. Similarly, the phenology of individual trees can determine the density of a number of different folivores including winter moth (*Opherophtera brumata*) on oak and large aspen tortrix (*Choristoneura conflictana*) on aspen. For both species, trees whose buds break in synchrony with the emergence of larvae in spring support higher populations than trees that leaf out prior to larval emergence or after it has already occurred. Slow growth of insects stemming from poor phenological synchrony with the host tree may lead to increased mortality from parasitoids or predators if the insect remains in a vulnerable stage for longer periods of time, as has been shown for tent caterpillars and autumnal moth. Even extreme generalist folivores like gypsy moth have a hierarchy of preferences for different tree species, based primarily on phenology and phytochemistry.

In addition to the direct influences mentioned above, trees may indirectly influence the population dynamics of folivores. Alterations to relationships between a herbivore and its natural enemies mediated by the host tree are known as tritrophic interactions. For example, leaves damaged by feeding folivores may release volatile chemicals that predators or parasitoids can use as cues to locate the herbivore. There are both intraspecific and interspecific differences in the type and strength of volatiles released by trees, contributing to variability in the susceptibility of folivores to predators and parasitoids. Tree chemistry can also alter the susceptibility of folivores to pathogens. Gypsy moth larvae are less likely to succumb to NPV when feeding on oaks which are rich in hydrolyzable tannins than when feeding on other species with lower concentrations such as aspen. In some, but not all studies, increases in tannins following defoliation of oaks reduce susceptibility of gypsy moth to NPV.

Another indirect influence of trees on herbivore populations can occur through so-called 'maternal effects' where the foliage quality experienced by the parental generation can have significant effects on the performance of their offspring. The influence of the environmental quality experienced by the parental generation on offspring is well documented for many organisms, including some foliage-feeding insects. An example is the change in yolk provisioning of gypsy moth eggs after the parental generation has experienced defoliation-induced declines in tree quality. While these effects have been documented in some studies of gypsy moth, they were not evident in several other folivores and their importance in population dynamics continues to be debated.

Population Cycles

A fractious debate in ecology during the mid-twentieth century focused on the relative role of density-dependent and density-independent factors in population dynamics. Density-dependent factors have effects that are a function of the size of a population. Such factors can act immediately or with a lag time or delay in the response. It is now generally accepted that cycles can only occur if a density-dependent process has sufficient lag time. Any process that functions in a delayed density-dependent manner can drive population cycles. Mathematical models have suggested that natural enemies, maternal effects, and host plant quality can all cause population cycles, although it has proved difficult to show whether or not any one density-dependent factor is critical to population cycling.

A long-standing hypothesis for explaining forest insect outbreaks was that periods of favorable climate allow populations to increase. This was thought to occur because the herbivore population grows faster than its natural enemies during favorable periods or because plant quality changes in a way that is advantageous to the herbivore, either through reduced defenses or increases in nutritive value. Although it is possible that periods of favorable weather could be driving the dynamics of species which outbreak at irregular intervals, weather patterns are too random (stochastic) to be responsible for the regular cycles that characterize the dynamics of many important defoliators.

Forest insects such as jack pine and spruce budworms, forest tent caterpillar, larch budmoth, and large aspen tortrix are prone to region-wide, synchronous outbreaks, some spanning distances of several hundred kilometers or more. The Moran effect, originally used to describe the synchronization of lynx populations across large regions of Canada, may offer an explanation for the remarkable degree of synchrony among these widespread populations. It postulates that an extrinsic factor such as weather may act to synchronize populations across a region so that they fluctuate in unison. In this case, the cycling of individual insect populations is driven by intrinsic density-dependent factors, but is brought into regional synchrony through Moran-effect processes.

Some have also proposed that dispersal among populations could also be responsible for synchronization. Certainly, large dispersals of adults from outbreak populations have been documented for conifer-feeding budworms. However, while dispersal among populations may account for synchrony over a small scale, the outbreak areas that are affected greatly exceed the dispersal capabilities of individual insects. In addition species such as Douglas-fir tussock moth (*Orygia pseudotsugata)*, spring canker worm (*Paleacrita vernata*), and gypsy moth also exhibit strong regional synchrony despite very poor dispersal abilities.

Impacts of Foliage-Feeding Insects on Trees

Effects of insect defoliation on tree health vary considerably depending on the species of tree, how much foliage is consumed, and the general health or vigor of the tree. In addition, the timing of the defoliation and the age or location of the affected foliage can also influence the severity of impact.

Hardwood and conifer trees differ greatly in their ability to tolerate severe defoliation. Healthy hardwood trees can generally recover from defoliation, even if 100% of the foliage is consumed. Most hardwood trees are able to produce a second set of leaves a few weeks after the initial foliage is lost – a process referred to as 'reflush.' As a rule, hardwood trees do not reflush until roughly 60% or more of the canopy has been consumed or otherwise damaged. The second set of leaves is typically smaller and less photosynthetically active than the original leaves, but they enable the tree to produce an adequate amount of energy to survive the winter and leaf out the following spring. Of course, there is a cost when a tree has to reflush. Carbohydrates and other nutrients must be utilized to form the second set of leaves, depleting the stored energy available to the tree and substantially reducing its radial growth. While healthy hardwood trees can generally reflush for 2 or 3 consecutive years, the stress eventually becomes too great. Trees that have sustained heavy defoliation for more than 2 or 3 years often succumb to secondary pests such as bark beetles, phloem-borers or root rot pathogens. These secondary pests rarely affect healthy trees but are able to take advantage of stressed trees. Hardwood trees that experience other stresses such as extended drought, wounds, or poor growing conditions are less likely to tolerate and recover from insect defoliation.

Unlike hardwood trees, conifers produce only a single set of buds in mid to late summer and cannot reflush in response to defoliation. Conifer trees that sustain complete defoliation will die and moderate to heavy defoliation increases the vulnerability of conifers to bark beetles and other secondary pests. Conifer forests killed by defoliating insects or associated secondary pests can be highly susceptible to wildfire, especially when conditions are dry. Some conifer feeders, such as jack pine budworm and yellow-headed spruce sawfly (*Pikonema alaskensis*), feed more heavily on needles at the top of the tree than in the middle or lower portion of the canopy. This can result in top-kill – a condition in which the tree survives and continues to grow radially, but the leader and upper whorls of branches die.

Because foliage-feeding insects reduce leaf area, photosynthesis is reduced during defoliation. This, in turn, leads to a decrease in the rate of radial growth. Most people are familiar with the annual rings of spring and summer wood growth that are visible in cross-sections of the trunk and branches of trees. Healthy trees produce wider rings and grow at a faster rate than unhealthy trees. When a tree loses more than about 10–20% of its canopy, less energy will be available for wood production and growth rings will be narrow. When defoliation exceeds 50–60% of the canopy, little or no radial growth will occur that year. Radial growth rates of hardwood trees may recover the following year while growth rates of conifer may only recover after 2 years or more.

Insects that feed in the spring or early summer generally have more effect on tree vigor than insects that feed later in the summer. Early in the year, young, succulent leaves or needles function as a sink for stored carbohydrates and nutrients. When young foliage is consumed by insects, the tree effectively loses that investment before the tissue begins to produce energy through photosynthesis. In contrast, defoliation in the latter part of the summer, when trees are beginning to prepare for winter dormancy, generally has little effect on tree health. Fall webworm and orange-striped oakworm (*Anisota senatoria*) typically cause less harm to trees than species like gypsy moth or forest tent caterpillar simply because they feed later in the year. Insects that feed on current-year foliage of conifers such as jack pine budworm or red-headed pine sawfly (*Neodiprion lecontei*) are generally more harmful than are insects such as European pine sawfly (*N. sertifer*) that feed primarily on needles 1 year old or more.

While severe defoliation can reduce radial growth, cause top-kill or tree death, foliage-feeding insects can also increase the overall long-term health of a forest. Suppressed or diseased trees are usually more vulnerable to mortality during outbreaks of defoliators. When these trees succumb, space, water, light, and nutrients are freed up for the healthier trees that survive the outbreak. Forest entomologists sometimes refer to this pattern as a 'thinning from below,' because mortality of the less vigorous trees can lead to increased rates of growth and productivity for the forest as a whole. This regulation of productivity by foliage-feeding insects is an important part of the long-term dynamics of many forest ecosystems.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Bark Beetles; Defoliators; Population Dynamics of Forest Insects; Sapsuckers.

Further Reading

Cappucino N and Price PW (eds) (1995) *Population Dynamics: New Approaches and Syntheses*. San Diego, CA: Academic Press.
Barbosa P and Wagner MR (1989) *Introduction to Forest and Shade Tree Insects*. San Diego, CA: Academic Press.
Haukioja E (2003) Putting the insect into the birch–insect interaction. *Oecologia* 136: 161–168.
Schowalter TD (2000) *Insect Ecology: An Ecosystem Approach*. San Diego, CA: Academic Press.

Defoliators

H F Evans, Forestry Commission, Farnham, UK

Published by Elsevier Ltd., 2004

Introduction

The dictionary definition of a defoliator is 'an insect that strips the leaves from plants.' This serves as a useful broad statement of both the nature of the biotic agent and of its overall impact on its primary target resource on trees. Its effects on tree growth and structure are manifested through removal of photosynthetic and transpiration tissues from trees, thus compromising the ability of the tree to grow, respire, control moisture loss, etc. Defoliation, therefore, is rightly regarded as detrimental to the plant but the severity of effects depends very much on both the timing and nature of defoliation. In the brief description in this article, defoliation is taken to mean the damage or removal of leaves by direct feeding, rather than the indirect defoliation that can occur from damage to other parts of the plant leading to browning of leaves and indirect loss.

Defoliating Species

Leaf feeders are found in a number of insect orders, particularly in the moths (Lepidoptera) (**Figure 1**), sawflies (Hymenoptera), grasshoppers (Orthoptera), and beetles (Coleoptera). Some feed on tree foliage exclusively in the larval stage, while others can include adult only or both adult and larval feeding. In all cases, however, timing of insect activity to coincide with the most suitable stage of leaf development and tree growth is critical. Some species, such as the winter moth (*Operophtera brumata*) overwinter as an egg and require close synchrony between egg hatch and bud burst to ensure maximum survival of the newly hatched larvae as they feed on the expanding leaves. It is fascinating to note, as an

Figure 1 A larval teak defoliator moth.

example of the potential effects of climate change, that oak bud burst in the southern part of Great Britain has advanced by an average of 20 days during the final 50 years of the twentieth century. This might be thought to give the tree an advantage in that bud burst could be too early for the young winter moth larvae. However, showing the high adaptability of many insect species, winter moth egg hatch has also advanced by around 20 days, thus retaining synchronization with its primary host tree. By contrast, a new association between winter moth and the exotic Sitka spruce (*Picea stichensis*) has not retained synchronization because bud burst in this tree species is not so dependent on temperature.

Impacts

As a general rule, suitability of leaves for feeding by the most vulnerable life stages of an insect is a strong determinant of the degree of defoliation and, ultimately of breeding success by the insect. Broadleaved tree species tend to tolerate episodes of defoliation without a high risk of tree mortality. This is mainly because the trees tend to be able to refoliate during the growing season and will develop adequate buds for shoot extension in the following year. This is not to say that the effects on tree growth are negligible. Attacks by teak defoliator moth (*Hyblaea puera*) during the early stages of development of teak trees (*Tectona grandis*) can result in up to 44% loss of growth increment during the first 9 years and up to 13% loss of total volume over the rotation of the crop. Losses of up to 30% in stem growth have also been recorded for defoliators of temperate broadleaved trees (e.g., 7–13% loss of beech growth arising from 90% defoliation by pale tussock moth (*Dasychira pudibunda*) in continental Europe).

The degree of tolerance to defoliation by conifers depends on whether either or both current and older foliage is consumed. Although known to have a significant effect on growth increment, European pine sawfly (*Neodiprion sertifer*) does not kill pine trees because it feeds exclusively on older foliage. By contrast, pine beauty moth (*Panolis flammea*) feeds on both young foliage and, later, on older foliage and can completely defoliate trees leading to heavy mortality. Similar specialization in feeding sites is apparent in the major lepidopterous pests of conifer forests in North America so that, for example, although spruce budworm (*Choristoneura fumiferana*) is regarded as highly damaging and occasionally renders trees vulnerable to mortality from actions of other biotic and abiotic factors, it does not lead directly to tree mortality, unless there are several consecutive years of heavy defoliation. This arises from larval feeding specialization on expanding young foliage in the spring which, although damaging, still allows the plant to photosynthesize through older foliage and to develop buds for the following year.

Management Approaches

The above examples illustrate the diversity of feeding habits for those defoliators that totally consume leaves or needles. This external feeding habit means that they can be vulnerable to natural enemies and to direct intervention in management programs. Thus, use of chemical or, particularly, microbial control agents can be contemplated when the economic or environmental case requires intervention. Integrated pest management approaches to control of defoliator populations are discussed elsewhere in this volume (*see* **Health and Protection**: Integrated Pest Management Practices. **Tree Breeding, Practices**: Biological Improvement of Wood Properties). Other defoliators have more cryptic habits, including leaf mining where larval feeding takes place entirely within the leaf, leaving the outer surfaces intact. An interesting example in this category is the horse chestnut leafminer (*Cameraria ohridella*) which was only described for the first time in 1985 in Macedonia. This micromoth has, from a slow start, now spread across most of Western Europe and is giving rise to heavy cosmetic damage and premature leaf fall in urban horse chestnut (*Aesculus hippocastanum*) trees. The rapid spread of the moth from its original restricted range has been attributed to human movement, particularly of leaves accidentally falling onto vehicles and being carried long distances before emergence of the next generation of moths. It was found for the first time in Britain in 2002 in the Wimbledon area of London. By mid 2003 it had spread to Kingston and Oxford and is likely to colonize horse chestnut trees in most towns in the south of England and possibly elsewhere in Britain. At this stage there are no effective longer-term control measures, although collection and burning of fallen leaves in the autumn is known to reduce populations significantly.

Defoliators and Biodiversity

Defoliators are, therefore, significant biotic agents affecting tree health and growth and can even lead to tree mortality. Fortunately, the number of species resulting in these extreme impacts on trees is relatively rare. Indeed, it is a fortunate ecological fact that trees support a wide range of defoliators without showing undue signs of ill health and thus act as a valuable resource for enhancing invertebrate biodiversity at both local and landscape scales. In general, broadleaved trees with wide distributions tend to support more species than conifers or broadleaved tree species with restricted distributions. This has been well studied in Britain and it is known that oak (*Quercus* spp.) and willow (*Salix* spp.) support the greatest biodiversities of insects. Some of these, such as winter moth and oak leaf roller moth (*Tortrix viridana*) on oak occasionally reach damaging population densities, but these subside under the actions of natural enemies and resource limitation without causing tree mortality.

International Movements and Pest Risk Analysis

Greater diversity of defoliators on trees also tends to be accompanied by greater diversity of natural enemies, again contributing to the maintenance of a balance between resource utilization, in terms of leaves consumed, and effects on tree growth and health. This natural balance will have evolved over very long time periods and can be compromised through the introduction of exotic elements into the ecosystem. These can be in the form of exotic host trees or of exotic defoliator species or a combination of the two. Pine beauty moth is a good example of the former category. This species of moth is innocuous on Scots pine (*Pinus sylvestris*) in Britain but became a lethal pest when North American lodgepole pine (*P. contorta*) was planted in the north of Scotland from the 1960s. International movement of insect pests is increasing with the expansion and increased speed of global trade and there have been a number of instances of defoliators establishing and causing damage in new geographical locations. The horse chestnut leafminer described above is one example. Others include white marked tussock moth (*Orgyia thyellina*) in Auckland, New Zealand which was the subject of an intensive and successful eradication campaign involving repeated aerial application of the microbial control agent *Bacillus thuringiensis*. The authorities in Auckland are currently grappling with an outbreak of painted apple moth (*Teia anartoides*), a pest from Australia. Prevention of international movement of defoliators is an important task for national and regional Plant Protection Organizations and, internationally, legislation is already in place to raise awareness and to prohibit or manage the main pathways for movement of these pests in trade. In particular, international movement of plants is controlled very carefully, which tends to reduce the likelihood of egg or larval stages of defoliators being transported. However, life stages that could survive transit are not always associated directly with plants, making it extremely difficult to both inspect and to legislate against such incursions. For example, gypsy moth egg masses can be found on virtually any substrate, including the undersides of vehicles, etc., thus making inspection a very onerous task. Detailed pest risk analysis helps to identify the high-risk pathways and can aid risk management protocols, but it is also important that pioneer populations of a new pest are detected early and, where appropriate, action taken to eradicate or manage the problem. Unfortunately, it is often the case that by the time a population of an exotic pest is discovered it is already well established, thus making eradication a difficult prospect. However, the eradication of white marked tussock moth in New Zealand does indicate that a concerted campaign carried out in a determined manner can be successful.

Conclusion

In conclusion, insect defoliators can compromise tree growth and even lead to tree mortality. However, in relation to total diversity of insects on trees, heavy defoliations tend to be the exceptions and are often caused by a single pest species, thus pointing to the possibility of developing monitoring and management regimes for detection and for direct or indirect action. Effects can be serious when volume increment is an important component, for example in the growing of a commercial crop of trees. When trees are not grown for direct commercial reasons, their relatively high tolerance to attack means that occasional episodes of defoliation, although temporarily impairing visual and amenity values, do not significantly affect the long-term contributions of trees to the landscape (**Figure 1**).

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Foliage Feeders in Temperate and Boreal Forests; Population Dynamics of Forest Insects. **Health and Protection**: Integrated Pest Management Practices; Integrated Pest Management Principles. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Evans HF (2001) Biological interactions and disturbance: Invertebrates. In: Evans J (ed.) *The Forests Handbook. Volume 1. An Overview of Forest Science*, pp. 128–153. Oxford, UK: Blackwell.

Evans HF (2001) Management of pest threats. In: Evans J (ed.) *The Forests Handbook. Volume 2. Applying Forest Science for Sustainable Management*, pp. 172–201. Oxford, UK: Blackwell.

Evans HF, Straw NA, and Watt AD (2002) Climate change: Implications for forest insect pests. In: Broadmeadow MSJ (ed.) *Climate Change: Impacts on UK Forests*, pp. 99–108. Forestry Commission Bulletin 125. Edinburgh, UK: Forestry Commission.

Speight MR, Hunter MD, and Watt AD (1999) *Ecology of Insects: Concepts and Applications*, pp. 1–350. Oxford, UK: Blackwell Science.

Watt AD, Stork NE, and Hunter MD (eds) (1997) *Forests and Insects*, pp. 1–406. London, UK: Chapman & Hall.

Williams DW, Long RP, Wargo PM, and Liebhold AM (2000) Effects of climate change on forest insect and disease outbreaks. In: Mickler A, Birdsey RA, and Hom J (eds) *Responses of Northern U.S. Forests to Environmental Change. Ecological Studies 139*, pp. 455–494. New York: Springer-Verlag.

Sapsuckers

A F G Dixon, University of East Anglia, Norwich, UK

Introduction

Insects of the order Hemiptera have mouthparts specialized for piercing and sucking, and within the suborder Homoptera of this order two groups, the Auchenorhyncha and Sternorhyncha, specifically feed on plants. As their general name implies these insects feed on the sap of plants. This can be the sap of individual mesophyll or palisade cells of leaves or the translocating elements of plants, in particular phloem. In feeding on phloem sap not only have these insects access to a more continuous supply of food but they can inject disease-causing organisms and saliva containing physiologically active chemicals, which are then translocated throughout a plant. In addition by telescoping generations aphids have overcome the developmental constraint and for their size achieved prodigious rates of increase. As a consequence aphids often become very abundant and so in addition to any indirect damage they can be extremely damaging because of the nutrient drain they impose on plants. That is, many phloem feeders in particular are such serious pests of trees that they threaten their survival, e.g., the scale insects *Carulaspis minima* and *Lepidosaphes newsteadi* attacking Bermuda cedar on Bermuda and *Orthezia insignis* attacking the native gumwood on St Helena. However, as they often do not apparently affect the leaf area or distort the leaves the damage goes largely unnoticed. The damage done by those sapsuckers that feed on mesophyll and palisade cells is often very conspicuous but possibly less damaging to the plant than that inflicted by the phloem feeders.

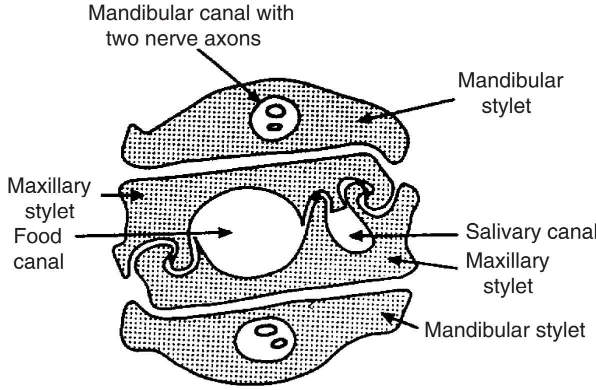


Figure 1 Diagram of a transverse section through the stylet bundle of an aphid. Reproduced with permission of Kluwer Academic Publishers from Dixon AFG (1998) *Aphid Ecology*, 2nd edn. London: Chapman & Hall.

Mode of Feeding and Nitrogen Metabolism

As indicated above the mouthparts of the Hemiptera are adapted for piercing and sucking rather than chewing. The mandibles and maxillae are modified to form slender bristlelike stylets, which rest in the grooved labium. Both pairs of stylets are hollow and capable of limited protrusion and retraction by means of muscles. In the coccids and psyllids the stylets may be extremely long and greatly exceed the length of the insect, being looped and coiled upon themselves within its body. The mandibular and maxillary stylets together form a needlelike structure. Cross-sections through the stylets reveal that the maxillary stylets have two parallel channels on their inner aspects and are interlocked. The approximation of the two stylets results in the formation of two extremely fine tubes. The dorsal one functions as a food canal and the finer ventral one as a salivary duct (**Figure 1**).

Of the two groups of Homoptera that specifically feed on plants it is the Sternorhyncha that have specialized on feeding on phloem elements of plants and produce large quantities of honeydew (**Figure 2**), which is often the first indication of their presence. The reason for the abundance of honeydew is that phloem sap is rich in sugars but contains relatively little amino-nitrogen. To overcome this problem the insects process very large quantities of phloem sap removing most of the amino-nitrogen and excreting the sugars as honeydew. Because phloem sap is rich in simple sugars it creates an osmotic problem for the insects, which is overcome by converting the simple sugars into complex sugars, which effectively reduces the osmolality of the phloem sap as it passes through the insect. In addition, these insects are very effective at assimilating and utilizing the low levels of amino-nitrogen in their food. First, they are able to process rapidly relatively large volumes of phloem sap and so fuel their total requirements for amino-nitrogen. Second, they generally have symbiotic bacteria in bacteriosomes within their haemocoel, which increase the efficiency of their nitrogen metabolism by converting the nonessential amino acids in phloem sap into the essential amino acids the insects need to sustain their growth. In addition the symbionts may also recycle some of the insect's nitrogenous waste. In this way the aphids in particular are able to sustain a prodigious rate of growth on what is a very poor quality diet. That is, they are able to process quickly very large quantities of phloem sap and upgrade the quality of the amino-nitrogen component of their diet.

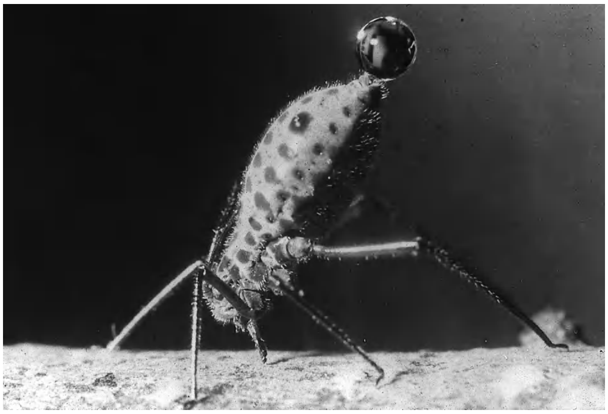


Figure 2 A giant willow aphid excreting a droplet of honeydew. In this case the aphid has its stylets inserted into a large willow twig.

Regional Distribution and Abundance

Correlation between the number of species of plants in an area is much better with the number of species of the least host-specific sapsuckers, the aleyrodids and coccids, than with the most specific, aphids and psyllids. In temperate regions sapsuckers, in particular aphids, are often an important and central component of the insect fauna of the canopies of trees. However, associated with the increase in plant diversity as one approaches the tropics is a decrease in aphid diversity, the reverse of what is seen in many other groups of animals and plants. This has been attributed to the lack of a marked seasonality in the growth of plants in the tropics or to a constraint imposed by the high host specificity and short period of time aphids can spend off their host plants searching for hosts. Although there are many species of plants in the tropics, all potential hosts of aphids, few of these plants are abundant enough to sustain a specific aphid. That is, for aphids to be able to survive its host plant has to be relatively abundant. However, other sapsuckers are more diverse, some considerably so, in the tropics. For example, there are 1000 species of Auchenorhyncha in the Panama Canal Zone, whereas there are only 350 species in the whole of Britain.

Ecology

Sapsuckers feeding on the leaves of trees that make up the forest canopy live in 'one of the least explored zones on land.' Obtaining estimates of the abundance of sapsuckers in the canopies of trees, which in the tropics can be very tall, presents considerable technical difficulties. Fogging the canopy with pesticides is often used to obtain such estimates but the accuracy of such estimates depends on the ease with which the insects are dislodged and whether they are likely to be intercepted by other leaves in falling through the canopy. Cranes have also been used to access the canopy and the estimates so obtained are likely to be more realistic and are only limited by the area that can be sampled from the crane.

Such samples show that ants can dominate the biomass of the arboreal fauna of tropical lowland forests. Since ants are largely regarded as predominantly predacious, this pattern challenges the usually accepted pattern of energy flow, in which the biomass of predators should only constitute a proportion of their prey. This has led authors to hypothesize that the availability of homopteran (Coccidae and Membracidae) honeydew provides a key resource for ants. As in temperate regions the homoptera on a particular tree are mostly monopolized by a single ant colony.

In summary, the few data that are available tend to indicate that there are more species of sapsucker in the tropics but they are less abundant than aphids such as the lime or sycamore aphids in temperate regions (**Table 1**). However, until projects with similar objectives and using similar methodologies are undertaken in the tropics and temperate regions these conclusions need to be treated with caution.

Direct Effects of Sapsucker Infestation

As phloem sap contains high concentrations of sugar and very little amino-nitrogen aphids have to process very large quantities of sap in order to obtain sufficient amino-nitrogen to sustain their very high rates of growth. In the case of the giant willow aphid (*Tuberolachnus salignus*), a single aphid consumes the photosynthetic product of 5–20 cm^2 of leaf per day. The annual energy drain imposed on a 14-m tall lime tree by a natural population of the lime aphid (*Eucallipterus tiliae*) is considerable (**Figure 3**). During the course of a year, the population turns over its own standing crop 482 times, or 3.4 times day^{-1}. This is considerably greater than that achieved by oribatid soil mites (38 times $year^{-1}$) and grasshopper populations (10 times $year^{-1}$). Thus although the lime aphid is not particularly effective at utilizing its energy intake, it turns over energy at a massive rate, much of which falls to the ground as honeydew. The annual production of honeydew by the lime aphid is equivalent in energy terms to 0.8 of

Table 1 Estimates of the standing crops of sapsuckers on trees in tropical and temperate forests

Forest	*Country*	*Method of sampling*	*Standing crop/unit weight or area of leaf*		*Reference*
			Number	*Weight*	
Tropical	Panama	Direct	3.4 m^{-2}		Basset (2001)
Tropical	Panama	Direct	3.5–11.8 m^{-2}	5.7–20 mg m^{-2}	Wolda (1979)
Tropical	Puerto Rica	Direct	6–500 kg^{-1}		Schowalter and Ganio (1999)
Temperate	UK	Direct	**Sycamore aphid**		Author's data
			115–742 m^{-2}	85–520 mg m^{-2}	
			508–7364 kg^{-1}	374 mg–5.15 g kg^{-1}	
			Lime aphid		
			150–801 m^{-2}	27.5–143 mg m^{-2}	
			955–7864 kg^{-1}	175 mg–1.39 g kg^{-1}	

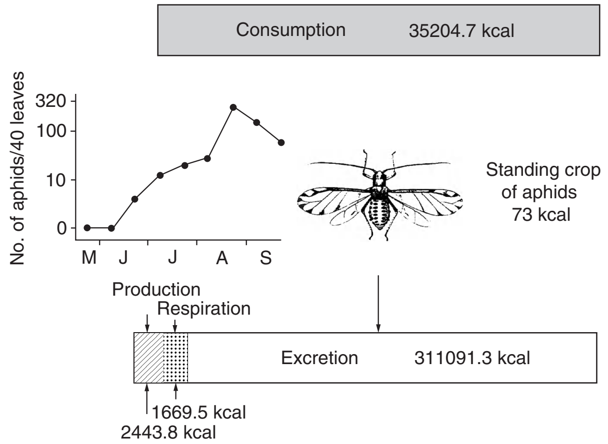


Figure 3 The annual consumption, production, respiration, and excretion, and average standing crop of a population of lime aphids on a 14-m tree, expressed in terms of energy. Inset is a graph of the lime aphid population trend for which this energy budget was computed.

that locked up in the leaves at leaf fall. In the case of the sycamore (*Acer pseudoplatanus*) it is on average equal to the energy in the leaves at leaf fall.

In the presence of the wood ant (*Formica rufa*) the energy drain imposed on sycamore can change dramatically. This ant preys on the sycamore aphid and tends another aphid found on sycamore, *Periphyllus testudinaceus*. In the absence of the ant the sycamore aphid removes approximately three times as much sap from trees than in its presence, whereas the ant-tended species removes 50 times more sap from ant-foraged trees than from unforaged trees. However, the ant-tended aphid on average only removes one-fifth of that removed by the sycamore aphid each year.

Aphid-infested sycamore saplings clearly grow markedly less than uninfested saplings. Although aphids do not affect the number of leaves borne by lime (*Tilia* spp.), oak (*Quercus* spp.), or sycamore, sycamore produces smaller leaves, which contain more nitrogen, when heavily infested in spring. However, the leaf area equivalent to the energy removed by sycamore aphids only accounts for a small proportion of the observed diminution in leaf area. If the drain imposed is expressed in terms of nitrogen rather than energy then aphids again remove far less nitrogen than expected from the reduced size of the leaves. This implies that the effect aphids have on tree growth is not a direct consequence of the energy and/or nutrient drain. Other factors, e.g., the saliva aphids inject into plants, contain physiologically active components that might also adversely affect tree growth.

The width of the annual rings of sycamore is positively correlated with the average size of the leaves, and negatively with the numbers of aphids on the tree throughout a year. This is possibly associated with the fact that each annual ring is composed of two types of vessel, which make up the spring and summer wood. The springwood is mainly laid down when the leaves are developing in spring, whereas the summerwood is mainly laid down after the leaves stop growing. In the absence of aphids some sycamore trees could produce as much as 280% more stem wood. Lime and oak aphids hatch later, relative to the time of bud burst of their host trees, than the sycamore aphid, and as a consequence rarely become abundant before the leaves are fully grown. This is reflected in the fact that the aphids on these trees do not affect the aboveground growth in girth and stem length of their respective hosts. However, infested saplings of lime and oak often weigh less at the end of a year than they did at the start, mainly due to a reduction in the mass of their roots.

Aphid infestation causes early leaf fall in all three species and, in oak and sycamore, results in the leaves becoming a darker green. In oak this is a consequence of a 25% increase in the quantity of both chlorophyll A and B. Associated with this is an increase in dry matter production per unit area of leaf, which in sycamore can be 1.7 times greater in infested than in uninfested saplings. Following years of heavy aphid infestations lime and sycamore break their buds later than usual, and in the case of lime the leaves are smaller and a darker green, and have a net production 1.6 times greater than the leaves of previously uninfested saplings.

Indirect Effects of Sapsucker Infestation

As indicated above, aphids produce large quantities of honeydew, which contains a high percentage of the trisaccharide sugar melezitose. Much of this honeydew reaches ground level, which can result in there being as much as 10 g of sugar per 100 g of soil. This has led to the proposal that trees release surplus sugars by enlisting the help of aphids. This sugar is utilized by free-living nitrogen-fixing bacteria in the soil, which increase in number beneath aphid-infested trees and make more nitrogen available to these trees. Melezitose, or a particular mixture of sugars characteristic of honeydew, is thought to have an optimal affect on nitrogen fixation. The aphids are seen as a necessary ‘part’ of a tree, releasing surplus sugars that promote a better supply of nitrogen.

The addition of the four sugars commonly found in honeydew – fructose, glucose, melezitose, and sucrose – to soil at rates equivalent to those found beneath lime trees infested with aphids causes an increase in the abundance of bacteria in woodland soils. In the laboratory fructose is more effective at promoting nitrogen fixation than melezitose. However, as a single sugar was used rather than a mixture this result does not refute the original hypothesis. In a more rigorous test of the mutualism hypothesis, in which alder aphids (*Pterocallis alni*) were removed from red alder (*Alnus rubra*) by spraying with malathion, aphid infestation resulted in a decrease in ammonification and nitrification in the soil, and a decrease in aboveground primary production. Although this does not rule out the possibility that melezitose may stimulate nitrogen fixation by soil bacteria, nevertheless, contrary to the prediction of the hypothesis, nitrogen availability in the soil is markedly reduced by large quantities of aphid honeydew and there is no positive effect on tree growth.

Much of the honeydew excreted by aphids feeding on the leaves and needles of trees falls on to the upper surface of other leaves where it promotes the growth of sooty molds. In some years these sooty molds blacken the upper surface of the leaves. On pecan (*Carya illinoensis*) these molds can reduce light penetration and photosynthesis by factors of from 25% to 98%. In addition, the darkening of the leaf surface can result in an increase in leaf temperature of 4°C. Epiphytic microorganisms, which include the sooty molds, are one of the most abundant groups of organisms. In areas where there is a lot of industrial pollution rich in nitrogen the limiting resource for epiphytic microorganisms is energy. Increasing the availability of energy in forest canopies in such areas results in a dramatic increase in the abundance of microorganisms (bacteria, yeasts, and filamentous fungi) of two to three orders of magnitude on the needles and leaves of aphid-infested trees. In addition to the changes in abundance there are also changes in species composition, more so on the leaves of beech (*Fagus sylvaticus*) than on oak, probably due to differences in the surface micromorphology of the leaves. In nonpolluted areas the nitrogen and sugar in honeydew are sufficient to stimulate an abundant growth of microorganisms when aphids are abundant on sycamore.

Less well understood are the effects of these microorganisms on throughfall chemistry, which is important because it determines the input of nutrients and ions into forest soils. For example, in June when aphids are most abundant on Sitka spruce (*Picea sitchensis*), the concentration of dissolved organic carbon (DOC) in throughfall collected beneath infested spruce trees is high and declines with the subsequent decline in aphid numbers. There is a very high correlation between DOC concentrations in throughfall and aphid abundance. The concentration of dissolved organic nitrogen (DON) in throughfall increases after the aphid population peaks and starts to decline in abundance. Concentrations of inorganic nitrogen are lower in throughfall collected beneath spruce heavily infested with aphids compared with uninfested trees but it becomes similar as the aphid numbers decline.

Field experiments show that following a high input of DOC from the canopy there is an increase in the DOC concentration in forest soil solutions, which is slightly delayed and longer-lasting than the aboveground aphid infestation. Similarly, there is an increase in the concentrations of DON and NO_3-N in the forest floor solution beneath aphid-infested trees. Laboratory experiments, in which simulated artificial honeydew is applied to cores of forest soil, reveal that low to medium inputs of honeydew increase base respiration within 1 h and cause a decline in NH_4-N fluxes. Large inputs of honeydew increased the immobilization of both NH_4-N and NO_3-N and slightly reduced DON fluxes. The DOC fluxes increase considerably but decline to base level within 72 h of applying the honeydew. That is, inorganic carbon from aphids in throughfall affects the mineralization, mobilization, and transport of organic matter in forest soils.

In conclusion, we are only just beginning to record the species and abundance of sapsuckers present in the canopy of forests, especially in the tropics. Nevertheless, they appear to be more species-diverse in this habitat in the tropics than in temperate regions but in terms of total biomass they are possibly more abundant in the temperate regions.

In temperate regions sapsuckers, in particular aphids, greatly reduce the growth of trees, whereas their honeydew encourages the growth/activity of epiphytic and soil microorganisms. This is in addition to their being an abundant source of food for insectivorous birds and the hosts and prey of various insect parasitoids and predators. That is, in spite of being relatively inconspicuous, sapsuckers possibly have a 'keystone' role in determining the community structure of temperate forests.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Bark Beetles; Foliage Feeders in Temperate and Boreal Forests. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Basset Y (2001) Communities of insect herbivores foraging on saplings versus mature trees of *Pourouma bicolor* (Cecropiaceae) in Panama. *Oecologia* 129: 253–260.

Dixon AFG (1971a) The role of aphids in wood formation. 1. The effects of the sycamore aphid, *Drepanosiphum* *platanoides* (Schr.) (Aphididae) on the growth of sycamore *Acer pseudoplatanus* (L.). *Journal of Applied Ecology* 8: 165–179.

Dixon AFG (1971b) The role of aphids in wood formation. 2. The effects of the lime aphid, *Eucallipterus tiliae* L. (Aphididae) on the growth of lime *Tilia* × *vulgaris* Hayne. *Journal of Applied Ecology* 8: 393–399.

Dixon AFG (1998) *Aphid Ecology*, 2nd edn. London: Chapman & Hall.

Dixon AFG (2004) *Insect Herbivore–Host Dynamics: Tree-Dwelling Aphids*. Cambridge, UK: Cambridge University Press.

Dixon AFG, Kindlmann P, Leps J, and Holman J (1987) Why are there so few species of aphids, especially in the tropics? *American Naturalist* 29: 580–592.

Eastop V (1978) Diversity of the Sternorrhyncha within major climatic zones. In: Mound LM and Waloff N (eds) *Diversity of Insect Faunas*, pp. 71–87. Oxford, UK: Blackwell Scientific Publications.

Elton CS (1927) *Animal Ecology*. London: Sidgwick & Jackson.

Elton CS (1966) *The Pattern of Animal Communities*. London: Methuen.

Llewellyn M (1975) The effects of the lime aphid (*Eucallipterus tiliae* L.) (Aphididae) on the growth of the lime (*Tilia* × *vulgaris* Hayne). 11. The primary production of saplings and mature trees, the energy drain imposed by the aphid population and revised standard deviations of aphid population energy budgets. *Journal of Applied Ecology* 12: 15–23.

Owen DF (1978) Why do aphids synthesize melezitose? *Oikos* 31: 264–267.

Schowalter TD and Ganio LM (1999) Invertebrate communities in a tropical rainforest canopy in Puerto Rico following Hurricane Hugo. *Ecological Entomology* 24: 191–201.

Stadler B, Solinger S, and Michalzik B (2001) Insect herbivores and the nutrient flow from the canopy to the soil in coniferous and deciduous forests. *Oecologia* 126: 104–113.

Wolda H (1979) Abundance and diversity of Homoptera in the canopy of a tropical forest. *Ecological Entomology* 4: 181–190.

Bark Beetles

M L Reid, University of Calgary, Calgary, AB, Canada

Bark beetles are small, dark, cylindrical beetles, usually less than 7 mm long. As their name implies, they are usually associated with woody plants. Despite their small size and modest appearance, they have an intriguing assemblage of feeding and breeding habits, some of which result in significant economic losses to forest and agricultural industries. This article reviews the taxonomy, life cycle, host–plant interactions, and ecosystem consequences of bark beetles, concluding with management options.

Taxonomy

Bark beetles have commonly been considered a family, Scolytidae, but recent taxonomy places them as a subfamily, Scolytinae, within the weevil family Curculionidae. Major characteristics that are shared with weevils include elbowed, clubbed antennae, larvae that feed within plant tissues, and the loss of the development of legs in larvae (**Figure 1**). The Scolytinae and closely related Platypodinae differ from typical weevils in their oviposition behavior: adults bore deeply into plant tissues to oviposit, while typical weevils use their elongated rostrum to create egg niches from the surface of the plant. Many of the Scolytinae do not actually breed in bark, as discussed below, but the common name 'bark beetle' is applied to this whole taxonomic group.

Bark beetles comprise approximately 6000 species, found worldwide. Their origin was in the Cretaceous, with an early association with the ancient conifer *Araucaria* distributed across Gondwana. Subsequent diversification into tribes and subtribes has occurred in North America, South America, Eurasia, and Africa. About 30% of extant genera are temperate in distribution.

Life Cycle

Upon arrival at a host plant, adults quickly begin to burrow into the plant to breed. Several species are known to histolyze their wing muscles upon arriving at breeding habitat. The sex that initiates a breeding site, the pioneer sex, differs among species. In many species, the beetle initially constructs a nuptial chamber where mating will occur (**Figure 2**). Many species emit pheromones at this stage that attract the opposite sex but also others of the same sex. When both sexes are attracted, the pheromones are called aggregation pheromones, and they result in a rapid colonization of the surrounding plant tissues. Such aggregation is a notable feature of bark beetles. Many pheromones are derived from precursors in the plant tissues, especially defensive compounds such as monoterpenes. However, the same pheromones can sometimes be synthesized *de novo*, or be produced by associated microbes. The link between plant defenses and pheromones means that pheromones can indicate the state of the tree to other beetles, which is especially important for those beetle species that

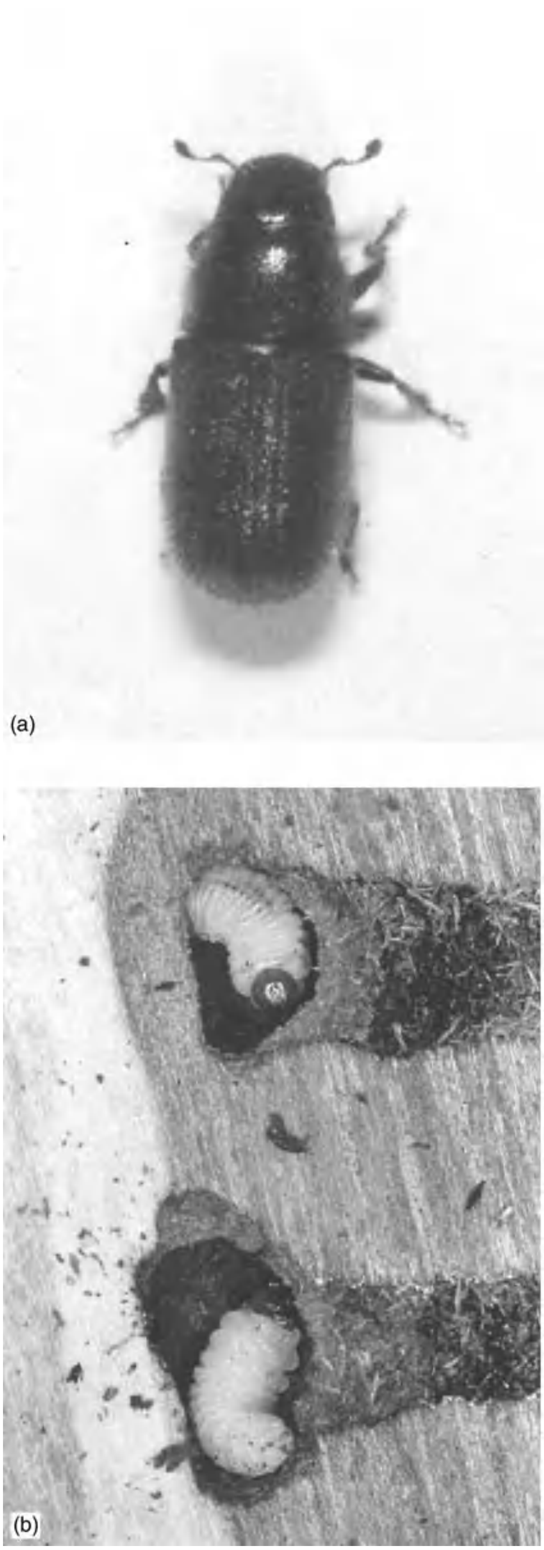


Figure 1 Douglas-fir beetle, *Dendroctonus pseudotsugae* (Hopkins): (A) adult; (B) Larvae. Courtesy of MM Furniss.

breed in live trees that they must kill. Aggregation pheromones diminish once an individual is established and mated. In some species, antiaggregation

Figure 2 Exposed egg galleries of pine engravers, *Ips pini* (Say), within the phloem of lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann. Typical of a polygynous species, several egg galleries radiate from a central nuptial chamber. Some larval galleries are visible extending perpendicularly from egg galleries. Courtesy of ML Reid.

pheromones are subsequently produced by one or both sexes.

Bark beetles have a fascinating diversity of breeding systems, including monogamy, polygyny, inbreeding polygyny (often associated with haplo-diploidy), and parthenogenesis. Monogamy and polygyny are clearest when males initiate breeding sites, with a species-typical number of females sharing the same nuptial chamber. Males contribute by removing debris produced by tunneling females and guarding the entrance against predators. Males may remain for some or all of the oviposition and larval development periods. When females initiate the breeding site, there is generally only a single female per nuptial chamber (monogyny), but males generally depart early in oviposition and may mate again elsewhere. In these outbred systems, mating generally occurs after dispersal at the new breeding site. In inbreeding polygyny, mating occurs between brothers and sisters at the natal site. Here the sex ratio is female-biased, usually achieved with haplo-diploidy, and males are dwarfed and flightless. These species commonly breed in xylem or seeds rather than phloem. Another variant of breeding system in bark beetles is pseudogamy, in which triploid females mate but only produce daughter clones.

Females tunnel through the tissue, and create orderly, characteristic egg galleries that generally extend linearly from the initial entry point, either parallel or perpendicular to the grain of the wood (**Figure 2**). In many genera, eggs are laid in individual niches along the sides of the egg galleries. Phloem-feeding larvae tunnel perpendicular to the egg galleries, while fungal-feeding larvae feed communally in chambers. Larvae progress through three to four instars before pupating, all within the host tissue.

Generation times depend largely on temperature, though also on feeding substrate and body size. For example, within North America, the southern pine beetle, *Dendroctonus frontalis*, a 3-mm beetle that breeds in the southeastern USA, may have eight generations a year. In contrast, the spruce beetle *D. rufipennis*, a 7-mm-long beetle breeding in northwestern Canada and Alaska, may take 2 or 4 years to complete a generation. Because the quality of the breeding substrate generally declines substantially over the course of offspring development, in part due to larval feeding, each generation typically disperses to a new breeding site. Parental adults may reemerge within a breeding season, after regenerating their wing muscles, and disperse to a new breeding site. The extent to which parent beetles successfully overwinter after breeding is unclear.

Host Plants

Evolutionarily, bark beetles appear to have originated in conifers, and many of the most conspicuous and economically important species breed in conifers. However, most bark beetle species (approximately 80%) breed in angiosperms.

As their name suggests, many bark beetles breed within the inner bark (phloem) of tree boles or branches. While these species are often the most important economically, phloem-feeding is characteristic of fewer than half of all bark beetle species. More commonly, bark beetles develop within tree xylem where they feed upon symbiotic fungi (xylomycetophagy). Such species are termed ambrosia beetles. Phloem-feeding species are characteristic of temperate environments (over 80% of temperate species), while ambrosia beetle species are numerically dominant in the humid tropics. Less common feeding and breeding substrates include the roots or stems of herbaceous plants, the pith of small stems, and seeds.

For species that breed within bark, host tree species are usually within a single genus. Ambrosia beetles often have a broader host range, likely because xylem is not as chemically distinctive as phloem, and because the beetles feed primarily on fungi rather than the tree itself.

Colonizing Host Plants

Bark beetles find their host trees primarily by chemical cues. These cues may come from trees themselves (tree kairomones), and may include both host volatiles to which beetles are attracted (primary attraction) and nonhost volatiles that deter beetles. The scale at which these cues operate is unclear. The proportion of host and nonhost volatiles may influence the distribution of bark beetles across the landscape (i.e., among stands). The problem of detecting an individual host tree that is suitable is more difficult, requiring finer chemical and spatial resolution. Conifers of different genera share many volatiles, and odor plumes from individual trees may be readily mixed depending in part on stand density and wind. The visual acuity of bark beetles is relatively poor. As a consequence, the range of detection of an unoccupied, suitable tree may be at the scale of centimeters. While one species of bark beetle has been shown to recognize tree suitability in flight, it appears that beetles of other species must actually land on a tree, and even consume part of it, to determine its suitability. Such a search process may be very time- and energy-consuming, and many species of bark beetles also respond positively to volatiles produced by breeding conspecifics (pheromones). This is true for species that colonize either dead or living host trees.

Bark beetles have several strategies for coping with plant defenses against herbivory and disease. The most common strategy is to colonize trees that are poorly defended, often because the tree is dying or severed from its roots. Such beetles are termed secondary species, since they are not the primary cause of tree death (e.g., *Ips* spp. in North America). Population sizes of secondary species correspond to the availability of poorly defended trees, sometimes increasing to significant numbers following extensive drought or large windfall events. At high numbers, these species may attack healthy trees, but even here there is evidence that trees that are attacked have been growing more slowly than average.

Of greater economic significance are those bark beetle species, termed primary species, that regularly attack healthy trees. The best known of these feed on phloem in conifers. Two attributes are key to the success of primary feeders against a defended tree: mass attack and symbiotic fungi. Mass attack is the arrival of large numbers of beetles at a tree over a few days. The synchrony of attack is important because trees not only have constitutive defenses, present before any attack, but also induced defenses where additional monoterpenes and oleoresin are synthesized around the site of an attack to kill or deter a pioneer attacker. To overwhelm the tree's capacity for defense, high attack densities are required. Thus the optimal attack density (maximizing an individual's reproductive success) may range from 20 to over 240 attacks per square meter, depending on beetle species and presumably on the vigor of the host tree. In contrast, the optimal density for beetles breeding in undefended hosts may be one individual in an entire tree.

Symbiotic fungi may be important to successful colonization of live trees, especially conifers, but their role is not entirely clear. Their evolutionary significance is indicated by special invaginations on the integument of adult beetles, called mycangia, in which particular species of fungi are carried. Among phloem-feeding beetle species, mycangia are most commonly found in species that kill trees. Interestingly, these mycangia occur at different places on different beetle species, including near the mandibles and in the thoracic pleural area. (Not surprisingly, many ambrosia beetles that feed on fungi also have mycangia.) In the temperate phloem-feeding bark beetles, the symbiotic fungi are usually ascomycetes within the genus *Ophiostoma*. Many, but not all, of these fungi stain the xylem blue, which diminishes the value of wood esthetically, though not structurally.

Mycangial fungi in tree-killing beetles species have been held responsible for early tree death that allows the beetles to breed, but this view has been disputed. The fungi penetrate and plug the vascular tissue, and their toxins may also adversely affect water relations and resin flow. However, mycangial fungi are found to be weakly pathogenic, and may spread into the vascular tissue after beetles are already established and breeding. Moreover, trees have been killed by primary bark beetles in the absence of these fungi. Thus it appears that the fungi may contribute to tree death, but high-density beetle attacks are also required. Additional benefits of fungi may be improved food quality, limitation of less beneficial fungi, and chemical communication. These latter benefits would also apply to secondary bark beetle species, but these species generally do not have mycangia.

Factors Limiting Population Growth

Although many bark beetles aggregate at breeding sites, individual reproductive success declines exponentially with breeding density in the absence of initial tree defenses. Part of this reduction can be attributed to changes in the oviposition behavior of females in response to density, such as by reducing egg density or the length of egg galleries. However, there is also competition where resources per larva are reduced by consumption of phloem or faster deterioration of heavily mined phloem. Cannibalism has also been reported. Offspring that do survive are usually smaller and have less fat when density is higher.

Mortality of bark beetles within their natal tree is often remarkably high, with fewer than 5% of eggs resulting in adult offspring (**Table 1**). As just mentioned, part of this mortality may be attributed to competition, but this is often difficult to identify directly. Host quality may significantly affect the survival of offspring from egg through to emergence.

Natural enemies are also an important source of mortality within the natal tree. Woodpeckers are an obvious predator of bark beetles, but usually have a minor impact on bark beetle survival (**Table 1**). Insect predators and parasites can cause substantial mortality, based on studies using exclusion cages (**Table 1**). Parasitism, a distinguishable source of mortality, varies widely in intensity (**Table 1**). Predation by insects generally leaves a poorer record. Some species of clerid beetles (Cleridae) are bark beetle specialists that detect bark beetle pheromones, arriving in large numbers, along with bark beetle colonizing trees. Adult clerids consume adult bark beetles on the surface of the bark while their larvae consume larval bark beetles. Consumption by adults reduces the number of beetles successfully colonizing by as much as 50% under realistic experimental conditions. Clerid larvae consumed about 10% of *Ips pini* larvae in one experiment. Clerids may determine the dynamics as well as the size of beetle populations (**Figure 3**). For example, clerids have longer development times than their bark beetle hosts, potentially resulting in a lag effect that can result in cyclic population dynamics (*see* **Entomology**: Population Dynamics of Forest Insects). They may also disperse differently than their hosts, causing patchy spatial distributions of bark beetles.

Dispersal between natal trees and breeding sites is also a significant source of bark beetle mortality. As mentioned, the breeding habitat of many bark beetles is no longer suitable after one generation, requiring dispersal every generation. Suitable hosts are typically rare, particularly for those bark beetles species relying on trees lacking defenses but with undeteriorated tissues, such as windfalls. While dispersal mortality cannot be observed directly, estimates from equilibrium population models and changes in sex ratio between emerging and breeding beetles suggest that more than half of beetles die during dispersal (**Table 1**). This is despite the ability of many species to fly 40 km or more.

Abiotic factors can also severely affect the success of small ectotherms such as bark beetles. Of these, temperature is fundamentally important. At higher latitudes and altitudes, temperatures may drop to lethal values over winter despite the cold-hardiness of bark beetles in these environments. For example, protracted temperatures of *c.* −40°C at unseasonable times of the year are an important contributor to the collapse of mountain pine beetle (*D. ponderosae*) populations (**Figure 3**). Cold-hardened larvae experienced 80% mortality at −34°C, compared to 27% mortality at −12°C. Temperature also influences reproductive rates in many ways. Dispersal in many temperate species is limited to temperatures above 16°C and below 40°C. Oviposition and larval development are also temperature-dependent processes. The

Table 1 Estimates of mortality in natural populations of bark beetles

Source of mortality	*Bark beetle species*	*Mortality (%)*	*Reference*
Total mortality in natal tree	*Dendroctonus ponderosae*	96.3–99.5	Amman GD (1984) Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. *Environmental Entomology* 13: 184–191.
	Dendroctonus ponderosae	98.6–99.4	Cole WE (1981) Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. *Researches on Population Ecology* 23: 116–144.
	Phloeosinus neotropicus	88	Garraway E and Freeman BE (1981) Population dynamics of the juniper bark beetle *Phloeosinus neotropicus* in Jamaica. *Oikos* 37: 363–368.
	Scolytus scolytus	96	Beaver RA (1966) The development and expression of population tables for the bark beetle *Scolytus scolytus* (F.). *Journal of Animal Ecology* 35: 27–41.
Woodpeckers	*Dendroctonus ponderosae*	2–15	Amman GD (1984) Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. *Environmental Entomology* 13: 184–191.
	Dendroctonus ponderosae	2–5	Cole WE (1981) Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. *Researches on Population Ecology* 23: 116–144.
	Dendroctonus frontalis	4.5	Moore GE (1972) Southern pine beetle mortality in North Carolina caused by parasites and predators. *Environmental Entomology* 1: 58–65.
	Scolytus scolytus	1	Beaver RA (1966) The development and expression of population tables for the bark beetle *Scolytus scolytus* (F.). *Journal of Animal Ecology* 35: 27–41.
Insect natural enemies	*Ips calligraphus*	74–96	Miller MC (1984) Mortality contribution of insect natural enemies to successive generations of *Ips calligraphus* (Germar) (Coleoptera, Scolytidae) in loblolly pine. *Zeistschrift für angewandte Entomologie* 98: 495–500. Miller MC (1986) Survival of within-tree *Ips calligraphus* (Col.: Scolytidae): effect of insect associates. *Entomophaga* 31: 39–48.
	Ips typographus	83	Weslien J (1992) The arthropod complex associated with *Ips typographus* (L.) (Coleoptera, Scolytidae): species composition, phenology, and impact on bark beetle productivity. *Entomologica Fennica* 3: 205–213.
	Ips spp.	31	Riley MA and Goyer RA (1986) Impact of beneficial insects on *Ips* spp (Coleoptera Scolytidae) bark beetles in felled loblolly and slash pines in Louisiana. *Environmental Entomology* 15: 1220–1224.
	Dendroctonus frontalis	24–28	Linit MJ and Stephen FM (1983) Parasite and predator component of within-tree southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae) mortality. *Canadian Entomologist* 115: 679–688.
Parasitism	*Dendroctonus ponderosae*	1–24	Reid RW (1963) Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of British Columbia. III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. *Canadian Entomologist* 95: 225–238.
	Dendroctonus ponderosae	3–6	Cole WE (1981) Some risks and causes of mortality in mountain pine beetle populations: a long-term analysis. *Research into Population Ecology* 23: 116–144.
	Dendroctonus frontalis	4	Moore GE (1972) Southern pine beetle mortality in North Carolina caused by parasites and predators. *Environmental Entomology* 1: 58–65.
	Phloeosinus neotropicus	10	Garraway E and Freeman BE (1981) Population dynamics of the juniper bark beetle *Phloeosinus neotropicus* in Jamaica. *Oikos* 37: 363–368.
	Scolytus scolytus	12	Beaver RA (1966) The development and expression of population tables for the bark beetle *Scolytus scolytus* (F.). *Journal of Animal Ecology* 35: 27–41.
	Scolytus ventralis	3–8	Stark RW and Borden JH (1965) Observations on mortality factors of the fir engraver beetle, *Scolytus ventralis* (Coleoptera: Scolytidae). *Journal of Economic Entomology* 58: 1162–1163.
	Scolytus ventralis	2	Ashraf M and Berryman AA (1969) Biology of *Scolytus ventralis* (Coleoptera: Scolytidae) attacking *Abies grandis* (Pinaceae) in northern Idaho. *Melanderia* 2: 1–22.
	Ips paraconfusus	0.2–70	Ball JC and Dahlsten DL (1973) Hymenopterous parasites of *Ips paraconfusus* (Coleoptera: Scolytidae) larvae and their contribution to mortality. I. Influence of host tree and tree diameter on parasitization. *Canadian Entomology* 105: 1453–1464.

continued

Table 1 Continued

Source of mortality	*Bark beetle species*	*Mortality (%)*	*Reference*
Dispersal	*Dendroctonus ponderosae*	10–85	Klein WH, Parker DL, and Jenson CE (1978) Attack, emergence and stand depletion of the mountain pine beetle, in a lodgepole pine stand during an outbreak. *Environmental Entomology* 7: 732–737.
	Ips paraconfusus	61	Cameron EA and Borden JH (1967) Emergence patterns of *Ips confusus* (Coleoptera: Scolytidae) from ponderosa pine. *Canadian Entomology* 99: 236–244.
	Phloeosinus neotropicus	73	Garraway E and Freeman BE (1981) Population dynamics of the juniper bark beetle *Phloeosinus neotropicus* in Jamaica. *Oikos* 37: 363–368.
	Scolytus ventralis	60	Berryman AA (1979) Dynamics of bark beetle populations: analysis of dispersal and redistribution. *Bulletin de la Société Entomologique Suisse* 52: 227–234.

Figure 3 Lodgepole pine forest in Alberta, Canada, recently affected by mountain pine beetle, *Dendroctonus ponderosae* Hopkins. Trees with red needles were killed the previous season, while the tree with yellow-green needles indicates a current year's attack. Courtesy of ML Reid.

size and fat content of adults are negatively related to temperature during development, presumably influencing future dispersal and reproductive success. Temperature also determines the rate of phloem desiccation and perhaps fungal growth, indirectly influencing bark beetles through food quality.

Ecosystem Processes

The contributions of bark beetles to community and ecosystem processes, such as succession, fire, and decomposition, have not been well quantified. Bark beetle species that kill large numbers of mature trees are likely to have the largest effects on many of these processes.

Fire

While a high density of dead trees, caused by bark beetles, would seem to increase the risk of forest fire, this relationship has not been well established empirically. One study in Yellowstone National Park (Wyoming, USA) observed that severe pre-fire bark beetle damage was correlated with increased risk of crown fire, but the reverse was true when damage was moderate. Risk of fire will likely change with time after a beetle outbreak, because of changes in tree moisture, abundance of fine fuels, and responses of the understory plant community. It is possible that stands with large numbers of beetle-killed trees may actually have a reduced risk of fire. Once a fire has started, fallen trees killed by bark beetles may increase heat intensity around them, increasing consumption of organic matter in soil.

The effects of fire on bark beetles are better studied. For beetles already breeding in trees that are subsequently burned, reproductive success is reduced. However, because of the insulative properties of bark and the mass of the tree bole, and the occurrence of beetles over most of the tree bole, fires need to be intense to cause significant mortality. After a fire, burned trees may attract bark beetles both to the area and to particular trees, although the reverse has also been observed. The difference in response may be related to whether the bark beetle species are primary or secondary species. Successful attack of individual burned trees varies with tree species and the severity of burn. Resin response may either increase or decrease in burned pine trees, depending on species. Some species avoid scorched bark while others are limited to these areas.

Forest Succession

Because tree-killing bark beetle species attack dominant trees within one host genus, they have the potential of altering forest composition and the rate and routes of succession to the canopy. Not surprisingly, subcanopy trees show increased growth rates following a bark beetle outbreak. Whether this results in a change in the species composition in the canopy depends on the species composition in the subcanopy and their relative responses. In one outbreak where half of the spruce trees were killed by bark beetles, there was no significant change in tree species composition.

Decomposition

Bark beetles are expected to hasten decomposition because they penetrate the wood material and are vectors for many species of fungi, but few studies have tested this. Douglas-fir beetles, *D. pseudotsugae*, had a small effect on log decomposition after 10 years, with wood borers contributing much more. Decomposition of spruce in Finland, as measured by percentage mass loss over 30 months, was positively correlated with the number of beetle attacks, although the difference in mass loss between logs with and without exposure to beetles was not large.

Management Options

Bark beetles that kill mature trees have many negative economic impacts. If the tree had been intended for timber, it remains usable for only a year or two after death before it becomes fractured. Discoloration by blue-stain fungi reduces the value of the wood for esthetic purposes. Penetration into sapwood by ambrosia beetles can reduce the structural and esthetic value of the affected area of wood. When outbreaks result in millions of trees being killed simultaneously, increased salvage harvesting may depress prices, and disrupt harvesting plans and expected future yield. The potential loss of individual trees valued by people also prompts management actions.

Management of bark beetles affecting trees includes three approaches. These are: (1) killing beetles directly; (2) manipulating beetle movement using semiochemicals (pheromones and kairomones); and (3) stand and landscape management to prevent increases in beetle populations.

Killing bark beetles is difficult because most of their life cycle is spent within plant tissue. For individual beetle-infected trees, it is possible to kill beetle broods by applying insecticides that are conducted through the tree's vascular system to the developing broods (e.g., monosodium methanearsenate). An interesting biological approach is to attract less aggressive but faster-developing bark beetle competitors into trees colonized by pest species. However, these individual tree treatments are not practical on a large scale. Small groups of trees may be felled and either debarked or burned. Infested stands may be harvested or burned with prescribed fire although, as noted above, fire may not kill most beetles. When stand removal is prescribed, beetles can be lured into the stand using semiochemicals to maximize the number of beetles removed. A difficulty with any plan to remove beetles in trees is that the presence of beetles may be hard to detect, as trees may not show obvious signs of attack until broods are well developed or already emerged. Consequently, experienced surveyors are required on the ground to assess beetle populations.

For some species of bark beetle, large numbers of beetles can be removed by using traps baited with semiochemicals, especially pheromones. To minimize the number of predators that are also captured, small discrepancies in the chemicals that are maximally attractive to bark beetles and their predators can be exploited. Mass-trapping is simple and inexpensive to implement once the baits have been developed, but it is difficult to assess how much the population is reduced, since many dispersing beetles fail to establish in trees anyway. In addition, the baits may attract high densities of beetles into a local area, increasing the risk that trees around the baited traps will be successfully attacked (spillover). Consequently, it is often recommended that the baited traps be placed far from host trees. An alternative approach is to use baited trees as traps (trap trees); these tend to be more attractive than baited traps initially, but then become unattractive once saturated with beetles, minimizing the risk of spillover. More effort is required to dispose of the trap tree to prevent beetle emergence than for pheromone traps.

Manipulation of beetle search behavior is an approach that takes advantage of bark beetles' reliance on chemical cues for host selection and mate finding. Beetles can be deterred from settling on trees, or even in stands, by conspecific antiaggregation pheromones, pheromones of competitor bark beetle species, or nonhost volatiles. For species that require high densities of beetles to overcome tree defenses, even some deterrence might allow trees to defend against beetle attacks.

A preventive approach to bark beetle control is to manage stands and landscapes to prevent the development of large beetle populations. However, by definition, pest species use trees that people want, so any plan to make host trees difficult for beetles to find will usually compromise the economy of harvest. Indeed, many bark beetle species have become pests because their host plants have been planted in monocultures, reducing dispersal mortality. It is possible to manage the risk of beetle attack by predicting when a stand is likely to be at risk, and taking action at that time. Risk and hazard rating systems are based on stand conditions (e.g., tree size, age, density, physiography) and on current beetle population size. Beetle population size can be assessed by surveying the number of trees recently killed in the area, by assessing the success of broods, and by monitoring baited traps.

A preventive method widely used to control mountain pine beetles (*D. ponderosae*) is stand-thinning. The mechanisms by which this method works are unclear, but may include increased vigor of remaining trees and a less favorable microclimate of thinned stands (warmer and windier). Some studies of thinning, focusing on other bark beetle species, have found no effect or a positive effect of thinning on beetle populations. If thinning is conducted on mature stands, costs of this approach include increased tree damage due to wind sway and wind throw, as well as the requirement to enter the stand multiple times. Thinning is therefore not an approach to be implemented indiscriminately.

See also: **Entomology**: Population Dynamics of Forest Insects. **Health and Protection**: Integrated Pest Management Practices; Integrated Pest Management Principles. **Pathology**: Insect Associated Tree Diseases.

Further Reading

Beaver RA (1988) Insect–fungus relationships in the bark and ambrosia beetles. In: Wilding N, Collins NM, Hammond PM, and Webber JF (eds) *Insect–Fungus Interactions*. London, UK: Academic Press.

Borden JH, Hunt DWA, Miller DR, and Slessor KN (1986) Orientation in forest Coleoptera: an uncertain outcome of responses by individual beetles to variable stimuli. In: Payne TL, Birch MC, and Kennedy CEJ (eds) *Mechanisms in Insect Olfaction*, pp. 97–109. Oxford, UK: Clarendon Press.

Byers JA (1989) Chemical ecology of bark beetles. *Experientia* 45: 271–283.

Kirkendall LR (1983) The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). *Zoological Journal of the Linnean Society* 77: 293–352.

Paine TD, Raffa KF, and Harrington TC (1997) Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology* 42: 179–206.

Raffa KF (2001) Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. *Chemecology* 11: 49–65.

Rudinsky JA (1962) Ecology of Scolytidae. *Annual Review of Entomology* 7: 327–348.

Schowalter TD and Filip GM (eds) (1993) *Beetle–pathogen Interactions in Conifer Forests*. San Diego, CA: Academic Press.

Wood SL (1982) The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs* 6: 1–1359.

ENVIRONMENT

Contents

Environmental Impacts

P Maclaren, Rangiora, New Zealand

Introduction and Definitions

There is considerable debate over definitions for the word ‘forest’ and even for ‘tree.’ Most vegetation types fall clearly into the categories of forest or nonforest, but there is dispute at the margins. The following are contentious questions:

- Does ‘forest’ apply to a type of land cover, or to a type of land use? (An apple orchard, for example, may consist of a high density of trees but is not normally considered to be forest, whereas areas of bare land in the phase between clearfelling and replanting are normally included as forest.)
- At what height is a woody species classified as a tree? Does this vary with the age of the plant?
- At what proportion of ground cover do trees collectively form forests? (For example, do widely spaced trees in the African savannah or Australian outback constitute a forest? Do heavily tree-lined cities constitute forests?)

A similar debate rages over the classification of forests into natural and artificial types. On the one hand, we could say that totally natural forests do not exist. There is probably not a single hectare of the earth's surface that has not been modified to some extent by human activity. In some parts of the world, hominids have been a part of the ecosystem for perhaps a million years, often using fire or browsing mammals. Peoples have introduced new species or eliminated species from every land mass, and have even modified the air (which provides a tree with its most important nutrient by weight – carbon). On the other hand, even a 'monocultural' and monoclonal plantation contains a surprising variety of adventitious species and cannot be said to be entirely artificial.

There is widespread public enthusiasm for natural forests, with ever-increasing pressure for their protection and enhancement. The environmental benefits of such forests are well recognized. This contrasts with the opprobrium that is often directed towards commercial plantations. Whereas 'natural' forests tend to be as complex as the climate and soils allow, the profit motive forces managers of plantations into greatly simplified forest systems. In order to minimize costs, and to maximize timber revenues, single commercial timber species are favored. These are best grown in large stands of homogeneous age, and managed in a way that provides a uniform and consistent industrial feedstock. In many nations, it is acceptable to grow horticultural or agricultural crops in large monocultural blocks, but – strangely – public attitudes change where the harvest product is stemwood rather than fruit.

The awe of the natural forest, and the emotional opposition to the artificial version, have spawned a set of beliefs about the negative environmental impacts of the latter, which are often based on prejudice, rather than on demonstrable fact. That said, even groundless fears have a political reality that foresters ignore at their peril.

Effect on Soil

The sustainable productive potential of a soil often cannot be discussed without specifying the intended land use. Thus 'soil quality' is a subjective term. It seems likely that persistent plant species modify the soil to a condition that ensures their long-term survival. Certain species of tree are said to be 'soil improvers' because subsequent agricultural crops grow better, and because the deep topsoil consists of well-mixed organic matter (mull), as in typical agricultural soils. Other tree species are said to be 'soil deteriorators' because they result in – or are found on – soils with a clear separation of surface organic matter from the underlying mineral substrate (mor). The latter appears to be an evolutionary mechanism for the forest to minimize nutrient loss, by controlling (by means of mycorrhizal associations) the decomposition of organic matter.

Given that a mor-type forest contains most of its nutrients in the biomass and relatively undecomposed forest floor, if it is subjected to persistent fire or removal of the forest duff (for fuel, fertilizer, or animal bedding), then it will certainly become less productive over time. It is very often the case that certain forest types gained the reputation for being soil deteriorators because of human extraction of such nutrients.

It is possible (although not satisfactorily proven) that trees can extract nutrients from deep roots and bring these to the surface via litterfall. This could be one reason for the observed boost in agricultural production following a forest cover. Such a boost can even be noted in much-maligned plantations, including those with eucalyptus and conifers. A common criticism of coniferous plantations is that they acidify the soil and create an environment unsuitable for earthworms. Charles Darwin did some excellent work establishing the worth of earthworms in agriculture, but his observations are not necessarily relevant to forestry. Forests develop their own soil fauna that is more appropriate to forest conditions. The slight acidification noted for conifers could be a device to prevent nutrient leaching and ensure controlled nutrient recycling. It is not a permanent effect, as the pH seems to bounce back after removal of the trees. By means of acidification and mycorrhizal action, anions (nitrogen, phosphorus, sulfur) under such trees can be more plant-available than in similar soils that have not experienced a forest cover.

Sustainability of the soil resource is largely determined by the balance of inputs and outputs of key elements. There are losses into the groundwater (i.e., leaching, under the action of rain or irrigation), and losses to the air (i.e., volatilization, often by burning). There are also losses via human removal of agricultural or forestry products. Inputs can come from: biological nitrogen fixation; aerial deposition; and breakdown of the mineral substrate by weathering, possibly stimulated by plant or mycorrhizal exudates. They can also come from deliberate fertilization.

The huge quantities of wood often extracted from a forest may provoke the comment that the land is being 'mined' of significant amounts of essential elements. This ignores the fact that wood differs from many other rural products. Wood consists predominantly of carbohydrates (cellulose, hemicellulose, and lignin), which are predominantly made up of carbon, hydrogen, and oxygen – these elements comprise more than 99.7% of the oven-dry weight of stemwood. They come from rainwater and carbon dioxide, with minimum contribution from the mineral soil. In contrast, products that contain foliage or fruit, or derive from an animal, can be rich in nitrogen, phosphorus, sulfur, potassium, calcium, and magnesium. If such elements are not replaced with fertilizers (organic or mineral), excessive exploitation of the land can easily 'mine' the soil.

To summarize: it is incorrect to state categorically that afforestation – even with monocultural conifer plantations – will cause soil deterioration, without defining what is meant. Soil from such plantations can produce higher yields of subsequent crops than adjacent, unplanted land. Nutrient levels, even in a highly exploited forest, need not decline provided that nutrients are replaced. Furthermore, the debate over soil deterioration can be somewhat academic if the main regional concern is the massive removal of topsoil via soil erosion. If soils are stripped down to the parent rock, this must be ultimate form of soil degradation.

Forests play a vital role in mitigating erosion in most of its dozen forms. Soil erosion is a major global problem, which occurs naturally but has been exacerbated by human actions. It is caused by wind, rain, or mechanical damage (e.g., plowing or livestock pugging (compaction and loss of soil structure in a clay soil)). Trees reduce wind speeds at ground level and thereby reduce wind erosion. They maintain the soil in a drier state, thus minimizing its mobility. Critically, they bind the soil together with their strong, interlocking and relatively deep roots. Erosion rates from mass wasting are typically 10 times lower in forest compared to, for example, pasture.

Effect on Water

There are more misconceptions related to the interaction of trees and water than to any other aspect of forestry. These myths are so widespread that they seem to have formed a self-sustaining body of belief, without recourse to empirical evidence. It is not true, for example, that – in some mysterious way – trees attract or even cause rain, resulting in abundant river flows. Rain is the result of the sun warming the planet and evaporating water, mainly from the oceans. Moisture-laden air masses are driven across the land by winds that would occur even if the earth were devoid of trees. Rain falls when the air cools, for example by rising over a mountain range. Trees affect the albedo (reflectivity) of the earth's surface, but this is not believed to be a major influence in planetary circulation patterns. Having said that, the presence of trees does maintain atmospheric humidity (by means of evapotranspiration). In other words, part of the rain that would have fallen to the ground and entered the groundwater is returned to the atmosphere by trees, and is available to enhance rainfall elsewhere. So, although forests do not greatly influence the total quantity of atmospheric water moved from the ocean to the land, they may well affect the quantity and distribution of rainfall on that land.

The effect of trees in a particular catchment is to reduce the yield of water, not to enhance it! Two effects cause this: interception and transpiration. Interception is where the rain wets the canopy and does not reach the ground. Readers will remember when they have stood under trees in a light shower and remained dry. Short vegetation (e.g., grass) also intercepts rainfall, but there is a critical difference: tree canopies readily evaporate the water, even during rain. Grass stays wet. This means that the trees are constantly intercepting and reexporting rain, whereas the first shower wets the grass and the second can penetrate to the ground. The reason why grass evaporates less water than trees is because it is shorter, and there is less wind at ground level. It is not a coincidence that people hang out their washing to dry on lines high above the ground!

Transpiration is the second way that trees reduce the water in a catchment. Plants have holes (stomata) beneath their leaves that allow the absorption of carbon dioxide from the air. These also permit the escape of moisture, which has been conducted upwards from the roots. When conditions are dry, plants close their stomata and moisture loss is minimized. This applies to both trees and to short vegetation, but the difference is that trees usually have deeper roots. Long after grass has closed its stomata and stopped transpiring, trees will continue to pump water from deep soil horizons. A light rain will recharge the water in the grass-covered soil, but it will require heavy or persistent rain to do the same for the forested soil.

The myth goes that 'forests act like a sponge, soaking up water during wet periods and releasing it slowly during dry periods.' A home experiment can soon confirm that even sponges do not work in this way: large pores release their water within minutes, under the influence of gravity. In smaller pores, capillary action is stronger than gravity and the water is not released. In soil, water in such micropores can be removed only by movement towards, and evaporation from, the surface or by active uptake by roots. Very small pores contain water that is inaccessible even to roots. Decreased water flow as a result of afforestation can be expected at all times of the year. So can forests act as a buffer, smoothing out flood peaks? That depends.

It is easy to observe that a bucket of water poured on to the forest floor usually penetrates quickly. Holes left by dead roots and gaps around living roots may provide the mechanism for rapid and deep infiltration. In contrast, water poured on to a bare or grass-covered soil may run along the surface for a considerable distance. Often, the soil may have been baked hard by the sun or compacted by grazing animals. Therefore we would expect that it would take longer for rain to reach the river in a forest, where it has to filter through the soil, than it would in a pasture, where much of the water flows overland. This has often been observed experimentally, but it is not always the case. In a heavy and prolonged downpour, the interception capacity of a tree canopy is quickly overwhelmed. The soil becomes saturated and instant penetration of water under the forest merely results in instant discharge along the riverbank – if a hosepipe is full, turning on the tap results in immediate release of water from the nozzle.

Another complication is that, while improved infiltration rates under trees may smooth flood peaks in small storms and small catchments, this does not usually occur in large river systems where the worst flooding damage takes place. As a storm passes over a large catchment, the rainfall peaks at different times in each tributary. Moreover, it can take many hours or days for the flood peaks from the mountainous headwaters to pass down the river and coalesce in the main channel. By this time, the smoothing effects attributable to the forest have all but disappeared. In short, the direct benefits of forestry for flood control have been grossly exaggerated. It is important to remember, however, that a major cause of flooding is the restriction in the cross-sectional area of river channels caused by upstream soil erosion. Forestry is highly important in this regard.

The lowering of water tables following from afforestation has at least one desirable side-effect: it can prevent and even (in nonchronic cases) reverse salinization. Salt is common in deeper horizons of soils that have not evolved under conditions of high rainfall. Irrigation has enabled crops to be grown in many drier parts of the world, but poor irrigation practices can allow this salt to migrate to the surface, by means of persistent soaking which dissolves the salt and distributes it throughout the soil profile. When the water evaporates from the surface the salt crystallizes out of solution, eventually creating conditions unsuitable for cropping and – in extreme situations – salt pans. Even in the absence of irrigation, salinization is a common result of deforestation and establishment of pasture. It may take many years of flushing by rainfall to lower the topsoil salt levels to a stage where trees can successfully be reestablished and the water table can be lowered by such means.

There is no doubt that freshwater is a scarce and underrated resource in many parts of the world, and that individual catchments will generate more usable water if they do not have a forest cover. But water quality is also important. Water that is polluted by salt, sediment, pathogens, or nutrient run-off is not as useful as clean water. Planning authorities, in a difficult balancing act, must ensure that river flow is maximized but water pollution is minimized. One way to do this is to afforest only the riparian areas. Water reduction from a forest cover depends on the proportion of the catchment that is forested, whereas water pollution is caused mainly by humans and animals having direct contact with the waterway.

The reason why human pathogens (viruses, bacteria, plasmodia, etc.) are more likely to be found in agricultural – as opposed to forestry – catchments is that many domestic mammals share the same intestinal diseases. The reason why polluted water normally has low transparency is that it is either filled with sediment from erosion, or with microorganisms fertilized by nutrient runoff. Enhancement of aquatic growth at first glance may be seen as beneficial to the environment, but there are usually negative impacts. Algae commonly excrete toxins, and when they decay they extract oxygen from the water (eutrophication), making it unsuitable for fish. The major plant nutrients are nitrogen and phosphorus, and while it is sometimes possible to keep the less-soluble phosphorus away from waterways, nitrogen is a more intractable problem. Nitrate salts are highly soluble and once they find their way into groundwater they can quickly bypass or overwhelm any barrier, such as riparian strips. To counteract the nitrogen via natural means usually requires filtration through a high-carbon medium, such as peat swamp. Nitrates and nitrites are often considered a health hazard in drinking water, although the evidence for this is not convincing.

Arguably, pollution of rivers is not as serious as pollution of lakes and aquifers. Whereas, if the source of pollution is removed, rivers can flush themselves clean within weeks, pollutants can persist in lakes for decades. Aquifers may contain water that fell as rainfall thousands of years ago, and it is most important to ensure that activity at ground level (including livestock farming) does not contaminate this valuable heirloom.

A major source of river pollution is siltation, often caused by deforestation in steep headwaters. As well as blocking the river channels and causing flooding, the sediment can cause major problems when it enters hydroelectric dams or the ocean. Siltation limits the useful life of many dams to a few decades, and silt particles rapidly erode the turbines. Deforestation can be the direct cause of siltation of harbors and decline in certain fisheries.

Effect on Air

It is now common knowledge that there is a connection between forestry and the enhanced greenhouse effect, but there is still considerable public confusion on the details. The concentration of atmospheric carbon dioxide (CO_2) has been rising for the last century, leading to the concern that it will cause global warming. The evidence is overwhelming that the increase in CO_2 is human-induced: the cause is both combustion of fossil fuels and deforestation (historically, one-third, but becoming less important). It is easy to imagine how burning coal – or burning a forest – could increase the atmospheric levels of the main combustion product, carbon dioxide. Why then is it so difficult to comprehend that establishing a forest is merely the reverse of this process? Deforestation puts carbon into the air, afforestation removes it from the air, but the mere maintenance of an existing forest usually has no net effect.

The process of photosynthesis has been understood for a long time. Plants use the energy of sunlight to combine water and carbon dioxide (obtained only from the air, via the stomata) into sugars. Oxygen is released as a byproduct. Half the dry weight of wood or other biomass is carbon, and therefore a forest represents a considerable amount of carbon that is not available to cause global warming. Whereas all green plants photosynthesize, only forests and swamps accumulate carbon to any great extent. It is conceptually simple to examine an ecosystem such as pasture or forest, and to observe the quantity of carbon it contains. Above knee-height, anyway, it is undeniable that a forest contains more carbon than a pasture, and that conversion of the pasture to the forest will result in extraction of atmospheric carbon. Because CO_2 is present in such small concentrations (0.036% of the atmosphere), the removal of approximately 100 tonnes of carbon per hectare by means of forest establishment has a major influence. Such afforestation could strip the air of all its carbon in an area six times the size. In contrast, the effect on oxygen is insignificant. It is often said that 'forests are the lungs of the planet' and provide us with our oxygen, but this is a gross exaggeration. If all the atmospheric carbon were removed by trees (an impossibility), this would increase the concentration of oxygen by only 0.036% from its existing 21%.

Once the forest has been established, it is not obvious whether this ecosystem is a sink (has more inputs than outputs), a source (the opposite) or merely a carbon reservoir (contains carbon but is not necessarily a sink or source). Forests consist of trees of all ages and sizes, and while all growing trees are individually sinks, the whole forest may not be a sink. Carbon is lost by the decomposition of biomass or by extraction of woody material. Over the long term, we can say that forests are not carbon sinks, because if they were to gain (say) only 1 t per hectare per year of carbon, then after 1000 years there would be an extra 1000 t. This would be clearly visible to the naked eye, and would not need sophisticated measurement.

The role of wood products in the global carbon cycle is also a cause for confusion. Wood products are carbon sinks only if the stock of such carbon is increasing every year. This may be the case, but it would be a trivial quantity. More important is the role of wood as a substitute for materials, such as steel, aluminum, concrete, and plastics that require large quantities of fossil fuels to manufacture. CO_2 emitted from burning wood is considered 'carbon-neutral' because it is merely recycled atmospheric carbon rather than additional carbon from beneath the earth's surface.

Effect on Wildlife and People

The main difference between forests and other terrestrial ecosystems is that trees have a more pronounced vertical component. In terms of the volume of space bounded by the ground and the top of the canopy, forests contain considerably more volume than all other terrestrial ecosystems combined. Within this space, there are many biological niches and an abundance of plant and animal wildlife can develop. These species are interesting because they add variety to the world, and because some of them can be useful to humans.

Just as in that other three-dimensional biospace – the oceans – the base of the biological pyramid is photosynthetic plant life. The primary productivity of the forest understory or the deeper ocean is often constrained by the sunlight that can penetrate – which is one reason why greater biodiversity is found in tropical forests. The high productivity of a natural forest (where little sunlight is wasted) can often support more human inhabitants than the degraded landscape that so often replaces it. Tropical forces often contain most of their nutrients in the trees and associated litter, and their removal (by repeated burning and browsing) can cause a long-term impoverishment of the soil and the people who live on it. Forests are often cleared to make way for food crops, but it is worth remembering that, while food is vital, so are shelter and fuel provided by wood. People can starve because they have not grown sufficient food, but they can also starve because there is no means to store that food or to cook it. Many staple foods (corn, cassava, potatoes, wheat, rice) must be cooked to be digestible.

There is often outrage when a timber plantation replaces a natural forest. Undoubtedly, such conversion reduces biodiversity – unlike the situation where plantations displace agriculture. But the high productivity of useful timber from plantations can take the pressure off overexploitation of natural forests. Most commonly, the opposition to plantation forestry is not because of the change in vegetation so much as the change in land ownership and control. Large plantations are associated with large companies, often transnational, whose prime interest is said to be profit rather than the well-being of local inhabitants. Locals who have traditional foraging rights in the forest may find themselves excluded by the plantation owners, and the wide range of useful products from a natural forests is reduced to a narrow range. Instead of the multipurpose role of natural forests (medicines, honey, game, fruits, rattans, slow-burning charcoal), locals must participate in the money economy to satisfy their various needs.

The comparison between natural forests and plantation forests is unfortunate, as the world needs more forests of any sort. Conversion of natural forest to plantations can be prohibited by legislation, as in most countries there is adequate degraded agricultural land than could be used for the latter purpose.

Summary

For environmental reasons, the world needs more forests and it needs more wood. Forests of all kinds protect the soil, water, and air – which are the basic life-sustaining resources of the planet. Wood is a benign product because it is biodegradable, and because it has been created by the combination of water and a greenhouse gas under the action of sunlight. Trees are a natural biological solar panel.

Plantation forests should not be seen as an alternative to natural forests. They are additional to natural forests, and there is sufficient degraded agricultural land to enable the area of plantations to increase without threatening natural forests.

See also: **Environment**: Carbon Cycle; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Hydrology**: Hydrological Cycle; Impacts of Forest Management on Streamflow; Impacts of Forest Plantations on Streamflow; Soil Erosion Control. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Soil Development and Properties**: Water Storage and Movement. **Tree Physiology**: Forests, Tree Physiology and Climate.

Further Reading

Calder IR (1993) Hydrological effects of land-use change. In: Maidment DR (ed.) *Handbook of Hydrology*. Auckland, New Zealand: McGraw-Hill.

Chow VT (ed.) (1964) *Handbook of Applied Hydrology: A Compendium of Water-Resources Technology*. New York: McGraw-Hill.

Cole DW (1995) Soil nutrient supply in natural and managed forests. *Plant and Soil* 168–169: 43–53.

Fisher RF (1990) Amelioration of soils by trees. In: Gessel SP, Lacate DS, Weetman GF, and Powers RF (eds) *Sustained Productivity of Forest Soils. Proceedings of the 7th North American Forest Soils Conference*, pp. 290–300. Vancouver, Canada: University of British Columbia.

Hamilton LS and Pearce AJ (1987) What are the soil and water benefits of planting trees in developing countries watersheds? In: *International Symposium on Sustainable Development of Natural Resources in the Third World*, pp. 39–58. Columbus, OH: Ohio State University, Argonne Laboratory.

Maclaren JP (1993) *Radiata Pine Growers' Manual*. FRI Bulletin no. 184. Rotorua, New Zealand: New Zealand Forest Research Institute.

Maclaren JP (1996) *Environmental Effects of Planted Forests in New Zealand*. FRI Bulletin no. 198. Rotorua, New Zealand: New Zealand Forest Research Institute.

Maidment DR (1993) Hydrology. In: Maidment DR (ed.) *Handbook of Hydrology*. Auckland, New Zealand: McGraw-Hill.

Pereira HC (1973) *Land Use on Water Resources in Temperate and Tropical Climates*. London, UK: Cambridge University Press.

Sargent C (1992) Natural forest or plantation? In: Sargent C and Bass S (eds) *Plantation Politics – Forest Plantations in Development*, pp. 16–40. London, UK: Earthscan Publications.

Sidle RC, Pearce AJ, and O' Loughlin CL (1985) *Hillslope Stability and Land Use*. Water Resources Monograph no. 11. Washington, DC: American Geophysical Union.

Will GM (1984) Monocultures and site productivity. In: Grey DC, Schönau APG, and Schutz CJ (eds) *Proceedings on Site and Productivity of Fast Growing Plantations*. Pretoria and Pietermaritzburg, South Africa, 30 April–11 May 1984, IUFRO.

Impacts of Air Pollution on Forest Ecosystems

P E Padgett, USDA Forest Service, Riverside, CA, USA
S N Kee, University of California, Riverside, CA, USA

Introduction

Air pollution problems are international in scale. All forests worldwide experience some degree of air pollution exposure above preindustrial levels. Atmospheric transport processes do not recognize geographic borders, but sources of pollutants, the pollutants of concern, and the specific effects of pollutants vary greatly depending on human cultural activities and natural climate patterns. For example, heavy-metal contamination is a result of poorly controlled mining and industrial emissions; when coupled with frequent rainfall, dispersion is minimized and local deposition is maximized. Deposition of suspended particles is most frequently a problem in forests in dry climates adjacent to agricultural areas where atmospheric conditions allow suspended particles to remain airborne for long periods of time. Ozone is a secondary pollutant formed from automobile exhaust (nitrogen oxides) and volatile organic carbon from a variety of chemical, combustion, and natural processes. The reaction requires ample sunlight, thus ozone is a serious problem in urbanized areas in sunny climates.

Air pollution effects on forests can, therefore, best be understood by looking at climate zone and the human cultural activities of agriculture, urbanization, and industrialization. Although there are many natural sources of air pollutants, such as vegetation fires, windstorms, and volcanic eruptions, for the purposes of this article we shall focus on human-caused, or anthropogenic, sources of air pollutants and their effects on forest ecosystems. The effects of elevated carbon dioxide, global climate change, and other abiotic stressors are covered elsewhere in this *Encyclopedia* (*see* **Environment**: Impacts of Elevated CO_2 and Climate Change).

There is still much to be learned regarding air pollution and forest health. For example, nitrogen deposition from agricultural and urban sources is recognized both in Europe and the American continents as having a large potential for changing existing ecological processes and species composition. However, understanding the mechanisms driving changes and the extent of the threat to existing ecosystems is subject to ongoing debate.

Air pollutants can have acute effects arising from very high pollutant loads such as the destruction of forests due to unregulated heavy industrial activities such as in the 'black triangle' of Czechoslovakia, East Germany, and Poland. Alternatively, pollutants can have chronic effects from long-term exposures at lower concentrations such as ozone damage found in southern Californian forests adjacent to the Los Angeles basin. Many of the chronic effects are difficult to identify and catalog. Plant species vary widely in their sensitivity to pollutants and the display of recognizable symptoms. The yellow pines of North America have been a key indicator species for identification of ozone toxicity because of a display of 'chlorotic mottle' (a stippling of the needles) and premature loss of annual whorls. However, the converse is not necessarily true; the lack of a specific suite of symptoms does not necessarily indicate a lack of pollutant effects. Many nonvascular mosses and symbiotic lichens simply disappear from the forests under polluted conditions.

Finally, many air pollutant effects are synergistic with other biotic or abiotic stressors. Heavy metal contamination may weaken a tree, but an insect or pathogen infestation may be the actual cause of death. Drought is part of the natural climatic cycle in semiarid forests, but forests that have experienced extended years of ozone toxicity may be more susceptible to drought-induced mortality.

In the sections that follow, air -pollution effects are described by major climatic zone (**Table 1**). A brief description of the primary environmental factors and human activities that affect pollution loads and distribution within each of the major climate zones is included. It is recognized that for the purposes of this article generalizations are made and many exceptions exist. The reader is referred to other sections in this series and the list of recommended reading for more detailed information.

Subarctic Boreal Forests

Air Pollution Causes

Subarctic forests occur across Asia, North America, and northern Europe; about 70% of the world's boreal forests are in Russia. The subarctic zones

Table 1 Pollutants described within the individual sections

Forest type by climate zone	*Pollutants of concern*
Subarctic	Heavy metals, sulfur dioxide
Wet tropic	Smoke
Semiarid	Ozone, dry deposition, particulates
Temperate	Acid rain

contain rich mineral deposits and extensive timber and coal resources for industrial processing and energy production. Resource extraction is the primary activity in these forests, creating intensely focused, localized sources of industrial pollutants. Little agricultural or urban activity occurs here. Coal mining and logging provide energy resources for local uses and export. Timber resources are also used for paper and wood products, creating air pollutants in the industrial processing of wood fiber. Most of the pollutants in boreal forests are generated from smoke stacks. However, since the human populations are low outside the immediate industrial site, regulations and restrictions based on human health concerns have, historically, been limited and concern regarding forest sustainability has only recently occurred. The climate plays a critical role in air pollution effects on boreal forests. The growing season is, at most, 3 months, with long hours of sunlight available during the summer for gas exchange and photosynthetic activity. During the winter not only does cold inhibit metabolic activity but also daylight hours are short. Boreal forests are slow-growing and slow to recover after disturbances.

Air Pollution Concerns

The effects of air pollutants on boreal forests are acute. The industries of the subarctic generate two primary pollutants of concern: sulfur dioxide and the generalized category of 'metals.' These two pollutants have very different dispersal patterns and modes of action (that is, how they affect trees and forest ecosystems).

Sulfur dioxide is a well-known byproduct of coal combustion, but it is also found in many minerals and is released during smelting. Once aloft, sulfur dioxide can be transported for hundreds of kilometers before depositing on foliage, soil, water, or other substrates. Deposition can occur in rainfall, snowfall, or fog. It is also absorbed by plants as a vapor, and can collect on surfaces in a dry form. Furthermore, sulfur dioxide reacts with a number of other atmospheric compounds to form sulfuric acid, ammonium sulfate, and other vapors or aerosols. Because of its wide dispersal patterns, sulfur dioxide emissions can result in damage to forests over a large geographical area.

Metals, on the other hand, are generally deposited within 10–15 km of the source. Although there are many potential metal contaminants, such as cadmium, uranium, or lead, most of the concerns regarding boreal ecosystems are focused on copper, nickel, and zinc. The tendency for metals to collect relatively close to the source limits their geographic impact, but increases the concentrations and thus the intensity of the effects.

Air Pollution Effect

Mining and forestry operations in Russia have resulted in about 1 million hectares of 'seriously damaged' forest and another 7 million hectares of 'affected' forests. The Noril'sk mining complex is one of the best examples of the catastrophic effects of unregulated mining and smelting on boreal forests. Tree mortality due to sulfur dioxide extends for 200 km downwind of the complex and copper, cobalt, and nickel concentrations in soils are 10–1000 times higher than background levels up to 30 km downwind.

In addition to differences in distribution, the effects of these two primary pollutants differ in several important ways. Sulfur dioxide is phytotoxic as an airborne pollutant while metals are generally most toxic when incorporated into soil systems. Acute exposure to sulfur dioxide results in necrosis (cellular death) of leaf tissue. Often the effects are first displayed as chlorotic spots and later as bleached-white or brown necrotic spots on leaves and needles or along the margins of leaves. As acute exposures progress, the entire foliar surface turns brown and the leaf or needle is abscised from the tree. Acute sulfur dioxide symptoms may begin to occur at ambient concentrations of 50 parts per billion (ppb). Emission episodes resulting in concentrations of 1 part per million (1000 ppb) have been measured around unregulated smelting plants and coal-burning facilities. Chronic exposures to lower concentrations of atmospheric sulfur dioxide cause interveinal chlorosis of leaves and tip burn on needles. Continued exposure at lower concentrations can result in premature shedding of foliage and reduced net primary productivity. Deposition of sulfur dioxide on foliage can cause erosion of the surface cuticle boundary, but more often the uptake through stomata is the primary mechanism for damage. Once in the foliage interior, sulfur dioxide is converted to HSO_3 – bisulfite – a free radical, $SO4_2^-$, or SO_3^-, all of which disrupt metabolic activity or alter plant nutrient balances. In the subarctic boreal forests, the long summer days provide extended periods of gas exchange and this extended period of foliar uptake can result in greater injury symptoms compared to regions closer to the equator. Conversely, during the winter, when days are much shorter and the cold temperatures limit water availability, stomata may not open at all for extended periods. During these times atmospheric sulfur dioxide interactions with the canopy of trees become less important, but deposition to, and accumulation in, soils can have adverse effects, which will be addressed in later paragraphs.

Metals generally do not attack foliage directly. Their effects are most pronounced on roots. Although lumping metals into a single category is scientifically inaccurate, as each element exhibits independent effects ranging from biochemical competition with nutrient ions (for example, zinc and phosphate) to direct inhibition of root tip growth (aluminum), for the purposes of this discussion they will be considered together. Most metals are not easily translocated to the shoots of plants but can have profound effects on root function and the healthy functioning of many soil organisms upon which plants rely for nutrient cycling. Studies of metal-contaminated soils have shown that the microbial communities are frequently altered. In addition, some metal-contaminated soils have reduced rates of litter decomposition, thus lowering nutrient availability. In particular, nitrogen and phosphorus can become growth-limiting. When metal concentrations reach a level such that they seriously inhibit root functions, the trees are no longer able to acquire enough water or nutrients, resulting in stunting of growth and ultimately death. Unlike sulfur dioxide, which may be metabolized and at least temporarily removed from the environment, the lack of uptake, assimilation, or translocation means that metals remain in the environment. Therefore, even relatively low levels of ambient air concentrations can result in metal accumulation in soils. Once a critical load has been achieved, tree mortality occurs.

The presence of both sulfur dioxide and metals is often synergistic, meaning that the effects together are more destructive than the individual effects. The second effect of sulfur dioxide emissions is 'acid rain,' although deposition occurs in any precipitation form. Acid rain has been greatly publicized and is probably the best recognized effect of air pollution. The significance of acid rain effects depends upon many other environmental factors, particularly those related to soil physical and chemical structure. Therefore a universal statement regarding acid rain effects in boreal forest is inappropriate. However, one of the more important chemical aspects of acidification of the soil is an increased mobilization of metals. When metals accumulate on the forest floor, many are bound up in organic compounds, or chemically bonded to the soil mineral fractions. In these forms metals are largely unavailable and will have little effect on plant roots. However, as the pH of soil decreases (becomes more acid) many metals lose their affinity for the organic ligands or minerals and become suspended in soil solutions. In these forms they are available to biological organisms, including tree roots, and begin to inhibit metabolic function.

Wet Tropics

The forests in the wet tropics vary from evergreen rain forests where growth occurs all year long, to deciduous rainforest with annual wet–dry cycles where growth is curtailed during part of the year. The seasonality of growth affects the extent of air pollution damage and the type of damage likely to occur. Many publications have highlighted the enormous diversity found in tropical forests, both within individual forest types, and globally when comparing rainforests of the world. One of the initial effects of acute air pollution toxicity is a loss of diversity. A few plant species are capable of tolerating the assault and ultimately prosper at the expense of less tolerant species. Whether this loss of diversity is a permanent or transient condition is subject to debate.

Air Pollution Causes

The tropics are generally defined as those areas between the tropic of Cancer (20° N) and the tropic of Capricorn (20° S). This climate zone covers most of South America, Africa, and parts of Southeast Asia and Oceania; thus many developing nations are found in the wet tropics. This section focuses on forest ecosystems where precipitation far exceeds evapotranspiration. Inland areas and landscapes along the western coasts of large continents, which tend to be arid or semiarid, will be discussed under that category. The wet tropics have relatively low industrial activity and traditional agricultural practices are small compared to many European nations. However, this is changing in many regions, and several examples of industrial pollution as well as effects of agricultural practices are beginning to be recognized. Urbanization and air quality problems associated with overcrowding and poor sanitation have created serious human health problems, but little research on ecological effects has been conducted. The use of fire as a land management tool and the prevalence of open fires for cooking, sanitation, and industry are the best-documented pollution concerns.

Air Pollution Concerns

Perhaps the most serious concern for the wet tropical regions is the potential for developing nations to repeat the environmental mistakes made by the developed world. At the same time developing nations are concerned that global air pollution problems of industrialized nations should not hinder their own efforts to improve the standard of living associated with industrialization. As has historically occurred in North America and Europe, when nations move from agrarian-dominated societies to urban manufacturing-based societies rapid influxes of people into cities causes crowding and sanitation problems. Until the necessary infrastructures are built, human and domestic animal wastes create nitrogenous pollutants and open fires remain the primary source for cooking and heating. Individually, small residential and entrepreneurial enterprises have little effect on the environment but, collectively, uncontrolled emissions from these sources generate the same air pollutants seen in larger industrial and urban complexes. These enterprises can produce sulfur dioxide, nitrogen oxide, and organic carbon compounds as primary pollutants. Secondary pollutants, nitric and sulfuric acids, aerosols and ozone generated by atmospheric processes are transported into adjacent forests or become part of the global circulation of anthropogenic atmospheric contaminants. Ammonia and other gases from poor sanitation, cropping systems, and animal husbandry resulting in nitrogen deposition and aerosol formation are typical of urban pollution problems anywhere in the world. The common use of managed fire, and the suggestion that wild fires have increased due to global climate change, are among the more serious concerns for sustainability of the unique forest structures in the wet tropics.

Air Pollution Effects

Clearly, burning to remove vegetation alters the immediate landscape but the effects of smoke on ecosystems downwind have only recently been addressed. The huge fires in Southeast Asia during the late 1990s and the annual burning of the cerrado grasslands in central Brazil offer examples of intentional and unintentional fire effects on native forests. Serious increases in tropospheric ozone have been documented as a result of cerrado fires. Concentrations measured are equivalent to those measured outside large urban centers (100–200 ppb). Data that document greatly increased atmospheric concentrations of volatile organic carbon and other pollutants due to the fires in Borneo have been published, but the long-term effects of these fires are not known. Few studies have been published relating the increase in ozone (and presumably other fire emissions such as organic carbon, nitrogen, and NO), to responses of native tropical forest trees, but experience from western North America would suggest that fire-generated ozone and its precursors are capable of being transported hundreds of kilometers, affecting native ecosystems far removed from the original burn site. Because the growing season is nearly year-round, foliar gas exchange would be expected to occur year-round as well, providing sites of entry for any number of airborne pollutants. The effect of anthropogenic emissions on the unique plant species of tropical rainforests is unknown. However, extrapolating from temperate forests where the nonvascular mosses and lichens appear to be the sentinel species, composition and structural changes are most likely occurring.

Semiarid Forests

Typically, forests found in semiarid regions are sparsely vegetated with trees and understory species well adapted to low, or seasonal water availability. Precipitation patterns vary from distinctly seasonal such as the wet winter/dry summer patterns of the Mediterranean climate, to bimodal rainfall patterns of wet winters and monsoon summer rains. On average, precipitation amounts equal evapotranspiration demands of the vegetation, but periodic drought is a normal feature. Forested landscapes are often at higher elevations where heat loads are not as intense and orographic processes increase total precipitation as moist air moves upslope. Many of these forests are found in coastal Mediterranean regions of the world where coastal influences modify the intense aridity found inland; southwestern North America, parts of the western coast of Africa and South America and of course, around the Mediterranean sea itself contain semiarid forests. Semiarid forests can be found inland as well, particularly at higher elevations where monsoonal rains provide enough moisture to survive the summers. Because metabolic activity is dependent on water and water availability is highly seasonal, direct interactions with the canopy and uptake of atmospheric pollutants are thought to be seasonal. However, deposited pollutants that accumulate in the terrestrial environment may result in unpredicted ecological responses.

Air Pollution Causes

These regions often contain extensive irrigation agriculture and large urban centers along shorelines focused on trade. Where logging has occurred it is not unusual for the forests to be extremely slow in returning, and total conversion of vegetation type to shrublands has been historically documented throughout the world. Although exceptions exist, for the most part semiarid regions do not contain large industrial complexes. Therefore both urban (primarily transportation sources) and agricultural pollutants are the most serious pollution causes in adjacent forested lands.

Air Pollution Concerns

The warm sunny climates, copious exhaust from roadways, and both natural and anthropogenic sources of volatile organic carbon provide the perfect combination for synthesis of the secondary pollutants ozone and nitric acid and primary and secondary aerosols. Nitrogen oxide and nitrogen dioxide from automobile exhaust can be taken up through leaf stomata but, except in the most extreme conditions, have only minor effects on plants. Because photochemical reactions that create ozone and nitric acid require sunlight, distinct diurnal patterns of atmospheric concentrations are typical. In coastal communities ozone concentrations may be near zero at night, increasing during the daylight hours to highs in the 100–400 ppb range. Since both ozone and the precursors are subject to transport aloft, similar ambient concentrations may be measured many kilometers away. This has been well documented in coastal southern California and southern Spain. Nitric acid is a byproduct of ozone synthesis. Currently there are no instruments that can measure nitric acid exclusive of other nitrogenous pollutants on an hourly basis. This has limited the ability to establish patterns of ambient concentrations and distribution. Denuder systems and passive collectors currently provide the best ambient concentration information, but they are labor-intensive and require longer exposure times. Therefore, the results are an integrated value over a 12-hour to 1-week period. Twenty-four-hour average concentrations above 1 ppb are considered high pollutant episodes. Daytime concentrations in the 10–12 ppb range have been recorded in southern California. Nitric acid is highly reactive. Once formed it can solubilize in water vapor, and readily deposit on exposed surfaces, combining with volatile ammonia products from cropping and animal production facilities to form ammonium nitrate aerosols.

Anthropogenic sulfur emissions are generally low in these regions largely due to the lack of significant coal-burning and metal-smelting operations but, along the coast and in saline valleys, natural sources of sulfate can provide the counterion for ammonium sulfate particles. Fugitive dust from roadways and land-disturbing operations such as construction and cropping practices are serious issues in these climates because the arid environment permits longer suspension times and therefore longer travel distances before the dust is deposited.

Air Pollution Effects

Ozone effects on semiarid forests are well documented in the Mediterranean climates of south-western North America, southern Spain, and Italy. Short-term exposures to ozone concentrations greater than 150 ppb can cause acute damage symptoms on many plant species. Long-term, chronic exposures to 50 ppb result in reduced growth of sensitive species and foliar mottling of many forest tree species. The primary sites of uptake and injury are the stomata of actively photosynthesizing leaves. When the stomata are open for gas exchange, ozone readily gains access to the stomatal cavity and mesophyll of foliage. Once inside the plant leaf, damage to cell and organelle membranes occurs, although the exact mode of attack is not well understood. Symptoms first appear as chlorotic spots on leaves and needles. As the damage progresses, cells in the chlorotic areas die, leaving necrotic spots. Although this kind of damage can be confused with other biotic and abiotic effects, the patterns of ozone damage and the distribution patterns of damage are often quite specific within a particular plant species. However, the lack of visible symptoms is not always an accurate indicator for tolerance to high ambient ozone concentrations. Ozone toxicity by itself is rarely the cause of death in mature trees, but weakens trees so that they are susceptible to insect, pathogen, or environmental assaults.

Much of the nitrogen deposition in semiarid forests occurs in the dry form, unlike nitrogen deposition in temperate regions. Dry deposition is very difficult to measure using current techniques. Among the many difficulties in understanding the effects of dry deposition is that nitrogen is a normal part of the ecosystem, unlike ozone or heavy-metal pollutants. For this reason establishing nitrogen deposition as a causal agent for changes in forests has been difficult. Deposited nitrogen accumulates during the dry season and becomes available when precipitation returns, in effect behaving as a fertilizer. Changes in nitrogen fertility have been shown to change ecological structure and function. Although forests are slow to respond to changes in fertility, monitoring nitrogen-impacted forests has indicated changes in species composition, beginning with the shorter-lived species, such as annuals and herbaceous perennials. Nitric acid and ozone are formed through the same photochemical processes in the atmosphere. Therefore, the presence of one is usually indicative of the other. Studies suggest that there is an interaction between the two air pollutants, but the nature of that interaction is poorly understood. Under some conditions it appears that nitrogen deposition may ameliorate ozone effects while under other conditions dry deposition of nitric acid to foliage may exacerbate ozone damage. The study of multiple pollutant effects is an emerging topic that will ultimately improve our understanding of air pollution effects on natural ecosystems.

Particulate pollutants occur in all parts of the world, but the low humidity and seasonal rainfall make suspended particulates a serious issue in semiarid ecosystems. The sizes of these pollutants can range from a few angstroms to several micrometers in diameter. The size affects physical behaviors such as travel distance and deposition as well as the pollutants' effects on biological organisms. Very small particles (less than 0.2 μm in diameter) are a serious public health concern. When breathed, they become lodged in the lung tissue and are not easily removed. It is not known whether similar phenomena occur in the plant kingdom. The effects of particulate pollutants in forests fall into two categories: physical abrasion/coatings and chemical effects. Blowing dust scratches leaf surfaces and damages the cuticles of leaves, increasing opportunities for pathogen infection. In addition, when dust lands and collects on foliage it blocks penetration of sunlight, reducing photosynthetic capacity. From a chemical standpoint, particulates serve as nutrient sources. Small ammonium nitrate or sulfate particles are capable of traveling hundreds of kilometers within a few days. Particles greater than 10 μm are restricted from rapid long-distance transport due to gravitational forces, but studies in Southwest North America have shown that multiple transport events over the course of a season can make a substantial contribution to the nutrient load at many kilometers distance from the particle source.

Temperate Forests

Most of the world's industrialized nations are partially or entirely in temperate climate regimes. Forests in the temperate climates experience all the air pollution insults and effects enumerated under other climate regimes. Ozone, particulates, nitrogen deposition, smoke, heavy-metal, and sulfur effects are well documented and in many ways best understood in these ecosystems. Europe and Central Asia have long histories of human settlement and industry. North America and Australia are more recently urbanized, but all participated in the industrial revolution that initiated large-scale air pollution effects in natural ecosystems.

Modern agricultural practices have improved crop yield and increased animal production by improving efficiency of land use. In many cases modern practices have led to highly concentrated animal husbandry operations where hundreds or thousands of animals are confined to small spaces and to the heavy use of synthetic fertilizers and pesticides. At the same time, urbanization concentrated humans into crowded cities where sanitation, fuel combustion for heating and cooking, and the need for transportation generates concentrated pollutants.

During the early expansion of industry and production agriculture, the ability of natural ecosystems to absorb the byproducts of human activities was either ignored or thought to be limitless. However, in the last several decades, many nations have recognized the serious effects of air pollution on forests and have taken steps to reduce or eliminate many of the pollutants through legislation and technology. Reduction in sulfur emission in the industrialized mid-west and northeastern parts of North America has resulted in measurable reductions in ambient concentrations and deposition to adjacent forests. Improved metal-smelting technologies have greatly curtailed atmospheric deposition of heavy metals in Canada, Europe, and parts of Asia. Improvements in energy production efficiency for heating, cooking, and transportation have reduced urban smoke emissions when compared to the air quality at the turn of the century. However, the problems of air pollution effects in temperate forests are far from solved.

Air Pollution Causes

The temperate forests are found in the most heavily populated climate zones on earth. All the known causes of air pollution are here. Intense animal production in western Europe, southeastern USA, and the UK produces enormous quantities of ammonia vapor that are then transported into native forests. Pesticide applications in valleys drift into the slopes of adjacent forests, and automobile exhaust continues to be one of the most serious causes of air pollution. Although reduction in sulfur emissions is a partial success story, nitrogen oxide emissions remain steady in the USA and are rising dramatically in western Europe and Asia as increased wealth allows increased numbers of automobiles and reliance on internal combustion engines for transport and energy production. Many of the most destructive smoke stack sources in Eastern Europe have been eliminated or reduced due to economic and outside pressure; however, these sources continue to impair forests seriously in developing Asian nations.

Air Pollution Concerns

The air pollution concerns of temperate regions are complex and intertwined. Frequently, it is difficult to isolate independent pollutant sources in an effort to control emissions and reduce impacts. Generation of the precursors for ozone synthesis, nitrogen oxide, and volatile organic carbon is a good example. Any combustion process – agricultural, urban, or industrial – can generate nitrogen oxide, although automobiles are the most frequently noted sources. Volatile organic carbon compounds can come from restaurants or dry cleaners, smoke stacks or motors, and fires or production of volatile compound by native vegetation. Once these compounds are aloft and the photochemical process initiated, the ozone created can impact forests tens or hundreds of kilometers away. This is clearly the case in the checkerboard pattern of land uses in the eastern half of the USA, much of Europe, and increasingly in Asia.

Pollution concerns in temperate agricultural systems are similar to those found in semiarid systems: particulates, nitrogen deposition, and pesticides. Unlike the semiarid systems, wet deposition plays a much more significant role. While wet deposition helps reduce high ambient particulate loads, it is the major source of nitrogen deposition in forests. The eutrophication effects of ammonia deposition are particularly acute in forests adjacent to large feedlots, dairy operations, and confined poultry and pig farms. Urban pollutant sources are generally associated with combustion processes, automobiles, and energy generation and its use. Although sanitation continues to be a problem in regions experiencing rapid population growth, many established urban centers have developed the necessary septic and sewer systems so that human waste is not generally an issue. Industrial waste does continue to impact local and global air quality. For many of the traditional smoke stack pollutants, sulfur, metals, and smoke particles, technology is available to reduce atmospheric loading; however, as new industries are being developed, new pollutants, particularly organic solvents, are emerging as serious health and ecological concerns. These new pollutants will continue to require new methods for detection and research into long-term impacts.

Air Pollution Effects

Acid rain and wet deposition are not unique to temperate forests but, because of milder temperatures, wet deposition, including fog and mists, can have pronounced effects on temperate ecosystems. Any substance that will solubilize in water will deposit as wet deposition. Acid rain studies have focused primarily on sulfuric and nitric acids but ammonia, metals, and pesticides – among other compounds – can be found in rain. One exception is ozone. Rainfall and very high humidity found in fog tend to ameliorate ozone, and without sunlight the chain reactions that form ozone are broken. The acidity in rain is caused by the presence of positively charged hydrogen ions (protons), which is why nitric and sulfuric acids have the most pronounced effect on pH; both are strong acids, releasing protons when solubilized in water. Normal rainfall tends to be slightly acidic, generally in the 6.2–6.5 pH range (neutral pH is 7). Acid rains have been measured as low as 3.5 and rainfall in the 4.5–5.0 ranges are not unusual in heavily industrialized or urban areas. How acid rain affects the forest is dependent upon many factors. In forest soils that are weakly buffered, wet deposition can reduce the soil pH, substantially changing below-ground processes, including mobilizing metals. Aluminum is an element that is found in large quantities in soils, but it is generally not toxic at higher pHs. When the pH is lowered, the availability of aluminum is increased, causing stunting of roots. Where soils are richer and better buffered, the percolation of rainwater through the soil profile leaches base cations (plant nutrients with positive charges) out of the rooting zone, causing impoverishment of the soil. The ability of forest soils to repair the damage once acid rain ceases is also highly dependent on the forest. Highly productive landscapes may reverse decline within a few years; however, many examples exist where the atmospheric inputs are no longer present, but the effects continue.

Wet deposition to foliar surfaces can result in erosion of the leaf surface. This is less of a problem in deciduous forests than in the evergreen conifer forests where excessive damage to needles results in premature abscission. Wet deposition of nitrogenous pollutants may not necessarily result in pH shifts, but long-term studies of nitrogen-affected forests indicate shifts in forest function and composition. The tendency of pollution-impacted forests to suffer 'winter kill,' for example, has been attributed to increases in nitrogen to those forests.

Remediation

Forests are slow to respond to management activities, and remediation measures are designed to shift the trajectories of forest ecological processes rather than completely change ecological patterns. Prescribed fire is being used as a remediation tool for several desired outcomes. Fire reduces the biomass of smaller trees and understory vegetation reducing the competition for water in semi-arid, ozone-impacted forests. Fire also reduces nitrogen loading in forests approaching nitrogen saturation and eutrophication. Selective harvesting and replanting of resistant varieties can also help shift pollution-impacted, declining forests into more productive forests. However, in recent years forests have demonstrated a surprising ability to recover all by themselves once the pollutant source is eliminated.

In recent years forests have demonstrated a surprising ability to recover once the pollutant source is eliminated. What was once thought to result in total destruction of forests in highly polluted regions is now understood to be yet another disturbance similar to fires or floods from which forests will recover over time. There are exceptions, such as sites heavily contaminated by metals; these areas will require more active remedial action. However, the annihilation of native forests due to air pollution, predicted during the 1970s and 1980s, has for the most part not occurred. Are these recovering forests the same before and after high pollution events? Probably not, but all landscapes are constantly responding to environmental conditions in ways that are difficult to quantify. It becomes the job of the forester and society to determine how air pollution effects are moderated so that all the resources that forests have to offer remain intact.

See also: **Environment**: Carbon Cycle; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Health and Protection**: Biochemical and Physiological Aspects; Diagnosis, Monitoring and Evaluation. **Site-Specific Silviculture**: Reclamation of Mining Lands; Silviculture in Polluted Areas.

Further Reading

Flagler RB (ed.) (1998) *Recognition of Air Pollution Injury to Vegetation: A Pictorial Atlas*, 2nd edn. Pittsburg, PA: Air & Waste Management Association.

Innes JL and Haron A (2000) *Air Pollution and the Forests of Developing and Rapidly Industrializing Countries*. IUFRO research series 4. Wallingford, UK: CAB International.

Innes JL and Oleksyn J (eds) (2000) *Forest Dynamics in Heavily Polluted Regions*. Report no. 1 of the IUFRO Task Force on Environmental Change. Wallingford, UK: CAB International.

Miller PR and McBride JR (eds) (1999) *Oxidant Air Pollution Impacts in the Montane Forests of Southern California. A Case Study of the San Bernardino Mountains*. New York: Springer-Verlag.

Olson RK, Binkley D, and Böhm M (eds) (1992) *The Response of Western Forests to Air Pollution*. New York: Springer-Verlag.

Seinfeld JH and Pandis SN (eds) (1998) *Atmospheric Chemistry and Physics From Air Pollution to Climate Change*. New York: John Wiley.

Smith WH (ed.) (1990) *Air Pollution and Forests Interactions between Air Contaminants and Forest Ecosystems*. New York: Springer-Verlag.

Vitousek PM, Aber J, Howarth RW, *et al*. (1997) *Human Alteration of the Global Nitrogen Cycle: Cause and Consequences. Issues in Ecology*, vol. 1, Washington, DC: Ecological Society of America.

Carbon Cycle

J L Innes, University of British Columbia, Vancouver, BC, Canada

Introduction

The forest environment carbon cycle can be viewed at a number of scales. Measurements can be made at the scale of an individual leaf or tree, stand-scale measurements can be made, and models can be developed that examine forest-level, regional, and global carbon cycles. The role of the forest in the global carbon cycle has become increasingly important as it is realized that forests and forestry have a role to play in mitigating the so-called greenhouse effect. This article examines the sources, sinks, and fluxes of carbon as they relate to forests and then places this information within the context of global change. Finally, the potential contribution of forests to the mitigation of climate change is assessed.

The Global Carbon Cycle

The main components of the natural global carbon cycle are the sources, sinks, and fluxes between the land, oceans, atmosphere, and geological reservoirs. Current estimates suggest that the atmosphere contains about 730 Pg C, the land 2000 Pg C, the oceans 38 000 Pg C, and that an unknown amount remains in geological reservoirs. The greatest natural flux (120 Pg C per year) is between the land and the atmosphere, with a smaller flux occurring between the atmosphere and the oceans (90 Pg C per year). Estimates of the sizes of the different carbon pools are given in **Table 1**. In terms of fluxes, the carbon cycle can be seen as an approximate balance between the processes of photosynthesis by plants and respiration by plants, animals, and microbes. It is the variations on either side of an exact balance between photosynthesis and respiration that cause natural variations in the global carbon pools, supplemented by anthropogenic activities, such as the clearing of forests and the burning of fossil fuels,

Table 1 Estimates of terrestrial carbon stocks and net primary productivity published by the Intergovernmental Panel on Climate Change

Biome	*Area (10^9 hectare)*	*Global carbon stocks (Pg C)*		
		Plants	*Soil*	*Total*
Tropical forests	1.76	212	216	428
Temperate forests	1.04	59	100	159
Boreal forests	1.37	88	471	559
Tropical savannas and grasslands	2.25	66	264	330
Temperate grasslands and shrublands	1.25	9	295	304
Deserts and semideserts	4.55	8	191	199
Tundra	0.95	3	121	127
Croplands	1.60	6	128	131
Wetlands	0.35	15	225	240
Total	15.12	466	2011	2477

which cause further changes (both in the balance between photosynthesis and respiration and in the total carbon fluxes).

The Forest Carbon Cycle

All higher plants take up carbon dioxide. Globally, the amount of CO_2 that is dissolved in leaf water has been estimated to be 270 Pg C per year, representing more than one-third of all the CO_2 stored in the atmosphere. Most of this carbon leaves the plants without being involved in photosynthesis. The fraction that remains and which is converted from CO_2 to carbohydrate is known as the gross primary production (GPP). The total amount of terrestrial GPP has been estimated at 120 Pg C per year. Approximately one-half of this is converted back to CO_2 by autotrophic respiration. Autotrophic respiration (often abbreviated to R_A) can be divided into two distinct processes: maintenance respiration (R_M), which is the respiration that is required for a plant to maintain its basic physiological processes and thus to survive, and construction respiration (R_C), which is the respiration that is needed for the plant to build new structures such as leaves, roots, the stem, flowers, and other organs. Autotrophic respiration therefore refers only to plants.

Scaling up to the ecosystem level, the difference between GPP and autotrophic respiration is termed net primary production (NPP). There are many measurements available for NPP, and the total amount of NPP globally has been estimated to be about 60 Pg C per year. Almost all of this carbon is returned to the atmosphere through heterotrophic respiration (R_H), which is the respiration of organisms that break down the products of net primary production, including both herbivores and decomposers, and through fires. Within forest ecosystems, fires can be a particularly important mechanism for the return of carbon to the atmosphere, with a global estimate of 936 Tg C being released annually by forest fires. However, the reliability of the data used to derive this estimate is very questionable. Where data are available, the figures suggest that fire is of major importance. For example, the 1987 fires in Indonesia, which burnt both above-ground biomass and below-ground peat, are estimated to have released between 0.81 and 2.57 Pg C, equivalent to 13–40% of the global annual emissions of fossil fuels. This figure is higher than the global estimate, as it includes the carbon released by the below-ground burning of peat. If only the above-ground vegetation is included, then the figure was reduced to 50 Tg C.

Heterotrophic respiration is especially important, as it is largely responsible for the return of organically bound carbon to the atmosphere. Much of this occurs in soils or on the soil surface, with the rate of breakdown being controlled by a number of different factors, including climate, chemical composition of the plant matter, soil conditions, and others. The microbial biomass and soil detritus tends to break down quite quickly (within 10 years), whereas modified soil organic carbon may take much longer (100 years or more, depending on the climate). Turnover times for forest litter vary from less than 6 months in some tropical forests to over 350 years in boreal coniferous forests. In many forests, the rates of breakdown have been influenced by management practices, and management presents an opportunity to control in part the carbon in forests.

The biomass pools in a forest can be divided into the above- and below-ground tissues of plants, woody debris, the forest floor, the mineral soil, and the tissues of heterotrophic organisms. The proportions in each of these pools vary dramatically, depending on the type of forest, with figures for the

Table 2 Forest volume and above-ground biomass by region, as published by the UN Food and Agriculture Organization

Region	Forest area (million hectare)	Volume		Biomass	
		By area (m^3 hectare^{-1})	Total (Gm^3)	By area (t hectare^{-1})	Total (Gt)
Africa	650	72	46	109	71
Asia	548	63	35	82	45
Oceania	198	55	11	64	13
Europe	1039	112	116	59	61
North and Central America	549	123	67	95	52
South America	886	125	111	203	180
Total	3869	100	386	109	422

above-ground biomass being presented in **Table 2**. Approximately 50% of the dry biomass of a tree is thought to consist of carbon, although carbon removed from the atmosphere of the tree may also be transferred to the soil carbon pool through litterfall. The actual amount sequestered by an individual tree will depend on the species, the growing conditions, and its environment. The environment is important: in urban areas, the leaves or needles shed by a tree are often removed, preventing uptake into the soil.

A mature forest is generally considered to be 'carbon-neutral.' This means that it releases as much carbon as it absorbs. This assumption is based on looking at the carbon balance over a fairly extensive area of forest, as local stand dynamics can result in substantial changes in the carbon balance as the forest is disturbed and regrows. Using the terms described above, NPP should more-or-less equal R_H. While this may be the case for some mature forests, more often forests are in a state of dynamic equilibrium, with some net carbon either being gained or lost from the forest ecosystem. This is termed the net ecosystem production (NEP); measurements of NEP range from 0.7 to 5.9 Mg C hectare^{-1} year^{-1} for tropical forests, 0.8 to 7.0 Mg C hectare^{-1} year^{-1} for temperate forests, and up to 2.5 Mg C hectare^{-1} year^{-1} for boreal forests. The rates are very variable, and in some areas there may be negative NEPs in particular years.

The NEP represents only the difference between NPP and R_H, and does not take into account carbon losses through fire, erosion, and other processes. The overall figure of relevance to global forest carbon cycles is the net biome production (NBP), which takes into account all the processes of carbon gain and loss from the terrestrial biosphere. This has been estimated at -0.2 ± 0.7 Pg C year^{-1} during the 1980s and -1.4 ± 0.7 Pg C year^{-1} during the 1990s. The negative values for these flux estimates indicate that the land is acting as a sink for atmospheric carbon.

While the figures for global NPP, NBP, and R_H all appear to be given with some certainty, considerable care should be taken over their interpretation. Most figures are based on models, and the underlying quality of the data used to draw those assumptions and build the models is not always very good. This is particularly true in the case of forests, where great reliance is placed on the Forest Resource Assessment of the UN Food and Agriculture Organization. The quality of this inventory of the world's forests has improved with each successive inventory, but major data quality problems remain, particularly in the tropical countries and Russia. For example, emissions of carbon associated with forest fires in Russia are very uncertain, with information on both the extent and severity of forest fires in Siberia being very unreliable.

Despite these difficulties, there are increasing numbers of indications that carbon stocks in the world's forests may be increasing. In the tropics, data from permanent sample plots indicate that tree growth is increasing, although the flux is more than balanced by losses caused by deforestation. In temperate and boreal forests, an increasing forest area has been accompanied by increasing carbon stocks in existing forests. In some regions, these trends have been present for some time. In the northern hemisphere, the regrowth of forests following the deforestation of the eighteenth and nineteenth centuries is estimated to be responsible for the uptake of 0.5 ± 0.5 Gt C year^{-1}. In other areas, such as the tropics and some temperate regions, the trend appears to be new.

Global Increases in CO_2

Over the past 200 years, the atmospheric concentrations of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) have been increasing at an exponential rate. These three gases, together with a range of others (particularly the halocarbons), are known as greenhouse gases. The term is used because the gases are able to absorb some of the longwave radiation that is emitted from the earth, resulting in an increase in the temperature of the atmosphere, the so-called 'greenhouse effect.' Since 1750, atmospheric CO_2 concentrations have increased from the preindustrial concentration of 280 parts per million (ppm) by 31%, and current concentrations (367 ppm in 1999) are higher than at any time in the last 400 000 years. Concentrations of CH_4 have increased 151% since 1750, and are also unprecedented within the past 400 000 years, whereas concentrations of N_2O have increased by 17%. The past history of atmospheric N_2O concentrations is less certain than for CO_2 or CH_4, and it is only possible to state that current N_2O concentrations have not been exceeded within the past 1000 years. In contrast to the other greenhouse gases, many of the halocarbon gases that are both greenhouse gases and ozone-depleting have been stable, decreasing or increasing more slowly since 1995, when the Montreal Protocol and its amendments introduced controls on their emissions. They have been substituted by a number of other gases, such as CHF_2Cl and CF_3CH_2F, which are not ozone-depleting, but which are greenhouse gases. These, together with synthetic compounds that are also greenhouse gases, such as perfluorocarbons (PFCs) and sulfur hexafluoride (SF_6), have been increasing in the atmosphere.

Atmospheric concentrations of these gases have varied considerably in the past, providing one of the reasons to question the cause of the current increase in concentrations. However, the rate of change in CO_2 concentrations appears unprecedented, certainly within the past 20 000 years. The preindustrial and recent (1998) concentrations of selected greenhouse gases are given in **Table 3**.

Table 3 Greenhouse gas concentrations in pre industrial times and currently

Gas	*Preindustrial*	*1998*
CO_2	*c.* 280 ppm	365 ppm
CH_4	*c.* 700 ppb	1745 ppb
N_2O	*c.* 270 ppb	314 ppb
CFC-11 (chlorofluorocarbon 11)	zero	268 ppt
HFC-23 (hydrofluorocarbon-23)	zero	14 ppt
CF_4 (perfluoromethane)	40 ppt	80 ppt

The Intergovernmental Panel on Climate Change (IPCC) is a group of government-appointed scientists responsible for looking into the nature, causes, and extent of climate change. They have reached a broad consensus that the increase in CO_2 and other gases is the result of anthropogenic activities, and that the increase is at least in part responsible for the observed increase in global average surface temperatures of $0.6 \pm 0.2°C$ over the past 100 years. It is likely that the 1990s was the warmest decade and 1998 was the warmest year in the northern hemisphere in the last 1000 years, and the IPCC has concluded that most of the observed warming over the past 50 years is likely due to increased greenhouse gas concentrations in the atmosphere.

The influence of different types of forcing factors on global temperatures is calculated using the concept of radiative forcing. The forcing is a measure (expressed in $W\,m^{-2}$) of the extent to which any particular factor influences the incoming and outgoing energy within the earth–atmosphere system. If the forcing is positive, then it results in an increase in temperature. Conversely, a negative forcing results in a lowering of temperature. The radiative forcing of different greenhouse gases is shown in **Table 4**. These figures need to be placed in the context of other forcing factors. For example, the radiative forcing associated with the burning of biomass is estimated to be $-0.2\,W\,m^{-2}$ (indicating a cooling effect), as the aerosols prevent energy from reaching the earth's surface.

During the period 1980–2000, approximately 75% of the CO_2 emissions were from the burning of fossil fuels, whereas the remainder (estimates range from 10% to 30%) was the result of land-use changes, particularly deforestation. Just over half of the emissions of CH_4 are from anthropogenic sources (such as fossil fuels, rice cultivation, cattle, and landfills), whereas only a third of current N_2O emissions are anthropogenic (sources include the chemical industry, cattle feed lots, and agricultural soils). The cumulative carbon losses occurring as a result of land use and management changes have been estimated to be between 180 and 200 Pg C. The loss of forests has been the primary factor, leading to terrestrial carbon emissions since 1850, amounting to about 90% of the total emissions.

Historical land-use changes have certainly had a major impact on the global carbon budget. Data collected by the United Nations Food and Agriculture Organization between 1990 and 2000 suggest that about 15 million hectares of natural forest are lost annually, although the data are very unreliable. This is in part compensated by a natural expansion of forest by 1 million hectares annually, and establishment of about 2 million hectares of forest plantations annually in the tropics. The greatest losses (42% of the total) occur in Latin America, with the proportions in Africa and Asia amounting to 31% and 27%, respectively. The land-use changes and forestry operations in the tropics are estimated to be releasing between 1.1 and 1.7 Gt C $year^{-1}$ (during

Table 4 Radiative forcing of greenhouse gases from 1750 to 2000

Greenhouse gas	*Radiative forcing*
CO_2	$1.46\,W\,m^{-2}$
CH_4	$0.48\,W\,m^{-2}$
Halocarbons	$0.34\,W\,m^{-2}$
N_2O	$0.15\,W\,m^{-2}$
Total	$2.43\,W\,m^{-2}$

the mid-1990s) although, again, the estimates are very approximate and based on incomplete data. The area of forested land in the temperate regions is, however, increasing by about 3 million hectare annually. This means that there was a net annual loss of forests in the period 1990–2000 of about 9.4 million hectare, equivalent to a biomass loss of about 1.6 Gt annually. This last figure should be treated with caution, as it is based on changes in forest area alone. There are also changes occurring within forests, such as the increase in productivity described above. Outside the tropics, a biomass gain within the forest of about 0.9 Gt occurred annually in the period 1990–2000. No equivalent figure is available for tropical forests.

Forests and the 'Greenhouse Effect'

The increase in global mean temperature is important as it will have a wide range of effects. For example, increased temperatures are leading to the loss of ice from glaciers and icecaps. At the same time, the increase in the temperature of the surface layers of the earth's oceans is resulting in thermal expansion of the surface waters. Combined, these processes have resulted in an increase in sea-level, with major potential consequences for low-lying land areas. In the Pacific region, several island groups are now threatened with submersion, with sea levels expected to increase by between 0.09 and 0.88 m between 1990 and 2100.

A number of potential solutions have been proposed, and an international mechanism to encourage solutions, the Kyoto Protocol, was agreed in December 1997. The Kyoto Protocol stated that industrialized countries would, by 2008–2012, reduce their combined greenhouse gas emissions by 5.2% relative to their 1990 emissions. Individual countries have specific targets, and some countries can even increase their emissions by the year 2012. A number of strategies can be adopted to reduce emissions, including increased energy efficiency, reduction in energy demand, and implementation of alternative technologies. In addition, several short-term steps can be taken through the development of carbon sinks.

The focus of the Kyoto Protocol and its amendments has been on CO_2. This is because CO_2 is the dominant human-influenced greenhouse gas, accounting for a radiative forcing of $1.46\,W\,m^{-2}$, or 60% of the radiative forcing of all the long-lived greenhouse gases. The rate of increase in the gas is variable, and in the 1990s, it ranged from 0.9 to $2.8\,ppm\,year^{-1}$, or 1.9 to $6.0\,Pg\,C\,year^{-1}$. The variation seems to be related to the occurrence of El Niño events, with higher rates of increase occurring in years with marked El Niño events (due to reduced terrestrial uptake).

Trees to Mitigate CO_2 Increases

The potential of forests to reduce the rate of increase in atmospheric CO_2 has been the subject of much debate, especially within the context of the Kyoto Protocol to the United Nations Framework Convention on Climate Change. At issue has been the extent to which countries should be allowed to offset their CO_2 emissions through the enhancement of sinks (which partly avoids the difficult issue of directly reducing CO_2 emissions). In addition, the many uncertainties associated with the quantification of the forest carbon sink has caused problems. The Kyoto Protocol (Articles 3.3 and 3.4) specifically recognized forests as carbon sinks, but it was not until November 2001 that some of the definitions were finally established (the Marrakesh Accords).

The increase in atmospheric CO_2 concentrations can be clearly linked to fossil fuel burning and to land-use change. The land-use change of greatest relevance is normally considered to be deforestation. Unfortunately, estimates of deforestation rates are extremely unreliable, making it difficult to determine precise figures. However, the net release of CO_2 from terrestrial sources, which amounted to between 0.6 and $2.5\,Pg\,C\,year^{-1}$ during the 1980s, has been attributed to deforestation in the tropics. A related problem is deforestation in high latitudes, where models of deforestation have suggested that the conversion of snow-covered forests to snow-covered open areas has resulted in an increase in the albedo (reflected energy), causing a cooling effect in the order of $-0.2 \pm 0.2\,W\,m^{-2}$. Reducing the rate of this deforestation would clearly have an impact on the global carbon cycle.

Trees are seen as a potential means to sequester carbon. This is based on the idea that a one-time benefit can be obtained by planting forests in areas where forests have previously been lost. Tree plantations in the boreal, temperate, and tropical zones are thought to have sequestered about 11.8 Gt C, with an annual sequestration rate of 0.2 Gt C $year^{-1}$. The IPCC has estimated that slowing the rate of deforestation combined with the promotion of natural forest regeneration and afforestation could increase terrestrial carbon stocks in the period 1995–2050 by between 60 and 87 Pg C. In Brazil alone, a reduction in the rate of deforestation by 50% could conserve as much as 125 Mt C $year^{-1}$.

A potentially much more valuable function of forests is as a supply of biomass for burning in power generation. While the carbon stored in the wood is immediately released into the atmosphere, the benefits are gained when the power that is generated replaces power generated from fossil fuels. This approach has been strongly advocated in some European countries, but there is still a need to look at the full costs of the power generation (i.e., including the carbon costs associated with the construction of the power generation plant and with the development and growth of the forest).

In addition to such direct methods, the IPCC has identified a number of silvicultural and management techniques that might be used to enhance carbon mitigation. These include fire prevention and control, protection against pests and disease, changes to rotation lengths, control of stand density, enhancement of nutrient supply, control of the water table, selection of useful species and genotypes, use of biotechnology, reduced regeneration delays, selection of harvesting methods such as reduced-impact logging, recovery of degraded forest, management of logging residues, recycling of wood products, increased use of wood, and efficiency of the conversion process from wood to products, and the establishment and maintenance of forest reserves. These methods all provide means by which the forest sector could contribute to the global effort to reduce anthropogenic impacts on the global carbon cycle.

See also: **Environment**: Impacts of Elevated CO_2 and Climate Change. **Mensuration**: Tree-Ring Analysis. **Non-wood Products**: Energy from Wood. **Tree Physiology**: A Whole Tree Perspective; Forests, Tree Physiology and Climate.

Further Reading

Aber JD and Melillo JM (1991) *Terrestrial Ecosystems*. Philadelphia, PA: WB Saunders.

Houghton JT, Ding Y, Griggs DJ, *et al*. (eds) (2001). *Climate Change 2001: The Scientific Basis*. Cambridge, UK: Cambridge University Press.

Karjalainen T (ed.) (2002) The role of boreal forests and forestry in the global carbon budget. *Forest Ecology and Management* 169(1–2), 1–175.

Kirschbaum MUF (2003) Can trees buy time? An assessment of the role of vegetation sinks as part of the global carbon cycle. *Climatic Change* 58: 47–71.

Metz B, Davidson O, Swart R, and Pan J (eds) (2001) *Climate Change 2001: Mitigation*. Cambridge, UK: Cambridge University Press.

Mohren GMJ, Kramer K, and Sabaté S (eds) (1997) *Impacts of Global Change on Tree Physiology and Forest Ecosystems*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Oberthür S and Ott HE (1999) *The Kyoto Protocol: International Climate Policy for the 21st Century*. Berlin, Germany: Springer-Verlag.

Schlesinger WH (1997) *Biogeochemistry: An Analysis of Global Change*. San Diego, CA: Academic Press.

Stocks BJ (ed.) (2002) The role of boreal forests and forestry in the global carbon budget. *Climatic Change* 55(1–2): 1–285.

Walker B and Steffen W (eds) (1996) *Global Change and Terrestrial Ecosystems*. International Geosphere-Biosphere Programme Series no. 2. Cambridge, UK: Cambridge University Press.

Watson RT, Noble IR, Bolin B, *et al*. (eds) (2000) *Land Use, Land-Use Change, and Forestry*. Cambridge, UK: Cambridge University Press.

Terminology

Pg C Petagrams of carbon (1 Pg C = 1 Gt C = 1000 Mt C $= 10^{15}$ g C).

Tg C Teragrams of carbon (1 Tg C = 1 Mt C = 10^6 tonnes C = 10^{12} g C).

Mg C Megagrams of carbon (1 Mg C = 10^6 g C = 1 ton-tonne C).

Gt C Gigatonnes of carbon (1 Gt C = 10^9 tonnes C = 3.7 Gt of carbon dioxide).

Mt C Megatonnes of carbon (1 Mt C = 10^6 tonnes C).

Impacts of Elevated CO_2 and Climate Change

G E Jackson and J Grace, Edinburgh University, Edinburgh, UK

Introduction

Forests have always been sensitive indicators of climate change. Tree pollen, preserved in lake sediments and bogs, provides a record of how tree species migrated northwards as warming occurred after the retreat of ice about 12 000 years ago. Many tree species reached a maximum northern limit in the warm period (5000–8000 years ago) and then retreated in the somewhat cooler period that followed. On a shorter timescale, most trees leave a faithful record of their annual growth over their lifetime, as annual growth rings in their stems. For northern species there is an excellent relationship between temperature and annual growth. From such records scholars have been able to use ancient wood samples found in old buildings and bogs to reconstruct past climates.

Another indication of the sensitive response of temperate trees to climate comes from phenological gardens where the timing of bud break and leaf unfolding is observed every year. These records show that trees begin their growth earlier nowadays than they did 20 years ago, matching the rise in temperature.

In this article we examine the current rate of climate change, and the predictions that have been made about the future climate. We discuss how forests may be responding to the changing climate, bearing in mind that factors other than the climate are changing too. These factors include the rising carbon dioxide concentration and the rate at which nitrogen (as ammonium or nitrate) is deposited on the land surface.

Climate Changes

Since the end of the last glacial period some 12 000 years ago, the temperatures of the northern hemisphere have increased markedly. Of particular interest are the changes over the last 100 years, which have been unusually rapid. The Intergovernmental Panel on Climate Change (IPCC) has produced a series of reports, the latest of which (the Third Assessment Report) was produced in 2001. This comprises three volumes, the first of which, *Climate Change 2001: The Scientific Basis*, provides the most up-to-date and reliable assessment of the recent state of the global climate. It finds that the global average surface temperature has increased over the twentieth century by 0.6°C (±0.2°C) (**Figure 1**). It also states that globally the 1990s were almost certainly the warmest decade and 1998 the warmest year in the instrumental record.

The second main feature of climate change is an altered rainfall pattern across the globe. After temperature we may expect rainfall to have an important influence on the growth of forests. Over the twentieth century rainfall patterns have changed according to broad latitudinal bands. In most mid and high latitudes of the northern hemisphere continents it is very likely that precipitation has increased by 0.5% to 1% per decade. Over subtropical land areas in the northern hemisphere (10° N to 30° N) it is likely that rainfall has decreased during the twentieth century by about 0.3% per decade. Over the tropical land areas (10° N to 10° S) it is likely that rainfall has increased by 0.2–0.3% per decade, although, interestingly, little change has been found in this region over the past few decades. Over the southern hemisphere no comparable systematic changes have been found in broad latitudinal averages.

Further important changes in the climate which influence forests include changes in cloud cover and changes in extreme weather events, for example seasonal patterns of temperature, heavy precipitation events, storms, fire, snow cover, floods, and droughts. Changes in cloud cover are less certain than increases in temperature and altered rainfall patterns but it is likely that there has been a 2% increase in cloud cover over mid- to high-latitude land areas during the twentieth century. A further potential threat to global climate, which has only recently been appreciated, is the possible increase in frequency and severity of El Niño-Southern Oscillation (ENSO) events. El Niño occurs in the tropical Pacific Ocean and happens when warm water from the western Pacific flows toward the east. Warm surface water builds up off the coast of South America and the earth's atmosphere responds by producing patterns of high and low pressure that can have a profound impact on weather far away from the equatorial Pacific. El Niño is associated with a fluctuation in the circulation in the Indian and Pacific oceans called the Southern Oscillation. Modeling and observational studies suggest that ENSO events are associated with abrupt shifts in climate, which since ecological systems are particularly vulnerable to rapid changes may prove of greater consequence than the gradual changes in other climatic factors.

Reasons for the Climate Changes

The recent and rapid changes in climate are thought, in part, to be induced by human activity. Burning of fossil fuels and changes in land use, especially deforestation, have resulted in increased atmospheric greenhouse gas concentrations. The main greenhouse gases that have increased in the last 100 years are carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). They have a warming effect on the earth by absorbing the longwave radiation being emitted from the earth that would otherwise escape to space and cool the planet. **Figure 2** shows the increase in greenhouse gases during the last millenium. Since 1750 the CO_2 concentrations in the atmosphere have increased by approximately 0.4% a year from 280 ppm to the present day concentrations of 367 ppm. Methane and nitrous oxide have

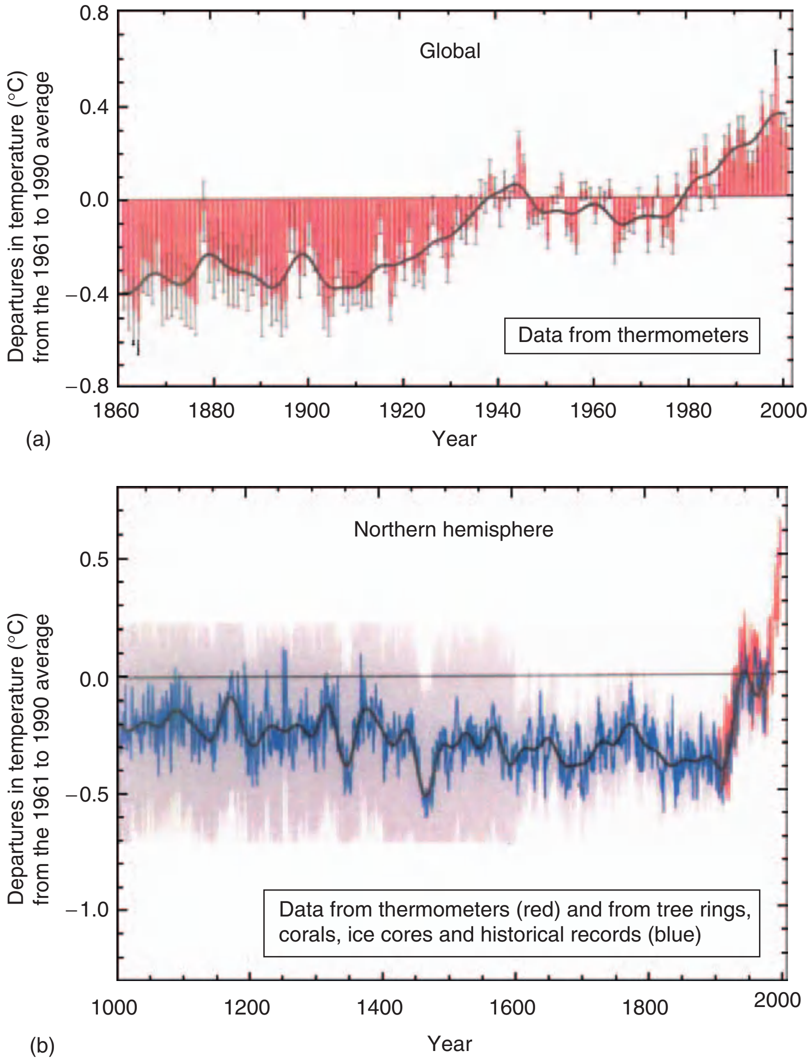


Figure 1 Variations of the earth's surface temperature over the last 140 years and the last millennium. (a) The earth's surface temperature is shown year by year (red bars) and approximately decade by decade (black line, a filtered annual curve suppressing fluctuations below near decadal timescales). There are uncertainties in the annual data represented by the thin black whisker bars (the 95% confidence range). (b) Additionally the year-by-year (blue curve) and 50-year average (black curve) variations of the average surface temperature of the northern hemisphere for the past 1000 years have been reconstructed from 'proxy' data calibrated against thermometer data (see list of the main proxy data in the diagram). The 95% confidence range in the annual data is represented by the gray region. These uncertainties increase in more distant times and are always much larger than in the instrumental record due to the use of relatively sparse proxy data. Reproduced with permission from Houghton *et al*. (2001) *Climate Change 2001*, *The Scientific Basis*. Cambridge, UK: Intergovernmental Panel on Climate Change.

increased by 1060 ppb (151%) and 46 ppb (17%), respectively, since 1750 and continue to increase. Carbon dioxide is not only a greenhouse gas, it is the raw material from which biomass is synthesized during photosynthesis. Any increase in CO_2 concentration is therefore likely to stimulate photosynthesis.

Predictions of Future Climate Change

The globally averaged surface air temperature is projected by models to increase by 1.4–5.8°C by 2100, relative to 1990 and the globally averaged sea level is projected by models to rise 0.09 to 0.88 m by 2100. Of course, prediction is dependent on the extent to which the burning of fossil fuels increases. These projections indicate that the warming would vary by region, and would be accompanied by increases and decreases in precipitation. There would probably also be changes in the frequency and intensity of some extreme climate phenomena. For example increases in the number of storms in northwest Europe are predicted, leading to the breaking or uprooting of increasing numbers of trees. These predictions assume that the current rate of emissions will not be reduced and that there will

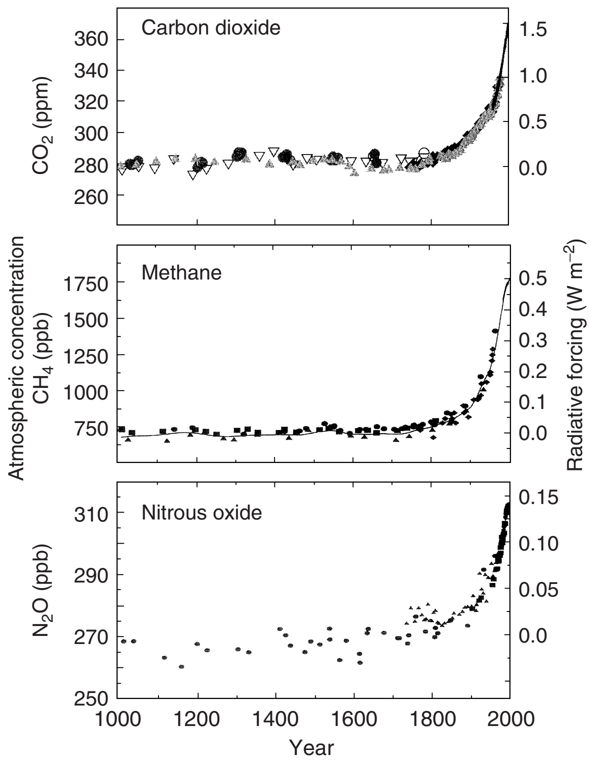


Figure 2 Indicators of the human influence on the atmosphere during the industrial era. Global atmospheric concentrations of the three main greenhouse gases (carbon dioxide, methane, and nitrous oxide) over the past 1000 years. The ice core and fern data for several sites in Antarctica and Greenland (shown by different symbols) are supplemented with the data from direct atmospheric samples over the past few decades (shown by a line for CO_2 and incorporated in the curve representing the global average of methane). The estimated positive radiative forcing of the climate system from these gases is indicated on the right-hand scale. Reproduced with permission from Houghton JT, Ding Y, Griggs DJ, *et al.* (2001) *Climate Change 2001, The Scientific Basis*. Cambridge, UK: Intergovernmental Panel on Climate Change.

be a rough doubling of current CO_2 concentrations by 2080. The exact effect on precipitation is not fully understood because of lack of knowledge about factors such as cloud formation and behaviour, but preliminary predictions have been made. It is thought that precipitation will continue to increase in the mid to high latitudes of the northern hemisphere, particularly in winter. In low latitudes there will be regional increases and decreases over the land areas. Changes in temperature, rainfall, and CO_2 concentration will naturally have profound effects on the growth, function, and distribution of forests.

Effects of Current Climate Changes on Forests

The results from modelling and other studies suggest that there are potentially beneficial impacts of climate change, such as an increase in the global timber supply from appropriately managed forests in regions of the world which are currently cold. However, this is tempered by the increased possibility of both disturbance factors, such as fires and insect outbreaks, and extreme climatic events which could lead to widespread forest decline. Recent work is now confirming these predictions. Using satellite observations it has been shown that there has been a 'greening trend' in the high northern latitudes associated with an advance of spring budburst by several days and a similar delay in autumn leaf fall. Other data from sample plots across Europe show that the growth of trees has been increasing. This is probably a worldwide phenomenon influenced by elevated CO_2 (the fertilization effect) and the deposition of active forms of nitrogen, ammonium, and nitrate (derived from farming, use of vehicles, and biomass burning). It is difficult to disentangle the effects of these three factors (temperature, CO_2, and nitrogen deposition) in natural systems but the results of many experimental studies focusing on one or both of them enable a clearer understanding of the processes underlying forest change. The experimental systems which have been used to conduct controlled experiments concerning the effects of elevated CO_2 are briefly reviewed below.

Experimental Systems Used to Investigate the Effects of Elevated CO_2 on Forest Systems

Initial studies into the direct effect of CO_2 on trees were necessarily performed on seedlings and often used seedlings rooted in pots. The environments in which the experiments were performed were often very artificial and in many cases the studies generated more questions than they answered. Their results were often qualitatively accurate, but quantitatively unreliable. Subsequent studies have used seedlings rooted in forest soil in larger open-topped transparent chambers (OTCs), and much of our understanding of how forests will respond to elevated CO_2 is from these studies.

Figure 3 shows a facility in Perthshire, central Scotland and is typical of many such OTC systems, in that it uses young trees rooted in forest soil. The chambers were set within a Sitka spruce forest and the trees were, as much as possible, treated in the same way as the surrounding forest. For example trees were planted around the outsides of the chambers to shade the trees within, in the same way as trees in the forest are shaded by their neighbors. The precipitation reaching the trees was that received through the chamber's open top and was therefore also realistic. Half of the chambers were continually flushed with ambient air, and half

Figure 3 Open top chambers (OTCs) at Glendevon, Perthshire, Scotland. Half of the chambers are flushed with ambient air and half with ambient air with additional CO_2 added to maintain a CO_2 concentration of twice ambient. The CO_2 tank can be seen in the foreground. The control room is just inside the site gates, and a nonchamber control area containing four plots with trees but no chambers can be seen at the rear, right of the photograph. This area was included to assess the affects of the chambers themselves on the trees. Photograph courtesy of the Forest Research Photo Library.

with ambient air with additional CO_2 added to maintain a CO_2 concentration of twice ambient. The airflow this generated helped to cool the chambers to more or less ambient levels, except if the ambient temperature was very warm. As the trees grew some were harvested to create space in the chambers, until only four trees per chamber were left and the trees were 4 years old. At this point the trees in elevated CO_2 had begun to grow out of the top of the chamber and the experiment could not be continued. Some OTC experiments have managed to grow trees in conditions similar to these for 6 years, but beyond this it is not practical.

More recently free-air CO_2 enrichment (FACE) systems have been developed in which air with additional CO_2 is delivered to a mature forest via a circle of pipework and vertical pipes containing CO_2-releasing jets projecting up through the forest. **Figure 4** shows FACE rings situated in a loblolly pine (*Pinus taeda*) forest in North Carolina, USA. The main advantage of such systems compared with OTCs is that they more nearly mimic the natural environment, but the main disadvantage is their huge expense both in infrastructure and in CO_2.

Figure 4 The free air CO_2 enrichment (FACE) rings in loblolly pine, North Carolina, USA. Three of the rings are flushed with ambient air and three with ambient air to which 200 ppm CO_2 is continually added. (The ring in the distance is a prototype.) The towers shown support white pipes with perforations for emitting CO_2 into the forest stand. Each 30 m diameter ring uses feedback control technology to control the CO_2 concentration.

Effects of Increased Atmospheric CO_2 on Forest Systems

During the course of their evolution plants have responded to atmospheric CO_2 concentrations ranging from lows of 190–200 ppm during the glacial maxima to 7000 ppm 400 million years ago when plants first colonized land. Photosynthesis itself developed at a time when CO_2 was the most abundant gas in the atmosphere. The present atmospheric CO_2 concentration of around 367 ppm limits photosynthetic CO_2 fixation in almost all tree species (some herbaceous plants are not limited by the CO_2 concentration as they have an evolutionarily more advanced mode of photosynthesis). Increasing the atmospheric CO_2 concentration therefore stimulates the photosynthetic rate of trees (and most herbaceous species) and can result in increased growth rates and biomass production.

Biomass It is usually found that trees in elevated CO_2 have a faster development, so they get bigger more quickly, but they are otherwise very similar to trees of the same size growing in ambient conditions. Results from FACE experiments show a 25% increase in growth in twice normal concentrations of CO_2. Similar results are found from trees growing near natural sources of CO_2 (geological sources, known as fumeroles).

Photosynthesis The reason for these increases in tree biomass in elevated levels of CO_2 is that the photosynthesis of trees is limited at current levels of CO_2. Growth is therefore almost always higher in air with an elevated concentration of CO_2. In one review of more than 500 reports, mostly from the USA, an average stimulation of 54% in elevated CO_2 was found. In long-term experiments (lasting years) plants often show less stimulation of photosynthesis than they do in short-term experiments (lasting hours), as a result of physiological adjustment.

Forest water use Plants absorb CO_2 into their leaves through tiny pores called stomata. They also lose water through the same pores which, when water is limiting is undesirable. In some experiments, elevated CO_2 causes a degree of stomatal closure and in experiments lasting several weeks or more the new leaves that have formed at elevated CO_2 often have fewer stomata per area. A reduction in the stomatal conductance could result in a reduction in the transpiration rate of the forest. Less water would therefore be removed from the soil for the same amount of carbon fixed. In the subtropics and other areas of the world where the rainfall has been decreasing this would enable photosynthesis and growth to continue for longer. A reduction in the quantity of water vapor entering the atmosphere above forests, as a result of reduced transpiration, would also affect regional and potentially global climate feedbacks. This plant atmosphere interaction can be the source of feedbacks from vegetation to atmosphere, which make the future climate very difficult to predict even though quite a lot is now known about the physiology of stomata.

Belowground processes A much-neglected area of research into the effects of elevated CO_2 on forest systems is the processes that occur below ground. These processes must be considered to fully understand forest ecosystem response to climate change. Elevated CO_2 concentrations cause a shift towards the production of more fine roots, compared with trees of a similar size growing in ambient CO_2. This is probably because trees in elevated CO_2 translocate much of their additional carbon below ground and it ends up not only as fine roots, but also as mycorrhizae (beneficial root–fungus associations), and as exudates of organic materials from the roots to the soil. The deposition of carbon directly into the soil stimulates the microbial population and it is frequently found that the respiration rate from soil beneath trees exposed to elevated CO_2 is greater than that beneath trees growing in ambient CO_2.

The quantity of litter (mainly leaves) falling to the ground from trees growing in elevated CO_2 is also increased since these trees have a larger biomass. This litter however usually has a lower concentration of nitrogen relative to carbon than litter from trees growing in ambient CO_2. The microbial soil decomposers of such litter generally require a higher nitrogen concentration and it is hypothesized that it will be degraded more slowly than litter beneath ambient grown trees, which could lead to the build up of recalcitrant carbon pools. Studies of this are inconclusive, and more research is needed. These belowground processes have feedbacks for the global carbon cycle, but mainly because of the difficulties inherent in working with this part of the ecosystem many questions still remain to be answered.

Effects of Increased Temperature on Forest Systems

The challenge facing forests during the current period of warming is the unprecedented rate at which the warming is occurring. Increased temperatures increase the rate of almost all enzymic reactions, up to the point where enzyme degradation occurs. Photosynthesis is therefore usually found to increase over relatively modest increases in temperature but soon reaches a maximum rate. Concomitant with the increase in photosynthesis is an increase in rates of cell division and expansion as well as an exponential increase in respiration, which uses up the products of photosynthesis. It is the balance between these processes of photosynthesis and respiration which determines whether increased temperature will have a positive effect on tree growth. Since respiration has been found to increase more rapidly with increasing temperature than photosynthesis, it is hypothesized that increasing temperature would have a negative impact on tree growth, but both positive and negative results have been found.

Phenology Evidence is now gathering that indicates that elevated temperature has increased the length of the growing season, particularly at high latitudes. Most of this evidence comes from a network of 'phenological gardens' which was established in 1957 across Europe, using plants that were genetically identical. Cloned specimens of trees and shrubs from a parent garden in Germany were planted at 49 sites across Europe, ranging from Ireland in the west to Macedonia in the east and Finland in the north to Portugal in the south. Dates of budburst in the spring and leaf fall in the autumn are noted annually. **Figure 5** shows the timing of leaf unfolding and leaf coloring of birch (*Betula pendula*) from 1951 to 1996 from a similar phenological

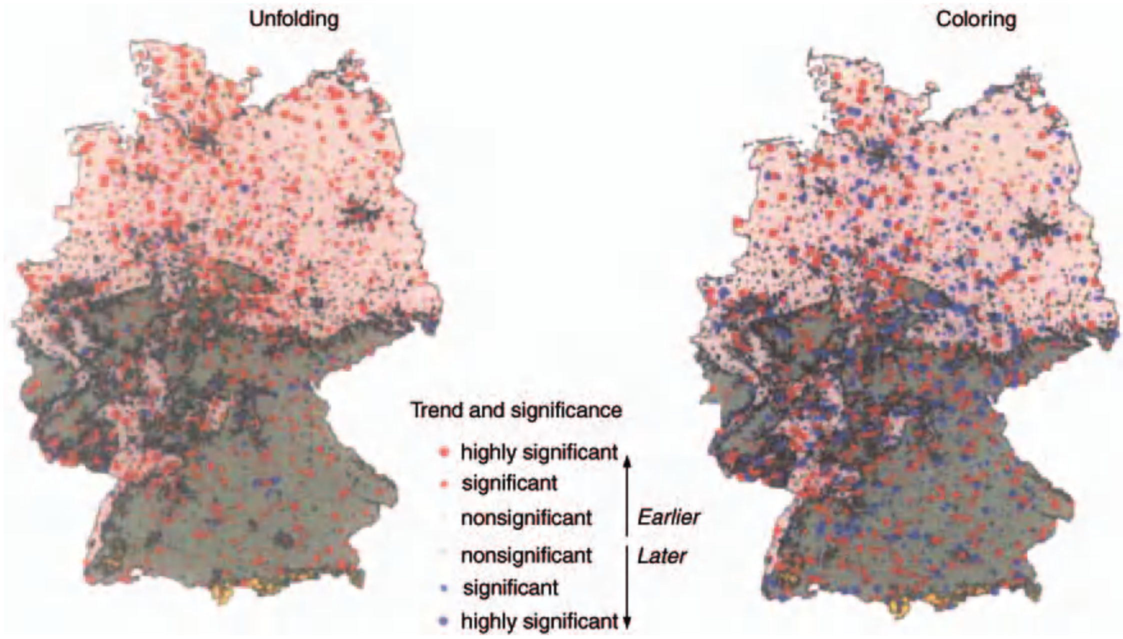


Figure 5 Linear trends in the timing of leaf unfolding (left) and autumn coloring (right) of birch (*Betula pendula*) in Germany. Data are from the phenological network of the German Weather Service and are for long observational series (20 years or more) during the period 1951 to 1996. Each point represents a series for one place. Reproduced with permission from Green RE, Harley M, Spalding M, and Zöckler C (eds) (2003) *Impacts of Climate Change on Wildlife* Cambridge, UK: WWF.

network of the German Weather Service. It shows a clear tendency for leaf unfolding to be earlier and leaf coloring to be later during this period, though the autumn shift was less than that in the spring. The Third Assessment Report of the IPCC suggests there has been a lengthening of the period during which deciduous trees bear leaves of 1.2 to 3.6 days per decade in the northern hemisphere. Moreover, spring 'greening' estimated from satellite data has advanced by 7 days since the 1960s. The regions of most greening are generally inland (except in the arctic) and are north of 50° N. In Alaska, northwestern Canada, and northern Eurasia there has been significant warming over large areas, with the greatest warming of up to 4°C occurring in the winter. This warming is associated with an approximate 10% reduction in annual snow cover from 1973 to 1992 and with an earlier disappearance of snow in the spring. However the earlier start to the growing season could increase the risk of frost damage to deciduous leaves by triggering unfurling before winter frosts have passed. Frost damage to the leaf photosynthetic apparatus would diminish photosynthetic capacity for the remainder of the season. Conifers face a similar problem timing spring dehardening and autumn hardening. There is a trade-off between fully using the extended growing season and minimizing the risk of damage by frosts.

Rapid effects at the treeline Treelines at high latitudes in the northern hemisphere shifted polewards during the early part of the twentieth century. Recent studies in the Swiss Alps show a dramatic increase in the growth of pine and spruce at the treeline. From 1820 to 2000 the temperature in the region increased by 1.02°C per century, which is much faster than the global average. The study found that the growth ring width of trees growing in the region 0–250 m below the current treeline prior to 1940 decreased with proximity to the treeline, as expected. After 1940 there was no decline in the ring width as the treeline was approached. A further study supported these finding and also found that the density of tree rings from the boreal region has decreased since 1960 – an indicator of faster growth. Despite this several studies have shown that the shift in the treeline poleward has been much less pronounced in recent decades than in the early part of the last century. It is hypothesized that increases in water stress and insect attack, amongst other factors may be possible explanations for this.

Pests and diseases Changes in climatic variables may increase frequency, intensity, and length of outbreaks of pests and diseases, especially in parts of the world which are cold. Outbreaks appear to involve range shifts northwards, poleward, or to higher elevations. For example eastern spruce budworm (*Choristoneura fumiferana*) is estimated to defoliate approximately 2.3 million ha of forest in the US and affects 51 million m^3 of timber in Canada annually. Outbreaks frequently follow droughts or dry summers, since drought and increased temperature intensify the stress on the host trees and enables the spruce budworm to lay more eggs (the number of spruce budworm eggs laid at 25°C is up to 50% greater than the number laid at 15°C). In years without late spring frosts some outbreaks have persisted and the budworm has consumed the tree's new growth. A further example is that of *Armillaria* root disease which is found throughout the world and causes significant damage on all forested continents through mortality and growth loss. In regions where the mean annual temperature is presently below the optimum (25°C) for growth of *Armillaria* a warmer climate is likely to result in increased root disease and rate of spread. In general, current forecasts of the response of forest insects and other pathogens to climate change are based on historical relationships between outbreak patterns and climate and further work to look directly at the effects of such attacks on forests which themselves are influenced by climate change is required.

Effects of Increased ENSO Frequency and Extreme Weather on Forest Systems

Many of the dry areas of the world will be particularly affected by ENSO events or other climate extremes, and forest productivity is expected to decrease. Countries in temperate and tropical Asia are likely to have increased exposure to extreme events, including forest dieback and increased fire risk, typhoons and tropical storms, floods and landslide, and severe vectorborne disease. Extreme climate events cause substantial damage to forests. For example during the 1997–8 ENSO event the drier conditions in Indonesia caused an increased frequency of forest fires resulting in a haze over the whole region lasting for many months. South America is also particularly vulnerable to ENSO and is associated with drier conditions in northern Amazonia and northern Brazil and the consequent reduction in forest biodiversity and forest productivity. In contrast southern Brazil and northwestern Peru have experienced anomalously wet conditions. Changes in precipitation levels in general are likely to lead to forest dieback and replacement of poorly adapted forest species with species more suited to the altered water availability. This will result in younger age-class distributions and altered productivity. Computer simulation modeling results have shown that ENSO events are likely to intensify under a doubled CO_2 scenario with the result that dry areas are likely to become drier and mesic areas will become wetter during ENSO events.

Computer Modeling

Computer simulation is a useful tool to address the experimental and practical limitations of research into the impacts of climate change on forest systems. For example a model called G'DAY (Generic Decomposition And Yield), developed in Australia, is an ecosystem model which integrates plant and soil processes for analysing the impact of high CO_2 on terrestrial ecosystems. The model has been used to simulate the response of nitrogen-limited forests to the expected CO_2 concentration in 2050 (about 700 ppm). It operates over periods ranging from a few years to centuries. The model predicts that there will be large initial growth increases of about 30% but that growth rates will reduce over longer timescales, as forests become limited by the shortage of nutrients. The model results change over time largely because the ratio of nitrogen to carbon in the soil changes due to the slow breakdown of organic matter.

Conclusions

Trees are sensitive indicators of climate change. There is evidence that the forests of boreal and temperate regions are responding to the current increase in temperature. They do this by unfolding their leaves earlier, shedding leaves later, and growing faster during the summer (provided there is enough water). They also respond to the increase in CO_2 concentration as enhanced CO_2 has a 'fertilization' effect on photosynthesis. In industrial and heavily agricultural regions of the world there is an additional fertilization effect because of the deposition of 'active' nitrogen (mainly ammonium and nitrate) from the atmosphere. However there are negative effects as well. As insects and pathogens complete their life cycle more rapidly at high temperatures we may expect damage by herbivorous insects and pathogens to be more acute. In the tropics, the annual growth is rarely limited by temperature but is probably very sensitive to changes in rainfall as well as CO_2 concentration. Some modeling studies suggest that Amazonian rainforest may be especially vulnerable to the effects of high temperature and drought, and decline over periods less than a century from now. Currently the temperature is increasing at an unprecedented rate, and the geographical limits of trees are likely to change. Cold regions from which trees are currently absent (at high elevation and latitude), may become colonized in the future. However, forests may die back in warmer regions.

See also: **Ecology**: Human Influences on Tropical Forest Wildlife. **Environment**: Carbon Cycle; Environmental Impacts. **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Mensuration**: Tree-Ring Analysis. **Soil Development and Properties**: Nutrient Cycling. **Tree Physiology**: A Whole Tree Perspective; Forests, Tree Physiology and Climate.

Further Reading

Houghton JT, Ding Y, Griggs DJ, *et al*. (eds) (2001) *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Jarvis PG (1998) *European Forests and Global Change: The Likely Impacts of CO_2 and Temperature*. Cambridge, UK: Cambridge University Press.

McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, and White KS (eds) (2001) *Climate Change 2001: impacts, adaptation and vulnerability contribution of working group II to the third assessment report of the intergovernmental panel on climate change*. Cambridge UK: Cambridge University Press.

Saxe H, Cannell MGR, Johnsen Ø, Ryan MG, and Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist* 149: 369–400.

EXPERIMENTAL METHODS AND ANALYSIS

Contents

Biometric Research

R E McRoberts, US Department of Agriculture Forest Service, St Paul, MN, USA

Published by Elsevier Ltd., 2004

Introduction

Any discussion of research in a scientific field is subject to caveats because research must of necessity be less definitive than a discussion of the field's established operational practices. First, enumerations of current research topics will be dated and subject to the perspective of the enumerator. Second, the foci of research change quickly and are subject to funding and societal priorities, perceptions of issues that demand immediate attention, and technical and technological advances. Finally, research, by definition, indicates that final solutions have not been achieved and that results may only be reported as preliminary or as works in progress. Thus, this assessment of biometric research in forest inventory should be considered a static summary in a rapidly changing discipline.

Given these caveats, current biometric research in forest inventory is focused in three major areas: forest sustainability, data delivery, and spatial estimation. With respect to forest sustainability, regional, national, and international public constituencies seek assessments of the effects on forest resources of forest management practices and environmental changes. Their demands have spawned international working groups and assessment procedures such as the Ministerial Conference on the Protection of Forests in Europe and the Montreal Process for assessing forest sustainability. Further, they have influenced national inventory programs to broaden the scope of data collection to include observation of attributes such as soil, lichens, pollutant-sensitive plant species, and down woody material. With respect to data delivery, inventory clients demand timely and precise estimates of forest attributes, summarizations, and estimates for their own areas of interest, and access to field data for their own analyses and to augment noninventory data. Finally, with respect to spatial estimation, the traditional emphasis of forest inventory has been the production of large-scale estimates of forest attributes such as area, volume, and species distribution and temporal changes in these attributes with the objective of answering the question, 'How much?' Increasingly, however, forest inventory clients are also asking the question, 'Where?' Answering the latter question requires spatial extensions of inventory plot information across the landscape. Thus, this article focuses on three biometric research topics: forest sustainability, data delivery, and spatial estimation. A vision for forest inventory that simultaneously addresses all three topics is also outlined.

Forest Sustainability

Frameworks for Sustainability Assessments

The 1992 Rio Earth Summit produced a statement of forest principles and conventions on biodiversity, climate change, and desertification. It further called upon all nations to manage development in a manner that sustains natural resources. Definitions of forest sustainability generally incorporate three components: (1) a process based on the integration of environmental, economic, and social principles; (2) satisfaction of present environmental, economic, and social needs; and (3) maintenance of forest resources to assure that the needs of future generations are not compromised. In 1993, Canada convened a seminar in Montreal on the topic of sustainable management of boreal and temperate forests. The seminar was sponsored by the Conference on Security and Cooperation in Europe and focused on defining criteria and indicators that can be used to measure progress toward sustainable development of forests. Criteria are categories of conditions or processes by which forest management may be assessed with respect to sustainability, while indicators are measurable aspects of the criteria. Following the Montreal seminar, the European countries opted to work under the framework of the Ministerial Conference on the Protection of Forests in Europe. North and South American, Asian, and Pacific Rim countries initiated a similar effort formally known as the Working Group on Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests. Informally known as the Montreal Process, this effort focused on the development and implementation of a set of internationally accepted criteria and indicators. The criteria for both the European and Montreal Process groups are identical, and the indicators for the four criteria that can be directly addressed via forest inventory observations are very similar (**Table 1**).

Traditionally, national forest inventories have emphasized the collection and analysis of individual tree attributes such as species, age, diameter, height, mortality, removal, and regeneration and collective tree attributes such as forest cover type, proportion crown cover, and plantation versus naturally regenerated. Although national inventories collected some nontree information before the early 1990s, the 1992 Rio Earth Summit provided the impetus for the development of sampling designs and estimation procedures for entire suites of information related to the health and sustainability of forest resources. Today, national forest inventories are the primary sources of information for regional, national, and international forest sustainability assessments and reporting requirements.

Designs and Analyses

The collection and analysis of data related to the forest sustainability criteria and indicators present a

Table 1 Categories of European and Montreal Process indicators for forest sustainability criteria

Criterion	*Categories of indicators*	
	Ministerial Conference on the Protection of Forests in Europe	*Montreal Process*
Conservation of biological diversity	Forest area	Forest area
	Tree species composition	Ecosystem diversity
	Landscape pattern	Fragmentation
	Threatened species	Species diversity
	Genetic resources	Genetic diversity
	Regeneration	
Maintenance of productive capacity of forest ecosystems	Roundwood and nonwood production	Area and growing stock available for timber production
	Balance between increment growth and fellings	Removal of timber and nontimber products relative to sustainable levels
	Value of marketed services	Area and growing stock of native and exotic species
	Forest under management plans	
	Air pollutants	Air pollutants
Maintenance of forest ecosystem health and vitality	Defoliation and forest damage	Pests, pathogens, exotic species, damage
	Protective area: soil erosion, water preservation, infrastructure, natural resources	Land managed for protective functions
		Soil erosion, organic matter, compaction, and accumulation of toxic substances
		Water bodies with significant deviation from historic properties

myriad of biometric research challenges. For example, the Forest Inventory and Analysis (FIA) program of the US Forest Service has augmented its sampling efforts to include the collection of information on tree crown condition, tree damage, ozone injury to vegetation, lichen diversity as a biomonitor of pollutant exposure, understory vegetation diversity, soil chemistry and erosion, and down woody material. These variables are sufficiently different that distinct sampling designs are usually necessary, as are separate approaches to estimation. For example, down woody material information is collected from line transects, soil information is collected from soil cores, while tree crown condition, tree damage, and ozone injury to vegetation are visually estimated. The additional biometric challenge is to develop methodology for using this raw inventory data to assess more complex phenomena such as carbon sequestration and forest wildfire risk.

Also, because the greatest proportion of the total cost of measuring an inventory plot is the travel to and from the plot location, the sampling designs for the additional variables must be integrated with sampling designs for the traditional variables, either on the same plots or in close proximity to them. In addition, because of the substantial additional cost of obtaining observations for these variables, the number of plots with the additional observations per unit area is substantially less than for traditional inventory plots; for the FIA program of the US Forest Service, the ratio is approximately 1 : 16. Thus, in order to relieve analysts and users from having to choose between only moderately precise regional estimates or imprecise estimates for smaller areas, biometric research must focus on developing methods for increasing the precision of estimates of the current status and change in these variables. Finally, sustainability analyses often depend on detection of spatially disparate pest-, pathogen-, or human-induced phenomena and may require risk-based sampling designs and designs constructed to detect rare events. Although inventory plots may be inadequate for detecting such rare phenomena, they are excellent for identifying areas with high probabilities of detecting these events.

In summary, the collection and analyses of data for evaluating forest management practices with respect to sustainability are increasing in priority. Observations of at least some variables necessary for these analyses will require special sampling designs which must be integrated to the greatest extent possible with traditional inventory sampling designs. Biometric research to develop procedures for estimating the current status and change in these variables at meaningful geographic scales for relevant temporal intervals is crucial.

Data Delivery

Internet Access

Because national forest inventories are typically funded by national governments, there are valid arguments for maximizing the utility of inventory data by making it publicly accessible. Internet access is becoming the medium of choice for distributing inventory data to the public, although a variety of constraints may be necessary depending on form of the data to which access is provided. Internet access to tabular summarizations for the same estimation units as is provided in published inventory reports has become routine with few constraints. However, internet access to tabular summarizations for user-defined estimation units requires real-time computations and is more complex. An approach using map-based estimation is discussed in the section on spatial analysis below. Another approach is to select the plots located in the user's estimation unit and then calculate estimates in the same manner as does the inventory program. If inventory programs calculate estimates on the assumption of simply random sampling, this approach is fairly trivial. However, because of budgetary constraints, inventory programs frequently cannot observe enough plots to satisfy precision requirements for many variables under an assumption of simple random sampling unless ancillary data are used to augment the estimation processes. Many programs rely on stratified estimation and use remotely sensed data, particularly classified satellite imagery, as the means of stratifying estimation units. Inventory data users requesting tabular summarizations for their own estimation units often wish to increase the precision of their estimates by using the same stratifications developed by the inventory programs. However, land cover classifications based on even medium-resolution satellite imagery (e.g., $30 \times 30\,\mathrm{m}$ Landsat thematic mapper imagery) require storage of and access to such large amounts of data that real-time estimation may be severely retarded. One solution is to provide users with summarizations of stratifications for geographic units of predetermined size and configuration. Two approaches are then possible. Either the boundaries of the user's estimation unit are forced to conform to the boundaries of the stratification summary units or the user's estimation unit is used with the stratification summaries for units that do not conform to the user's estimation unit. In the first case, an approximated user's estimation unit is used with the actual stratifications, and in the second case, the actual user's estimation unit is used with an approximated stratification. The research challenge is to select the size of the stratification summarization unit that minimizes the effects of the compromises. This problem may, of course, disappear as storage space and real-time processing speed increase, although it may also be exacerbated as classifications of finer-resolution satellite imagery are used for stratification.

Plot Integrity and Data Privacy

Inventory users often request access to raw inventory data rather than tabular summarizations, frequently for purposes of combining it with noninventory data such as satellite imagery for their own analyses. For example, researchers seek inventory observations for use as training or validation data for classifying satellite imagery or for map validation. For these applications, the exact coordinates of plot locations are usually necessary, either to associate field observations with satellite image pixels or to compare them with map predictions. Although inventory programs release plot information to the public, they generally resist releasing actual plot locations. First, release of plot locations may entice users to visit plot locations to obtain additional information which could result in artificial disturbance of the ecology of the sites and, in turn, induce bias in the inventory estimates. Second, forest inventory programs rely on the goodwill of private forest landowners for permission to observe plots on their land. Landowners generally do not welcome unwarranted or frequent intrusions and often only permit visits by inventory crews contingent on assurances that the plot locations and proprietary information will not be released.

Accommodating users' desires for the greatest utility and distribution of inventory data while simultaneously protecting the ecological integrity of inventory plot locations, preventing unwarranted intrusions on private land, and protecting the proprietary nature of information obtained from plots on private lands have emerged as crucial issues. Two measures have been considered: creating uncertainty in plot locations and creating uncertainty in the ownership of plots on private land. Creating uncertainty in plot locations discourages users from attempting to visit the plots, thus protecting them from artificial disturbance and protecting the landowner from unwarranted intrusions. This measure entails releasing to the public coordinates for plots that are known only to fall within a circle of area A centered at the actual plot location. Creating uncertainty in the ownership of plots on private land protects private landowners from unwarranted disclosure of proprietary information. This measure entails swapping observations between plots on private land. Plots on private land are first grouped into similarity pools with respect to criteria that are stable over time and retain as much utility of the data after swapping as possible, and then information for a proportion of plots within similarity pools is exchanged. Potential criteria for forming similarity pools include spatial location, site characteristics, and perhaps broad forest cover types. When creating uncertainty in plot locations, the area, A, of the circle containing the actual plot location is revealed to the public, although the center of the circle is not revealed. When creating uncertainty in plot ownership, the similarity criteria may be revealed to the public, but neither the swapping proportion nor the plots with swapped observations are revealed.

Although creating uncertainty in the locations and ownerships of plots satisfies the plot integrity, privacy, and nondisclosure requirements, there remain biometric research challenges. Knowing that inventory programs do not release the actual coordinates of plot locations, users often submit maps or satellite image classifications and request that the inventory program validate these spatial products by providing the map or classification categories for locations corresponding to inventory plots. If aggregated summaries of the results for large numbers of plots suffice, then no plot integrity or disclosure requirements are violated. However, if results for individual plots are required, then challenges arise. If the circle of area A is not wholly contained within a single map or classification category, then revealing the map category for an individual plot reduces the uncertainty in the plot location to an area of size less than A.

Users also request that inventory programs assist in satellite image classification efforts by appending the spectral values of satellite image pixels associated with actual plot locations to the inventory data for the plot. Technically, this does not require that actual plot locations be revealed to the user. However, even for medium-resolution satellite imagery, combinations of spectral values are sufficiently unique that the total area of pixels with the same spectral values as the pixel containing the actual plot location is often less than A. In addition, with two or more dates of Landsat thematic mapper imagery for the same scene (i.e., 12–14 spectral bands of data), it is not uncommon for the combination of spectral values for a single pixel to be unique, in which case revealing the spectral values for a pixel associated with a plot also reveals the plot location to within the 30×30 m resolution of the imagery.

The biometric research challenge is to assure compliance with plot integrity, privacy, and nondisclosure requirements while minimizing the area, A, of the circle containing the actual plot location, selecting similarity criteria that retain maximum utility of the swapped data, and minimizing the swapping proportion. Global selections for these parameters are unlikely. First, for areas in which ownership is fragmented into parcels of area less than *A*, creating uncertainty in plot locations may also create sufficient uncertainty in plot ownership. In this case, swapping is unnecessary and would serve only to degrade further the utility of the inventory data. Second, the criteria for establishing similarity pools will differ by region. For example, in mountainous areas, elevation may be an important similarity measure because of its high correlation with species composition, whereas in other regions elevation may be of little use.

In summary, timely delivery of inventory data and data summaries in a variety of formats for a variety of users for a variety of purposes has become mandatory. The biometric research challenge is to do so in the most timely and user-friendly manner that preserves the utility of the data while simultaneously accommodating integrity, privacy, and disclosure requirements.

Spatial Analyses

Traditionally, forest inventory has relied on sample-based estimation methods and has emphasized plot configurations and sample designs that produce efficient and precise estimates of tree-based forest attributes for large areas. Increasingly, however, inventory clients request resource estimates for small areas and estimates of the spatial distribution of the resource. Thus, two related research topics have emerged. First, maps of forest attributes that fill the spatial gaps between plot locations are required, and second, procedures for precisely estimating attributes for small areas are necessary. The challenges associated with both topics require innovative approaches for combining inventory plot data with ancillary data, particularly satellite imagery.

Maps

Mapping forest attributes observed on inventory plots inevitably requires a data source that can function as a bridge between arbitrary mapping units and mapping units containing inventory plots. Satellite imagery is emerging as the bridging data source of preference, although approaches to constructing the bridge depend on the image pixel size relative to the size of inventory plots. When the image pixel size is much greater than the plot size, then the approach is to associate the spectral values of groups of pixels containing inventory plots with aggregated information for groups of inventory plots. When the image pixel size is comparable to the plot size, then plots may be associated in one-to-one relationships with pixels and a variety of classification techniques, including maximum likelihood, regression, and nearest neighbors techniques, may be used. The cost of imagery with pixel sizes orders of magnitude smaller than plot size is generally beyond the budget constraints of national inventory programs, so use of this imagery is not discussed further.

Map-based estimation Maps of forest attributes could simultaneously resolve data access and estimation issues. Estimation using maps requires the uncertainty of predictions for individual mapping units, but these quantities may usually be estimated in conjunction with mapping operation. If the satellite image pixel size is of the same order of magnitude as the inventory plot size, then models of the relationship between plot-level aggregations of inventory observations and spectral values of pixels may be formulated, and inventory plot attributes may be predicted for each image pixel using the spectral values as predictors. When using regression to estimate the parameters of a model with statistical expectation described by a function $f(\mathbf{X};\beta)$, where $\mathbf{X}$ is a vector of image spectral values and β is a vector of parameters to be estimated, the variance of a prediction for an individual pixel is approximated by:

$$\mathrm{Var}(\hat{Y}_i) = \left[\frac{\partial f}{\partial \beta}(X_i)\right]' V^{-1}\left[\frac{\partial f}{\partial \beta}(X_i)\right] + \sigma_\varepsilon^2$$

where σ_ε^2 is the variability of observations around model predictions, and V^{-1} is the covariance matrix of the model parameters where the components of V are given by:

$$v_{ij} = \sum_{k=1}^{n}\left[\frac{\partial f}{\partial \beta_i}(X_k)\right]\left[\frac{\partial f}{\partial \beta_j}(X_k)\right]$$

and where k indexes observations. Thus, the estimate, $\hat{Y}_{\mathrm{tot}}$, for the total of an attribute (e.g., volume, forest area, biomass) for a user estimation unit and the variance of the estimate, $\mathrm{Var}(\hat{Y}_{\mathrm{tot}})$, are provided by:

$$\hat{Y}_{\mathrm{tot}} = \sum_{i=1}^{N}\hat{Y}_i$$

and:

$$\begin{aligned}\mathrm{Var}(\hat{Y}_{\mathrm{tot}}) &= \mathrm{Var}\left(\sum_{i=1}^{N}\hat{Y}_i\right)\\ &= \left\{\sum_{i=1}^{N}\sum_{j=1}^{N}\left[\frac{\partial f}{\partial \beta}(X_i)\right]V^{-1}\left[\frac{\partial f}{\partial \beta}(X_j)\right]'\right\}\\ &\quad + \left[\sum_{i=1}^{N}\sum_{j=1}^{N}\mathrm{Cov}(\varepsilon_i,\varepsilon_j)\right]\end{aligned}$$

where i now indexes image pixels, of which N is the total number. A crucial issue is whether the estimate of $\mathrm{Var}(\hat{Y}_{\mathrm{tot}})$ is larger when obtained from the map or when obtained directly from the plot observations using estimations based on simple random sampling or stratified estimation. The trade-off will be between the small number, n, of plot observations, assumed to be with little or no measurement error, and the large number, N, of mapping unit predictions, each with nonzero prediction uncertainty. If the variance estimate obtained from the map is as small or smaller, then user requests for estimates may be satisfied directly from the map, do not require direct access to plot data, and alleviate concerns about ownership because predictions for individual pixels do not disclose proprietary information. In addition, if the predictions for individual pixels are unbiased, then estimates may be obtained for small areas in which there may be no plots or there may not be enough plots per stratum for stratified estimation.

The spatial challenge to biometric researchers is to construct maps depicting the distribution of forest resources that not only answer the user question, ‘Where?’ but that also facilitate unbiased and precise estimation for both large and small areas. Research on mapping and map-based estimation of forest attributes is also of considerable interest to environmental scientists wishing to relate the status and change in forest resources to climatic, soil, and other environmental spatial data and to forest industry planners wishing to plan roads and select mill locations.

A Vision for Forestry Inventory Estimation

A visionary objective of an inventory program is to associate a tree list, or an aggregation of several tree lists, with each mapping unit. The map will be constructed by imputing to each mapping unit the entire suite of observations from inventory plots associated with similar mapping units. Inventory estimates will be derived from the map rather than from plot observations using sample-based methods, because the former method produces more precise estimates. Further, appropriate correlations among map-based predictions of forest attributes are preserved because entire suites of observations are imputed simultaneously. As with the model-based approach to estimation discussed in the section on spatial analyses, realization of the vision dispenses with many plot integrity, privacy, and disclosure issues.

Realization of the vision requires two crucial components: an adequate data source for bridging the gap between arbitrary mapping units and mapping units containing inventory plots, and an analytical tool that uses the bridging data to impute simultaneously to mapping units all attributes observed on inventory plots. Although a variety of spatial products including soil, climatic, and digital elevation maps may support and enhance the bridging function, the key data source will likely be satellite imagery and will further likely include imagery from active sensors that penetrate the forest canopy. Among the candidate analytical tools, the nonparametric k-nearest neighbors (k-NN) imputation technique popularized by the Finnish National Forest Inventory merits serious consideration.

The k-Nearest Neighbors (k-NN) Approach

With the k-NN approach, for an arbitrary mapping unit, u_i, the set of mapping units, $\{u_j\}$, associated with inventory plots is ordered with respect to the distance, d_{ij}, between u_i and each u_j. Distances are calculated using variables, X, common to all mapping units. A variety of distance measures, including unweighted and weighted Euclidean distance and Mahalonobis distance, are possible. For example, the weighted Euclidean distance, d_{ij}, between u_i and u_j is calculated as:

$$d_{ij} = \sqrt{\sum_{m=1}^{M} v_m (X_{mi} - X_{mj})^2}$$

where m indexes the variables, X, used to calculate distance, M is the number of variables, and v_m is the relative weight assigned to each variable. The value of the attribute imputed to mapping u_i is calculated as:

$$\hat{Y}_i = \frac{1}{k\left(\sum_{j=1}^{k} w_{ij}\right)} \sum_{j=1}^{k} w_{ij} Y_{ij}$$

where k is the number of nearest neighbors selected, the summations are over the k neighbors closest to u_i with respect to the distance measure, and w_{ij} is the weight assigned to each nearest neighbor in the estimation process. Common selections for w_{ij} include $w_{ij} = 1$, $w_{ij} = \mathrm{d}_{ij}^{-1}$, and $w_{ij} = d_{ij}^{-2}$. Calibration of the k-NN approach requires selections for the distance measure, the variables used to calculate distance, variable and nearest-neighbor weighting schemes, and k. Calibration selections are often based on minimizing a criterion such as mean square residual or maximizing a criterion such as proportion correctly classified using a leaving-one-out cross-validation approach.

Several research challenges are associated with operationally implementing the k-NN technique. First, not all aspects of k-NN estimation are intuitive.

Selection of variables for calculating distances between mapping units that are unrelated to the attribute to be estimated may have a detrimental effect on the calibration criterion. Also, selection of a value of k that is too small may result in values of residual mean square that are greater than if the overall mean had been used as the imputation for each mapping unit. Second, implementing the k-NN technique requires all mapping units $\{u_j\}$ containing inventory plots to be ordered with respect to distance separately for each mapping unit for which an imputation is to be calculated. If $\{u_j\}$ is a large set, then the ordering process may require large amounts of time. In addition, calibration may be a trial-and-error process requiring testing all combinations of values of k, distance variables, and weighting schemes to identify the particular combination that optimizes the calibration criterion. Third, defensible approaches to estimation of uncertainty have not been fully developed.

The future of forest inventory, today as it has been in the past, is to deliver more timely, more precise, more comprehensive inventory data and estimates to more users in more formats with less cost. The near-term solution is to provide internet access to spatial products that simultaneously depict entire suites of forest attributes across landscapes and that permit unbiased and precise estimation of those attributes for both large and small user-defined areas of interest. Although certainly nontrivial, imputing tree lists to individual mapping units would not only lead to realization of this vision but would also greatly facilitate compliance with plot integrity, privacy, and disclosure requirements.

Summary

The biometric research challenges in forest inventory are many, vary by program, and change over time. Research challenges were discussed in three topic areas: forest sustainability, data delivery, and spatial estimation. In the area of forest sustainability, the challenges are to integrate sampling designs for variables providing information on the health of the forest with traditional inventory sampling designs and to develop estimation methods that permit precise estimates for temporal trends in the variables using data from a sparse spatial array of plots. In the area of data delivery, the challenge is to provide users access to the greatest amount of data in a form with the greatest utility while satisfying plot integrity, privacy, and disclosure requirements. In the area of spatial estimation, the challenge is to construct maps of forest attributes that depict their spatial distribution and that permit precise estimation for small areas. The challenges are interdependent and will continue for the foreseeable future, although the approaches to addressing them will undoubtedly change.

See also: **Biodiversity**: Biodiversity in Forests. **Experimental Methods and Analysis**: Statistical Methods (Mathematics and Computers). **Inventory**: Modeling; Multipurpose Resource Inventories. **Landscape and Planning**: Spatial Information. **Mensuration**: Forest Measurements. **Resource Assessment**: Forest Change; GIS and Remote Sensing; Non-timber Forest Resources and Products.

Further Reading

Anonymous (1997) *Canada's Report on the Montreal Process: Criteria and Indicators for the Conservation and Sustainable Management of Temperate and Boreal Forests*. Ottawa, Canada: Montreal Process Liaison Office.

Csoka P (1997) *Interim Report on the Implementation of Resolution H3 of the Helsinki Ministerial Conference on the Protection of Forests in Europe: Results of the Second Inquiry*. New York: United Nations.

Franklin SE (2001) *Remote Sensing for Sustainable Forest Management*. New York: Lewis.

Iles K (2003) *A Sample of Inventory Topics – A Practical Discussion for Resource Samplers on Forest Inventory Techniques*. Nanaimo, Canada: Kim Iles.

McRoberts RE, Nelson MD, and Wendt DG (2002) Stratified estimation of forest area using satellite imagery, inventory data, and the k-nearest neighbors technique. *Remote Sensing of Environment* 82: 457–468.

Tomppo E (1991) Satellite imagery-based national forest inventory of Finland. *International Archives of Photogrammetry and Remote Sensing* 17: 2333–2351.

Design, Performance and Evaluation of Experiments

V LeMay, University of British Columbia, Vancouver, BC, Canada
A Robinson, University of Idaho, Moscow, ID, USA

Introduction

Experimental design is similar to sampling and inventory design in that information about forest variables is gathered and analyzed. However, experiments presuppose intervention through applying a treatment (an action or absence of an action) to a unit, called the experimental unit. The goal is to obtain results that indicate cause and effect.

For each experimental unit, measures of the variables of interest (i.e., response or dependent variables) are used to indicate treatment impacts. Replication is the observation of two or more experimental units under identical experimental conditions. A factor is a grouping of related treatments. For example, the factor could be fertilizer, with three levels representing three treatments (e.g., none, a moderate amount, and a heavy amount) applied to plots of trees (plot is the experimental unit). For each plot, height growth measures are taken and averages are compared among the three treatments; the null hypothesis is that there are no differences among the treatment means. The sum of squared differences (termed, sum of squares) between the average for the response variable by treatment versus the average over all experimental units represents the variation attributed to a factor. Experimental error is the measure of variance due to chance causes, among experimental units that received the same treatment. The degrees of freedom, associated with a factor, are the number of treatment levels within the factor minus one. The degrees of freedom for the experimental error relate to the number of experimental units and the number of treatment levels.

The impacts of treatments on the response variables will be detectable only if the impacts are measurably larger than the variance due to chance causes. To reduce the variability due to causes other than those manipulated by the experimenter, relatively homogeneous experimental units are carefully selected. Random allocation of a treatment to an experimental unit helps insure that the measured results are due to the treatment, and not to another cause. For example, if we have applied the no-fertilizer treatment to experimental units on north-facing sites, whereas moderate and heavy fertilizer treatments are applied only to south-facing sites, we would not know if differences in average height growth were due to the application of fertilization, the orientation of the sites, or both. The results would be confounded and very difficult to interpret.

Variations in designs, issues that arise, and methods of analyses are discussed in the context of forestry experiments. References from a selection of texts are given; however, there are many books on experimental design. The further reading section also includes more recent advances in analysis of experimental data.

Variations in Experimental Design

Introduction of More than One Factor

For many forestry experiments, more than one factor is included for design efficiencies over conducting separate experiments. This also allows for examining interactions among factors, and allows for a more efficient design if there are no interactions. A treatment represents a particular combination of levels from each of the factors. For example, if we have two species and three fertilization levels, then we have six treatments that represent the two factors, using a crossed experiment. We might be interested in the effects of species and fertilization, separately, and also whether these interact, resulting in different fertilizer impacts depending upon the species. **Figure 1** illustrates this example using a completely randomized design (CRD), where the treatments are randomly assigned to the experimental units, with factor A (three levels of fertilization: A1, A2, and A3), factor B (four species: B1, B2, B3, and B4), and four replications per treatment for a total of 48 experimental units.

If both species and fertilization are fixed effects, in that the experimenter would like to examine the mean response for each species and each fertilizer level, we obtain the analysis of variance table given in **Table 1** from the use of a general linear model and least-squares analysis.

If the assumptions of general linear models are met, in that residuals are independent, are normally distributed, and have equal variances among treatments, we can interpret the results. The null hypothesis is tested using an F-test for each factor and for each interaction. A type I error rate (α, significance level), the chance of rejecting a null hypothesis when it is true, must be selected; we reject an hypothesis if the probability value (P-value) for the test is less than the specified significance level. For this example, there is no significant interaction ($P = 0.0539$) using $\alpha = 0.05$; therefore, we can examine species and fertilizer effects separately. There are significant differences between the three fertilizer levels of factor A ($P < 0.0001$), and between the four

A1B1 = 10	A3B2 = 25	A3B4 = 35	A2B2 = 23	A1B2 = 14	A2B3 = 24
A1B4 = 24	A2B2 = 22	A1B2 = 15	A2B4 = 28	A3B3 = 32	A3B2 = 25
A3B2 = 27	A1B4 = 23	A3B3 = 29	A3B2 = 26	A1B3 = 17	A1B1 = 11
A3B4 = 35	A1B2 = 13	A1B4 = 22	A1B1 = 11	A2B3 = 24	A3B3 = 30
A1B3 = 19	A2B1 = 18	A2B4 = 30	A3B3 = 31	A2B3 = 23	A1B4 = 22
A3B1 = 22	A2B4 = 29	A3B1 = 23	A2B1 = 18	A1B2 = 15	A3B1 = 23
A2B2 = 25	A3B4 = 37	A1B1 = 9	A3B1 = 24	A3B4 = 36	A2B4 = 28
A1B3 = 17	A2B1 = 18	A2B2 = 20	A2B1 = 18	A2B3 = 26	A1B3 = 18

Figure 1 Completely randomized design with two fixed-effects factors, randomly allocated to 48 experimental units, with four replications per treatment. For example, A1B1 = 10 indicates that the response variable was 10 for this experimental unit that received factor A, level 1 and factor B, level 1.

Table 1 Completely randomized design with two fixed factors: analysis using a general linear model

Source	*Degrees of freedom*	*Sum of squares*	*Mean squares*	F	P
A	2	1258.17	629.08	514.70	<0.0001
B	3	934.75	311.58	254.93	<0.0001
A × B	6	17.00	2.836	2.32	0.0539
Error	36	44.00	1.22		
Total	47	2253.92			

species of factor B ($P < 0.0001$). The mean values based on these data are: A1 = 16.25, A2 = 23.38, A3 = 28.75, B1 = 17.08, B2 = 20.83, B3 = 24.17, and B4 = 29.08. Further analyses, such as Scheffé's test for multiple comparisons, could then be used to compare and contrast treatment means.

Significant interactions among factors lead to more difficult interpretations, and subsequent analyses must be based on a larger group of treatment means. In the example, if the interaction were significant, the 12 means for each fertilizer/species combination would be used in interpretation and subsequent analysis, resulting in fewer experimental units used to calculate each mean value. Since factors often interact in forests, interactions are often detected.

Issues that may arise in the analysis of this type of experiment include:

1. The assumptions for the residuals are not met.
2. For subsequent analysis, care must be taken to preserve the overall type I error rate.
3. There is difficulty in randomly assigning experiments in field layouts.
4. There are difficulties in inferring results to a larger population. The spatial and temporal scale of forest management is very large, whereas experiments are often small-scale.

These issues are also relevant for other types and variations in experimental design, and are discussed later in this article.

Fixed, Random, or Mixed Effects

Factors can be fixed, in that the experimenter would like to know the change that is due to the particular treatments applied (as in the CRD example), or random, in that the variance due to the factor is of interest. For example, if the impacts of species (factor) on height growth (response variable) were of interest, we could be interested in the differences among the species in the experiment, and how they rank relative to one another (fixed effect), or we could be interested in the variance in height growth due to species (random effect). Commonly, experiments in forestry include a mixture of factors, some random and some fixed (called mixed effects).

When factors are random or mixed, the default *F*-tests, as shown in the CRD example, are not appropriate. The expected mean-squares should be calculated in order to determine the correct *F*-tests. Most statistical packages allow the user to request the correct test. Alternatively, maximum-likelihood approaches may be more appropriate for mixed-effects experiments. A later section in this article presents more information on least-squares versus maximum-likelihood estimation.

Restricted Randomization Through Blocking: Randomized Block, Latin Square, and Incomplete Blocks Designs

Restricting randomization to within blocks is used when the experimental units can be grouped by another variable that may impact the results. In forestry experiments with large experimental units, blocking is often very useful in reducing error variance with only a small reduction in error degrees of freedom. Blocks (or variables that represent blocks, such as trials or sites) are most often random effects. **Figure 2** illustrates a randomized block design (RBD), with factor A (six levels of fertilization: A1 to A6), and two sites. Randomization of factor A is restricted to within sites.

Using a general linear model with fertilization as a fixed effect and sites as a random effect (mixed-effects model) gives the results in **Table 2**.

The interest with RBD is with the factor, not with the blocks; the blocks are simply used to reduce the variability among experimental units. For this example, there are significant differences among treatment means ($P = 0.0015$) As with CRD, subsequent comparisons and contrasts could be made among the treatment means.

The Latin square design extends grouping of experimental units to two variables. For example, two sites may represent north-versus south-facing stands, and there might be a moisture gradient within sites.

Another variation is incomplete blocks, where not all treatments are represented in each block. Such blocks are smaller, and, therefore, cheaper, and also subject to less environmental variation, making them quite attractive for forestry applications. Relatively recent technology on the recovery of interblock information has made the use of incomplete blocks more feasible.

As well as the issues noted for a multifactor completely randomized design, there is the concern that the blocking may not have been needed. In that case, the introduction of blocks does not result in a corresponding reduction in the experimental error. This should be addressed in the design of the experiment; variables used to group the experimental units into blocks should be those that are expected to affect the response variables.

Restricted Randomization Through Splitting Experimental Units

In many multifactor forestry experiments, the experimental unit is split, and different treatments for one factor are applied to the splits, while a single treatment from another factor is applied to the unit. For example, with six treatments representing three fertilizers and two species, we could use six small experimental units and randomly assign the six treatments to these units. However, this might result in an experimental unit that is too small for the mechanical application of fertilizer. An alternative is to apply the fertilizer treatments to three larger experimental units, and then split each unit and randomly assign the species to the split units (called split plots). This is a restriction on randomization. A further extension of this would be to split the units again, and randomly assign a third factor (e.g., particular seedling stocks for a species) to the smallest unit, resulting in split-split plots.

Although the analysis of an experiment using split or split-split plots is very similar to a multifactor experiment where there is complete randomization of treatments to each unit, care must be taken in using the correct experimental error for the units versus the subunits, and interpreting the results.

Nesting of Factors

Treatment levels for one factor may be particular to the level of another factor, resulting in nesting of treatments. For example, for the first level of fertilizer, we might use medium and heavy thinning, whereas, for the second level of fertilizer, we might use no thinning and light thinning.

Nesting of factors will affect both the analysis and the subsequent interpretation of the experiment. An example of a nested design is given in **Figure 3**, with the subsequent analysis in **Table 3**.

When factors are nested, it is not possible to isolate the nested factor from the other factors, nor is it possible to assess interactions between nested and nonnested factors. The correct *F*-tests differ from a crossed experiment, in that the error mean-squares is not used for all *F*-tests. For factor A, there were no significant differences between the treatment means

Site 1

A1 = 9	A6 = 21
A3 = 15	A2 = 12
A5 = 20	A4 = 17

Site 2

A4 = 25	A3 = 19
A1 = 12	A5 = 27
A2 = 16	A6 = 29

Figure 2 Randomized block design with one fixed-effect factor randomly located to six experimental units within each of two sites.

A1B1 = 10	A1B1 = 11	A1B2 = 13	A2B4 = 23
A1B2 = 15	A2B3 = 18	A2B4 = 25	A1B1 = 11
A2B4 = 20	A2B3 = 18	A1B1 = 9	A2B3 = 18
A2B4 = 22	A1B2 = 15	A2B3 = 18	A1B2 = 14

Figure 3 Nested design with two factors, where the second factor is nested in the first factor, with four replications per treatment.

Table 2 Randomized block design with one factor, randomly located with each of two blocks: analysis using a general linear model

Source	*Degrees of freedom*	*Sum of squares*	*Mean squares*	F	P
Block	1	96.33	96.33	38.03	0.0016
Fertilization	5	320.00	64.00	25.26	0.0015
Error	5	12.67	2.53		
Total	11	429.00			

Table 3 Nested design with two fixed-effects factors, where the second factor is nested in the first factor: analysis using a general linear model

Source	*Degrees of freedom*	*Sum of squares*	*Mean squares*	F	P
A	1	256.00	256.00	7.06	0.1172
B (A)	2	72.50	36.25	23.51	<0.0001
Error	12	18.50	1.54		
Total	15	347.00			

($P = 0.1172$), using the mean-squares for factor B, nested in A for the *F*-test. The means for factor B, nested in A, were significantly different ($P < 0.0001$) using the error means-squares for the *F*-test.

Interpreting nested designs is more complicated than crossed designs. However, nesting may result in efficiencies by reducing the number of experimental units over the number that would be needed for a crossed experiment. Also, nested factors result from a hierarchical design, which is discussed next.

Hierarchical Designs and Subsampling

Commonly in forestry experiments, the experimental unit represents a group of items that we measure. For example, an experiment includes several pots in a greenhouse, each with several plants germinating from seeds. A treatment (specific level of factor A) is randomly allocated to each pot (could be more than one factor, fixed and/or random), even though measures are to be taken on plants. The three factors, which affect the measures on plants, are factor A, pots, and plants. The pots are nested within factor A treatment levels, since pot 1 receiving treatment 1 is not the same treatment as pot 7 receiving treatment 1. Similarly, plants in a pot are nested within pots and factor A treatment levels. The three factors are not all crossed in this hierarchical design; some factors are nested.

A variation on hierarchical designs is measuring a sample of items, instead of measuring all items in an experimental unit. For example, if we have 50 trees in an experimental unit, we may choose to measure only 10 of them for diameter growth.

The analysis of hierarchical designs differs from an experiment with fully crossed factors. All levels in the hierarchy must be included in the analysis. Since lower levels in the hierarchy are often random-effects factors, hierarchical models are commonly mixed-effects models. Although methods for least-squares analysis have been developed, maximum-likelihood estimators for mixed-effects models may be more appropriate, as discussed later.

Introduction of Covariates

The initial conditions for an experiment may not be the same for all experimental units, even if blocking is used to group the units. Site measures such as soil moisture and temperature, and starting conditions for individuals such as starting height, are then measured (called covariates) along with the response variable, and these covariates are used to reduce the experimental error. Covariates are usually interval or ratio scale (continuous).

Issues Arising in Forestry Experiments

Failure to Meet Assumptions

When the usual assumptions of the least-squares method are not met, usual *F*-tests may not be reliable. Transformations of the response variables are commonly used, often requiring a 'trial-and-error' approach until the residuals do meet the assumptions. However, results for the transformed response variable are more difficult to interpret, as mean values do not relate well to the original measurement scale. This is particularly true if a nonparametric analysis via a ranking the response variable (called rank transformation) is used. Alternatively, generalized linear models can be used if the residuals appear to follow a distribution from the exponential family, including binomial, poisson, or gamma distributions. For temporally related data, repeated measures analysis is commonly used. Analysis for spatially correlated data can be more difficult, since data can be correlated in many directions.

Preservation of Overall Error Rate in Subsequent Analyses

The use of a particular type I error rate to test for differences among treatment means within a factor should be preserved in subsequent analyses. For example, if an *F*-test is used with a type I error rate of 0.05, appropriate subsequent pairwise tests should use the type I error rate of 0.05 over all tests.

Difficulty in Randomly Allocating One or More Treatments

Although randomizing the allocation of treatments to experimental units is fundamental to removing confounding of treatments with other impacts, sometimes randomization of all treatments is not possible. For example, the impact of burning as a site preparation method prior to planting is difficult to randomize; burning may necessarily need to be confined to one side of the experimental area, resulting in a restriction in randomization. As noted, the results are then subject to confounding, since there may be another factor in the burned area that influences the response. Experimenters often use the analysis appropriate for unrestricted randomization; however, caution must be used in interpreting results.

Missing Information

For some circumstances, particular combinations of factors may be missing, because of a lack of experimental units, because some of the experimental units are damaged, or because of the nature of the treatments. For example, all trees with the high fertilizer, species 1, die because of a failure in one section of a greenhouse sprinkler system. Analysis of the experiment as a nested experiment may be possible, allowing for different levels of one factor within a level of another factor. Imputation methods may be used to find estimates for missing data. However, at some point, statements of statistical inference may not be possible, if too much of the experimental data is missing.

Size of Experimental Units and Time Scale

For studies of young trees and plants, experimental units can be relatively small, and may be conducted in greenhouses with many experimental units. For larger trees, large experimental units are needed to reflect the scale of processes impacting growth. Difficulties arise in finding homogeneous units. As a result, the number of experimental units is often small, resulting in low power. This becomes more pronounced in studying wildlife habitat and watershed processes, where the scale of some processes is even larger. For these very large-scale processes, often a number of case studies are conducted. Results are more difficult to interpret, since unknown or known confounding may have occurred.

Another complication of forestry experiments is that long time scales are often needed to study forest changes meaningfully. As a result, missing information is more common, measurement standards may change over time, and measures might not be taken at regular time intervals, due to changes in funding. These long-term experiments are difficult to analyze and interpret. Models and graphs are commonly used to interpret trends.

Inferences Made from Experimental Results

Since the aim of experimental design is that results indicate cause and effect, experimental units are carefully selected for homogeneity. Results of experiments can, therefore, be somewhat artificial, since the usual heterogeneity of the biological system has been removed from the experiment. Often researchers include observational studies to attempt to model the biological system, and experimental components to isolate causes and effects. The results of the two types of studies are then combined for a more thorough interpretation.

Power of Experiments

The power of a test is the ability to reject a null hypothesis when it is false. An experiment may have too little power to detect an important difference among treatment means, or conversely, too much power, resulting in detection of significant differences that are of no practical importance.

The ability to detect differences between treatment means increases as the size of the experiment increases, where size is defined as the number of replicates and the number of treatments. Power analysis is the assessment of the power of test for the planned experiment, given the size of differences that have practical importance, and an estimate of the expected variation.

The method of determining the size of the difference that will be detected by an experiment will vary with the design of the experiment. For example, if a randomized block design is used, then more experimental units per block could be used to increase power (sometimes called generalized randomized block design), or more blocks could be established. For split-plot experiments, the power for the factor assigned to the split plot (subunit) is higher than for the factor randomly assigned to the whole plot (experimental unit). Careful design of the experiment should allow for varying sizes of differences for different factors. If power analysis is done following the experiment, the correct analysis given the experimental design must be followed.

Least-Squares versus Maximum-Likelihood Estimation

Many forestry experiments require and benefit from a mixture of fixed and random effects. These different effect types simplify the analysis of hierarchical designs as well as correlations in time and space. Analysis of these models using least-squares techniques can be complicated. Analysis using maximum-likelihood estimators and their variants (restricted maximum-likelihood estimators), is often much more straightforward and flexible. Furthermore, the statistical properties of the maximum-likelihood estimation-style estimators can be superior.

Although maximum-likelihood estimation allows for greater model flexibility, it requires a search algorithm to find a global maximum (overall maximum), unlike generalized least-squares models. For very complex models, only a local maximum may be found, or there may be no convergence. Many statistical packages have built-in procedures for mixed-linear or nonlinear models, allowing for easier application of these relatively new procedures.

Overall Considerations in Designing and Analyzing Forestry Experiments

In order to obtain results that can be interpreted with little or no confounding, experimental units should be carefully selected to remove factors that are not of interest to the experimenter, but would affect the variables of interest. Random allocation of treatments is also needed to equalize the impacts of any remaining factors that were not removed through careful selection. Identifying factors as fixed versus random and using the appropriate design is essential to correct interpretation of results. Also, the correct analysis of hierarchical designs should be stressed; incorrect analyses sometimes appear in literature. For least-squares analysis, expected mean-squares should be calculated to determine appropriate *F*-tests. Power analysis is strongly recommended, during the design of the experiment, to ensure that statistically significant results indicate differences of practical importance.

Because of the large time and spatial scale of many forest processes, experimental units often are large and long-term, in order to have meaningful results. This leads to problems with traditional designs, in that experimental units are large and very heterogeneous, and some are lost over time. Also, there is low power as there are few experimental units. Assumptions of least-squares analysis are commonly not met, resulting in difficulties in analysis and interpretation.

New technologies using maximum-likelihood methods allow greater variability in the analysis of data. These methods have improved our ability to conduct analyses when the assumptions of least-squares analysis are not met, and have increased the flexibility in the design of forestry experiments.

See also: **Afforestation**: Species Choice; Stand Establishment, Treatment and Promotion - European Experience. **Ecology**: Human Influences on Tropical Forest Wildlife. **Environment**: Environmental Impacts. **Experimental Methods and Analysis**: Biometric Research; Statistical Methods (Mathematics and Computers). **Health and Protection**: Diagnosis, Monitoring and Evaluation. **Inventory**: Forest Inventory and Monitoring; Modeling. **Landscape and Planning**: Spatial Information. **Mensuration**: Yield Tables, Forecasting, Modeling and Simulation. **Recreation**: Inventory, Monitoring and Management. **Soil Development and Properties**: Soil Contamination and Amelioration. **Tree Breeding, Practices**: Biological Improvement of Wood Properties. **Wood Formation and Properties**: Wood Quality.

Further Reading

Box GEP and Cox DR (1964) An analysis of transformations. *Journal of the Royal Statistical Society Series B* 26: 211–252.

Cochran WG and Cox GM (1957) *Experimental Designs*. New York: John Wiley.

Cressie NAC (1993) *Statistics for Spatial Data*. revd. edn. Toronto, Canada: John Wiley.

Hurlbert SH (1984) Pseudoreplication and the design of ecological experiments. *Ecological Monographs* 54(2): 187–211.

John JA and Williams ER (1995) *Cyclic and Computer Generated Designs*. London, UK: Chapman & Hall.

Kirk RE (1982) *Experimental Design: Procedures for the Behavioral Sciences*. Belmont, CA: Brooks/Cole.

McCullagh P and Nelder JA (1991) *Generalized Linear Models*. New York: Chapman & Hall.

Meredith MP and Stehman SV (1991) Repeated measures experiments in forestry: focus on analysis of response curves. *Canadian Journal of Forestry Research* 21: 957–965.

Neter J, Kutner MH, Nachtsheim CJ, and Wasserman W (1996) *Applied Linear Statistical Models*, 4th edn. San Francisco, CA: McGraw-Hill.

Schabenberger O and Pierce FJ (2002) *Contemporary Statistical Models for the Plant and Soil Sciences*. New York: CRC Press.

Scheffé H (1959) *The Analysis of Variance*. Toronto, Canada: John Wiley.

Sheskin DJ (1997) *Handbook of Parametric and Nonparametric Statistical Procedures*. New York: CRC Press.

Statistical Methods (Mathematics and Computers)

H T Schreuder, USDA Forest Service, Fort Collins, CO, USA

Inference

Scientific inference becomes statistical inference when the connection between the unknown ‘state of nature' and the observed information is expressed in probabilistic terms.

Statistical inference from sample surveys can be model-based, in which inference relies on a statistical model to describe how the probability structure of the observed data depends on uncontrollable chance variables and frequently on other unknown nuisance variables. Inference can also be design-based, in which reliance is placed on probabilistic sampling. The following is a brief summary of both approaches.

In nonprobabilistic or model-based sampling, inference is made by specifying an underlying superpopulation model ξ for the values of the variable in the actual population being sampled where the actual values are considered random variables from the superpopulation. Then the actual population or a sample from it is considered a sample from this superpopulation of interest. Sample elements do not have to be chosen at random or with known probability as long as they are not selected based on their values of interest $y_i, i = 1, \ldots, N$. Inferences and conclusions rely heavily on the model assumed, which can be a serious liability if the model is not correctly specified. But if correctly specified, an increase in precision can be expected over the design-based approach.

The design-based approach to inference relies heavily on probabilistic sampling, in which each unit and pairs of units in the population have a positive probability of being selected and the probability of each sample can be calculated. The statistical behavior of estimators of a population characteristic is based on these probabilities and the probability-weighted distribution of all possible sample estimates. A weakness of this approach is that samples that were not drawn are considered heavily in evaluating the properties of the inference procedure, yet should not inference about a population parameter be based solely on the actual sample drawn? But the approach is objective and the only assumption made is that observational units are selected at random so the validity of the inference only requires that the targeted and sampled populations are the same. And careful attention to sample selection within the framework of probabilistic sampling will eliminate the least desirable samples from consideration. The idea behind probabilistic sampling is to make the sample representative of the population being sampled.

A crucial difference between design-based and model-based inference is that design-based inferences are made about the finite, usually large, population sampled, whereas model-based sampling inference, although initially restricted to the usually small sample being taken, is generalized to superpopulations by the use of models. Note that there is a distinction between enumerative (or descriptive) and analytical (or comparative) surveys. In enumerative surveys a 100% sample of the existing population provides the complete answer to the questions posed, but is still inconclusive in analytical surveys (see **Figure 1** for informative distinctions between analytical and enumerative surveys). Design-based sampling is widely accepted now and we limit our discussion to it.

Basic Concepts

Why Sample?

Most decisions are made with incomplete knowledge. Your physician may diagnose disease from a single drop of blood, for example. We hope that the drop represents the nonsampled portions of the body. A complete census is rare – a sample is commonplace. A ranger advertises timber sales with estimated volume. Bidders take the truth and reliability of this information at their own risk and judgment.

Sampling will frequently provide the essential information more timely at a far lower cost and can be more reliable than a complete enumeration. There are several reasons why this might be true. With fewer observations to be made and more time available, crews will get less tired and remain more committed to careful measurement of the units in the sample. In addition, a portion of the saving resulting from sampling could be used to buy better instruments and to employ or train higher-caliber personnel. But it is critical that the sample represents the population well!

Populations, Parameters, Estimators, and Estimates

The central notion in any sampling problem is the existence of a population, a collection of units with values of variables of interest attached. The units are selected and the values of interest obtained from the selected elements, either by measurement or observation. Whenever possible, matters will be simplified if the units of the population are the same as those that can be selected for the sample. If we wish to estimate the total weight of earthworms in the top 15 cm of soil for some area, it would be best to think of a population made up of blocks of soil of some specified dimension with the weight of earthworms in the block being the unit value. Such units are easily selected for inclusion in the sample and projection of sample data to the entire population is relatively simple. If we think of individual earthworms as the

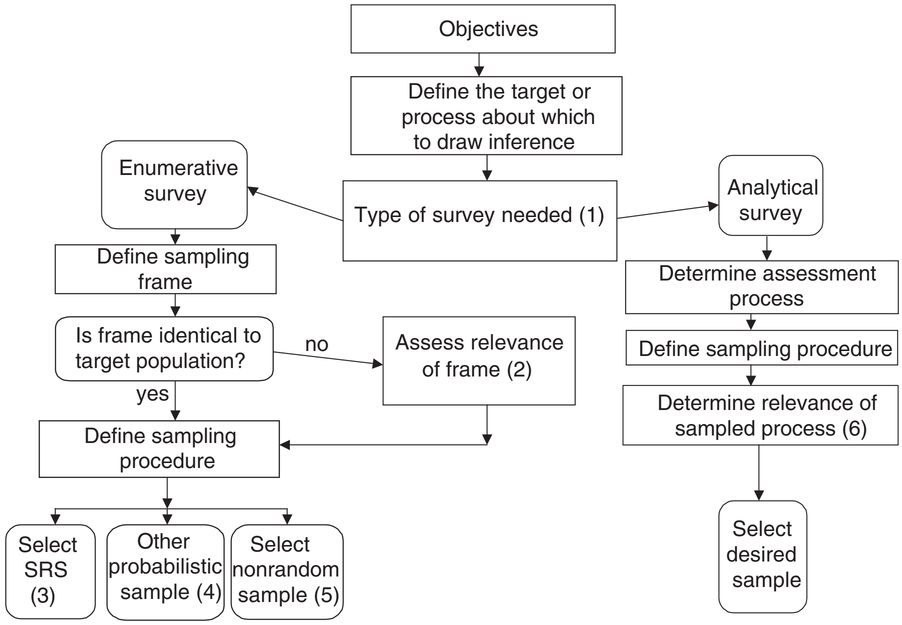


Figure 1 A comparison of enumerative and analytical surveys. The numbers refer to the following:

(1) Are the objectives to draw conclusions about an existing finite population (enumerative survey) or to act on or predict the performance of a (frequently future) process (analytical survey)?
(2) Statistical intervals apply to the frame from which the sample was drawn. Inferences could be biased if the target population is different from the population used for the frame.
(3) Often simple random sampling (SRS) is assumed in constructing confidence intervals.
(4) Confidence intervals can also be constructed for other probabilistic procedures; for example, bootstrapping intervals for the most complex ones.
(5) Statistical confidence intervals are not meaningful here.
(6) Statistical confidence intervals apply to the sampled process and not necessarily to the process or population of interest.

Adapted from Hahn GJ and Meeker WO (1993). Assumptions for statistical inference. *American Statistics* 47: 1–11. Reprinted with permission from *The American Statistician*.

units, selection of the sample and expansion from the sample to the population may both be very difficult.

To characterize the population as a whole, we often use certain constants of interest called parameters. The proportion or the number of living seedlings in a pine plantation are parameters. Usually the parameters estimated are the population mean or total of one or more variables or change therein over time but we are now often also interested in potential explanations of why interesting changes in parameters happen. Parameter estimates are generated from samples using mathematical formulas called estimators.

Bias, Accuracy, and Precision

A good estimate of a population trait or parameter is one that is close to the true value and obtained from a sample at a reasonable cost. But what happens if the person selecting the sample is prejudiced in some manner in terms of either selecting the sample or making measurements? Either one of these would introduce bias into our estimate.

Statisticians have well-defined expressions for bias, accuracy, and precision. Bias is a systematic distortion. A distinction is made between bias in measurement, in method of selecting the sample, or in estimation of the parameter.

Measurement bias can result, for example, when an observer counts trees on plots and systematically excludes or includes border trees.

Bias due to sampling selection arises when certain units are given a greater or lesser representation in the sample than in the population and this is not compensated for in estimation. If we only sample recreation preferences of visitors to a park on weekends, bias would occur because weekday users had no opportunity to appear in the sample.

The technique of estimating the parameter after the sample has been taken is also a possible source of bias. If the most common recreation preference of users on two national forests is estimated by taking a simple arithmetic average of the preferences from the two forests, the resulting average may be seriously biased if there is a considerable difference in their size and use.

Selection and measurement biases are rarely acceptable. Estimation bias may be acceptable when some biased estimator is more precise with only slight bias relative to unbiased ones.

A biased estimate may be precise but it is not accurate. Accuracy refers to the success of estimating the true value of the parameter; precision refers to the clustering of sample values about their own average, which, if biased, cannot be the true value. Accuracy, or closeness to the true value, may be absent because of bias, lack of precision, or both (**Figure 2**).

Variables, Continuous and Discrete

Variation is a fact of life. Coping with some of the sampling problems created by variation is an important part of making valid inferences. For example, tree height is a variable.

Continuous variables are those expressed in a numerical scale of measurement, any interval of which may, if desired, be subdivided into an infinite number of values, say amount of time spent recreating. Discrete variables are qualitative or those represented by integral values or ratios of integral values, either attributes such as the proportion of trees having a specific attribute or counts such as number of people in a recreation group.

Continuous and discrete data may require different statistical procedures. Most of the sampling methods and computational procedures discussed are for use with continuous variables and we focus on those. The procedures for discrete variables are generally more complex. Often count variables can be treated as continuous variables, especially for larger sample sizes.

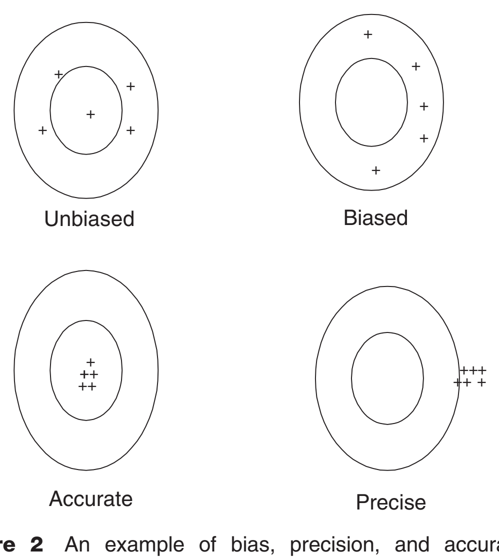


Figure 2 An example of bias, precision, and accuracy if average distance to plot center is used in estimating distance to center of target for five shots.

Distribution Functions

A distribution function shows, for a population, the relative frequency with which different values of a variable occur so that the proportion of units within certain size limits can be determined. Each population has its own distinct distribution function that can often be approximated by certain general types of function, such as the normal, binomial, Poisson, and negative binomial. The bell-shaped normal distribution is often encountered in dealing with continuous variables such as volume per hectare in old-growth stands of timber. The binomial is associated with data where a fixed number of individuals are observed on each unit, characterized by the number of individuals having some particular attribute such as number of seed germinating on a dish. The Poisson distribution may arise where individual units are characterized by a count having no fixed upper limit, particularly if zero or very low counts tend to predominate, such as number of dead trees per hectare. For such data the negative binomial may be useful if low counts do not dominate.

The form of the distribution function dictates the appropriate statistical treatment of a set of data. The exact form of the distribution will seldom be known, but some indications may be obtained from the sample data or from a general familiarity with the population. The methods of dealing with normally distributed data are simplest and fortunately the distribution of means of large samples may be approximated well by this distribution.

Sample estimates are subject to variation just like the individual units in a population. The mean diameter of a stand as estimated from a sample of three trees will frequently be different from the mean estimated from other samples of three trees, and a sample of size 6 would usually produce a more precise estimate than a sample of size 3.

The measure of variation most commonly used is the variance, a measure of the dispersion of individual attribute values about their mean estimated from a sample. Large and small variances indicate wide and little dispersion respectively. The variance of an attribute is a parameter.

The estimator of the variance from a simple random sample is given by:

$$s^2 = \frac{\sum_{i=1}^{n}(y_i - \bar{y})^2}{n-1}$$

where s^2 = sample estimate of the population variance, y_i = the value of the i^{th} unit in the sample, $\bar{y}$ = the arithmetic mean of the sample, i.e., $\bar{y} = \sum_{i=1}^{n} y_i/n$, n = the number of units observed in the sample, and s is the standard deviation, the square root of the variance. Measures of the same form, called the variance of the estimate (s^2/n for simple random sampling (SRS)) and the standard error of estimate (standard error of estimate = square root of the variance of the estimate) are merely the variance and standard deviation among estimates rather than among individual units. Repeated sampling is unnecessary; the variance and the standard error can be obtained from a single set of sample units where the variability of an estimate depends on the sampling method, the sample size, and the variability among the individual units in the population. A sample estimate should be presented with an indication of its reliability as measured by the standard error.

With the standard error, confidence limits can be estimated suggesting how close we might be to the parameter being estimated. For large samples (usually more than 30) the parameter estimated will be on average roughly within 2 standard errors of the estimated parameter (based on an approximation to the normal distribution) unless a 1 in 20 chance occurred (95% confidence limits).

Design

Objectives can be to:

1. Generate current status estimates such as area or volume in a forest, where the forest is, and how it is distributed, and monitor change in such parameters.
2. Identify possible cause-and-effect relationships such as a growth decline in pine forests that could be due to drought or pollution.

Sampling Frame and Representative Sampling

Sampling Frame

Each unit in the population should have a positive, known probability of being selected for the sample so a list of units in the population, called a sampling frame, is required. This frame gives for all N units in the population:

1. The known positive probability of selection, π_i, $i = 1, \ldots, N$ for each unit.
2. The joint positive probability of selection, π_{ij}, i, $j = 1, \ldots, N$, $i \neq j$ for all pairs of units.

In the following we only discuss without replacement sampling of units since it is more efficient than with replacement sampling. Potential sample units can have equal or unequal probabilities and joint probabilities of selection. One of the big advantages of unequal probability sampling is that all single-phase probabilistic procedures used are special cases. Understanding the concept of unequal probability sampling will facilitate comprehension of the other procedures and why and when it is advantageous to use them. This flexibility leads us to the designs discussed: SRS, stratified sampling, cluster sampling, sampling with probability proportional to size (PPS), and systematic sampling with a random start. We then discuss estimation so that we have a sampling strategy consisting of both the sampling design and the estimation procedure used.

Sample Designs

Unequal probability sampling If π_i is the probability of selecting unit i and π_{ij} is the joint probability of selecting units i and j, then the unbiased Horvitz–Thompson estimator of the population total Y is:

$$\hat{Y}_{HT} = \sum_{i=1}^{n} y_i/\pi_i \tag{1}$$

with variance:

$$V(\hat{Y}_{HT}) = 1/2 \sum_{i \neq j}^{N} w_{ij}(y_i/\pi_i - y_j/\pi_j)^2 \tag{2}$$

with $w_{ij} = \pi_i\pi_j - \pi_{ij}$.

Unbiased variance estimators are:

$$v_1(\hat{Y}_{HT}) = 1/2 \left\{ \sum_{i \neq j}^{n} [(\pi_i\pi_j - \pi_{ij})/\pi_{ij}](y_i/\pi_i - y_j/\pi_j)^2 \right\} \tag{3}$$

and

$$v_2(\hat{Y}_{HT}) = \sum_{i=1}^{n} [(1 - \pi_i)/\pi_i^2] y_i^2 + \sum_{i \neq j}^{n} [(\pi_{ij} - \pi_i\pi_j)/\pi_{ij}](y_i y_j/\pi_i\pi_j) \tag{4}$$

Examination of the above equations for understanding If $\pi_i = ky_i$, with k a constant, then $\hat{Y}_{HT}$ in eqn [1] is a constant, and Y and V in eqn [2] would be 0, the ideal situation. This won't happen in practice but we can approximate it. For example, we can practically select trees proportional to their diameter breast height squared if we are interested in tree volume and then the ratios y_i = volume for tree i/x_i = basal area for tree i are essentially constant, so that $(y_i/\pi_i - y_j/\pi_j)^2$ in eqn [2] is close to 0. Similarly, if we are interested in tree counts, then giving each tree an equal weight in selection is efficient. The efficiency of the methods discussed depends on the strength of the relationship between the variable of interest y and the covariate x used for probability of selection, how the covariate is used in selection, and joint probabilities of units. With this background on the ideas behind the sampling designs, we now list them specifically.

Simple random sampling This is the simplest probabilistic approach. All samples of size n have the same probability of selection from the N units in the population. SRS sampling has the advantages that since all units have the same probabilities of selection, applicable analysis techniques are easy to implement and estimation is straightforward and understandable, for example when estimating the mean or total of a population. The estimator of the mean $\bar{y}$ is:

$$\bar{y} = \sum_{i=1}^{n} y_i/n$$

with sample size n and y_i the value for variable of interest on sample unit i.

An unbiased estimator of the population variance of the mean is:

$$\begin{aligned} v(\bar{y}) &= [(N-n)/(Nn)]\left[\sum_{i=1}^{n}(y_i - \bar{y})^2/(n-1)\right] \\ &= [(N-n)/(Nn)]s^2 \end{aligned}$$

where N = number of elements in population, s^2 is the sample variance and $(N-n)/N$ is called the finite population correction. An estimator of the total Y, $\hat{Y}$, would be obtained by multiplying $\bar{y}$ by N, so $\hat{Y} = N\bar{y}$ and its variance would be $v(\hat{Y}) = N^2 v(\bar{y})$.

In various circumstances we may have complete knowledge on a covariate associated with the variable of interest for which we know all the values in the population or we can get those with relative ease. Usually this information is combined with the information on the variable of interest measured on a subsample of the units in the population. This information can be used in various manners in sample selection and in estimation.

Denoting by y = variable of interest and x = covariate, numerous sample selection schemes and estimators are possible.

Stratified sampling This is a simple but powerful extension of SRS where the population of interest is divided into subpopulations or strata of interest. The idea behind stratification is as follows:

1. We are interested in those subpopulations (strata) too.
2. The subpopulations are internally more homogeneous than the population so we can gain efficiency in estimation by distributing the sample in a good manner over them.
3. We are thus able to apply different sampling procedures in the different subpopulations for convenience.

Estimator of the population mean is:

$$\bar{y}_{st} = \sum_{h=1}^{k} N_h \bar{y}_h / N$$

with estimated variance of the mean:

$$v(\bar{y}_{st}) = \sum_{h=1}^{k} (N_h^2/N^2)[(N_h - n_h)/N_h] s_h^2/n_h$$

where: $\bar{y}_h$ = sample mean for stratum h, k = number of strata, $s_h^2 = \sum_{i=1}^{n_h}(y_{hi} - \bar{y}_h)^2/(n_h - 1)$ and N_h and n_h are number of elements in the population and sample respectively in stratum h.

Cluster sampling In this extension of SRS, clusters of (say) trees are sampled by SRS. The idea behind cluster sampling is twofold:

1. It is useful when no list of sample units is available, as is often true with trees, but lists of clusters are available or easily constructed (e.g., stands or plots respectively).
2. It is usually cheaper to visit clusters of trees than individual trees as in SRS because travel expense is often the biggest item in sampling forests.

Ideally, clusters are very heterogeneous, in contrast to strata, because it is more efficient that way. Usually, reduced cost is the reason behind cluster sampling.

If we select n out of N clusters at random and each cluster sampled is measured completely for the variable of interest, then a biased estimator, $\bar{y}_{cl}$, of the mean per unit is:

$$\bar{y}_{cl} = \sum_{i=1}^{n} M_i \bar{y}_{i.} \Bigg/ \sum_{i=1}^{n} M_i$$

where M_i is the number of units in cluster i, with an estimator of the variance:

$$v(\bar{y}_{cl}) = [(N-n)/Nn] \sum_{i=1}^{n} (M_i^2/M_n^2)(\bar{y}_{i.} - \bar{y}_{cl})^2/(n-1)$$

with N = number of clusters in the population, n = number of clusters selected by SRS, $M_n = \sum_{i=1}^{M} m_i/n$

is the average number of units per cluster in the sample, and $\bar{y}_{i.} = Y_{i.}/M_i$, where $Y_{i.}$ is the total for all observations in cluster i.

PPS sampling In PPS sampling it is assumed that there is a covariate (or independent variable) available which is positively correlated with the variable of interest and units are selected proportional to the value of the covariate. The information collected on the covariate and on the variable of interest are combined into an estimator such as the Horvitz–Thompson estimator in eqn [1].

PPS sampling is useful when individual selection probabilities are nearly proportional to the variable of interest.

Estimator of the population mean is:

$$\bar{y}_{HT} = \sum_{i=1}^{n} y_i/(N\pi_i) \text{ with estimated variance :}$$

$$v(\bar{y}_{HT}) = (1/2)\sum_{i\neq j}^{n}[(\pi_i\pi_j - \pi_{ij})/(N^2\pi_{ij})](y_i/\pi_i - y_j/\pi_j)^2$$

with n and N = number of elements in the sample and population respectively and all π_i and π_{ij} are assumed to be larger than 0.

Systematic sampling with a random start In systematic sampling with a random start, a random starting unit is selected and then every kth unit is selected. Systematic sampling assumes that the population can be arrayed in some order, which may be natural, say, days of the week in recreation sampling, or artificial, such as numbered plot locations on a map. The ordering may be haphazard in the latter case but needs to be carefully considered in the earlier one. For example, in sampling use of a recreation area we probably do not want to sample every seventh day, say every Sunday. Systematic sampling has not in the past been generally endorsed by theoretical statisticians because it is not a strictly probabilistic procedure in that several units have joint probabilities of selection of 0. But practitioners and applied statisticians have prevailed in getting it used widely because it is a very practical way of collecting information in the field and avoids the problem of poorly distributed samples in the field, as can happen with some of the earlier procedures discussed. Generally, systematic sampling (with a random start) is treated as SRS, the assumption being that the variance estimate for SRS should usually give an overestimate of the variance achieved with systematic sampling.

Estimator of the population mean is:

$$\bar{y}_{syst} = \sum_{i=1}^{n} y_i/n$$

with variance estimator:

$$v(\bar{y}_{syst}) = [(N-n)/N]s^2/n$$

Note that the formulas are the same as for SRS.

Another estimator Although the Horvitz–Thompson estimator is quite efficient in many situations, it can be quite unreliable in some cases. A specific example involves populations where some of the covariate values, x, are quite small relative to the values of the variable of interest, y. It is clear that if some of the sample units contain y and x values where x is quite small, for those ratios in the estimator, y/x can be quite large yielding large estimates. For example, if $x = 0$ for one or more units, the ratio would be ∞. Units with $x = 0$ would not be selected by PPS sampling (causing bias in the estimation) but would be with SRS. Having extreme values is a general problem with such mean of ratio estimators which are generally not recommended to be used at all with SRS.

In general, more complex – but also more robust – estimators such as the very general, efficient generalized regression estimator developed by C. E. Sarndal should be used if possible:

$$\hat{Y}_{gr} = \sum_{i=1}^{n} y_i/\pi_i + a_{gr}\left(N - \sum_{i=1}^{n} 1/\pi_i\right) + b_{gr}\left(X - \sum_{i=1}^{n} x_i/\pi_i\right) = \sum_{i=1}^{N} \hat{y}_i + \sum_{i=1}^{n} e_i/\pi_i$$

where:

$$\hat{y}_i = a_{gr} + b_{gr}x_i, e_i = y_i - \hat{y}_i$$

$$a_{gr} = \left[\sum_{i=1}^{n} y_i/(\pi_i v_i) - b_{gr}\sum_{i=1}^{n} x_i/(\pi_i v_i)\right] \Bigg/ \sum_{i=1}^{n} 1/(\pi_i v_i)$$

$$V(\hat{Y}_{gr}) = (1/2)\sum_{i\neq j}^{N}(\pi_i\pi_j - \pi_{ij})(e_i/\pi_i - e_j/\pi_j)^2$$

and a variance estimator:

$$v(\hat{Y}_{gr}) = (1/2)\sum_{i\neq j}^{n}[(\pi_i\pi_j - \pi_{ij})/\pi_{ij}](e'_i/\pi_i - e'_j/\pi_j)^2$$

where:

$$e_i = y_i - \tilde{y}_s - b_{gr}(x_i - \tilde{x}_s)$$

and:

$$e_i' = e_i - e_i \left\langle \left\{ \left[(\hat{N} - N) \sum_{l=1}^{n} x_l^2/(\upsilon_l \pi_l) - (\hat{X} - X) \sum_{l=1}^{n} x_l/(\pi_l \upsilon_l) \right] \bigg/ \upsilon_i \right\} + \left\{ \left[-(\hat{N} - N) \sum_{l=1}^{n} x_l^2/(\upsilon_l \pi_l) + (\hat{X} - X) \sum_{l=1}^{n} 1/(\pi_l \upsilon_l) \right] \right\} (x_i/\upsilon_i) \right\rangle \times \left\langle 1 \bigg/ \left\{ \sum_{l=1}^{n} x_l^2/(\pi_l \upsilon_l) \sum_{l=1}^{n} 1/(\pi_l \upsilon_l) - \left[\sum_{l=1}^{n} x_l/(\pi_l \upsilon_l) \right]^2 \right\} \right\rangle$$

where:

$$\hat{N} = \sum_{l=1}^{n} 1/\pi_l, \tilde{N}_s = \sum_{l=1}^{n} 1/(\pi_l \upsilon_l),$$

$$\hat{X} = \sum_{l=1}^{n} x_l/\pi_l, \tilde{x}_s = \left\{ \sum_{l=1}^{n} x_l/(\pi_l \upsilon_l) \right\} \bigg/ \tilde{N}_s$$

and:

$$\tilde{y}_s = \sum_{l=1}^{n} y_l/(\pi_l \upsilon_l)/\tilde{N}_s$$

The generalized regression is biased but consistent in the sense that as $n \to N$, the bias goes to 0.

Variance estimation in general Classical variance estimators discussed above are typically derivable and usually give unbiased or at least consistent estimates of the actual variance. In many cases the actual sampling strategy used is quite complex and such variance estimators cannot be derived. For such situations and even in cases where the actual variances can be derived and computed, other methods can be used, the best-known one being bootstrapping.

Bootstrapping takes full advantage of the computing power now available. It is a computer-based method that allows us to assign measures of precision to statistical estimates. Confidence intervals can be constructed without having to make normal theory assumptions. To illustrate for SRS, if we have a sample of n units of y, with sample mean $\bar{y}$ and variance $\upsilon(\bar{y})$, then in bootstrapping we take B samples of n units with replacement from the n sample units. Then, for each of the B samples we compute means $\bar{y}_b$, $b = 1, \ldots, B$ with overall mean $\tilde{\bar{y}}_B = \sum_{b=1}^{B} \bar{y}_b / B$. The variance between these bootstrap estimates is: $\upsilon(\bar{y}_B) = \sum_{b=1}^{B} (\bar{y}_b - \tilde{\bar{y}}_B)^2/(B-1)$, which can also be used for $\bar{y}$. In addition, the B sample estimates generate a distribution of estimates that can be used for easy confidence interval construction. There are various ways of bootstrapping.

Multi-Information Sources and Sampling over Time

Often covariates are available or information on them can be more easily and cheaply obtained than for the variable(s) of interest, but not for all units in the population, so more than one sampling phase is required. A voluminous literature is available on this topic and on sampling over time too (see Schreuder *et al.* (1993) in Further Reading, below).

See also: **Experimental Methods and Analysis**: Biometric Research; Design, Performance and Evaluation of Experiments. **Mensuration**: Yield Tables, Forecasting, Modeling and Simulation.

Further Reading

Dawid AP (1983) Inference, statistical: I. In: Kotz S and Johnson NL (eds) *Encyclopedia of Statistical Science*, vol. 4, pp. 89–105. New York: John Wiley.

Deming WE (1975) On probability as a basis for action. *American Statistics* 29: 146–152.

Duncan GJ and Kalton G (1987) Issues of design and analysis of surveys across time. *International Statistical Review* 55: 97–117.

Fraser DAS (1983) Inference, statistical: II. In: Kotz S and Johnson NL (eds) *Encyclopedia of Statistical Science*, vol. 4, pp. 105–114. New York: John Wiley.

Hahn GJ and Meeker WO (1993) Assumptions for statistical inference. *American Statistics* 47: 1–11.

Kruskal WH and Mosteller F (1988) Representative sampling. In: Kotz S and Johnson NL (eds) *Encyclopedia of Statistical Science*, vol. 8, pp. 77–81. New York: John Wiley.

Koch GG and Gillings DB (1983) Inference, design based vs model based. In: Kotz S and Johnson NL (eds) *Encyclopedia of Statistical Science*, vol. 4, pp. 84–88. New York: John Wiley.

Schreuder HT and Gregoire TG (2001) For what applications can probability and non-probability sampling be used? *Environmental Monitoring and Assessment* 66: 281–291.

Schreuder HT and Thomas CE (1991) Establishing cause–effect relationships using forest survey data. *Forestry Science* 37: 1497–1525. (includes discussion).

Schreuder HT, Gregoire TG, and Wood GB (1993) *Sampling Methods for Multiresource Forest Inventory.* New York: John Wiley.

Schwarz CJ and Seber GAF (1999) Estimating animal abundance. Review III. *Statistical Science* 14: 427–456.

Smith TMF (1994) Sample surveys: 1975–1990; an age of reconciliation? *International Statistics Review* 62: 5–34.

F

FRAGMENTATION *see* ECOLOGY: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife; Natural Disturbance in Forest Environments. SILVICULTURE: Natural Stand Regeneration. SUSTAINABLE FOREST MANAGEMENT: Causes of Deforestation and Forest Fragmentation.

G

Genetic Modification *see* **Genetics and Genetic Resources**: Genetic Systems of Forest Trees; Molecular Biology of Forest Trees. **Tree Breeding, Principles**: Forest Genetics and Tree Breeding; Current and Future Signposts.

GENETICS AND GENETIC RESOURCES

Contents

Genetic Systems of Forest Trees

V Koski, Vantaa, Finland

Introduction

The term ‘genetic system’ was coined in 1932 by C.D. Darlington, one of the renowned pioneers of cytogenetics. His original definition was limited:

> Properties of heredity and variation, methods of reproduction and the control of breeding, we now realize, are in various ways bound up together in each group of organisms. They constitute a genetic system. The genetic systems of different groups of organisms differ widely.

The concept and its definition have later been elaborated as follows. Genetic system refers to any of the species-specific ways of organization and transmission of the genetic material, which determine the balance between coherence and recombination of genes and control the amount and type of gene combinations. Evolution of the genetic systems means the evolution of those mechanisms effecting and affecting genetic variability.

The latter definition contains three crucially significant points:

1. The system is considered species specific.
2. The balance between recombination and maintenance of advantageous gene combinations requires both promoting and restricting mechanisms.
3. Genetic systems are under genetic control and thus subject to evolutionary processes. Species formation is fundamentally based on changes in the genetic system, especially in isolation mechanisms.

A genetic system comprises various components, such as:

- the mode of chromosome organization (genetic information all in one linkage group or distributed to several such groups)

- chromosome cycle (normal meiosis in both sexes)
- recombination index
- mating pattern: outcrossing (allogamy) or self-fertilizing (autogamy), population size, the mode of reproduction (sexual, asexual)
- isolation mechanisms.

Cytological Factors

The genetic information in the nucleus is packed in structures called chromosomes. Each chromosome contains genes in a linear arrangement, with its genes linked together in a consistent sequence, such that the gene programming a given protein (and all its resulting functions) is at a particular position or locus within its chromosome. For higher plants the basic state is diploid, such that there are two homologous versions of each chromosome, one from the mother and another from the father. This comes about from the fusion of haploid gametes, which contain one version of each chromosome from the male and one from the female parent. During meiosis, which is a part of the formation of haploid gametes, maternal and paternal homologs of each chromosome in the parent join together, and these bivalents reassort at random. The higher the chromosome number the larger the number of various combinations of maternal and paternal elements. Furthermore, in a process of duplicating each original chromosome, crossing-over causes exchange of parts of maternal and paternal strains of the chromosome. Towards the end of meiosis the double sets are pulled towards the opposite ends of the mother cell, and finally the single sets draw apart, which leads to a tetrad of four haploid nuclei. Recombination index, a nonlinear function of the chromosome number and the average chiasma frequency, is proportional to the potential number of various recombinant gametes (**Figure 1**). Normal meiosis mixes the maternal and paternal parts of the chromosome set so effectively that the probability of repeating exactly the parental gametes is negligible. Recombination also breaks apart many favorable combinations ('complexes') of genes, but can create some new complexes that are even more favorable in the context of natural selection. Within the overall plant kingdom there are numerous deviations from this classical pattern of meiosis.

Mating Pattern and Gene Flow

The mating pattern, or breeding system, is the second fundamental part of the genetic system. Mating pattern refers to the mode of combining haploid female and male gametes, which leads to the formation of a diploid zygote, embryogeny, and a new individual. The classical function of sexual reproduction is based on cross-fertilization, i.e., the female gamete and male gamete originate from different parents. This process requires cross-pollination, with pollen transported from one individual to the pollen-receptive site of the seed parent. As plants are almost all immobile, an external factor is needed. Wind, insects, birds, and bats are the main pollen vectors, although water rarely and other small mammals occasionally are effective.

Within the plant kingdom numerous kinds of deviations from cross-pollination have evolved, from complete self-pollination to partial cross-pollination. Cross-pollination requires large amounts of pollen, especially in wind pollination. Complete self-pollination leads to loss of heterozygosity (diversity between

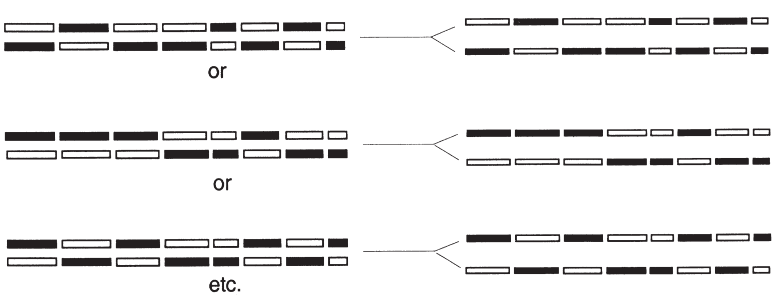


Figure 1 Diagrammatic illustration of chromosomal recombination during meiosis of a species with a diploid chromosome number $(2n) = 16$. The eight chromosome pairs are made up of the maternal part (here white) and the paternal part (here black). During the early part of meiosis the original pairs of chromosomes rejoin and the pairs (bivalents) are assembled to the so-called metaphase plane. The orientation of the maternal and paternal components is random. Consequently, the haploid daughter nuclei (on the right) contain various combinations of maternal and paternal chromosomes. The ideograms show some examples of the orientations. In fact there are 256 different combinations of 8×2 chromosomes. The number of possible combinations (N_R) is a function of the haploid chromosome number (n), $N_R = 2^n$. For instance in case of pines the number of chromosomal recombinants would be 2^{12}, i.e., 4064. Owing to crossing-over, the total number of variations is much higher still. Consequently, the probability of any two of the parental gametes being identical is extremely low in ordinary meiosis.

duplicate copies of the same gene) and recombinants during a few generations, and thus wipes out the original benefit of sexual reproduction. On the other hand, selfing can preserve favorable gene combinations, with minimal allocation of energy to pollen production.

Outcrossing plant species have several mechanisms to enhance cross-pollination. One sure solution is dioecy, i.e., female and male flowers on separate individuals (e.g., *Cedrus* spp., *Populus* spp., *Juniperus* spp.) (**Table 1**). Monoecy means that, while there are separate female and male structures, they both occur in one and the same individual, but it is often combined with features that favor cross-pollination. For instance, female strobili may develop in the upper part of the crown and male strobili in the lower part (e.g., *Abies* spp., *Picea* spp.), reducing chances of self-fertilization. Timing of female and male flowering can be slightly different. When female flowers open prior to pollen shedding in the individual parent, foreign pollen is at an advantage, especially if the space for pollen grains is limited. This phenomenon is called metandry. In monoecious plants sexual asymmetry is common; some individuals carry predominantly female strobili, some others mostly male strobili. Some flowering plants have structural heteromorphism in their hermaphrodite flowers, which results in pollen being deposited on separate parts of the pollinating insects. Cross-pollination requires some external agent to transfer pollen grains of one individual on the receptive organs, ovules, or pistils of another individual of the same species.

Table 1 Occurrence of dioecy and monoecy among 24 genera of conifers. Some genera (e.g., *Cedrus, Juniperus and Podocarpus*) include both monoecious and dioecious species, and exceptional individuals exist in most species.

Genus	*Dioecy*	*Monoecy*
Abies		x
Agathis	x	
Araucaria	x	
Callitris		x
Cedrus	x	x
Cephalotaxus	x	
Chamaecyparis		x
Cupressus		x
Fitzroya	x	
Juniperus	x	x
Larix		x
Libocedrus		x
Metasequoia		x
Picea		x
Pinus		x
Podocarpus	x	x
Pseudolarix		x
Pseudotsuga		x
Sciadopitys		x
Sequoia		x
Taxodium		x
Taxus	x	
Thuja		x
Tsuga		x

Wind pollination is characteristic of gymnosperms, but is also quite common among angiosperms. Wind carries light pollen grains over considerable distances, but successful wind pollination must be based on some key factors: (1) synchronization of flowering time, (2) abundant pollen production and (3) avoidance of harmful effects of pollen from other species. Animal pollination is rather recent in the evolutionary time scale, and it represents a huge diversity of coevolution of generative organs in the plants and the respective animal pollinators. In addition to various kinds of insects, birds and mammals (mainly bats) also transfer pollen while collecting food from flowers. There are many fascinating examples of highly specialized pollination systems. Even though many pollinating insects use pollen for their nutrition because of its high protein content, essentially lower pollen production is sufficient than in wind pollination. On the other hand, the probable distance of pollen transfer is much shorter.

Except for dioecious plants, the pollen deposited on the pistils (or ovules of gymnosperms) contains more or less pollen grains of the same individual; in other words, partial self-pollination is common. If the plant's own pollen is accepted, self-fertilization follows. In outcrossing flowering plants (angiosperms) a special self-incompatibility system prevents the germination of own pollen or retards the growth of the pollen tube. This incompatibility mechanism is usually based on one locus, denoted *s*, with a large number of alleles. If a pollen grain (or even its parent, in some cases) carries the same allele as the pistil, incompatibility prevents fertilization. This kind of system evidently does not exist in conifers, because pollen grains deposit directly on the ovules. After entering the pollen chamber self pollen grains germinate normally and, after the species-specific, shorter or longer rest period, fertilize archegonia as successfully as foreign pollen. During embryogeny, however, most of the selfed embryos abort owing to homozygosity of embryonic lethals. Because there are several archegonia and pollen grains in each ovule, a sound seed may still develop despite the abortion of one or more embryos, if there is at least one outcrossed zygote (or a 'balanced heterozygote' from selfing).

Self-incompatibility and embryonic lethals may be considered a part of the genetic load because they restrict seed production. In combination, however, they maintain high outcrossing rates despite partial self-pollination. Outcrossing and subsequent heterozygosity must be advantageous in long-lived plants, especially trees, as either self-incompatibility or embryonic lethals in combination with archegonial polyembryony are so predominant. Neither of these systems is absolute; spontaneous selfing does take place, and controlled self-pollination results in some germinable seeds. The inbred seedlings usually display strong inbreeding depression, and most soon die under competition. Self-fertilization can occasionally produce offspring of full vigor, through fortuitous lack of genetic load in parents or fortuitous occurrences of balanced heterozygotes. In this respect the typical genetic system of a gymnosperm is highly flexible in its stochastic (probabilitistic) discrimination against results of self-fertilization rather than self-incompatibility.

Gene flow is a process that affects the rate of recombination and population structure of species. A theoretical, so-called Mendelian population is closed and tends to preserve its genes and its genotype frequencies in a Hardy–Weinberg equilibrium. Exchange of genetic material between populations, however, alters gene frequencies and enhances recombination. As trees are immobile organisms the only option is through reproductive material. The most mobile medium is pollen but many trees have seed that can be transported over considerable distances. Windborne pollen, in particular, may travel hundreds of kilometers without losing viability. On the other hand, pollen must meet receptive female flowers in order to generate a new individual; a pollen grain carries only a haploid genome.

Mode of Reproduction

Simple organisms, such as bacteria, reproduce asexually though cell division. Multiplication of genetically uniform lines is exponential in favorable circumstances. Occasional mutations and recombination events provide adaptability when they are coupled with short generation time and exponential reproductive capacity. Typical sexual reproduction of flowering plants requires considerable allocation of resources to reproductive organs, and the complex array of events is vulnerable. Altogether, sexual reproduction is not optimal in all respects. A large number of plant genera and species have in fact diverged from ordinary sexual reproduction and continue their existence with various forms of reproduction. Cleistogamy, apomictic seed, bulbs, buds, root suckers and other forms of vegetative propagation are common means of reproduction among plants, although in the long term most of these are generally interspersed with at least occasional outcrossing events.

Isolation

Each species is by definition essentially a closed biological unit, within which mating and subsequent sexual reproduction is possible. In the formation of new species the development of isolation mechanisms, following for example disruptive selection, is a crucial step. As long as the new lines that are produced are able to interbreed they are not separate species in the strict sense. Thus, isolation is the factor that is antagonistic to overwhelming recombination and gene flow. The function of isolation is to maintain the species' specific gene complexes and to prevent contamination from other species that will threaten the species' integrity if not its fitness as well. Isolation is predominantly a one-directional phenomenon. The escape of pollen grains from a population of any species does not cause change in the gene pool of the donor population. The participation of the pollen in the paternity of the offspring in the receptor population must be prevented by means of isolation.

Several types of isolation exist. Geographic isolation, i.e., isolation by distance, is a special case. It has come as a result of ancient external forces, such as tectonic processes or climate changes, that separated parts of the original range by even thousands of kilometers. The evolutionary processes caused divergence in morphological and ecological characteristics of those sister species or allopatric species, but there was no pressure to develop cross-incompatibility barriers. Consequently, sister species from Europe and North America often hybridize if artificially grown next to each other. Species hybrids of larch (*Larix*), fir (*Abies*), and poplar (*Populus*) are well known examples in many arboreta. The lack of isolation causes trouble in certain instances of gene conservation, when autochthonous populations are subject to pollution from stands of introduced species. The problem may be even more serious in case of *ex situ* conservation of species, especially rare (e.g., *Abies*) species with extremely small, endangered natural stands. When species share a common territory, in other words they are sympatric, they must have effective mechanisms to preclude interspecific hybridization.

Spatial Isolation

Spatial isolation at least reduces interspecific pollination in animal-pollinated species, especially when they grow on ecologically different habitats. On the other hand, bats and solitary bees can travel significant distances while visiting different trees of a species. Windborne pollen of forest trees can travel over 10 km, and spatial isolation is rather ineffective.

Temporal Isolation

Temporal isolation is caused by nonoverlapping flowering times. Typically wind pollination occurs during a short seasonal period, being heavily dependent on close synchrony among individuals in their flowering times. This kind of behavior, in addition to being needed for effective pollination, facilitates the avoidance of interspecific pollination.

Incompatibility

Incompatibility, i.e., a biochemical mechanism that prevents the normal functioning of pollen grains of foreign species, is the most effective barrier against interspecific hybridization. This barrier may sometimes partly fail such that hybrids appear at low frequency. Sometimes the hybrids may lack fitness in the wild, but sometimes they may even show hybrid vigor.

Hybrid Sterility

Hybrid sterility is the final alternative of culling species hybrids. Sterility is thought to be mostly caused by meiotic disturbances, when the homology of chromosomes is imperfect, or when the chromosome numbers do not match. There are still other isolation mechanisms even though the hybrid may be fertile. They may for example have poor field survival, or segregation may cause unbalanced phenotypes in the second generation. On the other hand, rare coincidences of successful hybrids and 'failure' of isolation, often coupled with polyploidy, have resulted in new species.

Forest Trees

Forest trees are large, long-lived organisms, which have immense ecological and economic value. The sustainability of forest ecosystems and the maintenance of genetic diversity may be threatened by exploitation and changes in land use. As the genetic system and its components determine the capability of a population to adapt and to undergo evolutionary changes, the components promoting genetic variability and regeneration are considered to be of utmost importance. From the biological point of view, however, isolation mechanisms must not be neglected. Introduced tree species may hybridize with autochthonous ones, which is usually undesirable (e.g., in black poplar, *Populus nigra*).

Forest trees comprise a huge number of species, which in terms of plant systematics do not form any uniform group. Even though conifers represent only a small fraction of the total, the components of their genetic systems have been investigated much more comprehensively than those of angiosperms. This is mainly due to the great economic value and ecological significance of many conifers. Also, their chromosomes are much easier to study, and their reproductive organs, pollen grains and ovules are large enough to study with small magnification.

Conifers

The number of remaining genera of conifers is around 50 and the number of species close to 600. The numbers of genera and species vary among textbooks and catalogs, depending on each author's taxonomic views. The crucial fact is that the extant species are only a small fraction of the ancient diversity.

The chromosome numbers of conifers are extremely uniform when compared to those of angiosperms. With very few exceptions, the somatic chromosome number ($2n$) is 22, 24 or 26. Thus, almost the entire group is diploid. There are differences in the chromosome morphology, e.g., in the length of the arms among species, so that the karyotypes are variable. Normal meiosis, including crossing-over, takes place in both female and male gametes. The chiasma frequency is above 2; in other words there are, on average, at least two crossing-over events in each bivalent. These figures indicate that the potential for recombination is high, owing to recombination of maternal and paternal chromosomes and is further increased by numerous chiasmata. The huge amount of gametes, especially pollen grains, makes possible the manifestation of immense numbers of potential recombinants.

Conifers are wind-pollinated plants. Most species are monoecious, but there are dioecious species (e.g., *Cedrus* spp., *Juniperus* spp., Podocarpaceae) too. As the transport of pollen grains from male catkins to the female inflorescence is largely a random process, the effective pollination of ovules requires abundant and simultaneous pollen shedding. One big tree produces several hundreds of grams of pollen at one time, even though the individual pollen grains of conifers are very light. One tree releases some 10^{10} pollen grains, and on a per-hectare basis the order of magnitude is 10^{12}. Air currents carry pollen grains far from a source and only a very small fraction happens to hit the female strobili of the neighborhood. Conifer pollen is quite resistant to desiccation and ultraviolet radiation. So the pollen cloud immigrating from another stand of the same species can cause effective gene flow. This kind of gene flow has been detected as pollen contamination in many seed orchards (**Figure 2a**).

Partial self-pollination is common in monoecious species despite the temporal and spatial differences

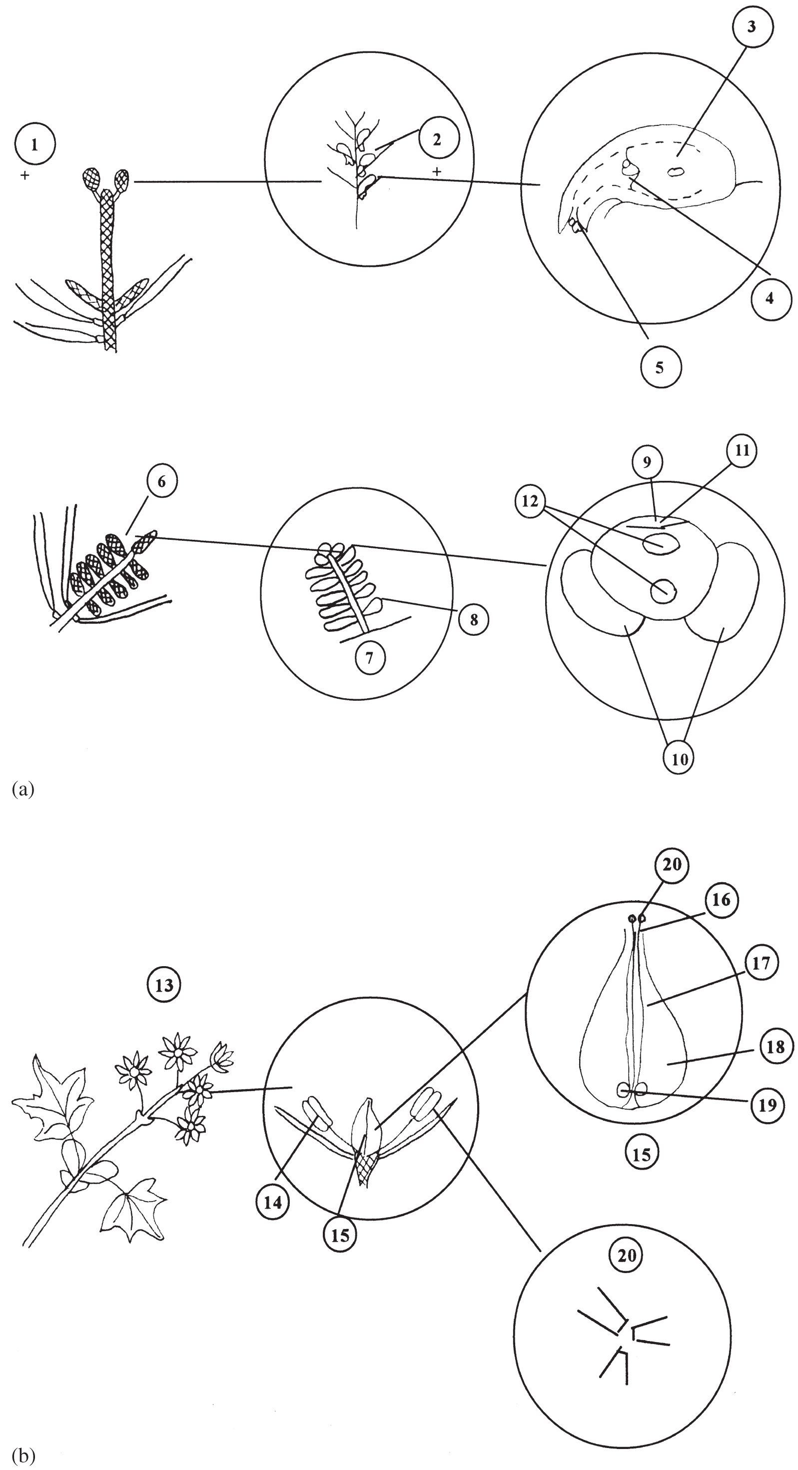


Figure 2 Schematic illustration of the differences in the floral organs of (a) conifer (pine) and (b) angiosperm (maple). (a) A female strobilus (1) of pine consists of an axis, supporting scale and ovuliferous scales. There are two ovules (2) at the base of each fertile scale. An ovule consists of nucellus (3), pollen chamber (4), and micropyle (5). Pollen grains attach on the micropylar filaments and they are transported into the pollen chamber by a pollination drop. Male strobili (6) of pine are on the basal part of the new shoot, mainly in the lower part of the crown. A male (7) strobilus (catkin) has nothing but an axis and scales (microsporophylls) (8) with saclike microsporangia that are filled with pollen. Pollen grains (9) are rather big and they have two air sacs (10). The body of the pollen grain contains a few haploid cells (11) and two haploid sperm nuclei (12). (b) In angiosperms the basic type of flower has both female and male parts. Often numerous flowers make up an inflorescence (13). A single flower of maple has four sepals, four petals, eight anthers (14), and a pistil (15). The pistil consists of stigma (16), style (17), and ovary (18). The ovules (19) are inside the ovary, and the pollen grains (20) are deposited on the stigma (by insects). Pollen tubes have to grow through the style until they reach the egg cells within the ovary. Immense variability of structure of the reproductive organs exists especially among angiosperms.

of female and male flowering. Inbreeding is, however, significantly restricted by embryonic lethals, which cause abortion of selfed embryos. The embryonic lethals are recessive genes which make their homozygotes nonviable. They are a part of the genetic load. Conifer species with large distributions and a continuous population structure usually carry numerous such embryonic lethals. Some species with a small distribution area have been purged and they may be relatively self-fertile. Altogether, most conifers studied so far display high rates of outcrossing and large genetic diversity among individuals in populations. Conifers have never been found to have self-incompatibility mechanisms as such to prevent self-fertilization, but incompatibility does exist to some extent between even closely related species.

Angiosperms

Broadleaved trees are representatives of flowering plants, which are younger than conifers from the evolutionary point of view. Diversity is characteristic of broadleaved trees when compared to conifers. An estimate of species is 25 000, all belonging to the group dicotyledons. The number of genera is in the thousands, and numerous families include trees. Often there are both herbaceous and woody plants in the same genus. In fact there are probably still numerous broadleaved tree species undiscovered, especially in tropical forests. On the other hand, the components of the genetic system have been investigated only in relatively few species. The commercially important species of the temperate and boreal zones are fairly well known, but many basic features of flowering biology and cytology of most species are unknown.

The chromosomes of broadleaved trees are very small, which does not mean that they contain less genetic information than the large chromosomes of conifers. The minute size causes problems in cytological studies. Even the counting of the exact number is tedious, and a detailed survey of meiosis is most difficult.

The chromosome numbers vary widely. This is not surprising because the group consists of various taxonomic categories. Polyploidy has played an important role in species formation, and different levels of ploidy are found even within one genus (e.g., *Betula*). Sometimes the geographical races of one species can have different levels of ploidy. In any case, the chromosome numbers are large enough to produce a large number of chromosome recombinations in meiosis (**Figure 2b**).

Flowering biology and pollination mechanisms are extremely diverse. The wind-pollinated species of the temperate and boreal zones have rather similar pollination to that of conifers. Where the pollen vectors are animals, the pattern is highly variable. Most of these tree species grow in mixed forests and do not occur in stands or even groves but as scattered individuals. In general, animals do not carry pollen over such long distances as wind does. Thus gene flow through pollen migration tends to be lower than in wind-pollinated species. On the other hand, fruit and seed may be dispersed by animals or float on water over considerable distances.

The structure of the gynoecium of angiosperms facilitates the functioning of incompatibility mechanisms. Outcrossing tree species have self-incompatibility, and interspecific incompatibility very often prevents the germination of foreign pollen grains.

Conclusion

The life-form and strategy of forest trees is typically coupled with high degrees of heterozygosity and potential to produce broad genetic variation in the offspring. The genetic system of successful species must have met this requirement. These features of the genetic system appear to have been crucial to the long-term success of forest tree species. The profuse production of pollen and seed becomes understandable against this background.

A sound knowledge of the structure and functioning of the genetic system of trees not only helps to understand trees' life but it is also essential when planning the management of genetic resources. This applies especially to all efforts to conserve genetic resources and to maintain genetic diversity of forest trees. Even though many species are capable of vegetative regeneration, e.g., coppicing or root suckers, sexual reproduction is essential and outcrossing seems to be the predominant mating pattern. Therefore, in addition to a sufficient number of trees to sample an adequate proportion of the gene pool, the requirements of the functioning of the genetic system deserve attention. As regards wind-pollinated species the stands should be fairly large and separated from undesirable pollen sources. In any case of animal pollination the pollen vector should be known, too, and its environment be maintained.

See also: **Ecology**: Reproductive Ecology of Forest Trees. **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Forest Genetics and Tree Breeding; Current and Future Signposts.

Further Reading

Burley J and Styles BT (eds) (1976) *Variation, Breeding and Conservation of Tropical Forest Trees*. London: Linnean Society.
Frankel R and Galun E (1977) *Pollination Mechanism, Reproduction and Plant Breeding*. New York: Springer-Verlag.
Hattemer HH and Melchior GH (1993) Genetics and its application to tropical forestry. In: Pancel L (ed.) *Tropical Forestry Handbook*, pp. 333–380. New York: Springer-Verlag.
Hayward MD, Bosemark NO, and Romagosa I (eds) (1993) *Plant Breeding: principles and prospects*. London: Chapman & Hall.
Koski V (1970) A study on pollen dispersal a mechanism of gene flow in conifers. *Communicationes Instituti Forestalis Fenniae* 70.4: 1–78.
Koski V (1973) On self-pollination, genetic load, and subsequent inbreeding in some conifers. *Communicationes Instituti Forestalis Fenniae* 78.10: 1–42.
Mandal AK and Gibson GL (eds) (1998) *Forest Genetics and Tree Breeding*. New Delhi: CBS Publishers.
Owens JN (1993) Pollination biology. In: Bramlett DL, Askew GR, Blush TD, Bridgwater FE, and Jett JB (eds) *Advances in Pollen Management*, Agriculture Handbook no. 698, pp. 1–13. Washington, DC: US Department of Agriculture Forest Service.
Owens JN and Blake MD (1985) *Forest Tree Seed Production: A Review on the Literature and Recommendations for Future Research*. Petawawa National Forest Institute, Canadian Forestry Service.
Rehfeldt GE and Lester DT (1969) Specialization and flexibility in genetic systems of forest trees. *Silvae Genetica* 18(4): 118–123.
Sarvas R (1962) Investigations on the flowering and seed crop of *pinus silvestris*. *Communicationes Instituti Forestalis Fenniae* 53: 1–198.
Stebbins GL (1950) *Variation and Evolution in Plants*. New York: Columbia University Press.
Stebbins GL (1974) *Flowering Plants: Evolution above the species level*. Cambridge, MA: Harvard University Press.
Sybenga J (1992) *Cytogenetics in Plant Breeding*. New York: Springer-Verlag.

Quantitative Genetic Principles

R D Burdon, New Zealand Forest Research Institute Ltd, Rotorua, New Zealand

Introduction

Response to selection is the basic prerequisite for successful genetic improvement. Within a species, the entities that are selected can be populations (or provenances) or individuals that can be used as seed parents or as clones for mass propagation. Where selection of individuals is involved the genetic improvement amounts to breeding, in which cumulative genetic gain is sought over successive generations. Efficient breeding is dependent on an understanding of the factors governing response to selection, in both the short term and the long term. Prediction of response can indicate what genetic gain is achievable and, when applied to alternative selection scenarios, it can be used to indicate how best to achieve the gain.

The classical tool for predicting response to selection, and optimizing various selection procedures, is quantitative genetics. This is based upon a model of individual gene action. It embodies the neo-Darwinian synthesis, which reconciles the usual pattern of continuous variation with Mendel's discovery that units of heredity represent discrete factors. Practical implementation is usually based on assuming that each trait is controlled by large numbers of genes ('polygenes'), each of very small effect, at widely dispersed sites or loci in the genome. This treatment will often be a major oversimplification of reality. Nevertheless, it is typically a powerful and remarkably robust framework for predicting response to selection and illustrating various guiding principles.

After a basic exposition of the genetic model, important topics are:

- how response to selection is governed by the different parameters, which need to be known at least reasonably well
- how the same principles can be extended to responses to progeny testing
- the factors governing the efficiency of various forms of indirect selection for breeding goals
- how the principles can be applied to multitrait selection
- how genotype × environment interaction can affect response to selection, appropriate structuring of a breeding program, and appropriate deployment of genetic material
- factors governing longer-term response to selection, as opposed to short-term, which need to be considered in structuring populations.

Complementary information needed by the breeder (but often very imperfectly known) includes the cost structures for the various breeding operations, and the economic worth functions for metric values of various traits. Such information allows efficient allocation of effort, and enables the breeder to decide on the appropriate emphasis to place on different traits.

The principles are far from specific to forest tree breeding, but certain features of forest tree breeding, notably the amount of physical resources entailed, have favored much explicit use of the quantitative genetic model.

The Basic Model

It is appropriate to state the basic role of genetic influences in governing the phenotype (P), the phenotype being the tree as one sees it and can measure it for any particular trait. We have the relationship

$$P = G + e = A + NA + e$$

where G denotes the effect of the genotype, and e denotes the effect of the environment. The latter is typically a local environmental effect, e.g., an effect of poor planting of the individual tree or a patch of ground with missing topsoil, as opposed to measurable effects of the general environment.

It can be seen that G has two components: (1) A, which results from additive gene effects, whereby offspring tend to be intermediate between their parents, and which are the effects that form the basis of cumulative genetic gain over generations, and (2) NA, which results from nonadditive gene effects, whereby offspring tend to depart from intermediacy between their parents, and which cannot be recaptured and accumulated over successive generations. Such effects can include dominance of expression of one allele over another at a single locus, or epistasis, whereby the effect of one allele at a locus can be conditional upon what allele(s) is/are represented at one or more other loci.

Note that $A/2$ represents the general combining ability (GCA) of the parent when it is crossed with the rest of the population to produce a half-sib family.

Complications that can arise, but are generally disregarded here, are epigenetic effects. Such effects can often masquerade as true genetic effects. They can include maternal effects which, in the case of seed-weight effects, are usually transient. However, clonally propagated material is subject to 'C-effects,' which typically reflect the state of the material at time of propagation and often can be erased only by sexual reproduction (seed production).

Key Genetic Parameters

Variances In terms of variances (which represent the squares of standard deviations, and for which usual notation is either V or σ^2), the basic model means that

$$\sigma_P^2 = \sigma_G^2 + \sigma_e^2 = \sigma_A^2 + \sigma_{NA}^2 + \sigma_e^2$$

where σ_P^2 is the phenotypic variance, and so on.

Heritability Heritability, the percentage of phenotypic variance that is heritable, is a key parameter, with bounds 0 and 1. It has two forms:

- narrow-sense, given by the ratio σ_A^2/σ_P^2, and usually denoted h^2, which is applicable to propagation by seed
- broad-sense, given by the ratio σ_G^2/σ_P^2, and usually denoted H^2 ($\geq h^2$), which is applicable to mass propagation of selected clones.

A heritability is specific to a trait, and, in some measure, to the population and the macroenvironment (e.g., site). Narrow-sense heritabilities tend to be low (0.2 or less) for growth rate traits, but much higher (≥ 0.5) for wood properties.

Genetic correlation A genetic correlation (denoted r_A or r_G) between traits is a measure of the degree of common genetic control for the two traits concerned. Its bounds of 1 and -1 relate to complete common control to perfect inverse control respectively. Genetic correlations, if they are adverse, impose severe constraints on the genetic gain that is simultaneously achievable in the traits concerned. Common examples of adverse correlations in forest trees include wood density and diameter growth, or growth potential and hardiness. On the other hand, favorable or even neutral genetic correlations can provide major opportunities for the breeder.

Some Simple Expectations

Assuming the usual quantitative genetic model of polygenic control we have the following expectations for composition of variances (ignoring certain minor components of nonadditive gene effects):

- among half-sib families (each parent in question mating with a random sample of a large population) $-\frac{1}{4}\sigma_A^2$; this amounts to GCA variance
- within such families $-\frac{3}{4}\sigma_A^2 + \sigma_{NA}^2 + \sigma_e^2$
- among full-sib families (crosses between random pairs of parents) $-\frac{1}{2}\sigma_A^2 + \leq\frac{1}{4}\sigma_{NA}^2$
- within such families $-\frac{1}{2}\sigma_A^2 + \geq\frac{3}{4}\sigma_{NA}^2 + \sigma_e^2$.

Note: It is very convenient for forest geneticists and tree breeders that, with pollination by wind, seed collections from individual trees often approximate closely to half-sib families.

Thus a heritability (or repeatability) of half-sib family means (h_{HS}^2), with n individuals per family, is given by:

$$h_{HS}^2 = \tfrac{1}{4}\sigma_A^2/[\tfrac{1}{4}\sigma_A^2 + (\tfrac{3}{4}\sigma_A^2 + \sigma_{NA}^2 + \sigma_e^2)/n]$$

Intercrossing among parents can be done in a range of systematic mating designs, which almost all give some forms of both half- and full-sib family information.

Applying the same approach to heritability of clonal means (H^2_C), we have the expectation

$$H^2_C = \sigma^2_G/(\sigma^2_G + \sigma^2_e/n)$$

which will tend to be much higher for given n than h^2_{HS}, illustrating how clonal material can give information with a much better signal-to-noise ratio than seedling families.

Also of interest is the variance attributable to interaction between parents, reflected in the component of family performance that cannot be predicted from the additive genetic merit or GCA values of the two parents; such variance is specific combining ability (SCA) variance, of composition $\leq 1/4\sigma^2_{NA}$.

Response to Selection

Direct Selection

For a single trait, expected response to selection (E(R)) is the product of selection differential (D) which is the difference between the mean for the selected individuals and that of the population from which they are selected, the heritability (h^2, or H^2 for clonal selection), and the phenotypic standard deviation (S), such that:

$$E(R) = D \times h^2 \times S$$

If the distribution is normal, such that equal (or symmetrical) responses can be expected to equivalent selection for high or low values of the trait, D can be expressed in terms of number (i) of phenotypic standard deviations of the population in which selection is done. Thus

$$D = i \times \sigma_P$$

The formula for expected genetic gain (E(R)) can be expanded and manipulated into various forms, but the following features may be noted:

1. If h^2 is low, with σ^2_e fixed and large, gain will vary in proportion to σ^2_A.
2. If σ^2_A (or σ^2_G) is fixed, but h^2 varies through variation in σ^2_e, E(R) will vary in proportion to h, and will therefore be reduced far less than in proportion to an associated drop in h^2 (σ^2_e may be inflated by measurement error).
3. While i (number of phenotypic standard deviations, or selection intensity) always increases as the number screened for each one saved increases, it does so non-linearly, according to the law of diminishing returns (**Table 1**).

Table 1 Selection intensity (standardized selection differential, or *i*) in relation to number screened per individual saved, for global proportion and within finite subgroups

Trees screened per tree saved	*Global proportion*		*Finite subgroups*
	i	*Marginal* i *per tree screened*	i
2	0.798	0.399	0.564
5	1.400	0.201	1.163
10	1.755	0.071	1.539
100	2.665	0.010	2.542
1000	3.367	0.000 78	3.241
10 000	3.958	0.000 068	3.852
100 000	4.479	0.000 0058	4.384
1 000 000	4.948	0.000 000 052	4.863
10 000 000	5.380	0.000 000 004 8	5.301

4. If selection is done within finite subgroups (e.g., the best out of every two individuals instead of the top 50% of a very large population), i is less, especially when the subgroups are small (**Table 1**).
5. Percentage gain obtainable is dependent on the coefficient of variation (phenotypic standard deviation divided by population mean) as well as i and h^2.
6. If, with cost constraints, there is a choice between screening more trees cheaply or fewer trees thoroughly, there is effectively a trade-off between i and h^2.

Indirect Selection

It is often possible to select for a 'target' trait (y) that represents part or all of a breeding goal by using another ('index') trait (x) as a proxy, in what is termed indirect selection. Examples may include stem volume as y and stem diameter as x, or a mechanical property of wood as y and wood density as x, or else harvest-age performance as y and early performance as x, or even a DNA marker or an identified gene (x) that is strongly associated with desirable expression of a trait (y).

For indirect selection to be more efficient than direct selection there must be at least a fairly strong genetic correlation between the target and index traits. Other conditions, of which one or more needs to be met are:

- markedly higher heritability for the index trait than for the target trait, either as an inherent heritability or through more precise measurement
- much cheaper determination of the index trait, allowing more intensive selection than is possible with direct selection

- earlier expression of the index trait, allowing a shorter generation interval and thence more rapid gain per unit time.

The roles of these conditions are illustrated by the equation for the relative efficiency of indirect selection E(*x*/*y*) compared with direct selection. In a single generation it is given by

$$E(x/y) = (i_x/i_y)(h_x/h_y)r_{G_{xy}}$$

where i_x and i_y denote the intensities of selection achieved for the respective traits, h_x^2 and h_y^2 are the corresponding heritabilities, and $r_{G_{xy}}$ is the genetic correlation between the two traits.

Multiplying the right-hand side by the ratio t_y/t_x, for the generation intervals under the two forms of selection, gives E(*x*/*y*) in terms of gain per unit time.

Cases of indirect selection with forest trees include using wood density, which is usually very heritable yet not very expensive to determine, as the selection criterion where strength and/or side hardness may figure in the underlying breeding goal. In the case of *Pinus radiata*, selecting for closely spaced branch clusters, a highly heritable feature, has been used as a selection criterion to control branch size which is very subject to environmental influences. DNA markers will have the advantage of perfect heritability and can be determined very early in the life cycle, but may not be well correlated genetically with the trait of interest. Efficient early selection is very widely sought with forest trees.

Using Information on Relatives

Progeny Testing

The essence of progeny testing (and clonal testing) is to improve the effective heritability. Selection wholly on progeny test results, which often amounts to reselection of parents, can be termed backwards selection. For instance, with half-sib families, the heritability of family means (formulated above), will increase with the number of individuals per family. However, the number of parents, will be limited by the number of selections made from the preceding generation. This will often impose a practical constraint on i, even though trading off smaller family size and thence lower h_{HS}^2 for higher i may have a theoretical advantage.

Note that gain expected from selection on half-sib family information for seed orchards has a coefficient of 2 inserted in the adapted form of the equation for response to selection; this is to take account of the fact that both pollen and seed parents will be selected.

More General Use of Information on Relatives

Selection purely on the basis of progeny test performance is a special case of using information on relatives, in this case placing 100% reliance on information from offspring. It is in principle possible to use information from almost any class of relatives, including parents and siblings in selecting individual offspring. A simple but common case in forest tree breeding is selecting individual offspring on both sib-family and individual information, weighting individual information heavily if heritability is high and family information heavily if heritability is low, in a combined family-plus-individual selection index.

Information from multiple classes of relatives, with varying representation of relatives among candidates, can be used to estimate the genotypic merit of candidates by best linear unbiased prediction (BLUP).

Genotype × Environment Interaction

This phenomenon represents differential performance of genotypes with respect to each other in different environments. To accommodate it, the basic genetic model can be expanded to:

$$P = G + E + GE + e$$

where E is the effect of the macroenvironment (e.g., a site category), which can be allowed for, and GE is the genotype × environment interaction.

The interaction can have two components: that tending to cause changes in genotypic ranking among environments (which is usually of prime interest), and that reflecting differential expression of genetic difference among the environments. As above, G is composed of $A + NA$, and (in principle, at least) GE of $AE + NAE$.

Applying this extended model to variance components, and partitioning off macroenvironmental effects, we have

$$\sigma_P^2 = \sigma_G^2 + \sigma_{GE}^2 + \sigma_e^2 = \sigma_A^2 + \sigma_{NA}^2 + \sigma_{AE}^2 + \sigma_{NAE}^2 + \sigma_e^2$$

where $\sigma_G^2 + \sigma_{GE}^2$ denotes σ_G^2 and $\sigma_A^2 + \sigma_{AE}^2$ denotes σ_A^2, within a single site.

Hence the heritability (narrow-sense) for selecting an individual for performing in its particular environment is given by

$$h^2 = \sigma_A^2 + \sigma_{AE}^2/(\sigma_A^2 + \sigma_{AE}^2 + \sigma_e^2)$$

Deleting σ_{AE}^2 from the numerator gives the heritability for selecting the individuals for performing across the various environments. Substituting

$\sigma_G^2 + \sigma_{GE}^2$ for $\sigma_A^2 + \sigma_{AE}^2$ gives H^2. This extended model can readily be applied to expected response to selection.

It may be noted that the ratio $\sigma_A^2/(\sigma_A^2 + \sigma_{AE}^2)$ is actually a genetic correlation between the performance from one environment to another, if corresponding variances are all expressed equally in all the environments. Such a correlation can be calculated either for a set of environments, or between a pair of environments. A favorable test environment is one that shows both high genetic correlations for tree performance with other important growing environments and a high heritability.

There are important implications for whether or not to institute regional subdivisions in a breeding program. Key points are:

1. A high ratio σ_{AE}^2/σ_A^2 favors regionalization, particularly if fairly discrete site categories can be identified.
2. However, even with quite substantial interaction, if progeny testing can be well spread across environments it may be possible to produce a set of selections that are near-optimal for all the individual environments.
3. That said, failure to screen in an environment that is strongly interactive with respect to the others can sacrifice much potential gain in that environment.

Genotype × environment interaction is the subject of a voluminous literature. Much of that, however, focuses on characterizing the interactive behavior of specific plant genotypes (which are often cultivar varieties). For forest tree breeding, the main interest often lies in the roles of environments in generating interaction.

Multitrait Selection

Selection for more than one trait usually dilutes the gains obtainable for individual traits (**Table 2**). However, if several traits are uncorrelated but of equal economic worth and equal heritability, it may be better to spread the selective effort among several traits, especially if large numbers of candidates can be easily screened for each of several traits. This is also illustrated in **Table 2**. In practice, traits will differ markedly in heritability, economic worth, and cost of evaluation per individual, which means that selection needs to be focused on just a very few key traits.

Table 2 Selection intensities (standardized selection differentials, or *i*), for varying numbers of individuals screened for each one saved, assuming either a single trait or three uncorrelated traits for selected at equal culling rates. All cases relate to selection within single large population

Trees screened per tree saved	i		
	Single trait	*Three traits*	
		Per trait	*Summed over traits*
8	1.65	0.798	2.39
30	2.22	1.114	3.34
125	2.72	1.400	4.20
1000	3.37	1.755	5.26
1 000 000	4.95	3.367	10.10

Genetic correlations between traits are crucial. Adverse correlations, if strong, severely restrict the gains that can be achieved simultaneously in the traits concerned. In forest tree breeding such correlations may exist between growth potential and hardiness, or between wood density and stem volume production. Conversely, if intercorrelations are favorable, selecting for additional traits may dilute gains achievable in individual traits little if at all.

Four ways of selecting for multiple traits in any one generation are:

1. Independent culling levels, setting thresholds of acceptability for each trait.
2. Sequential culling (sometimes called tandem selection), first for one trait and then another, and so on. This may be cost-efficient if evaluation costs differ widely among traits, so one might, for example, select first for stem diameter and only then evaluate wood properties and cull for them.
3. Tandem selection which, in the true sense of the term, involves selecting for different traits in successive generations. For forest tree breeding, deliberate adoption of this method from the outset is unlikely to be realistic, although elements of it may be practiced as a fortuitous result of changed perceptions of breeding goals.
4. Multitrait index selection, attaching weights to the values for individual traits, like the partial regression coefficients in multiple regression. Thus an indifferent ranking for one trait may be offset by a candidate being outstanding for one or more other traits. Various bases exist for weighting. A theoretical optimum takes account of economic weights of the respective traits and variance–covariance matrices that encapsulate the heritabilities of all traits and all the phenotypic and genotypic intercorrelations among those traits. There can thus be elements of both direct and

indirect selection. In practice, this optimality depends on various assumptions, notably concerning cost structures and the quality of the information on heritabilities and all the intercorrelations between traits. Various modifications of the multitrait selection index are possible, including use of elements of independent culling levels, and setting restrictions on expected gains in one or more traits.

In fact, it is possible in principle to combine multitrait information with information from various classes of relatives, and unequal representation of relatives among the candidates, to obtain a multitrait BLUP solution.

Long-Term Gain

Assuming polygenic control, pair-crosses will continue to show genetic segregation, each containing roughly half the base population additive genetic variance. This segregational variation is expected to persist over generations, although it will decay over time, especially if populations are small and/or selection is intense, but it will tend to be replenished by mutation. It is the key to cumulative genetic gain over generations of crossing and selection, which lead to increases in frequencies of favorable genes (alleles) at the various loci. Some genes of quite large effect can be present without causing behavior that is obviously different from that expected with polygenic inheritance. However, the use of DNA technology to recognize such genes offers greater selection efficiency.

Initial response to selection will involve mainly the loci of intermediate gene frequencies, which contribute most to expressed genetic variation. If favorable alleles approach 100% frequencies at such loci, these loci will contribute little to continued genetic gain. However, initially rare favorable alleles at other loci may increase in frequency to the point where they become the prime basis of response to selection.

There are some situations where the quantitative genetic model may not suffice for the tree breeder. In breeding for disease resistance there may be genes of large effect, and some can mask the expression of resistance genes at other loci. These genes of large effect need to be recognized and managed carefully, in order to select efficiently and ensure durability of resistance against mutation and genetic shifts in the pathogens. DNA technology offers a general means of recognizing and capturing favorable genes of significant individual effects, thus going beyond the classical polygenic model.

Inbreeding

With normally outbreeding organisms, which include almost all forest trees, the quantitative genetic model may not be straightforwardly applicable when significant inbreeding occurs. With outcrossing, the genetic load, which mainly represents genes that are individually rare but very deleterious in the homozygous state, contributes almost nothing to the expressed genetic variation. Inbreeding, however, allows such genes to be expressed strongly, thus contributing a different element of expressed genetic variation.

See also: **Genetics and Genetic Resources**: Genecology and Adaptation of Forest Trees; Genetic Systems of Forest Trees; Population, Conservation and Ecological Genetics. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts; Genetics and Improvement of Wood Properties; *Pinus Radiata* Genetics.

Further Reading

Baker RJ (1986) *Selection Indices in Plant Breeding*. Boca Raton, FL: CRC Press.

Bulmer MG (1985) *The Mathematical Theory of Quantitative Genetics*. Oxford, UK: Clarendon Press.

Cotterill PP and Dean CA (1990) *Successful Tree Breeding with Index Selection*. East Melbourne, Victoria: CSIRO Publications.

Crow JF (1986) *Basic Concepts in Population, Quantitative and Evolutionary Genetics*. New York: WH Freeman.

Falconer DS and Mackay TFC (1996) *Introduction to Quantitative Genetics*, 4th edn. Harlow, UK: Longman.

Fins L, Friedman ST, and Brotschol JV (1992) *Handbook of Forest Genetics*. Dordrecht, The Netherlands: Kluwer.

Kang MS and Gauch HG (eds) (1996) *Genotype-by-Environment Interaction*. Boca Raton, FL: CRC Press.

Lindgren D and Nilsson J-E (1985) *Calculations Concerning Selection Intensity*. Umeå, Sweden: Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology.

Mrode RA (1996) *Linear Models for the Prediction of Animal Breeding Values*. Wallingford, UK: CAB International.

Namkoong G, Kang H-C, and Brouard JS (1988) *Tree Breeding: Principles and Strategies*. New York: Springer-Verlag.

White TL, Neale DB, and Adams WT (2003) *Forest Genetics*. Wallingford, UK: CAB International.

Population, Conservation and Ecological Genetics

C Mátyás, University of West Hungary, Sopron, Hungary

Introduction

Intraspecific genetic variation is an often overlooked, but none the less essential, biodiversity component of forest ecosystems. Genetic diversity provides the fine-tuning in adjustment to dynamic processes in species and intraspecific competition and determines the pace of adaptation and microevolution on a population level.

Developments in genetic analysis techniques of recent decades yielded an impressive amount of knowledge about reproductive processes in forest tree populations. It turned out that forest trees are unique in their ability to accumulate and maintain exceptionally high levels of genetic variability, compared to other organisms, both plants and animals. Undoubtedly, this strategy must have an evolutionary significance and is related to the long lifespan of trees.

Typically intense gene flow, phenotypic plasticity and other heritable and nonheritable effects contribute to the robustness of tree species, i.e., to their ability to evade genetic degradation and drift even in isolated populations and at low density of occurrence. Nevertheless, genetic analyses also demonstrate effects of human activities on the genetic resources of trees (see **Figure 9**). Silviculture and various indirect environmental loads have some bearing on the genetic make-up of populations. This fact supports the need to include genetic considerations in both sustained management and conservation strategies of forest ecosystems.

Significance of Genetic Regulation in Forest Ecosystems

Living systems have a remarkable ability to maintain and restore their uniqueness and identity under both spatially and temporally changing environmental conditions. Ecosystem stability is largely dependent on biodiversity which is detectable at the three main levels of biotic organization: the landscape (associations), species, and genetic levels. Species diversity is generally perceived as biodiversity *per se*. However, it is within-species genetic diversity that safeguards the adaptability and integrity of individual species. Intermating populations are the basic units of adaptation and evolution. An important task of forest genetics is therefore to understand the complexity of genetic regulation and to detect patterns that give it meaning from the gene to the ecosystem level. Within-species genetic patterns determine the rules for use of forest reproduction material and the strategy of conservation of genetic resources.

Defining and Interpreting Genetic Diversity

Diversity on the genetic level is usually described by the number and frequencies of alleles (different forms of the same gene) per locus in the population or species. Accordingly, two basic components of diversity are the allelic number (A) and the proportion of loci that are polymorphic, i.e., with more than one allele. Polymorphism (P) is expressed as a percentage of all investigated loci. Expected heterozygosity (H_e) is used as the numeric expression of gene diversity within a population or species. Within-species diversity is further characterized by genetic differentiation between populations, i.e., the ratio of variation found among population averages.

Calculation of gene diversity measures At a locus, effective number of alleles: $A_E = 1/\sum p_i^2$

Expected heterozygosity: $H_e = 1 - \sum p_i^2$

Genetic differentiation between populations:

$$G_{ST} = 1 - \frac{H_{eP}}{H_{eT}}$$

where p_i is the frequency of allele i across loci, H_{eP} is the average expected heterozygosity within populations; and H_{eT} is the total expected heterozygosity if all populations are pooled.

Beside gene diversity there are, however, reasons to use a broader definition for genetic diversity. First, the described measures are based on predominantly neutral genetic markers (isozymes, randomly amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFLP), microsatellites) which are chosen for being polymorphic. Yet the key importance of diversity is maintaining adaptability and stability, which are expressed in adaptive (nonneutral) quantitative traits in response to the environment. For trees, it is especially true that there is no expression of genotype without environment. Therefore, genetic diversity in the broad sense also includes quantitative genetic variability, i.e., that part of phenotypic variability which can be identified as genetic, based on quantitative genetic analysis.

Gene diversity characteristics of forest trees Using genetic marker techniques, the genetic structure of species and populations (gene diversity, level of inbreeding, deviations from Hardy–Weinberg equilibria) can be drawn up and used for comparison. Of great practical importance is the distribution of diversity within and between populations and regions. Compared with other organisms, forest trees generally display high heterozygosity (**Figure 1**), reflecting relatively high allele numbers.

Also within the plant kingdom, average polymorphism, allelic number, and heterozygosity of trees are conspicuously high, but among-population genetic differentiation is low (**Table 1**). Weak differentiation in most species with large natural ranges reflects high rates of gene flow in trees. Although the differences in average allele numbers may seem minor, it should be remembered that the potential number of genotypes (G) rises sharply with increasing average allele numbers (A) and number of loci considered (n):

$$G = \left[\frac{A(A+1)}{2}\right]^n$$

Counting with just 10 loci, the difference between annual plants and trees of only 0.2 in A means an increase in potential genotypes from 70 000 to 340 000.

Gene diversity is profoundly influenced by the genetic system (mating pattern, reproductive strategy, genomic organization) of the species and its distribution (e.g., local endemic versus large, continuous). For example, population density of individual species decreases from the boreal zone toward the tropics. With decreasing density, polymorphism and allelic numbers tend to diminish. The effect of evolution, distributional pattern, mating, and reproduction system on species diversity is illustrated by data in **Table 2**. Failing concrete genetic information, likely genetic characteristics of a species may be inferred from these basic relationships.

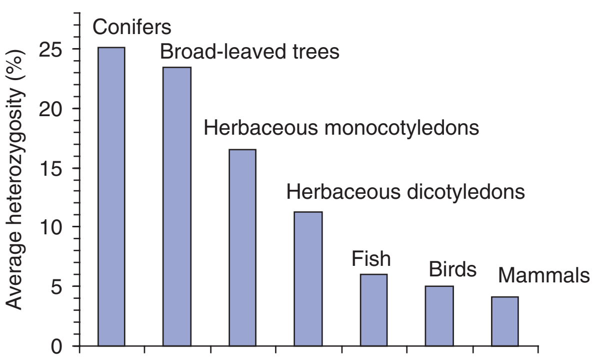


Figure 1 Average heterozygosity (in percent) for some organism groups.

Table 1 Average genetic diversity within species of different plant life forms

Life form	P	A	H_e	G_{ST}
Annuals	49.2	2.02	0.15	0.36
Perennials, herbaceous	43.4	1.75	0.12	0.25
Trees	65.0	2.22	0.18	0.08

Genetic diversity is expressed by the measures polymorphism (*P*), average allele number (*A*), expected heterozygosity (H_e) and genetic differentiation (G_{ST}). For further details, see chapter on defining and interpreting diversity.

Directed and Random Genetic Changes in Large Populations

Owing to various, partly random genetic effects, such as natural selection (i.e., genetic adaptation), mutation, genetic drift, gene flow, or unequal sexual contribution of individuals, allele frequencies change over time, unlike in idealized populations in Hardy–Weinberg equilibrium. In large populations, gene flow and adaptation are the prime forces influencing genetic diversity and intraspecific variability.

Hardy–Weinberg Law

In infinite, random-mating populations, allele and genotype frequencies remain constant from generation to generation in absence of selection, migration, drift, and mutation effects. For two alleles of p, q frequency at a locus, the equilibrium ratio of homozygotic (p^2 and q^2) and heterozygotic ($2pq$) genotypes will be $p^2 + 2pq + q^2 = 1$.

Table 2 Connection between genetic diversity and distribution, density, and mating type in trees

	P	A	H_e	G_{ST}
Type of distribution	***	*	***	*
Endemic	42.5	1.82	0.08	0.141
Medium	55.7	1.87	0.17	0.065
Large	67.8	2.11	0.26	0.033
Zonal occurrence ($\approx$**density**)	**	**	NS	
Boreal (high)	82.5	2.58	0.21	
Temperate (medium)	63.5	2.27	0.17	
Tropical (very low)	57.9	1.87	0.19	
Mating type, vector	***	**	***	NS
Selfing	11.0	1.15	0.02	—
Allogamous/animal	63.2	2.18	0.21	0.099
Allogamous/wind	69.1	2.31	0.17	0.077

Statistical significance (probabilities of zero difference) of differences within subcolumns indicated as follows: * 5%, ** 1%, *** 0.1% probability; NS, nonsignificant. For explanation of letters in table heading, see **Table 1**. Compiled from data of 191 tree species. The calculation is based on the assumption that the population is in Hardy–Weinberg equilibrium.

Gene Flow

Gene flow describes the spatial movement of genes, typically through seed and pollen dispersal, either within a population or between separated stands. (An alternative term, 'migration,' is reserved here for shifts in time of the geographic range of species or populations.) Wind-pollinated species, producing abundant pollen, such as most temperate forest trees, show major gene flow. In favorable weather, pollen clouds may travel hundreds of kilometers and contribute significantly to local pollination (**Figure 2**).

Animal-pollinated (mostly tropical) tree species depend on the movement of their pollen vectors. Investigations have shown pollen transport of several kilometers and medium-level gene flow between trees and stands. The very rare apomictic and self-pollinating tree species show the lowest gene exchange rate.

The evolutionary and practical significance of gene flow is high. Its function is to counter genetic drift (random fluctuations in allele frequencies) within the range, to disperse fitness-improving mutant alleles, to maintain high levels of genetic variation and adaptability, and to avert inbreeding in fragmented populations. Gene flow has therefore a decisive role in shaping within-species genetic variation patterns (**Table 2**), and consequently influences appropriate strategies for forest reproductive material use and conservation.

Natural Selection, Adaptation

The prerequisite of the selective force described by Darwin and Wallace is easily visible in forests, namely conspicuous differences between individual trees in competitive and reproductive ability, the two key components of fitness. Natural selection acts through higher mortality and fewer offspring of less-fit individuals. Consequently, the gene pool of the next generation will be selected for greater fitness.

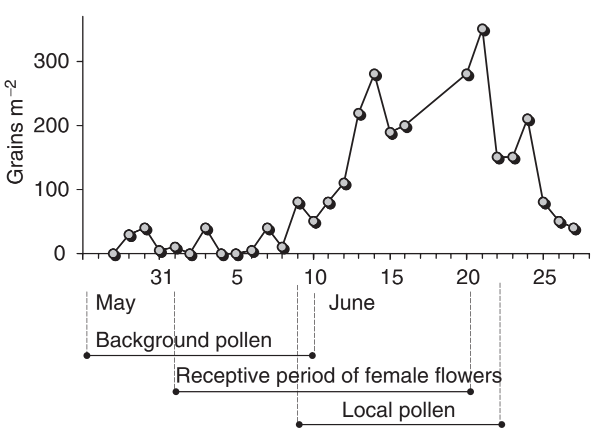


Figure 2 Density (grains m^{-2}) of pollen in a Scots pine seed orchard. Fifty percent of the female strobili was receptive before the appearance of local pollen. Reproduced with permission from Lindgren D, Paule L, Xihuan S, *et al.* (1995) Can viable pollen carry Scots pine genes over long distances? *Grana* 34: 64–69.

The shift in genetic variability tends to change the population profiles and over several generations may lead to evolution. Darwinian natural selection is an important, although not exclusive, driving force of evolution, as random effects play an important role too.

Genetic adaptation and fitness While natural selection explains the 'statistical' aspect of selection, adaptation describes the sum of biological processes that safeguard the survival of the population under constantly changing conditions. Some of these mechanisms are nonheritable.

Genetic adaptation operates on populations through fitness selection. Fitness encapsulates the differential effect of many traits expressed during the life cycle. The selective value of individual traits depends on the actual environment, which can change constantly. In environments influenced by humans, e.g., in managed forests or plantations, fitness will be modified (cultivation- or domestic fitness).

Fisher's fundamental theorem of natural selection postulates that the increase of average fitness ($\Delta\bar{W}$) is a function of the average relative fitness of the parent population ($\bar{W}$) and the within-population additive genetic variance (V_W):

$$\Delta\bar{W} \approx \frac{V_W}{\bar{W}}$$

i.e., progress of natural selection depends on adaptedness ($\bar{W}$), and adaptability of a population depends on the available genetic variance – if genetic variability is depleted, adjustment to a changed environment becomes difficult or impossible (**Figure 3**).

The consequences of reduced genetic diversity on adaptability on species level can be illustrated by the examples of two contrasting boreal pine species, jack pine (*Pinus banksiana*) and red pine (*P. resinosa*), which have similar life histories and ecological niches in boreal forests of eastern North America. While the former displays very broad genetic variability, the latter seems practically devoid of diversity. Regarding distributions, red pine has only restricted, fragmented occurrences and is becoming rare in certain areas, while jack pine is the dominant species in many forest associations. The difference in distribution pattern may be attributable to the loss of diversity in red pine, probably through 'genetic bottlenecks' of glacial periods.

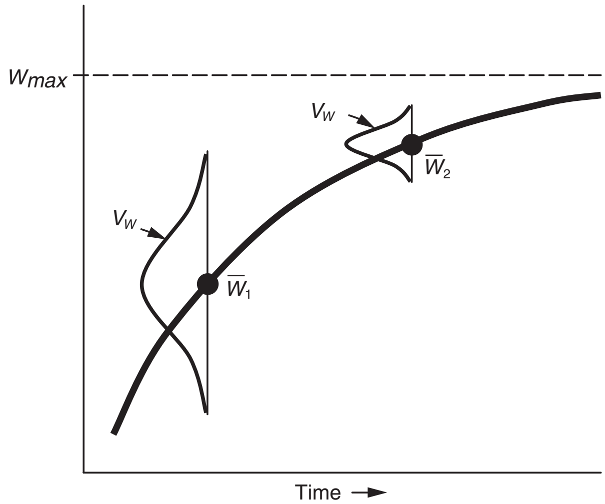


Figure 3 Improvement of the fitness average of populations over time in a theoretical niche. The progress of population 1 is slower toward the fitness maximum (W_{max}), because its genetic variability is smaller, and its average fitness is closer to the maximum. Population 2 has a larger genetic load (L), but also the selection pressure is stronger. In practice, the progress is not very effective owing to environmental fluctuation and heterogeneity, resulting in ever-changing fitness optima. The precondition for the improvement of fitness is sufficient genetic variability!

Variation in Reproductive Fitness: Unequal Sexual Contribution of Individuals

Differences between genotypes in flowering and seeding vary over 10-fold, even among dominant trees in a forest stand. Owing to unbalanced flowering and seeding, neither natural regeneration nor the seed crop collected in a stand or in a seed orchard is genetically identical to the gene pool of the parents. Many genotypes contribute insignificantly to the next generation. The top quartile of genotypes may be represented in over two-thirds, and the bottom quartile in less than 3% of the progeny. Therefore the effective population size (N_e) is usually far smaller (by roughly an order of magnitude) than the total number of individuals, and can be calculated for a monoecious species from the reproductive contribution of each individual (W_i):

$$N_e = \frac{1}{\sum(W_i^2)}$$

Effectiveness of Fitness Selection in Natural Populations

The effect of fitness selection on individual traits depends strongly on both the (adaptive) importance of the trait for total fitness (e.g., budbreak timing versus leaf morphology) and on the simplicity of the traits' inheritance. Rapid adaptation could be demonstrated, e.g., in 'industrial melanism' in various insect species, or in heavy-metal tolerance in grasses growing on mine spoils. In trees, diversity patterns of adaptive traits indicate more gradual adaptive shifts.

Constraints on 'Perfect' Adaptation

The idea of perfectly adapted natural populations is a widespread misconception. There are several genetic reasons why 'perfect' adaptation is impossible, such as:

- genetic interdependence of traits, making simultaneous adaptive shifts relatively slow
- polygenic inheritance of quantitative traits, preventing ready fixation (attaining 100% frequency) of favorable alleles
- trade-offs between reproductive and vegetative traits in contributions to fitness, which maintain a conspicuous variation of reproductive ability within populations
- environmental heterogeneity and fluctuations (on the life-cycle scale of trees, the changes are two orders of magnitude faster than for annual plants)
- gene flow: the more continuous the distribution, the stronger the effects to limit differentiation between populations
- biotic complexity: e.g., long-term competition, and spasmodic epidemics of pests and diseases, which point toward evolutionary complexity rather than toward precise adjustment to local conditions.

Adaptation lag can be demonstrated in comparative experiments, where populations of local origin often show less adaptedness than introduced ones.

Local Patterns Arising from the Balance of Gene Flow and Adaptation

Genetic neighborhoods are intermating groups of related individuals within larger populations. The size and even the existence of such neighborhoods depend on the sexual system and dispersal pattern of the species. In outcrossing, wind-pollinated species, occurring at high density, neighborhoods cannot readily develop. In some species with more restrictive sexual systems (e.g., mixed-mating eucalypts) neighborhoods are much more extensive than usually suspected (**Figure 4**).

The balance of gene flow and adaptation forms adaptively homogenous areas (AHAs) within the species, which should serve as a basis for seed and conservation zones. Within the AHAs populations vary little in adaptive features. Owing to gene flow, AHAs are much larger than selective environments with roughly uniform ecological conditions.

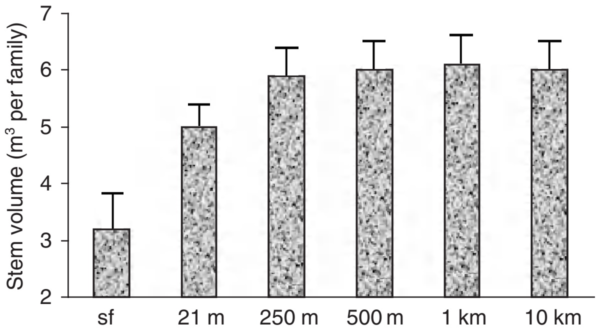


Figure 4 Average stem volume of 4-year-old progenies of a selected tree of *Eucalyptus globulus* from controlled crossings (*sf*., selfed). The crossing partners were chosen at various distances (horizontal axis) from the subject tree. The poorer performance from pollination by closer neighbors is probably caused by inbreeding depression, which indicates the existence of genetic neighborhoods in this species. Reproduced from Hardner CG, Potts BM, and Gore PI (1998) The relationship between cross success and spatial proximity of *Eucalyptus globulus* parents. *Evolution* 52: 2, 614–618.

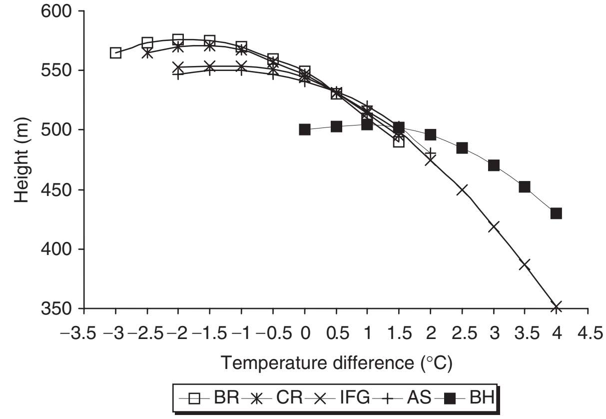


Figure 5 Response regressions calculated for 12-year height of *Pinus ponderosa* progenies in five Californian tests (different plotting symbols). The horizontal axis shows differences in average temperature between the original and the test site (0 means local). Almost without exception, populations transferred from warmer environments performed better.

Nonheritable Ways of Adaptation

Phenotypic Adjustment

A genotype may grow and develop in different ways, in interaction with the environment, resulting in the actual phenotype. The change of the phenotype of a population or an individual genotype may be plotted along site factor gradients. Genotypes clearly vary in their phenotypic responses to environment, and this is termed genotype-× environment interaction. (Naturally, the ability itself is genetically determined.) Populations or genotypes maintaining their relative performance (relative to a standard genotype or experimental average) across sites are considered phenotypically stable and, if inherently productive, are highly desirable.

Genetic Imprinting

Genetic regulational changes triggered by environmental signals that lead to persistent phenotypic change are termed genetic imprinting or epigenetic effects. Indications that epigenetic effects may contribute across generations to the phenological and growth differentiation of populations in different environments were recently traced in certain boreal conifer species. The extent and inheritance of this effect in trees are still unexplored.

The importance of nonheritable adaptation is that it allows adjustment to the environment by reducing the role of natural selection; this offers a saving of resources and of response time. Nonheritable adaptation 'masks' the true genotype and contributes therefore to the maintenance of a broader adaptability.

Intraspecific Genetic Variation Patterns

Large-Scale Adaptive Geographic Variation

Provenance research, which has a tradition of more than a hundred years of study in forestry, has revealed a clear geographic differentiation between populations for adaptive traits in widely distributed species. Provenance is a population originating from a defined geographic location or area.

Clinal variation Genetic variation showing gradual trends linked to ecological gradients is termed clinal. In continuously distributed, wind-pollinated species clinal variation is caused by gradually changing selection effects despite gene flow, leading to gradual allele frequency changes; however, a gradual allele frequency trend itself may also reflect gene flow effects. In temperate species, variations in daylength and temperature cause latitudinal clines in stem form, phenology, and growth potential. In temperate pines, for example, southern origins exhibit faster growth, extended vegetation period, longer needles, but poorer stem form than northern ones. Particularly steep clinal variation may occur on mountain slopes. Significant differences appear over altitudinal differences of only 200–300 m (at high elevations, even less). Such differentiation tends to be weaker in broad-leaved than in coniferous species (**Figure 5**).

Ecotypic variation An ecotype is a population adapted to local site (usually edaphic) conditions that occur in patches rather than in gradients. Traditionally, within-species genetic variation is considered by most silviculturists as ecotypic. However, site differences seldom exert enough selection pressure to override gene flow. Accordingly, there are very few proven cases of ecotypes in forest trees. Their existence may be restricted to species with minimal gene flow between populations (**Table 2**). European ash (*Fraxinus excelsior*), for example, occupies conspicuously different habitats. Still, even thorough field tests could not reveal any clear genetic differentiation between populations of 'water ash' of the floodplains and 'lime ash' of dry, calcareous mountain ridges.

Nonadaptive Geographic Variation

Racial differentiation Historical fragmentation of species ranges during Ice Ages (and associated migration) affected the genetic diversity of species, causing genetic bottlenecks, as mentioned for *Pinus resinosa*. For many others (e.g., beech or firs) the loss of alleles along the migrational route could be demonstrated. In many cases migration and isolation have led to fragmentation and strong within-species differentiation and even speciation. The effect of the migrational past persists especially on neutral loci (**Figure 6**). These patterns reflect combinations of adaptive and random effects and therefore have limited or no ecological significance. This variation is therefore not ecotypic and should be better termed racial.

Polymorphism

Phenotypic (quantitative) polymorphism A well-known feature of many forest trees is the broad variation of traits and the parallel presence of alternative phenotypes (morphs) in the population. Some of these have clear ecological-adaptational significance (early- or late-flushing, branching types), while others obviously not (cone scale form, male flower color in conifers). Ecologically relevant differences between populations can be expected only for traits of adaptive value (**Figure 7**).

Polymorphism at genetic marker level In contrast to quantitative traits, most of the marker-allele polymorphism of forest trees exists within populations. In widespread species, differentiation between populations (G_{ST}) seldom exceeds 4–5%. Exceptions are species with fragmented or dispersed distribution (e.g., *Pinus radiata* isozymes: 16%), and some tropical forest trees of low density (<1 flowering tree ha^{-1}; e.g., *Cavanillesia platanifolia*: 26%). Obviously, an adaptive geographic variation pattern, as is observable with quantitative traits, is seldom evident in genetic markers. This phenomenon raises the question of interpreting results of genetic marker analysis. From the neutralist viewpoint, gen(et)ic diversity at the marker level is held in equilibrium by mutation and genetic drift. The selectionist interpretation maintains that frequency differences have selective value; even neutral alleles may mark adaptive effects if genetically linked to loci of adaptive significance.

In fact, for a few izozyme systems the selective value of alleles could be proven. For example, the B_1 allele of the enzyme gene *IDH-B* (isocitrate

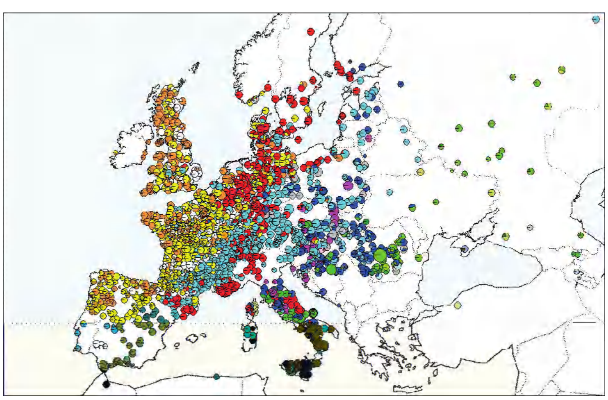


Figure 6 Beside the nuclei, chloroplasts also contain genetic material which is inherited maternally in broad-leaved species. A Europe-wide analysis of chloroplast haplotypes of white oaks revealed the prolonged effects of postglacial migration from South European refugia. Reproduced with permission from Kremer A *et al.* (2002) Chloroplast DNA variation in European white oaks. *Forest Ecology and Management* 156: 5–26.

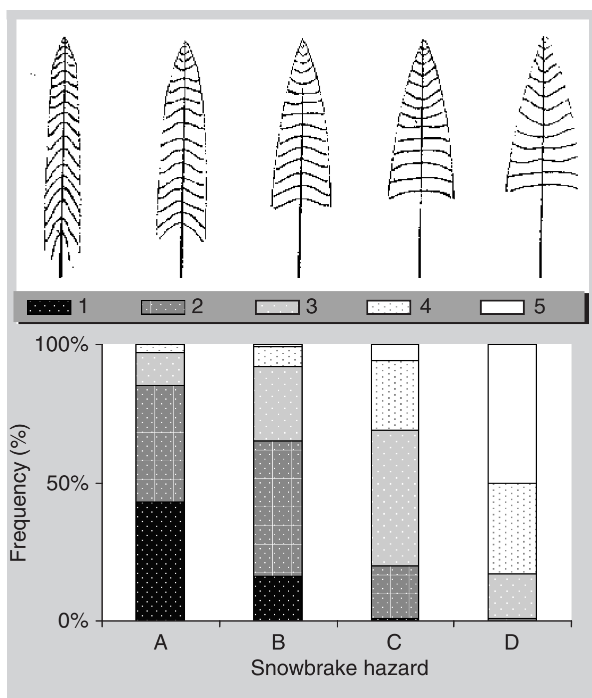


Figure 7 Frequency of spruce crown types in the Slovenian Alps. The diagrams represent different categories of snow-break hazard: (A) extreme cold, hazardous sites, (B) exposed sites on a plateau, (C) transitory sites, and (D) low hazard sites.

dehydrogenase-B) has a lower temperature sensitivity than allele B_2. In silver fir (*Abies alba*) populations, the higher frequency of B_1 in Mediterranean populations as compared to temperate-montane populations was confirmed.

Gene Pool Changes in Small Populations

Small, isolated populations are often considered as resulting from human activity, but many species have naturally restricted, or scattered distributions. Reduced population size becomes problematic if random genetic forces prevail over selection and adaptation.

Genetic Drift

Differential pollen and seed production means a 'random genetic sampling' of the parent population. The smaller the sample, the more the offspring depart from the Hardy–Weinberg allelic ratios. If the population size remains low, drift recurs every generation. Drift effects may persist long after the population regains its size, if the original allelic richness is not replenished through gene flow, e.g., after a demographic bottleneck (through a catastrophic fall in numbers), or if very few individuals colonize a new habitat (founder effect). For example, the loss of alleles during postglacial recolonization is still evident in many temperate species, despite gene flow over many generations.

Figure 8 shows that diversity loss in small populations depends on the effective number of population members. Through random fluctuations, alleles might be lost or fixed even if their initial frequencies were high or low respectively.

As a result, small populations typically show an excess of homozygotes due to a higher number of fixed (monomorphic) loci. Random fixation of some deleterious alleles (harmful mutants) is also probable if the effective number is small or if selection pressure (s) is mild. At the species level, drift in single fragmented populations does not necessarily lead to loss of diversity and may even increase among-population additive variance. For example, in island populations of sugar maple (*Acer saccharum*), fragmented by agricultural fields, polymorphism was found to be higher than in closed, large stands.

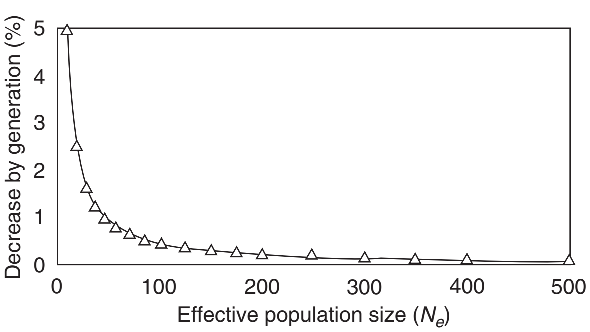


Figure 8 Decrease of gene diversity (heterozygosity) by generation (as a percentage) in function of effective population size. Adapted from Wright JW (1976) *Introduction to Forest Genetics*. New York: Academic Press.

Genetic drift may be compensated by gene flow. Model calculations show that relatively low migration rates suffice to offset drift effects. The maintenance of gene flow between scattered stands is therefore important for avoiding divergence of species fragments.

Inbreeding

Inbreeding happens if individuals of common ancestry mate. Selfing is an extreme form of inbreeding, which can only happen in monoecious species. The inbreeding coefficient (F) depends, like genetic drift, on the size of the effective population (N_e): $F = 1/2N_e$.

The mating probability of identical alleles matters if the allele adversely affects fitness, causing inbreeding depression. Forest trees are typically outbreeders and carry relatively high genetic loads (deleterious alleles) to avoid inbreeding. Experiments with conifers show that growth depression of selfed plants typically reaches 20–25%. The practical importance of selfing is generally low, owing to mechanisms that effectively limit fertilization with self-pollen (in angiosperms, self-incompatibility alleles; in conifers, embryonic lethals). Viable offspring from selfing and matings between close relatives are therefore uncommon, and few survive competition.

Human Effects on Forest Gene Resources

Selective cutting has been practiced over millennia in most of the accessible forest complexes in inhabited areas. Negative effects of associated dysgenic selection ('high-grading') on both gene diversity and quantitative traits have been proven. Consequences may be especially serious if the species occur at low density, such as in tropical forests. For instance, as a result of overexploitation, Cuban mahogany (*Swietenia mahagoni*) presently reaches only shrub size in the Caribbean.

Various other silvicultural practices may cause dysgenic effects, such as the unconsidered introduction of certain exotics (causing introgression between related, otherwise separated species), but especially the uncontrolled collection and commerce of reproductive material blurred the pattern of natural genetic variation in managed forests (**Figure 9**).

Figure 9 Scots pine provenances in a comparative test in the Ukraine. Compared to the autochthonous population (right), the German population (Darmstadt, left) shows the effect of severe dysgenic selection.

Proper forest management, however, may also have positive effects. In some cases genetic improvement of growth and resistance traits has been found to follow proper silviculture, certainly for introduced species.

Contrary to many beliefs, well-managed artificial stands display gene diversity characteristics comparable or even superior to natural forests. **Table 3** illustrates that statistics of controlled artificial regeneration and of first-generation seed orchards are not inferior to those of natural populations.

Table 3 Comparison of gene diversity statistics of natural and artificial populations of Douglas fir in British Columbia. A negative effect on genetic diversity can be traced after intense genetic selection only

Population type	P *(%)*	A	H_e
Natural stand	53	2,14	0,171
Artificial regeneration	65	2,65	0,167
First-generation seed orchard	63	2,28	0,172
Second-generation seed orchard	56	2,25	0,163

For explanation of letters in table headings see **Table 1**. Reproduced with permission from Mátyás C (ed.) (1999) *Forest Genetics and Sustainability*. Forestry Sciences vol. 63. Dordrecht, The Netherlands: Kluwer.

Conservation and Management of Genetic Resources

Genetic resources are elements of genetic variability that are (or might be) used to meet human needs and objectives. In forestry, the term covers naturally occurring populations and individuals, plantations, and collections, which carry currently or potentially valuable genetic information, and their protection is considered necessary from standpoints of economics, ecology, or conservation.

A basic concept for conservation is minimum viable population (MVP) size – the number of individuals that is necessary for the long-term survival of a population. It has to be large enough to conserve genetic diversity and to safeguard evolutionary ability. One approach to estimate MVP size is to calculate the probability of loss of low-frequency alleles. **Table 4** shows that MVP should include several hundred individuals. The numbers refer to effective population sizes; so gene reserves may need to be at least an order of magnitude larger. *MVP* size may largely vary according to species, depending on diversity conditions, mating patterns, dispersion, and density.

Table 4 Estimation of minimum viable population size (MVP) based on probabilities of allele loss (*P*)

P	q	*Population size*			
		M = 1	M = 10	M = 100	M = 1000
0.01	0.05	45	67	90	113
	0.01	230	343	458	573
	0.005	460	689	919	1148
0.005	0.05	52	75	97	119
	0.01	264	379	493	622
	0.005	529	758	988	1217

The table gives estimates for three allele frequencies (*q*) and different number of rare alleles at unlinked loci (*M*). The calculation is based on the assumption that the population is in Hardy–Weinberg equilibrium. Reproduced with permission from Mátyás C (ed.) (1999) *Forest Genetics and Sustainability*. Forestry Sciences vol. 63. Dordrecht, The Netherlands: Kluwer.

Why Specific Forest Gene Conservation Strategy is Needed

Although nature conservation areas protect valuable genetic resources, they are not sufficient because:

- the areas do not necessarily represent ecological conditions typical and important for silviculture
- there may be legal obstacles to management interventions in protected areas (regeneration/or seed collection).

A strategy of forest gene conservation should be based on some knowledge of past and present human influence, the diversity conditions and genetic system of the species, the probable size of MVP, and of adaptively homogenous areas.

Methods of Gene-Resource Management

1. Dynamic, *in situ* (on site) conservation of natural or naturalized populations is the ideal. Although natural forest dynamics should usually be preferred, human intervention to regulate succession or density, and even to regenerate artificially (with authentic material), is acceptable. The species-oriented protection of evolutionary potential is best served by a network of gene reserves.
2. *Ex situ* conservation: reproductive material is brought to units outside the natural habitat. Gene banks include seed-, pollen-, and tissue-culture banks, as well as field collections (clonal archives, stool beds, etc.). *Ex situ* conservation stands (progeny stands) may be established with evacuated populations where the original site is threatened, or with plantations of valuable selected populations or exotic species.

Gene conservation and sustainability Gene conservation forms part of the conservation of biodiversity and, more generally, of nature conservation. The general aim of conserving genetic resources of forest trees, i.e., to safeguard adaptability and long-term evolutionary potential, has high priority given the current pace of environmental changes in relation to trees' generation intervals.

The emerging concept of ecosystem management includes the sustained management of genetic resources. Genetic sustainability depends on the maintenance of processes determining genetic diversity, such as population size, conditions of gene flow, mating, and reproduction. In a world dominated by humans, genetic sustainability cannot rely on nature conservation and gene reserves alone. Genetic principles must form part of national forest policy, especially with regard to the management of close to natural forests.

International scope of gene conservation As the distributions of some key forest trees straddle many countries, reasonable conservation of genetic resources requires international collaboration. At present no binding international agreement exists for forest genetic resources. However various international initiatives (notably the Convention on Biodiversity) and institutions (such as the Food and Agricultural Organization of the UN, International Plant Genetic Resources Institute, Rome) promote internationally coordinated conservation efforts. Perhaps the most advanced is the European initiative (EUFORGEN), with nearly 30 actively participating countries.

See also: **Genetics and Genetic Resources**: Genecology and Adaptation of Forest Trees; Genetic Systems of Forest Trees; Molecular Biology of Forest Trees. **Tree Breeding, Practices**: Genetics of Oaks. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts.

Further Reading

Baradat P, Adams WT, and Müller-Starck G (eds) (1995) *Population Genetics and Genetic Conservation of Forest Trees*. Amsterdam, The Netherlands: SPB Academic.

Ericson G and Ekberg I (2002) *An Introduction to Forest Genetics*. Uppsala, Sweden: Department of Forest Genetics, SLU.

Langlet O (1971) Two hundred years of genecology. *Taxon* 20: 653–722.

Loeschke V, Tomiuk J, and Jain SK (1994) *Conservation Genetics*. Basel, Switzerland: Birkhäuser.

Mátyás C (ed.) (1999) *Forest Genetics and Sustainability.* Forestry Sciences vol. 63. Dordrecht, The Netherlands: Kluwer.

Mátyás C (2002) [Forest and conservation genetics.] Budapest, Hungary: Mezőgazda. (in Hungarian).
Morgenstern EK (1996) *Geographic Variation in Forest Trees*. Vancouver, Canada: University of British Columbia Press.
Müller-Starck G and Schubert R (eds) (2001) *Genetic Response of Forest Systems to Changing Environmental Conditions*. Forestry Sciences vol. 70. Dordrecht, The Netherlands: Kluwer.
National Research Council (1991) *Managing Global Genetic Resources – Forest Trees*. Washington, DC: National Academy Press.
Wright JW (1976) *Introduction to Forest Genetics*. New York: Academic Press.
Young A, Boshier D, and Boyle T (2000) *Forest Conservation Genetics*. Collingwood, Australia: CSIRO.

Genecology and Adaptation of Forest Trees

S N Aitken, University of British Columbia, Vancouver, Canada

Introduction

Genecology is the study of intraspecific genetic variation in relation to environmental conditions. It reveals patterns of adaptation of populations to their environments that result from differences in natural selection among locations. Genecological studies are conducted for the practical purposes of: (1) determining how far seed can be moved from the collection site to a reforestation site without risking maladaptation of the trees to the planting site; (2) delineating geographic breeding zones for which a single breeding program would suffice; (3) selecting optimal provenances within the native range for nonnative (introduced) species; and, more recently, (4) predicting the ability of populations of forest trees to adapt to rapidly changing climates.

To meet these objectives, seed is collected from different provenances (geographic origins) throughout all or a portion of a species range and planted in one or more field or nursery common-garden experiments. The survival and growth of trees of different provenances are observed under the same set of environmental conditions, allowing for the separation of genetic and environmental effects. Genetic variation in resistance to biotic (e.g., insects and diseases) or abiotic (e.g., cold and drought) stresses can also be observed in different environments or tested artificially. Variation among provenances is quantified and related to patterns of geographic variation in climate or other environmental factors. Species that show a high degree of genetic differentiation among provenances require the management of genetic resources on a more local scale than those that show relatively little genetic variation. If seed for reforestation is moved too far from the environments to which it is well adapted then losses in growth, health, and survival may result. The ability of populations to adapt to climate change will depend on current geographic patterns of genetic differentiation as well as the amount of genetic variation for adaptive traits that exists within populations.

Background

The recognition of genetic variation among populations of trees occupying different environments is not new. A full century before both Darwin's theory of evolution was published in *On the Origin of Species*, and Johann Gregor Mendel determined the mechanics of heredity, Carl von Linné (also known as Carolus Linnaeus, the father of modern taxonomy), reported in 1759 that yew trees (*Taxus baccata*) from France were less cold-hardy than those from Sweden. Around the same time, Henri Louis Duhamel du Monceau, Inspector-General of the French navy and noted botanist, established the first forest genetic trials on record. He collected seed from Scots pine (*Pinus sylvestris*) from various locations across Europe and established plantations in France in which to compare the performance of different provenances (seed origins). Later in the eighteenth century, the importance of provenance was recognized by guidelines of the Swedish Admiralty for selection of seed sources of pine and oak, and in Germany for the use of tree species introduced from North America. Similarly, the importance of using local, well-adapted provenances was recognized in Japan centuries ago.

While early botanists and foresters lacked an understanding of evolution and genetics, they recognized that the survival, health, and growth of planted individuals of a tree species depended jointly on the location where seed was collected and the environment in which the resulting seedlings were planted. Maladaptation can result in slow growth, and injury or mortality due to biotic (e.g., insects, diseases, or competition) or abiotic (e.g., cold or drought) agents. When seed was planted in an environment very different or very far from the one in which it was collected, the likelihood of maladaptation was clearly high; however, nonlocal provenances sometimes outperformed local material.

Investigations of provenance variation continued through the nineteenth century, most notably for

Scots pine in France, Germany, and Switzerland, and Norway spruce (*Picea abies*) in Germany, Austria, and Switzerland. Adolf Cieslar studied variation in Norway spruce among provenances from different elevations and latitudes, and found that seed from higher latitudes and higher elevations produced slower-growing seedlings than seed from lower or more southerly locations when planted in the same location. He also suggested that the different performance of provenances was inherited.

Early provenance trials were often located in a single environment, on one site, with limited replication. Thus, while the effects of source environment of provenances could be studied, and the optimum provenance for the test plantation site determined, the effects of planting environment and interactions between source and planting environments could not, nor could the results be extrapolated to select provenances for other planting sites. Not until well into the twentieth century was the first published systematic genecological study established, involving multiple experimental sites as well as many provenances, with sufficient replication for robust statistical analysis. The focus of this study was not a tree species, but the herbaceous perennial yarrow (*Achillea millefolium*). Clausen, Keck, and Heisey collected seed from yarrow plants along an east–west transect in California from the Pacific Ocean (sea level) over the coastal range, across the Central Valley, up to the crest of the Sierra Nevada (3300 m) and down its dry eastern slope. They then established common-garden experiments, in which plants from all populations sampled were grown together in a replicated experiment, on experimental sites along the original transect sampled. Similar to earlier studies of Norway spruce, at low-elevation experimental sites the populations from higher elevations were the slower-growing. They also observed that, at each experimental site, the population that grew to the greatest size was the one from closest to the experimental site. Thus, the relative rankings of populations, from largest to smallest based on mean plant size, changed with planting environment, which has been observed since then for many tree species. This is an example of genotype × environment interaction (G × E) (**Figure 1**). If there was no G × E, the fastest-growing population at one experimental site would be the fastest-growing throughout.

The basic genecological experimental design used by Clausen, Keck, and Heisey was repeated for many tree species around the world in the second half of the twentieth century, very often revealing similar patterns of local adaptation: **Figure 1** illustrates a typical pattern. The majority of these tests have been in temperate forest regions in Europe and North America, with fewer published studies of tropical or boreal species. While these trials were initially established to generate information for operational forestry, they have been used for new applications in recent years, including predicting response to climate change, determining the underlying genetic basis of adaptive traits (i.e., ecological genomics) and testing evolutionary and ecological theories about factors limiting the evolution of species range. The extensive body of scientific literature on local adaptation in forest trees may well exceed that for any other type of organism.

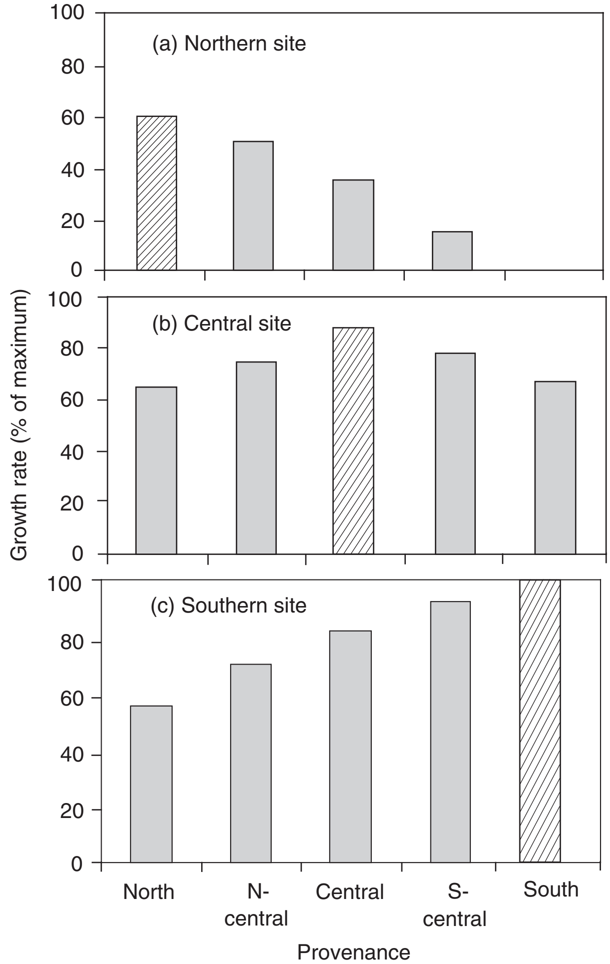


Figure 1 Results of a hypothetical genecological experiment illustrating typical results for widespread, temperate tree species. In this example, seed was collected from five locations (provenances or populations) along a latitudinal transect in the northern hemisphere and grown in common-garden experiments at three of those locations (north, central, and south). Growth is illustrated as a percentage of the mean of the fastest-growing provenance on the fastest-growing site. Average growth is highest at the southernmost site, and lowest at the northernmost site, but the fastest-growing provenance on any one site is local (indicated by the cross-hatched bar). There is genotype-by-environment interaction: the ranking of provenances is different at each site.

Evolutionary Forces

The pattern of genetic variation among and within populations within a species results from the cumulative effects of five evolutionary forces: (1) mutation; (2) gene flow (migration); (3) genetic drift (random changes in allele frequencies from generation to generation due to sampling effects); (4) natural selection; and (5) mating system (the degree to which sexual reproduction occurs through self-pollination, consanguineous mating between related individuals, or mating between unrelated individuals). Genecological studies of tree species with large distributions and historically large populations reveal the efficacy of natural selection in a given environment in favoring locally adapted phenotypes (**Figure 1**). Patterns of genetic variation among populations often mirror environmental gradients, revealing the strong effects of natural selection despite considerable gene flow introducing alleles conferring adaptation to other environments. Genecological studies of species with small ranges, small or isolated populations, or species that have experienced major bottlenecks (e.g., during glacial periods in the Pleistocene) often reflect the effects of genetic drift to a greater extent than other evolutionary forces, and as a result have more random patterns of genetic variation among populations rather than clines along environmental gradients.

Species that show strong patterns of genetic variation among populations in growth and other adaptive traits associated with environmental gradients are referred to as adaptive specialists, while those with weak or no geographic patterns are referred to as adaptive generalists. Generalists may lack such patterns owing to one of two reasons: either they have a high degree of phenotypic plasticity, i.e., the same genotype (genetic make-up) can produce a range of phenotypes (outward appearance, performance, or physiological behavior) depending on the environment, or local adaptation has not had an opportunity to develop as natural selection has been countered either by gene flow or by genetic drift in small populations. In North America, lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) are examples of adaptive specialists, while western white pine (*Pinus monticola*) and western red cedar (*Thuja plicata*) are generalists. Adaptive specialists require more restrictive seed transfer guidelines and smaller breeding zones than adaptive generalists, as there is a greater risk of maladaptation with seed transfer or deployment of genetically selected material. The variation among species in the degree and patterns of specialization means that provenance trial results for one species cannot be extrapolated to another.

Some species have intraspecific taxonomic structure resulting from past isolation of portions of the range leading to more abrupt genetic differentiation among regions due to both random genetic drift and natural selection. This taxonomic structure can persist after previously isolated varieties or subspecies come into secondary contact through range expansion or migration. Examples of such species include *P. contorta* comprising subspecies *contorta*, *latifolia*, *murrayana*, and *bolanderi*, and *Pseudotsuga menziesii* coastal variety *menziesii* and interior var. *glauca*. In species with intraspecific taxonomic structure, genetic differentiation resulting from both isolation and past adaptation can overlay and complicate the interpretation of variation resulting from adaptation to current or recent environments in continuously distributed populations. Hybridization resulting from secondary geographic contact between previously separated species can also produce strong geographic patterns of adaptive variation, for example, in the introgression zone between *Picea glauca* and *P. sitchensis* in the coastal mountains of British Columbia and Alaska.

Genecological Methods

Provenance Trials

Traditional provenance trials require five steps: (1) collection of seed; (2) growing of seedlings; (3) planting of a replicated experiment on multiple field sites; (4) measurement of traits; and (5) analysis and interpretation of results. Seed is typically collected from 10 to 25 trees per location, to ensure a representative sample of the natural population from each provenance. Parent trees sampled are usually 50–100 m (or more) apart, to minimize sampling of closely related individuals. Seeds are sometimes kept separate by seed parent (called a provenance–progeny trial), to allow for the estimation of within-provenance genetic variation and trait heritabilities as well as to facilitate some initial selection for selective breeding; however, bulk seedlots are often used, with seed pooled across parents within provenances. Seed is collected from accessible locations scattered throughout the zone of interest within the species' range, with anywhere from just a few to over 100 locations sampled, depending on the size of the area and the resources available.

Seeds are usually sown in greenhouses or nursery beds and seedlings grown in randomized, replicated blocks for 1–2 years before outplanting. Field provenance test sites are usually selected to cover the range of planting environments that are typical for a species within a given political jurisdiction, although some trials are rangewide, particularly those coordinated by international organizations. To ensure that a range of environments is sampled for native species, sites are usually selected to cover the full range of latitude, longitude, elevation, and ecological conditions across which the target species is found or actively managed. For exotic species, sites are selected across the range of potential planting sites for that species.

Blocks are delineated within planting sites, hopefully grouping similar environments together; for example, with block boundaries following contour lines along slopes, or separating wetter and drier areas. Within blocks, a complete, randomized block design can be used where trees from individual provenances are represented by single-tree plots; a split-plot design can be used where provenances are allocated to main plots and individual-tree progenies within provenances to single-tree subplots. Where such families are identified, equal numbers of seedlings from each family represent a provenance in all blocks, and families are randomized within provenances, usually in single-tree plots.

Traits assessed in provenance trials are often limited initially to survival, height, and diameter. Tree size is used as a cumulative index of tree health and degree of adaptation, and individual tree growth is an indicator of potential stand-level productivity. As trees age, insect or disease outbreaks, and unseasonable weather events such as frost and drought offer opportunities for studying population variation in resistance to biotic and abiotic stresses. However, response to these agents is often best studied under more controlled conditions. While mortality is usually periodically recorded, differences among provenances in survival must be large or replication (blocks and sites) high for these to be statistically significant. In addition, trees can often survive a much broader range of environments than those in which they can be highly productive. In most areas of the world with a focus on industrial plantation forestry, survival is more dependent on good silvicultural practices than on the choice of provenance. Choice of the wrong provenance can reduce the realized production of a high-productivity site, just as planting an optimum provenance can increase site productivity, so growth is usually emphasized. Wood cores can be sampled from older provenance trials and wood properties analyzed including wood density, fiber length, microfibril angle, lignin content, extractives content, and other economically important traits, although within-population variation in wood properties is usually of greater interest than among-population variation.

Short-Term Genecological Experiments

Some traits related to adaptation to specific environmental stresses can be assessed in long-term field provenance trials such as phenology (e.g., timing of bud burst, bud set, leaf abscission, pollination, and seed maturation); cold-hardiness; and drought-related traits (e.g., water-use efficiency as measured by stable carbon isotope ratios in wood samples). Adaptive traits such as these are more commonly assessed in short-term nursery, greenhouse or growth-chamber experiments under more controlled conditions. These trials have several advantages over field provenance studies. They can typically be completed in 2–3 years, can involve more uniform environments and thus have a greater ability to detect genetic differences, can be located close to laboratory facilities for repeated observations or for assessment of time- and equipment-intensive traits, and can allow the isolation, control, and testing of specific environmental factors such as temperature, moisture, photoperiod, and nutrients. Disadvantages include a lack of long-term information on survival and health in natural environments, and the inability to assess mature characteristics. Ideally, these short-term experiments are linked with long-term provenance trials containing similar genetic materials.

The experimental designs for short-term genecological experiments can be similar to or quite different from those for provenance trials. If a genecological mapping approach is taken, instead of sampling from many trees at relatively few locations, many locations are sampled with seed collected from just one or two trees per location. This method, pioneered by R.K. Campbell, allows for the fine-scale mapping of genetic variation and, using spatial analytical techniques, results in detailed spatial maps with isoclines that connect and delineate environments with similar natural selection pressures. Including progeny of two trees at some or all locations allows for the estimation of within-location genetic variation for estimation of trait heritabilities.

Short-term genecological experiments can allow the separation of temperature- and moisture-related adaptation more easily than long-term provenance trials, where factors contributing to tree injury or death may be unclear; treatments controlling environmental factors allow detailed assessments of physiological responses to these treatments. Soil–temperature treatments have been successfully created through the use of soil heating cables, and such treatments have revealed provenance × treatment interaction in some species.

Rather than develop experimental systems to grow seedlings under different temperature regimes, most investigators use artificial freeze-testing of shoots or other tissue samples collected from genecological experiments or provenance trials to assess genetic clines in cold-hardiness. Shoot samples, or small pieces of leaves, buds, or stems, are placed in computer-controlled freeze chambers and the temperature is slowly reduced to a target freezing level. Damage is then assessed using one or more of several available methods, including visual scoring of damage following freezing, measuring the release of electrolytes from injured cells, measuring chlorophyll fluorescence of foliar samples following freezing.

Drought treatments can be created in seedling trials through the use of soils with low water-holding capacity in raised nursery beds with barriers to moisture entry, by withholding irrigation, and by using clear covers to block precipitation. The use of individual-seedling containers for the study of adaptation to drought is not recommended, as this approach usually confounds plant size with drought stress intensity owing to fixed soil volume and no competition.

Data Analysis

The first step in analyzing provenance and genecological trials is usually analysis of variance (ANOVA) to test the significance of phenotypic variation among sites and provenances, as well as within-site environmental effects, including block effects. Provenance–progeny trial analysis also tests for the effects of families nested within provenances and their interactions with site, along with certain other effects. If provenances have been chosen randomly for inclusion in the experiment, unbiased estimates of variance components can be calculated for each effect and the proportion of variation due to provenances, and to families within provenances if applicable, can be estimated.

The next step in the analysis is to test for and characterize genetic clines. A cline is a geographic or environmental pattern of change in the mean of a trait associated with an underlying environmental gradient (**Figure 2**). Where specific environmental descriptors of provenances are lacking, geographic variables such as latitude, longitude, elevation, and distance inland from oceans are used as surrogates. Climatic records provide a better indication of source environments than these geographic variables but weather stations are typically underrepresented in extensively forested areas away from major human settlements. Some provenance trials have selected provenances with available weather records to address this problem, but this may result in a biased sample. More recently, climatic models have been available in some regions, or have been generated by forest geneticists in partnership with meteorologists, to provide better descriptors of provenance environments. For example, predictions from the PRISM model are now available for much of North America.

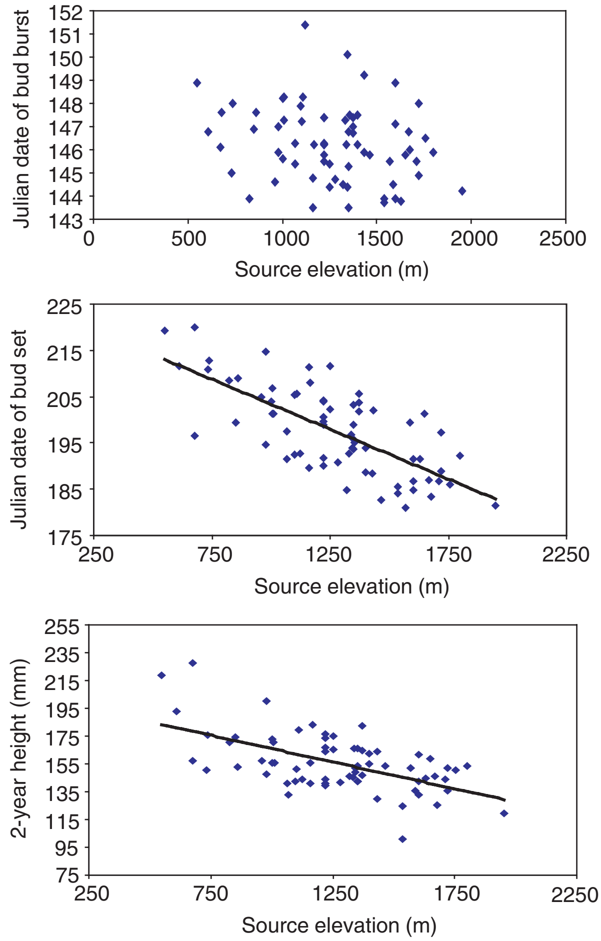


Figure 2 Genetic clines associated with elevation in *Picea engelmannii* (with possible introgression from *P. glauca* at lower elevations) in southeastern British Columbia, Canada, for 2-year-old seedlings in a common-garden experiment established in nursery beds. Plotted against source elevation are the mean values of the open-pollinated progeny of individual seed parents. There is no pattern of variation in mean date of bud burst with elevation; however, date of bud set reveals a fairly strong, significant ($P \leq 0.05$) elevational cline ($r^2 = 0.45$) while height shows a weaker but significant cline ($r^2 = 0.30$).

To test for genetic clines, univariate or multiple regression analyses are conducted on each provenance trial or controlled environment separately, with geographic, environmental, or climatic descriptors as independent variables, and provenance means for assessed traits as dependent variables. A significant genetic cline, particularly if provenance means are significantly associated with a parallel environmental gradient in more than one geographic area, is considered evidence of varying natural selection pressures at different locations along that gradient.

Genetic clines associated with the elevation of parent origin observed in a short-term seedling genecological study of Engelmann spruce (*Picea engelmannii*) are illustrated in **Figure 2** for timing of bud burst, timing of bud set, and height. It is worth noting that, at any elevation, there is still substantial within-population variation for all traits, providing the raw material for adaptation to new conditions or for breeding programs. As traits vary in the strength of clines and spatial patterns of variation, and many traits are often assessed, statistical methods such as principal component analysis are often used to combine traits into multivariate indices.

Genecological Trends

For widely distributed tree species in temperate and boreal regions, most species have broad genetic clines associated with gradients in mean annual temperature, growing-season length (i.e., frost-free period) and, to a lesser extent, total and growing-season precipitation. In mild test environments, overall growth is generally highest for populations with the mildest source environments, and lowest for those from particularly cold (or dry) locations. In harsher test environments, populations from warmer source environments often suffer higher mortality, while populations from similarly cold or dry environments have higher survival and good growth rates for those particular environments.

While local provenances in general are the safest to use for reforestation in the absence of good provenance data, as they have higher survival and productivity than provenances from afar, there are two common exceptions to this pattern. For a number of species, superior provenances have been identified, trees from which have higher than expected growth rates and perform well above the norm for the genetic cline over a wide range of test environments. The second trend is that for many western North American species, the most rapidly growing genotypes with comparable survival and health to local provenances are from slightly milder environments than the test site, e.g., 1–2° S, or 100–300 m lower in elevation. This may reflect adaptational lag, that is, the local adaptation of populations to past rather than current environments, given the long generation interval of trees, or it may reflect a lack of extreme climatic events as agents of natural selection since the provenance trials were planted.

The steepness of genetic clines varies with trait assessed (**Figure 2**). The steepest genetic clines often exist for phenological traits and cold-hardiness. The period of active primary growth from bud break (or growth initiation for indeterminate species) to bud set (or growth cessation) varies with annual frost-free period of source environments. There is typically more variation within species for timing of growth cessation (or bud set) than for timing of growth initiation (or bud burst). Populations within species typically differ in the timing of growth cessation and initiation of cold acclimatization in autumn, or in the timing of dehardening in the spring, rather than in the level of maximum cold-hardiness achieved mid-winter. It should be noted that autumn and spring cold-hardiness are really different traits from a genetic standpoint, as variation in these traits is relatively uncorrelated. In Douglas fir, genetic mapping of quantitative trait loci (QTL) controlling cold-hardiness has revealed that autumn and spring cold-hardiness are controlled by largely independent sets of genes. These processes have different cues: acclimatization (hardening) in the autumn is triggered by photoperiod, while first sufficient chilling, then exposure to warm temperatures, initiates dehardening.

Areas with late summer drought generally have populations with earlier growth initiation and cessation, and greater allocation of biomass below ground (higher root/shoot ratios) than locations with more summer precipitation. The mean total growth of trees in populations tends to be correlated with length of the growing season (period between primary growth initiation and cessation), which explains at least part of the lower growth potential of populations from colder or drier source environments, even under favorable conditions. Populations adapted to dry environments are often phenotypically similar to those adapted to frost-prone locations.

Drought-avoidance mechanisms such as a shorter, earlier growing season, preemptive stomatal closure (resulting in cessation of photosynthesis at a higher water potential), and greater allocation of biomass to roots (as opposed to increasing photosynthetic leaf area) tend to decrease net growth; thus provenances from drier regions often have a lower inherent growth capability. Tolerance mechanisms include higher water-use efficiency (less water used per unit of photosynthesis) and a lower vulnerability to cavitation (the water potential at which xylem water columns embolize). Significant interprovenance variation has been observed for all of these drought-related traits in genecological studies of temperate forest trees, with changes in growth phenology and biomass allocation being the best documented.

Phenotypic versus Genetic Estimates of Differentiation

Many studies rely on the use of selectively neutral DNA markers rather than genecological experiments to determine population differentiation. The results of such studies provide an indication of historic population size based on levels of genetic diversity, as well as the strength of gene flow. Genetic marker variation is commonly partitioned among and within populations, and the amount of total genetic variation due to among-population differences estimated by F_{st}. The proportion of total genetic variation in a phenotypic trait due to differences among populations can also be estimated in a genecological test using a similar parameter, Q_{st}. If Q_{st} exceeds F_{st}, it is evidence of past differences in natural selection on different populations. F_{st} values in forest trees are usually between 5 and 10%, while Q_{st} values are usually higher and vary widely, with published values up to 80%. Thus, while useful for other purposes, selectively neutral genetic markers can greatly underestimate population differentiation and the potential for local adaptation.

While most genetic markers that are widely used for population genetic studies are not useful for studying variation in adaptive traits, as genomic methods develop and gene sequence databases grow, there will soon be new classes of markers available that reveal single nucleotide polymorphisms (SNP) in genes that affect adaptive traits. While most of the adaptive traits of interest are likely influenced by many genes, it will be possible to look for clines in allele frequencies for some of these genes, rather than just characterizing phenotypic variation, using methods of the emerging field of ecological genomics.

Predicting Response to Climate Change

Local populations facing rapid environmental change have three possible fates. They can adapt *in situ* to new conditions. They can migrate, and track the environment to which they are adapted across the landscape. Or they can be extirpated due to maladaptation to new conditions. The pollen and macrofossil records indicate that tree species have migrated in response to past climate change, but the fossil record cannot reveal the extent to which adaptation has also played a role. It has been suggested that population structure and differentiation may have persisted during range expansions and contractions in the Pleistocene, and maintained adaptive structure within species during migration. With rates of anthropogenic climatic change predicted to be much higher than most of those in the past, combined with considerable range fragmentation by human development in some areas, it is likely that species migration will often be unable to keep pace with expected changes.

Established long-term provenance trials have been the focus of renewed interest in recent years; not only do they provide an opportunity to study differences among populations from different environments, but they also provide the ability to study the effects of a changing environment on these populations by substituting spatial for temporal environmental variation. As a result of moving seed from the point of origin to a series of new environments, the genetic and ecological response of these populations to these environments can be assessed.

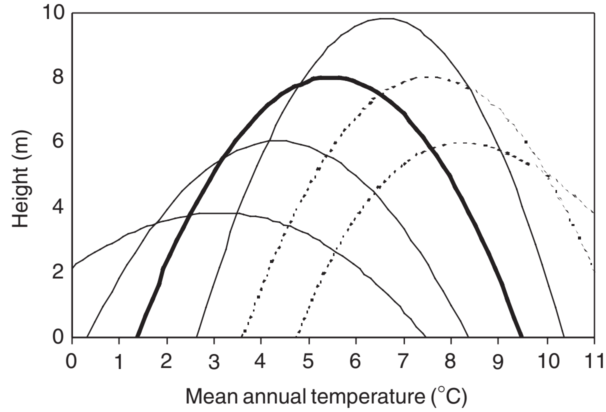


Figure 3 Norms of reaction of six *Pinus contorta* subsp. *contorta* populations to mean annual temperature (MAT) as derived by Rehfeldt GE, Ying CC, Spittlehouse DL and Hamilton DA (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change and reforestation. *Ecological Monographs* 69: 3375–3407, based on height at 20 years in a field provenance trial planted on 60 field test sites. Genotypes typical of each population will be found in geographic areas with an MAT for which that population has higher productivity than other populations. Each population has an optimum MAT at which its productivity is maximized; however, it may not occupy areas with that MAT due to displacement by more competitive genotypes. If climates warm 3–5°C, as predicted by models, productivity losses due to maladaptation will be substantial.

This type of climate change analysis has been most thoroughly conducted by noted genecologist G.E. Rehfeldt, who analyzed provenance data for lodgepole pine in a provenance trial involving 140 populations and 60 field sites. **Figure 3** illustrates the derived responses, called norms of reaction, of height growth of just six of those populations to mean annual temperature of the planting environment. If mean annual temperature increases at the predicted rate of 3–5°C in the next century, it is clear that massive maladaptation will result in this species. It is predicted that it will take 4–12 generations of natural selection, or massive redeployment of genetic resources across the landscape for reforestation, for populations of lodgepole pine once again to be genetically matched to their environments.

See also: **Genetics and Genetic Resources**: Population, Conservation and Ecological Genetics. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance;

Genetic Improvement of Eucalypts; Tropical Hardwoods Breeding and Genetic Resources. **Tree Breeding, Principles**: Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tree Physiology**: A Whole Tree Perspective; Physiology and Silviculture. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources.

Further Reading

Aitken SN and Hannerz M (2001) Genecology and gene resource management strategies for conifer cold hardiness. In: Bigras F and Columbo S (eds) *Conifer Cold Hardiness*, pp. 23–53. New York: Kluwer Academic Press.

Clausen D, Keck D, and Heisey WM (1948) *Experimental Studies on the Nature of Species*. III. *Environmental Responses of Races of* Achillea. Carnegie Institute Washington Publication no. 581. Washington, DC: Carnegie Institute.

Davis MB and Shaw RG (2001) Range shifts and adaptive responses to climate change. *Science* 292: 673–679.

Endler JA (1977) *Geographic Variation, Speciation, and Clines*. Monographs in Population Biology no. 10. Princeton, NJ: Princeton University Press.

Kirkpatrick M (1996) Genes and adaptation: a pocket guide to the theory. In: Rose MR and Lauder GV (eds) *Adaptation*, pp. 125–148. San Diego, CA: Academic Press.

Langlet O (1971) Two hundred years genecology. *Taxon* 20: 653–722.

McKay JK and Latta RG (2002) Adaptive population divergence: markers, QTL and traits. *Trends in Ecology and Evolution* 17(6): 285–291.

Morgenstern EK (1996) *Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge and Science*. Vancouver, Canada: University of British Columbia Press.

Rehfeldt GE, Ying CC, Spittlehouse DL, and Hamilton DA (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change and reforestation. *Ecological Monographs* 69: 3375–3407.

Williams ER and Matheson AC (1994) *Experimental Design and Analysis for Use in Tree Improvement*. East Melbourne, Australia: CSIRO Information Services.

Cytogenetics of Forest Tree Species

Ž Borzan, University of Zagreb, Zagreb, Croatia
S E Schlarbaum, University of Tennessee, Knoxville, TN, USA

Introduction

The discipline of cytogenetics was first defined by Sutton in 1903, as a field of investigation which developed from the separate sciences of genetics and cytology. It is concerned with studies on the correlation of genetic and cytological (especially chromosomal) features characterizing a particular genetic system under investigation. With respect to forest trees, cytogenetic studies have generally been limited to chromosome studies, on the number, appearance, and behavior of chromosomes during mitosis and meiosis, chromosomal and karyotypic evolution, and the role of chromosomes in the transmission and recombination of genes.

Plant breeding can be traced to the ancient Babylonians, but a clear understanding of genetics has its beginning in the nineteenth century with Mendel's hybridization experiments and their subsequent rediscovery by de Vries, Correns, and von Tschermack in 1900. Cytology required the invention of the microscope, and began when Robert Hook observed cork cells in 1665. Early scientists studied cell structure, organelles, and division. Nageli first described chromosomes as visual bodies during cell division in 1844, and Fleming in 1882 described the complete process of mitotic nuclear division. However, it was not until the independent observations of Sutton and Boveri that chromosomes were first linked with the emerging field of genetics.

Cytogenetic investigations of forest tree species were first conducted in the early 1900s, after cytological investigations in most crop plants and animals were well established. Leading discoveries were made in the research of insect cytogenetics, and then followed by maize (*Zea mays*) cytogenetics, especially from the standpoint of the applied methods and materials. Thomas Hunt Morgan and his group of students and scientists made fundamental discoveries in the early decades of the twentieth century, investigating giant chromosomes of fruit fly, *Drosophila melanogaster*. The fly's short life cycle and variant phenotypes/genotypes allowed rapid progress in understanding cell differentiation, cell divisions, and breeding results. In contrast, the relatively long time to reproductive maturity of many forest tree species, and logistical problems in sampling, make trees less desirable for cytogenetic research. However, papers written at the turn of the twentieth century pointed to the suitability of conifer species for cytological research.

The main interest in forest tree cytogenetics in the early 1900s was in discovering and interpreting the process of fertilization in pines. Ferguson conducted very detailed observations on the development of the egg cells, fertilization, and microsporogenesis in various pine species (*Pinus strobus*, *P. nigra*, *P. rigida*, *P. resinosa*, and *P. uncinata*). She determined the precise number of chromosomes in the haploid state for these pine species ($n = 12$). Early embryological research, such as Ferguson's, also revealed that chromosomes of coniferous species are relatively large and easily investigated by techniques used at that time, including sectioning and chromosome smears. Working with large conifer chromosomes was made easier after 1921, when the squash technique was developed and camera lucidas utilized for illustrations.

The classic study of that era was by Sax and Sax in 1933, who pioneered karyological studies of 53 gymnosperm species and presented their results using rudimentary idiograms. They discussed the similarities and differences in karyotypes among species and advocated the use of female gametophyte tissue, which showed advantages in analyzing cells without thick cell walls and containing only the haploid number of chromosomes. Their paper was a prototype for further karyological research of coniferous species.

Karyological research of angiospermous (= hardwood) species in that era was hampered by chromosomes that were numerous and generally too small for detailed observations of morphology. Chromosome counts of many species, however, were registered and published in reference books of cumulative presentations of plant chromosome numbers, beginning with Darlington and Wylie's *Chromosome Atlas of Flowering Plants* in 1955, and followed by Moore in 1973, Fedorov in 1974, and by others.

Forest trees occur in a wide variety of taxonomic families and span different orders and classes. Correspondingly, there is a wide variation in the number and size of chromosomes among and even within different species (**Figure 1**). In some taxonomic groups, e.g., Pinaceae, there is great similarity in the chromosomes of different species, which makes identification and comparison difficult. Standardization in karyotype analysis was suggested by some authors, but was inconsistently adopted in later papers. This caused difficulties in comparing results of different cytological investigations. Additionally, differences in terminology, in statistical analysis procedures (if used), and in number of analyzed cells per species contributed confusion.

Forest tree cytogenetic research over much of the twentieth century was dominated by somatic studies on coniferous species, particularly in Pinaceae and Taxodiaceae, using conventional staining methodology. Studies by Saylor, Khosho, Mergen and Burley, Mehra, Hizume, Muratova and Kruklis, Stebbins, Schlarbaum and Tsuchiya, Borzan, and Toda and other representative studies were quoted by Schlarbaum, in his review of cytogenetic studies of forest trees. Many studies were botanical in nature, investigating inter- and intraspecific variation, cytotaxonomy, and phylogeny. In the latter part of the twentieth century, cytogenetic studies of trees exposed to air, heavy metal, and radioactive pollution were made under difficult conditions, and demonstrated the effects of pollution on the meiotic and mitotic processes.

Cell Division and Chromosomes

Cell division includes nuclear (karyokinesis) and cytoplasmic (cytokinesis) division. Simply, it is a cell reproduction process that enables growth (cell multiplication) and development (cell differentiation and growth) of an organism through mitotic division (mitosis), and parental transfer of hereditary determinants to their offspring through meiotic division (meiosis). The process of mitosis and meiosis is fundamentally similar in all organisms, but can differ in details among species.

Mitosis is a genetically controlled process that provides two identical daughter cells with chromosome numbers identical to their parental nucleus. It is followed by cytokinesis and gives rise to genetically equivalent cells in the growing somatic regions of eukaryotic species. This continuous process can be observed under the microscope and is usually described in five stages: prophase, prometaphase, metaphase, anaphase, and telophase. The period between division cycles is the interphase stage, when single-stranded chromosomes become double-stranded chromosomes due to DNA duplication prior to mitosis, with two identical chromatids attached to a common centromere (= primary constriction). Under a light microscope, the chromosomes appear as chromatin granules. As mitosis begins, each chromosome becomes visible as a distinct structure due to coiling, shortening, and thickening during the prophase stage. The spindle (= microtubules) is formed in prometaphase and becomes attached to the kinetochore within the centromere region of each chromosome. During prometaphase, the chromosomes migrate to the spindle equator. The metaphase chromosomes are most often analyzed for determining number and karyotype, as they are maximally condensed and appear as stretched or curved bars divided usually in long and short arms by centromere. In anaphase, the two sister chromatids of each chromosome are separated by movement to the opposite spindle poles. The "daughter chromosomes" of each chromosome arrive at each spindle pole, a cell wall is formed between the two new cells as the nucleus is reconstituted, and the cell proceeds into interphase.

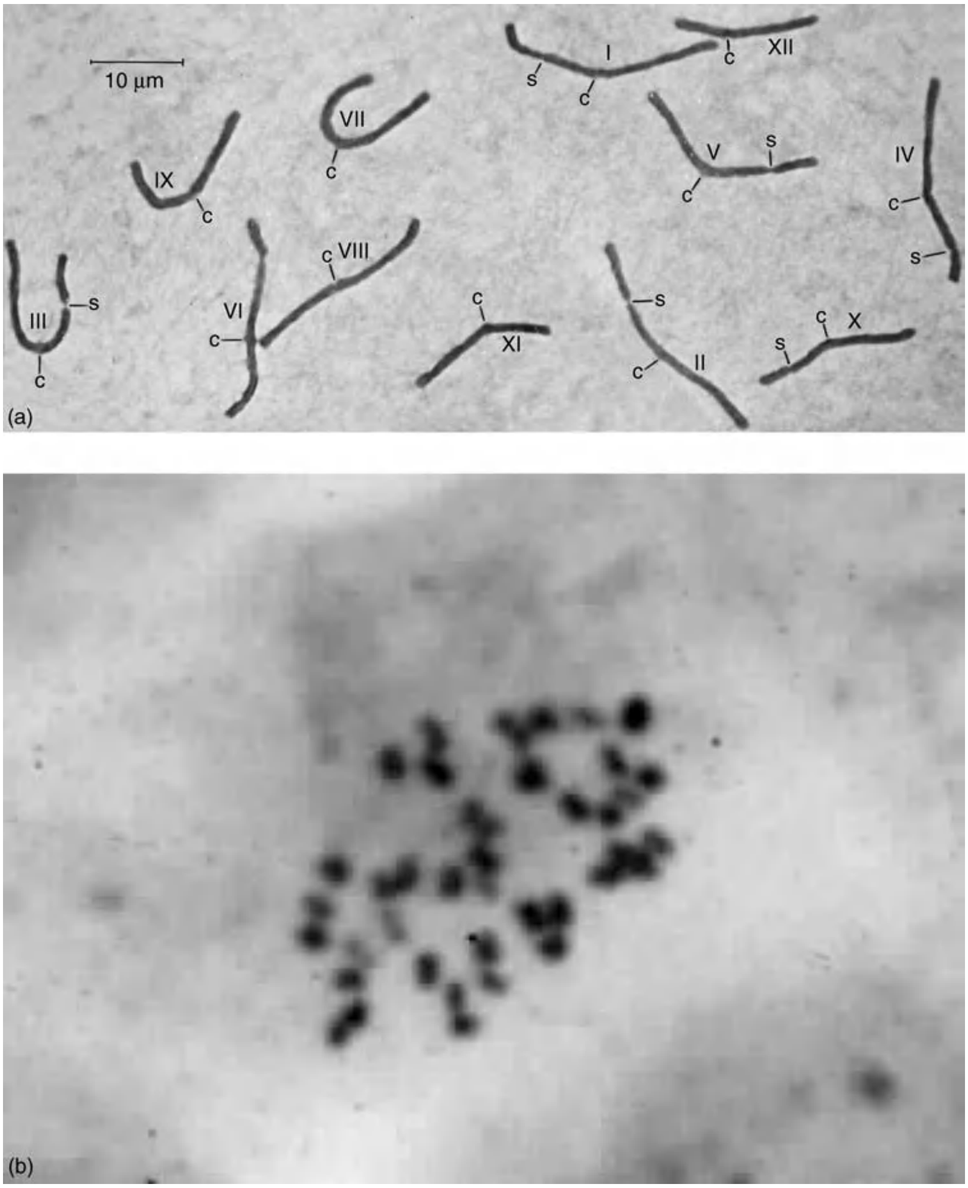


Figure 1 (a) Haploid chromosomes in the female gametophyte tissue of *Pinus nigra*; (b) Diploid chromosomes in somatic cells of root-tips in *Salix sitchensis* ($2n = 2x = 38$).

Meiosis differs from mitosis in having two successive nuclear divisions, with a reduction of chromosome number in the first division from the somatic (= sporophytic) state ($2n$) to the gametic (= gametophytic) state (n) in cells that will proceed to form gametes. Meiosis is a continuous process under genetic control and occurs over a number of stages in each division. The first meiotic division contains the stages leptotene, zygotene, pachytene, diplotene, diakinesis, prometaphase I, metaphase I, anaphase I, and telophase I. The chromosomes are loosely coiled in leptotene and become progressively more densely coiled through telophase I. Pairing of homologous chromosomes (= bivalents) begins in zygotene and is completed in pachytene, where genetic recombination can take place through reciprocal exchanges of genetic material that may occur between homologous nonsister chromatids (= crossing over). Chromosome contraction continues to occur in diplotene and diakinesis. During prometaphase I, the spindle fibers (= microtubules) are organized and become attached to the bivalent centromeres. In metaphase I and anaphase I, the chromatids do not divide as the homologous chromosomes are pulled to the opposite poles, thereby reducing the chromosome number to the haploid state.

The interkinesis stage between the first and second division of meiosis may or may not occur. During this

Figure 2 Asynapsis in *Cunninghamia lanceolata*.

stage, the chromosomes are partially uncoiled. Interkinesis is followed by the second meiotic division, which contains the stages prophase II, metaphase II, anaphase II, and telophase II. The second meiotic division is similar to mitosis, although prophase II does not occur in organisms where interkinesis is omitted. In telophase II, haploid (n) interphase nuclei are reconstituted, and cell walls are formed to separate the four cells, which in turn go through microsporogenesis (male) or megasporogenesis (female).

There can be many variations and anomalies in the meiotic process, particularly when polyploidy, instead of the typical diploidy, is involved. These variations and anomalies can be under genetic control, such as asynapsis where chromosome pairing fails completely among all chromosome pairs, or pairing is incomplete, where only certain homologous chromosomes fail to pair, and thus univalents are formed. Asynapsis can lead to fertility problems due to uneven distribution of the chromosomes in the gametes (**Figure 2**).

Variation in Chromosome Numbers

Generally, each species has a characteristic number of chromosomes in each cell (except for gametes) referred to as the somatic number ($=2n$), which is typically diploid. Most higher organisms have one species-specific set of homologous chromosomes donated by the male (pollen) ($=n$, the gametic number which is typically haploid), and the other set by the mother (egg). Through evolutionary processes, the number of chromosomes can increase by whole sets (polyploidy) and/or increase or decrease by individual chromosomes (aneuploidy).

Polyploidy can occur in different ways, spontaneously or induced. Autopolyploids are polyploids that have occurred through chromosome doubling (*AA*–*AAAA*). Allopolyploids are created when different species (*AA* and *BB*) hybridize and the chromosome number doubles or the hybridization involves unreduced gametes (*AABB*). A segmental allopolyploid occurs when the chromosome complements of very closely related species or subspecies combine ($A_1A_1A_2A_2$).

As with polyploidy, aneuploidy can occur spontaneously or can be induced. There is a large body of terminology for individuals that have lost or gained individual chromosomes, e.g., nullosomic ($2n-2$; missing both homologs of a chromosome pair), monosomic ($2n-1$; missing one homologous chromosome), trisomic ($2n+1$; containing three homologous chromosomes).

In conifers, true polyploid coniferous species are rare, occurring only in Taxodiaceae (*Sequoia sempervirens*) and Cupressaceae (*Fitzroya cupressoides*), although individuals within Taxodiaceae, e.g., *Cryptomeria*, and Cupressaceae, e.g., *Juniperus*, are polyploid in nature. Aneuploidy is widespread in species of Podocarpaceae. In other coniferous families, however, polyploid and aneuploid individuals are generally stunted and not competitive in natural settings.

A review of Darlington and Wylie's *Chromosome Atlas of Flowering Plants* in 1955, coupled with a more recent overview by Schlarbaum in 1991, reveals a significant number of hardwood species where polyploid and aneuploid processes have been involved in the speciation process. Additionally, it is evident that there are species with polyploid races, e.g., *Fraxinus americana*, *Populus tremuloides*, and *P. tremula*. The chromosome nature of most hardwood species, however, is still unknown. While chromosome counts have been made on many species, those counts are often based on a single sample of individuals or a single individual.

Basic chromosome number (x) represents the smallest (monoploid) chromosome number in a taxon. Basic number can become variable as the taxon grouping becomes larger, e.g. *Cupressus* to Coniferales, etc. The basic chromosome number has evolutionary connotations, and there are many publications that speculate about the true basic number of different taxa, particularly those with high chromosome numbers.

Notation of chromosome number in the scientific literature is often incorrect, when the notation involves the somatic ($2n$) or gametic (n) number and basic number (x) of a species. For example, notation for somatic chromosome number of a diploid species with 24 chromosomes in somatic cells ($2n$), 12 chromosomes in haploid cells (n), and a basic number of 12 chromosomes, is written as: $2n=2x=24$. If there is a euploid (whole chromosome set) increase in chromosome number to 36, the notation would be $2n=3x=36$; not $3n=3x=36$. The notation for somatic number remains $2n$, despite the increase in chromosome number. With aneuploid changes in chromosome number, the $2n$ and $2x$ notation remains the same, but the number of chromosomes added or missing is noted, e.g., $2n-1=2x-1=23$.

Slide Preparation Methodology

Uniform Chromosome Staining

Until the mid-1970s, the majority of forestry cytogenetic studies were conducted to determine the chromosome number and karyotype by using a staining methodology that produced a uniform stain. Root-tip meristematic tissue and, to a lesser extent, terminal bud or young leaf tissues were used. Before fixing, the root tips are usually pretreated with a mitogen to inhibit spindle fiber formation in metaphase, resulting in slides with a large number of cells at the metaphase stage. In addition, the mitogens selected, e.g., colchicine, 8-hydroxyquinoline, were often used to shorten the extremely long chromosomes found in conifers, as well as to inhibit postmetaphase cell division. After fixation, usually in Farmer's or Carnoy's solutions, the sampled materials were hydrolyzed in different chemicals, e.g., $1\,\mathrm{mol\,l^{-1}}$ HCl, or later enzymes, e.g., pectinase, to secure the satisfactory separation of cells. Somatic investigations have used a variety of methods for slide preparation, including the smear and squash techniques.

Different cytological methods were described in detail by Darlington and La Cour in 1962, followed by various improvements made by many authors, depending on the species and tissue investigated. More recently, Fukui and Nakayama edited in 1996 an excellent laboratory manual describing methods for plant cytology investigations. An example of most commonly observed features of the prometaphase and metaphase chromosomes is shown in **Figure 3**.

Karyotype Analysis

The karyotype of an organism is a descriptive analysis of the chromosome complement. Each karyotype is defined numerically with statistical parameters of values based on the measurements of the chromosome's morphology. A graphic presentation is often used to give a better illustration of the chromosomes and their morphological features. Problems of comparison among studies can arise due to the lack of standardization in presenting a karyogram, graphically or numerically. An insight into this problem was published in *Forest Genetics* journal in 1996, with recommendations for standardized presentation of karyotypes for the species of the Pinaceae family. An example of the graphic presentation is shown in **Figure 4**.

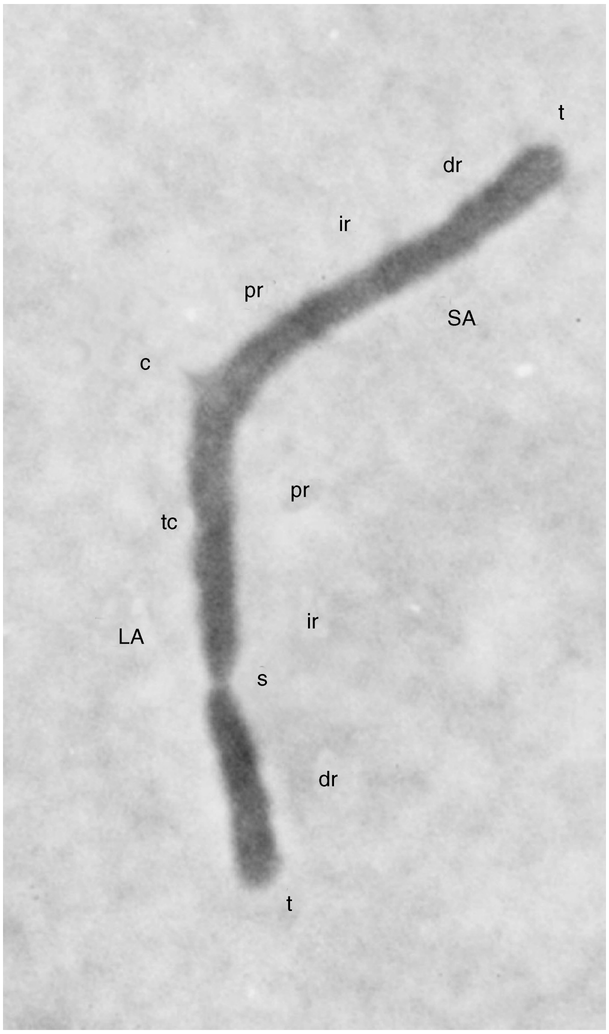


Figure 3 Chromosome terminology shown on the *Pinus nigra* metacentric chromosome V. SA, short arm; LA, long arm; t, telomere; dr, distal region; ir, interstitial region; pr, proximal region; c, centromere (primary constriction); tc, tertiary constriction; s, secondary constriction (nucleolar organization region or NOR).

Classification of chromosomes by centromere position is a basic feature of karyotype analysis. Depending on the centromere position, chromosomes can range from metacentric to telocentric. Centromeric nomenclature, however, can vary from study to study. In studies of *Pinus* species, the classification presented by Saylor's classic papers is most often used. Another classification system often cited is the nomenclature presented by Schlarbaum and Tsuchiya in 1984, which was developed according to protocols given by Levan and his coworkers in 1964. Recognizing the inconsistency in centromeric nomenclature in a wide range of studies and the need for a standard, Levan and his coworkers developed precise standards for nomenclature and devised a system for modifying the standards to allow for better distinction among chromosomes if needed. Other modifications can be used if warranted by chromosome morphology, but the modifications should be according to their protocols.

The ability for rapid communication among scientists through the internet presents an exciting possibility in sharing karyomorphological data of investigated species. An idea for consolidating data in a standardized manner in a centralized database that can be instantly analyzed and made available worldwide via the internet was presented during the Second IUFRO Cytogenetics Working Party S2.04.08 Symposium, held in Graz, in 1998.

Banding Methods

In the last quarter of the twentieth century, chromosome banding techniques began to be applied to forest tree species. These techniques allowed for better distinction between homologous chromosomes and among nonhomologous chromosomes of similar size and morphology. Chromosome banding

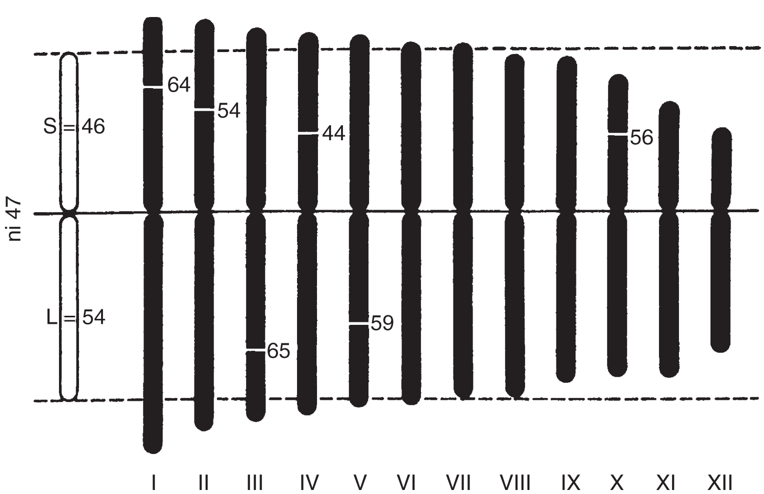


Figure 4 Graphic presentation of karyotypes shown by the idiogram of *Pinus nigra*.

is especially important in physical mapping of genes and can provide additional insight into the molecular organization of chromosomes.

Chromosome banding can be defined as a lengthwise variation in staining properties along a chromosome, induced by application of a variety of chromosome treatments by specific reagents, dyes, singly or in combination. It refers both to the process of producing banding patterns and to the patterns themselves. All of the many different banding methodologies have a common objective of accurately identifying chromosomes and parts of chromosomes. The use of banding methodology can also give insight into chromosome organization. Some banding methods have contributed greatly to both the molecular biology and cytogenetics, giving chromosome research a new and wider importance. However, successful attempts to band chromosomes of tree species using protocols for mammalian or plant species have been limited. Thus, banding of chromosomes of forest trees is currently still an enigma in terms of band numbers and/or consistency.

Important insights into chromosomal reactivity to applied reagents for revealing banding patterns was possible after Heitz in 1928 showed that certain specific chromosome segments, termed heterochromatic, do not decondense during the telophase. Constitutive heterochromatin is a permanent structural characteristic of a given chromosome pair, and is present in all cells at identical positions on both the homologous chromosomes, whereas facultative heterochromatin is heteropycnotic in special cell types or at special stages, and is related to differential gene activity, according to Brown in 1966. Constitutive heterochromatin is chromosome-specific and species-specific and can be used for chromosome identification; it is cold-sensitive, late-replicating, and genetically inert, and usually contains highly repetitive DNA sequences. After Pardue and Gall's paper in 1970 showed that Giemsa dye stained centromeres of mouse chromosomes more strongly than other chromatin, the Giemsa C-banding technique became the most widely used banding method for both animal and plant chromosomes. The first successful Giemsa C-banding of a forest tree species was on *Pinus nigra* chromosomes (**Figure 5**) by Borzan and Papeš in 1978 on haploid chromosomes in the female gametophytic tissue. Other scientists – Muratova, Tanaka and Hizume, Wochok and coworkers, and MacPherson and Filion – applied Giemsa banding to various coniferous species, mostly on root-tip meristematic tissue, and made further steps in that field. The use of Giemsa C-banding in hardwood species has been very limited. Generally, the small size of metaphase chromosomes in hardwoods limits the usefulness of this technique. An example of a Giemsa C-banding method applied to chromosomes from female gametophytic tissue of *Picea abies* is shown in **Figure 6**.

A review of Giemsa C-banding studies in conifers shows that this method successfully reveals bands of constitutive heterochromatin located in the region of the centromere, in secondary constrictions and, occasionally, in intercalary regions. In general, coniferous chromosomes contain a relatively small amount of constitutive heterochromatin. Owing to the lack of research on forest trees in this area, it is still not possible to formulate conclusions on heterochromatin distribution at the level of population, let alone of taxon.

Chromosome banding became more practical in the early 1970s, when staining protocols developed for banding chromosomes of one organism could be applied to other organisms with only minor modifications. As the use of banding protocols became more prevalent and more specific for certain chromatin or regions, classification of chromosome bands occurred as follows:

1. Heterochromatic bands, where constitutive heterochromatin (not facultative) is stained distinctively.
2. Bands occurring throughout the length of chromosome, which Sumner regarded provisionally as euchromatic bands.
3. Specific staining of the kinetochore structure.
4. Nucleolar organization region (NOR) bands.

Nomenclature of different banding methods is standardized and usually abbreviations are used to designate the method in use. In 1990 Sumner described banding nomenclature and reviewed C-banding and related methods, G-banding, R- and T-banding, Q-banding, banding with fluorochromes and methods for NOR and kinetochore staining. Fukui and Nakayama presented in 1996 banding plant chromosomes principles and detailed protocols for revealing C-bands, N-bands, fluorescent-bands 4′,6-diamidino-2-phenylindole (DAPI) for the detection of AT-rich and chromomycin A_3 (CMA) for the detection of CG-rich regions of constitutive heterochromatin in plant chromosomes, F-bands, Hy-bands, G-bands, RE-bands, and Ag-NOR-bands.

Fluorescence chromosome banding using CMA, Hoechst 33258 and DAPI has been successfully used in different coniferous species. Fluorescence *in situ* hybridization (FISH) is a technique for detecting a site of specific DNA sequences (rDNA, other classes

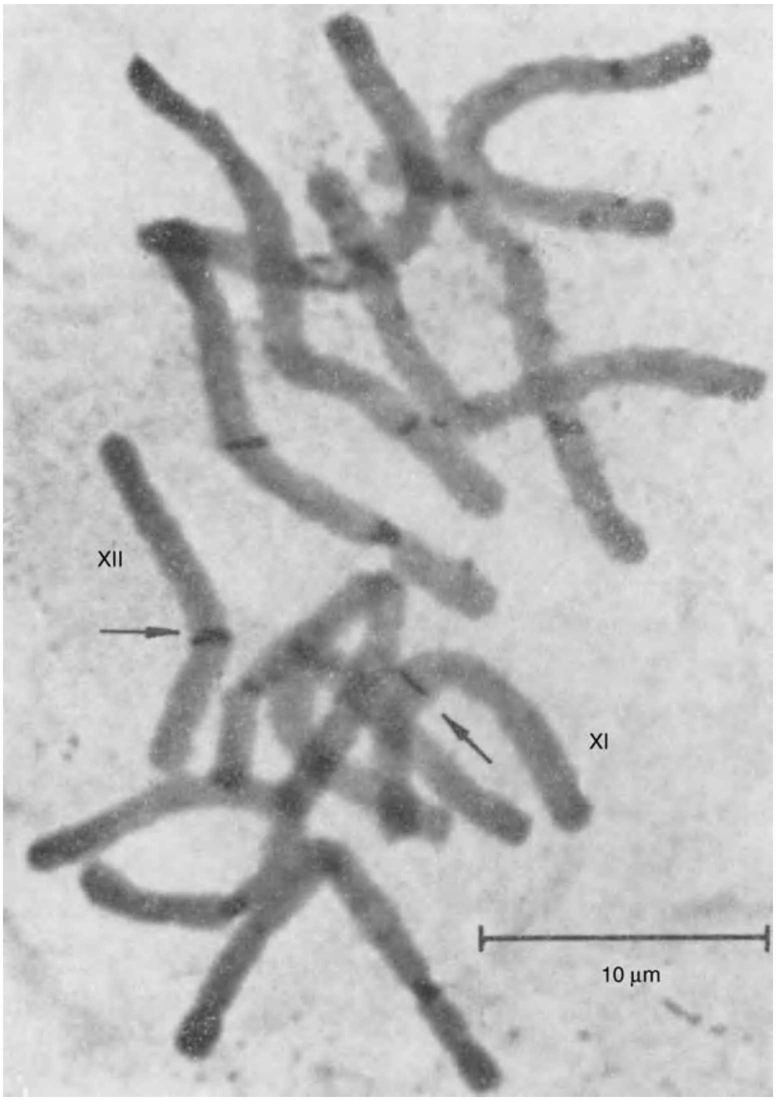


Figure 5 Giemsa C-banded chromosomes in the female gametophyte tissue of *Pinus nigra*. Arrows indicate centromeric bands on submetacentric chromosomes.

of repeated DNA, or single genes) in plant and animal chromosomes, thereby allowing physical mapping. CMA bands appearing at the secondary constrictions coincide with FISH signals when an 18S-5.8S-26S rDNA probe is used on chromosomes of coniferous and hardwood species, and in many other plant and animal species. **Figure 7** shows banded chromosomes from *Quercus pubescens* by the FISH technique, using 18S-5.8S-26S and 5S rDNA probes. Nakamura and Fukui applied in 1997 a laser dissection method to dissect specific regions of the chromosomes of giant sequoia (*Sequoiadendron giganteum*), showing that visible SAT-chromosome contains 18S rRNA genes and is the only location for those genes in the chromosome complement.

Applications of Cytogenetics to Basic Genetic Research in Forest Trees

Prior to the advent of molecular biology and *in-situ* hybridization of probes directly on chromosomes, physical gene mapping was essentially nonexistent in forest tree species. Agronomic and horticultural approaches that use chromosomal aberrations, e.g., translocations, or aneuploidy, such as monosomics or trisomics, in combination with breeding are generally not possible with coniferous species. Most conifers do not tolerate aberrations and aneuploid changes which usually affect growth and reproduction. With hardwood species, cytogenetic characterization of the different species was too limited to conduct mapping experiments. Long-term

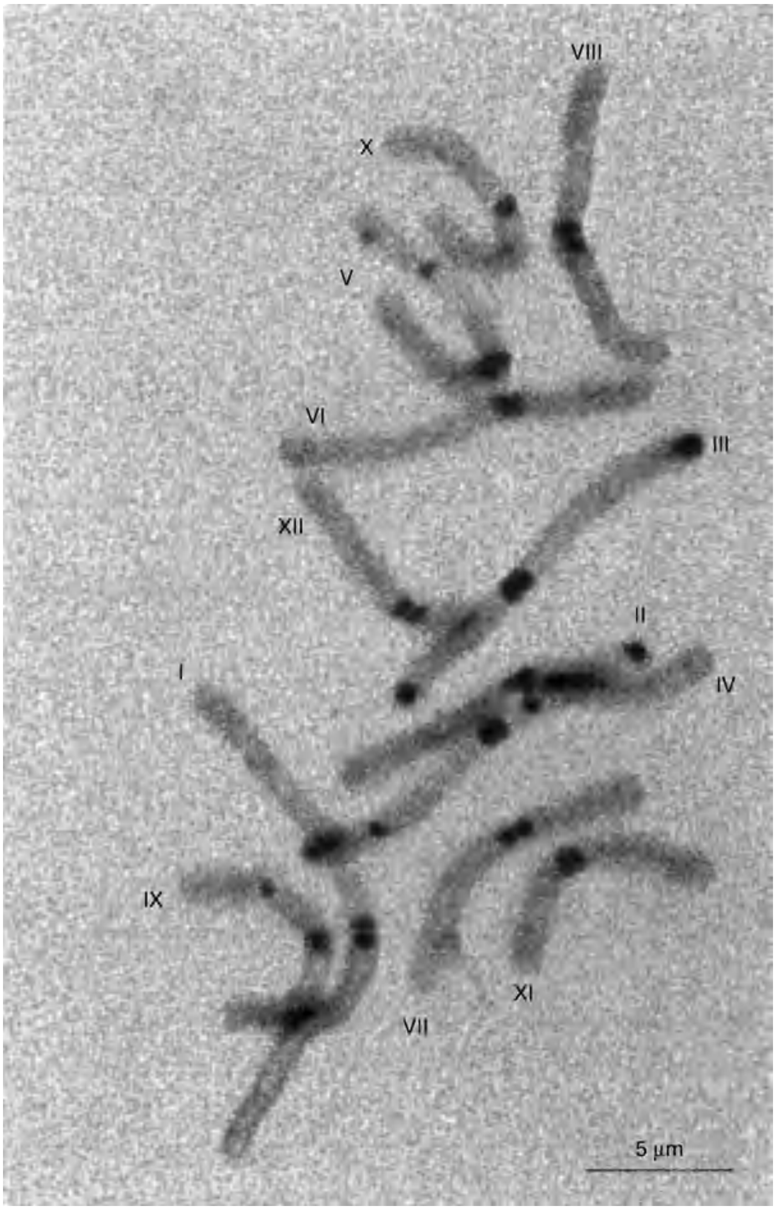


Figure 6 Giemsa C-banded chromosomes in the female gametophyte tissue of *Picea abies*.

reproductive cycles and, often, the physical size, contributed to difficulties in mapping forest tree species.

The application of chromosome banding techniques developed in the 1970s specifically to identify chromosomes was an initial step toward physical mapping. The development of chromosome imaging techniques for tree species by Fukui and by Guttenberger has also contributed to chromosome identification. *In-situ* hybridization with a variety of fluorescing probes has physically mapped gene sequences to chromosomes in a number of coniferous and some hardwood species. Nakamura and Fukui's laser microdissection of a SAT-chromosome in *Sequoiadendron* shows the potential for using a combination of cytogenetic and molecular techniques with instrumentation. Physical mapping efforts have been concentrated on coniferous species owing to their chromosome size, but advances in instrumentation from human genome projects may make studies on hardwood species more feasible.

Applications of Cytogenetics to Tree Improvement

Using a cytogenetic approach to improve a plant species usually involves breeding and/or euploid

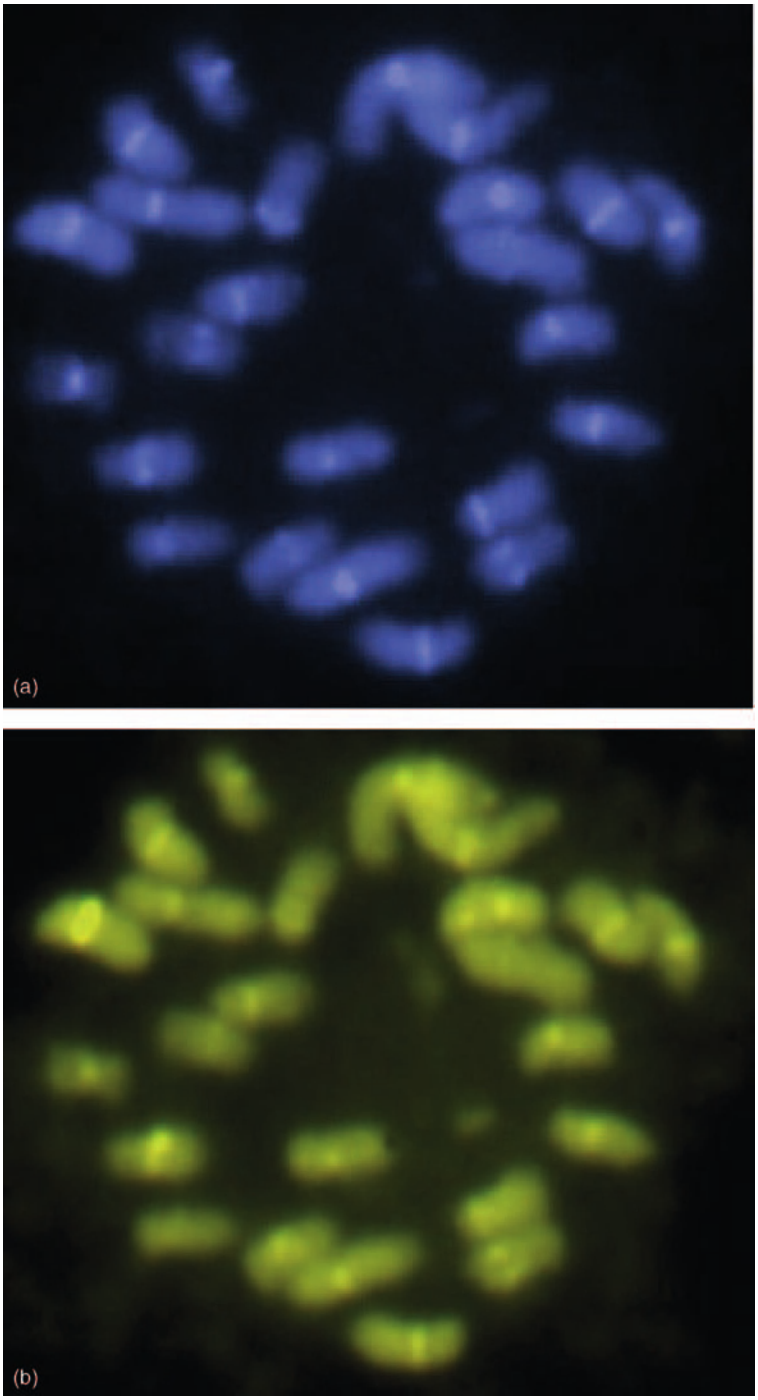


Figure 7 Banded chromosomes from the root-tip meristem tissue of *Quercus pubescens*. (a) Coloration with 4′,6-diamidino-2-phenylindole (DAPI) reveals fluorescent bands exclusively in centromeric regions of all 24 chromosomes of *Q. pubescens* complement. (b) Coloration with chromomycin A_3 (CMA) reveals fluorescent bands in all 24 chromosomes at the juxtaposition with those produced by use of DAPI. The most prominent CMA bands at the centromeric region of one metacentric pair correspond to 18S-26S rDNA sites. Note the same metaphase plate for both DAPI and CMA banding. Reproduced with permission from Zoldos V, Papes D, Cerbah M *et al.* (1999) Molecular-cytogenetic studies of ribosomal genes and heterochromatin reveal conserved genome organization among 11 *Quercus* species. *Theoretical and Applied Genetics* 99: 969–977.

increases in chromosome number. Unfortunately, the majority of cytogenetic studies of forest trees have been on coniferous species and little improvement has been made. Most species have a juvenile period that can be measured in years, which has precluded improvement via a cytogenetic approach when breeding is involved. The delay in breeding may be circumvented by using accelerated breeding techniques that have been developed for some species. Shortening the breeding cycle, however, is only a partial solution. Chromosome changes in this group of trees are not well tolerated, with the exceptions of Taxodiaceae and Cupressaceae. It is only in *Cryptomeria japonica* that euploid changes from the normal diploid state have been exploited.

Cytogenetic improvement of hardwood species shows more promise than coniferous species. Some species have relatively short juvenile periods that would not greatly inhibit an integrated cytogenetic/breeding approach to improvement. Ploidy changes, either natural or induced, are not a problem in many species, and euploid changes from the diploid state have been shown to increase yield in some species. Studies have shown that triploidy is the optimal level for growth in *Populus* and could be for some *Quercus* species. In general, cytogenetic manipulation of hardwood species is a vast reservoir of potential waiting to be explored.

Conclusion

A general conclusion on the benefits from cytogenetic studies on forest trees is somewhat problematic. Studies on forest trees are able to follow successfully the methods applied in human, animal, and plant cytogenetic studies, but usually have not been pursued in depth, e.g., in an integrated long-term breeding and cytogenetic program with tangible objectives. During the era when cytogenetics was prevalent in science and resources were available, many studies concentrated on coniferous species in Pinaceae, in which chromosome aberrations and changes in chromosome number are usually disastrous. Early efforts in studying and developing triploid aspen were successful, but diminished in the 1960s. Despite the success of the triploid aspen program, interest in cytogenetic studies did not spread to other hardwood species. Although sporadic studies on ploidy changes in some hardwood species have shown promise for increasing timber yields, corresponding tree improvement programs have generally not had a cytogenetic component. Advances in instrumentation, e.g., chromosome imaging systems and laser microdissection, coupled with wise choices for experimental material can make cytogenetics an important component of basic and applied forestry research. Therefore, it can be concluded that the contribution of cytogenetics to the forestry profession and science in general has been small, but the potential for contribution still remains significant.

See also: **Ecology**: Reproductive Ecology of Forest Trees. **Genetics and Genetic Resources**: Genetic Systems of Forest Trees; Molecular Biology of Forest Trees. **Tree Breeding, Practices**: Southern Pine Breeding and Genetic Resources. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Forest Genetics and Tree Breeding; Current and Future Signposts.

Further Reading

Borzan Ž and Kriebel HB (eds) (1996) Cytogenetics. *Forest Genetics* 3(3): 125–171.

Borzan Ž and Schlarbaum SE (eds) (1997) Cytogenetics of forest trees and shrub species. *Proceedings of the First IUFRO Cytogenetics Party S2.04.08 Symposium*, Brijuni 1993. Zagreb: Croatian Forests, Inc., Zagreb and Faculty of Forestry, University Zagreb.

Darlington CD and La Cour LF (1962) *The Handling of Chromosomes*. London: George Allen & Unwin.

Darlington CD and Wylie AP (1955) *Chromosome Atlas of Flowering Plants*. London: George Allen and Unwin.

Fedorov AA (1974) *Chromosome Numbers of Flowering Plants*. Koenigstein: Otto Koeltz Science Publishers.

Ferguson M (1904) Contribution to the knowledge of the life history of *Pinus* with special reference to sporogenesis, the development of the gametophytes and fertilization. *Proceedings of the Washington Academy of Science* 6: 1–202.

Fukui K and Nakayama S (eds) (1996) *Plant Chromosomes Laboratory Methods*. Boca Raton, FL: CRC Press.

Guttenberger H, Borzan Ž, Schlarbaum SE, and Hartman TPV (eds) (2000) Cytogenetic studies of forest trees and shrubs – review, present status, and outlook on the future. *Proceedings of the Second IUFRO Cytogenetics Party S2.04.08 Symposium*, Graz, 1998. Zvolen, Slovakia: Arbora Publishers.

Levan A, Fredga K, and Sandberg AA (1964) Nomenclature for centromeric position on chromosomes. *Hereditas* 52: 201–220.

Moore RJ (1973) *Index to Plant Chromosome Numbers 1967–1971*. Oosthoek's Uitgeversmaatschappij B.V.: Utrecht, Netherlands. 539 pp.

Rieger R, Michaelis A, and Green MM (1976) *Glossary of Genetics and Cytogenetics – Classical and Molecular*. Berlin: Springer Verlag.

Sax K and Sax HJ (1933) Chromosome number and morphology in the conifers. *Journal of Arnold Arboretum* 14: 356–375.

Schlarbaum SE (1991) Cytogenetics of forest tree species. In: Tsuchiya T and Gupta PK (eds) *Chromosome Engineering in Plant Genetics and Breeding*, vol. II, pp. 593–618. Netherlands: Elsevier Science Publishers.

Sumner AT (1990) *Chromosome Banding*. London, UK: Unwin Hyman.

Zoldos V, Papes D, Cerbah M, *et al.* (1999) Molecular-cytogenetic studies of ribosomal genes and heterochromatin reveal conserved genome organization among 11 *Quercus* species. *Theoretical and Applied Genetics* 99: 969–977.

Forest Management for Conservation

R Uma Shaanker, N A Aravind and K N Ganeshaiah, Ashoka Trust for Research in Ecology and the Environment, Hebbal, Bangalore, India

Introduction

Forest management for conservation is in practice different from management of forest for optimizing economic returns. It refers to the preservation of forest for the explicit functions of conserving the constituent biodiversity elements and ecosystem processes. The concept of managing forest for conservation is very old and was practiced by many traditional cultures and societies across the world. The resurgence however of the concept in the nineteenth century followed the European colonization events and thereafter more recently owing to the disproportionately large human pressure on the forest resources. Several models of forest management for conservation have emerged, both globally and locally. From very formal models such as the protected area network to completely informal models of grassroots people's movements, managing forests for conservation has gained an unparalleled momentum in the last couple of decades. In this article we trace the development of the concept of managing forests for conservation with a critique on the various models of management for conservation.

Historical Developments

Historically, forest management for conservation can be traced to two major schools, the first embedded in traditional cultures and the second emerging subsequent to European colonization of the tropical world. In both, the motive seems to have emerged from the need to prevent the overexploitation of natural resources, be it waterfowl hunting by the Egyptians or timber felling by the British in India. Ashoka, one of the illustrious Emperors of India (274–232 BC) was known for his great diligence in conserving forests. He not only passed an official promulgation forbidding the killing of a set of animals, but also decreed that forests must not be burnt. A large number of civilizations across the world, including the Greeks, Romans, Mongols, Aztecs, and Incas, developed such decrees from time to time. With the wave of exploitation of natural resources by the European powers during the eighteenth and nineteenth centuries, the need for conserving the natural resources, if only to build up the growing stocks, was acutely realized. This resulted in a number of promulgations in the European colonies from the Ivory Coast in Western Africa to Indonesia in Eastern Asia. In India, for example, the British established the Imperial Forest Department in 1864 to oversee the utilization of timber for railway crossties. By another legislation, in 1874, the British classified forests in India into three categories, viz., the reserved forests (where extraction of timber was permitted), protected forests (which were under state control and protected against extraction pressures from the local people), and village forests (apparently open to the village settlements for sourcing their needs).

In the recent past, a significant shift in the conservation ethos occurred when attention was paid to conserving or preserving species other than those that were merely economically useful. Thus, perhaps for the first time in recent history, attention was paid to the conservation of invertebrates, small plants, amphibians, and reptiles. One of the earliest milestones in this movement can be traced to the 1960s and 1970s when several countries including the USA passed national legislation on endangered species. Thus from a predominantly economic approach to forest management there was a shift in emphasis to forest management for conservation.

Models of Forest Management for Conservation

Among global models of forest management for conservation, three types can be readily identified: (1) formal models that include protected areas; (2) semiformal models that includes conservation through community participation with the state, such as sacred groves, joint forest management and extractive reserves; and (3) informal models arising from grassroots people's movements (**Figure 1**). The formal models are almost invariably controlled by the state while the semiformal approaches involve varying degrees of state and local community regulations. The informal models are mostly led by individual groups of people or institutions. In the following sections, we describe the salient features of these models with a brief commentary on the relevance of these models to conservation issues and practices.

Formal Model of Forest Management for Conservation: Protected Areas

History

According to the IVth World Congress on National Parks and Protected Areas, 1992, a protected area is

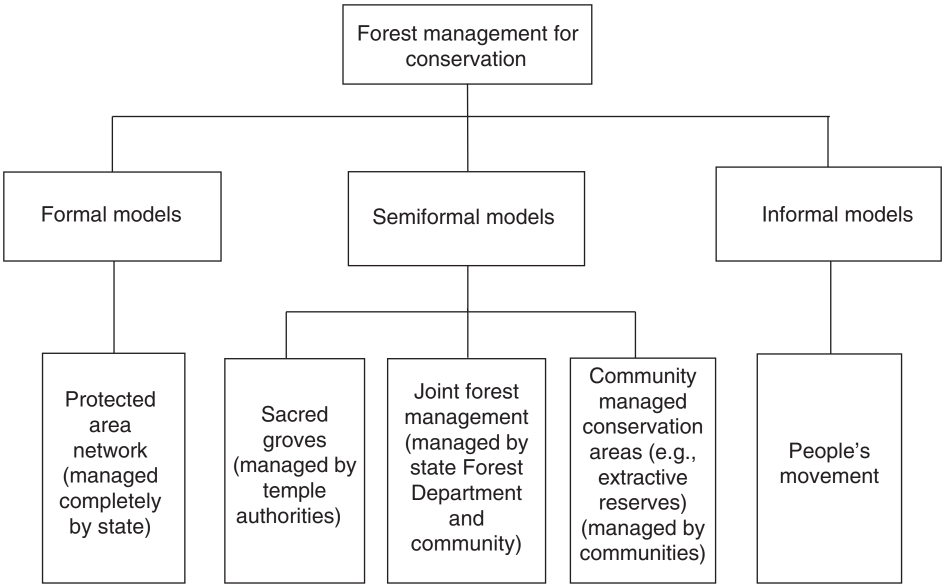


Figure 1 Schematic diagram of the various models of forest management for conservation.

defined as: An area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means. The designated protected areas are usually accorded protection by the state authorities and often exclude local people and institutions from decision-making processes or procurement of direct economic benefits. By enforced exclusion of all forms of dependence, the protected area is supposed to serve the conservation goals in its purest form. Delimiting a protected area was historically used by rulers to exclude people from parks to conserve, primarily, a healthy population of wild animals for purposes of hunting. Thus among the first 'conservation areas' in Europe were the medieval hunting parks such as the New Forest established in 1079 by William I of England. In recent history, the first area protected specifically for 'the preservation of' its biodiversity and 'for the enjoyment of the people' was Yellowstone National Park, established by the US Congress in 1872, and later followed by the creation of the National Park Service in 1916. The latter was instrumental in the establishment of the network of protected areas across the USA.

Classically the protected area concept involves setting aside natural or seminatural areas with high conservation value in which genes, species, communities and even habitats are conserved. Based on the emphasis of conservation, the IUCN has categorized protected areas into several groups (**Figure 2**). With increasing international efforts to preserve biological diversity, protected areas have become central to any global strategy for conservation.

Global Network of Protected Areas

Globally there are currently 9869 protected areas (>1000 ha) covering an area of about 9 317 874 km^2, about 6.29% of the earth's land surface area (**Figure 3**). Protected area networks vary considerably from one country to another, depending on needs and priorities, and on differences in legislative, institutional, and financial support. Europe has the maximum area under protection (about 16.4% of the continent's land area) while Asia has the least, accounting for only 4.29% of the land area (**Figure 4**). The global distribution of protected areas does not necessarily reflect the underlying patterns in species richness and biological diversity. For example, in the world's 25 biodiversity hotspots, which harbour 30–40% of all earth's biodiversity, an average of less than 10% of land area is protected. Partly to rectify this discrepancy, a number of protected areas have been established in the framework of international instruments include the World Heritage Sites, designated under the 1972 Convention for the Protection of the World Cultural and Natural Heritage and the World Network of Biosphere Reserves, operated under the UNESCO's Man and Biosphere (MAB) program.

Effectiveness of Protected Areas

Critics claim that protected areas cannot serve as effective means of conservation, because often these forests are vulnerable to anthropogenic pressures. The World Bank/World Wildlife Fund (WWF) Alliance have shown that less than one-quarter of declared national parks, wildlife refuges, and other

IUCN has defined a series of eight protected area management categories, based on primary management objective. These are:

1. Strict Nature Reserve/Scientific Reserve. To protect nature and maintain natural processes in an undisturbed state in order to have ecologically representative examples of the natural environment available for scientific study, environmental monitoring, education, and for the maintenance of genetic resources in a dynamic and evolutionary state.

2. National Park. To protect outstanding natural and scenic areas of national or international significance for scientific, educational, and recreational use. These are relatively large natural areas not materially altered by human activity where extractive resource uses are not allowed.

3. Natural Monument/Natural Landmark. To protect and preserve nationally significant natural features because of their special interest or unique characteristics.These are relatively small areas focused on protection of specific features.

4. Managed Nature Reserve/Wildlife Sanctuary. To assure the natural conditions necessary to protect nationally significant species, groups of species, biotic communities, or physical features of the environment where these may require specific human manipulation for their perpetuation. Controlled harvesting of some resources can be permitted.

5. Protected Landscapes and Seascapes. To maintain nationally significant natural landscapes which are characteristic of the harmonious interaction of humans and land while providing opportunities for public enjoyment through recreation and tourism within the normal lifestyle and economic activity of these areas. These are mixed cultural/natural landscapes of high scenic value where traditional land uses are maintained.

6. Resource Reserve. To protect the natural resources of the area for future use and prevent or contain development activities that could affect the resource pending the establishment of objectives which are based upon appropriate knowledge and planning. This is a "holding" category used until a permanent classification can be determined.

7. Anthropological Reserve/Natural Biotic Area. To allow the way of life of societies living in harmony with the environment to continue undisturbed by modern technology. This category is appropriate where resource extraction by indigenous people is conducted in a traditional manner.

8. Multiple Use Management Area/Managed Resource Area. To provide for the sustained production of water, timber, wildlife, pasture, and tourism, with the conservation of nature primarily oriented to the support of the economic activities (although specific zones may also be designated within these areas to achieve specific conservation objectives).

Figure 2 IUCN system of classification of Protected Area Management Categories.

protected areas in 10 key forested countries were well managed, and many had no management at all. In other words, only 1% of the protected land area is secure from serious threats such as human settlement, agriculture, logging, hunting, mining, pollution, war, and tourism, among other pressures. However, officially designated conservation areas have been shown to be successful at reducing forest clearance and, to a lesser degree, effective at mitigating the effects of logging, hunting, fire, and grazing (**Figure 5**). Even modest increases in funding to the parks are likely to increase the ability of the parks to protect biodiversity.

Despite their shortcomings, protected areas do provide the last refugia for many species threatened with extinction. About 40 critically endangered trees are found almost exclusively within the protected areas across the world. These include *Hibisicadelphus woodii* (Malvaceae) with population fewer than 10 in the Napali Coast State Park, Hawaii; *Parsania formonsana* (Fagaceae) in the Kenting National Park, Taiwan; and *Shorea bakoensis*, in Sarawak, Malaysia. In Thailand, a large number of important timber species, which have been extensively harvested from the native forests, are today found only in protected areas. The last remaining population of the white rhinoceros (*Diceros simus*) is found in the Garamba National Park in the Democratic Republic of Congo as much as the remaining population of the Asiatic lion (*Panthera leo*) in the Gir National Park, Gujarat, India (**Table 1**).

Protected areas also serve as repositories of intraspecific genetic diversity for economically important forest species. For example, populations of sandal (*Santalum* spp.), a tree treasured for its heartwood oil in India and that has been extensively felled as a result, have higher genetic diversity in national parks and sanctuaries than outside. Protected areas also afford higher population genetic diversity for several species of bamboos and rattans. Thus in addition to species conservation, protected areas fulfil an important function in the conservation of intraspecific genetic diversity.

Deficiencies of Protected Areas

Critics also point to the fact that protected areas tend (1) to be biased towards conserving charismatic taxa

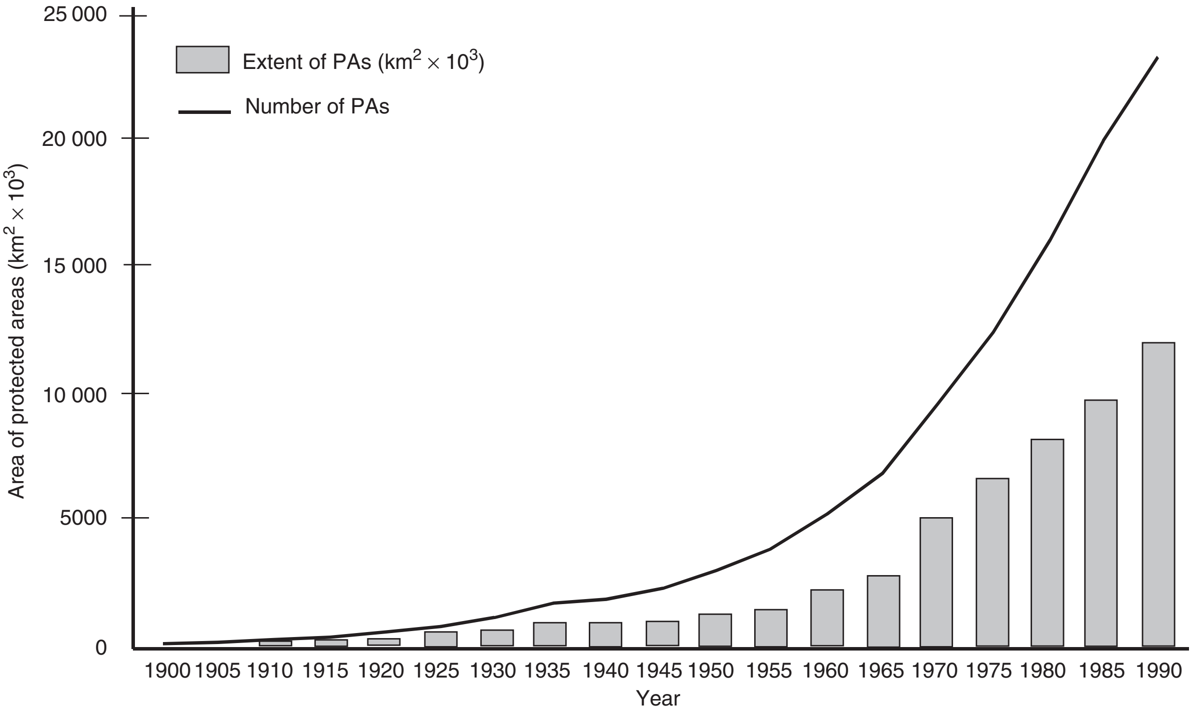


Figure 3 Cumulative area (bars) and cumulative number (line) of protected areas in the world since 1900. About 59% of the protected areas are less than 1000 ha. Redrawn from Michael JBG and Paine J (1997) State of the world's protected areas at the end of the twentieth century. In IUCN World Commission on Protected Areas *Symposium on Protected Areas in the 21st Century: From Islands to Networks*, 24–29 November 1997, Albany, Australia.

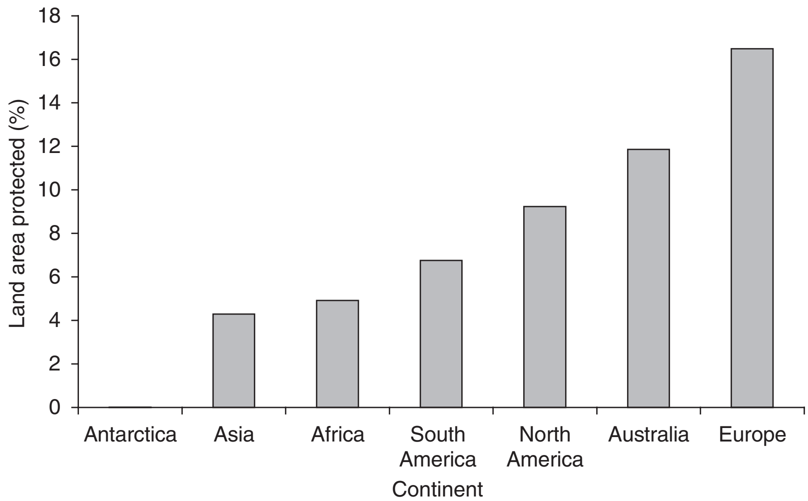


Figure 4 Percentage of land area protected in different continents.

at the expense of lesser known taxa, (2) to be too small to host viable populations, (3) to act as insular and isolated habitats that do not allow for genetic mixing across populations, and (4) to be costly and demanding in terms of logistics to secure the protected area from extraneous pressures.

Among the commonest of criticisms is that protected areas do not necessarily address the conservation needs of nontarget taxa. This is because protected areas have been generally designated on the basis of geomorphical or phytogeographic considerations or, frequently, due to the presence of charismatic large mammals (tiger and elephants in India, panda in China, grizzly bear in British Columbia, wolf in the USA, gorilla, white rhinoceros, and okapi in the Congo Basin, etc.) and not on

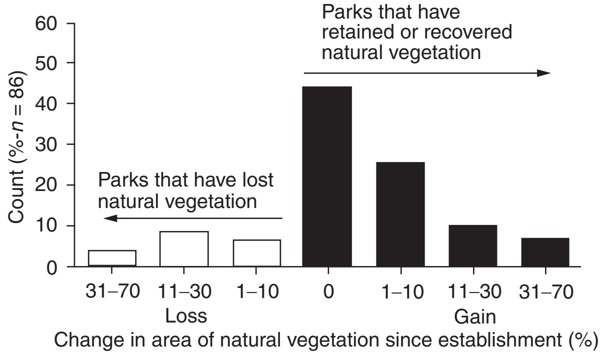


Figure 5 Effectiveness of protected areas in the world. The figure describes the change in the area of natural vegetation for 86 tropical parks. The majority of the parks have either experienced no net clearing or have actually increased natural vegetation cover. Reproduced with permission from Bruner AG, Raymond EG, Rice RE, and da Fonseca GAB (2001). Effectiveness of parks in protecting tropical biodiversity. *Science* 291: 125–128.

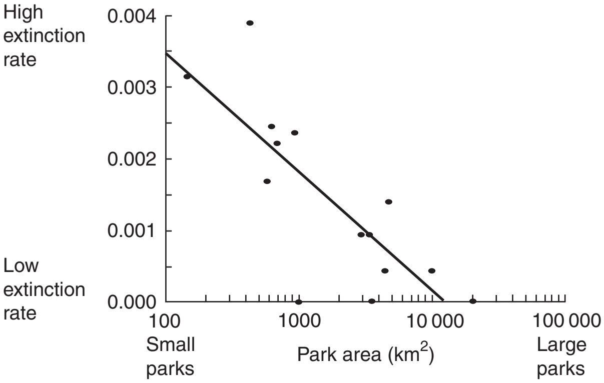


Figure 6 Extinction rates of mammals versus park size. Each dot represents the extinction rates of animal populations for a particular US national park. Mammals have higher extinction rates in smaller parks than larger ones. Reproduced with permission from Newmark WD (1995) Extinction of mammal populations in western North American national parks. *Conservation Biology* 9: 512–526.

Table 1 Protected areas as refugia for critically endangered species; the examples illustrated are those in which the concerned species is not present outside the protected areas

Species	*Protected area*
Animals	
Asiatic lion (*Panthera leo*)	Gir National Park, Gujrat, India
Javan rhinoceros (*Rhinoceros sondaicus*)	Udjung Kulon National Park, Java (Indonesia) and the Cat Tien National Park in Vietnam; it may also still exist in other locations
Hangul or Kasmir stag (*Cervus elaphus hanglu*)	Dachigam National Park, Jammu and Kasmir, India
Orangutan (*Pongo pygmaeus*)	Sepilok Forest Reserve, Malaysia
Straight-horned markhor (*Capra falconeri*)	Sheikh Buddin National Park, Pakistan
Plants	
Dypsis ovobontsira (Palmae)	Mananara Biosphere Reserve, Madagascar
Rhododendron protistum var. *giganteum* (Ericaceae)	Nature Reserve, Gaoligongshan, Yunnan Province, China
Maillardia pendula (Moraceae)	Aldabara Strict Nature Reserve, Seychelles
Hibisicadelphus woodii (Malvaceae)	Napali Coast State Park, Hawaii, USA
Parsania formonsana (Fagaceae)	Kenting National Park, Taiwan
Shorea bakoensis	Sarawak, Malaysia

a holistic basis. The disproportionate emphasis on few large mammals may divert attention from other similarly endangered taxa. Thus it is suggested that the boundaries of protected areas need to be revised to fulfil the conservation requirements of a more representative range of taxa.

The trade-off of size with number of protected areas has been the subject of considerable debate. A single large reserve allows for a wider habitat heterogeneity that is more representative of landscape complexity, and larger population sizes, particularly important for maintaining viable populations of wide ranging low-density species such as carnivores (**Figure 6**). On the other hand, several small reserves offer a degree of protection from large-scale catastrophic events, such as disease, fire, or extreme weather events that may destroy populations confined to a single reserve.

Protected areas could be made more effective by establishing them in sites known to harbor exceptionally high species diversity and/or endemism. Efforts should be made to optimize the selection of new protected areas by iterative processes that maximize the biological diversity conserved in a given area.

Semiformal Model of Forest Management for Conservation

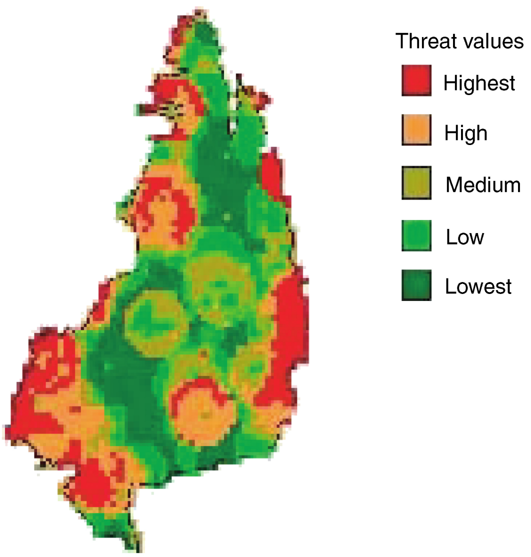
Protected areas that exclude humans alienate local people who may have traditionally depended on forest resources. A recent study estimated that 54% of protected areas considered had residents who contested the ownership of some percentage of the park area. In India, with about 572 protected areas occupying 4.58% of the geographical area, an estimated 3 million people live within the protected areas with several million more living adjacent to the parks. Rather than evicting people traditionally dependent upon forests a more pragmatic and sympathetic approach is to manage forest use and impacts in a way that maximizes conservation gains while realizing economic benefits (**Figure 7**). Community involvement in the management of protected areas, where the state and the local inhabitants work together for both conservation and basic livelihood security, is seen as a positive and necessary strategy for successful conservation programs in both tropical and temperate regions.

Semiformal methods of forest management for conservation are predominantly located in tropical countries that have a long history of association of people with the forests and that retain sufficiently large areas of forest such that these associations persist. The origin of these models can often be traced to the codification of the use of forest resources. Among the semiformal models, the predominant are the temple forest or sacred forests, joint forest management (*see* **Social and Collaborative Forestry:** Joint and Collaborative Forest Management), and extractive reserves.

Sacred Groves

Probably begun as manifestations of nature worship, sacred groves have played an important role in conserving the forest and its constituent biodiversity elements. This unique community-linked forest conservation concept is practiced in several tribal and agrarian regions of the world. A number of societies in Asia, Africa, Europe, America, and Australia have long preserved sections of their natural environment as sacred groves. The practice of sacred groves is widespread in India (**Figure 8**). About 4215 sacred groves covering an area of 39 063 ha are estimated to

In India a number of protected areas (PAs) continue to be inhabited by the tribal and indigenous communities who depend almost completely on the forests for their livelihoods and thus constitute direct threats to the PAs. It is clear that unless attempts are made to reduce these threats, the protected areas in succumb to the increasing human pressures. Unfortunately most of the threats arising from anthropogenic activities in the protected areas are not easily quantifiable as they are very dynamic and heterogeneous. Effective conservation of such protected areas demands that we evaluate the threats and accordingly formulate appropriate management plans to mitigate them. However, there is hardly any standardized methodology to evaluate the complex threats that protected areas might face.



Threat map of BRT wildlife sanctuary, south India

Ganeshaiah and his coworkers developed a protocol for measuring and mapping threats in a protected area, a wildlife sanctuary, in South India. They computed three threat values viz:

1. Settlement associated threat from human, cattle, and sheep.
2. Developmental activity associated threats due to major and minor roads.
3. Accessibility-related threats due the steepness of the terrain.

Combining all the three threat values, they derived a composite threat index for each grid over the sanctuary. The composite threat index clearly reflected the pressures on the sanctuary as evident from the strong correlation between the threat levels and the human related disturbance activities and a strong negative relation between the composite threat index of a grid andits tree diversity. Periphery of the sanctuary (in deep red) is more threatened than those in the core (green). Based on the composite threat index, Ganeshaiah and coworkers have proposed strategies to manage the forest to maximize the conservation gains.

Figure 7 Measuring, mapping and managing threats in a protected area. Reproduced with permission from Ganeshaiah KN and Uma Shaanker R (2003) *A Decade of Diversity*. Bangalore, India: Ashoka Trust for Research in Ecology and the Environment and University of Agricultural Sciences, Bangalore.

Figure 8 A typical sacred grove in Coorg District, Western Ghats, India. Photograph by courtesy of G. Ravikanth.

be distributed in India and are located in habitats ranging from resource-rich forested landscapes, in the Western Ghats, to extremely resource-poor desert conditions, in western and central India. In Ghana, about 1.5% of the land is covered with nearly 2000 groves. Typically the local village temple authority directly manages the groves. However with passage of time, the regulations were extended to the state as well. In India, for instance, the local revenue department and the forest department have joined the temple authorities in managing the groves.

Being bound by taboo, sacred groves have been as effective as modern protected areas in conserving biological diversity and serving as a refugia for endangered species. In Coorg district along the Western Ghats of India, about 14% of tree species, 26% of bird species, and 44% of macrofungi were exclusively found in the groves. Certain species such as *Dysoxylum malabaricum*, *Anacolosa densiflora*, *Holigarna arnottiana*, *Diospyros bourdilloni*, *Poeciloneuron indicum*, and *Vateria indica,* which are in heavy demand for their commercial value, continue to survive and flourish mostly in the sacred groves. The sacred groves called 'orans' managed by the Bishnoi community of Rajasthan, India are well known for their conservation ethos of protecting the khejari trees (*Prosopis cineraria*) and the blackbuck (*Antelope cervicarpa*) (**Table 2**).

Over the years the sacred groves have been threatened from both powers within and outside. In India, from early nineteenth century, the British gained control over the use of forests of the Western Ghats including the vast network of sacred groves. At certain other places, taboos relating to the groves began to weaken. With declining forest resources outside the groves, people began to remove leaf litter and dead wood from the groves to meet the needs of the charcoal industry. Encroachment of the sacred groves, notably by forest-based plantations such as

Table 2 Sacred groves as refugia and sites of relict vegetation; the species listed below are known to occur either exclusively or predominantly in the sacred groves

Species	*Area*
Kunstleria keralensis	Southern Kerala, India
Belpharistemma membranifolia, *Buchanania lanceolata*	Kerala, India
Syzygium travancoricum, *Cinnamomum quilonensis*,	Kerala, India
Philautus sanctisilvaticus	Amarkantak, Madhya Pradesh, India

coffee, also took its toll. Between 1905 and 2000, the total area under groves in Coorg, decreased from 6277 to 2550 hectares with about 45% of the groves smaller than 0.4 ha and 80% less than 2 ha. Perhaps in large measure degradation of the groves has been associated with decreased religious rigor among the people over time. The highly fragmentary nature of the groves with their poor insularization in a matrix of grassland and forest makes them very vulnerable.

Maintaining the sacred groves might not only help in conserving the biological diversity in the forests, but also serve to be symbolic of the traditional conservation cultures associated with some of the oldest religions and faiths across the world. In the context of conserving the genetic resources, the groves act as micro-hotspots of biological diversity, and thus merit serious attention. The groves, by their nature, can complement protected areas in forming a network of forest conservation areas in the tropics.

Joint Forest Management Program in India

In a pioneering move, the government of India formulated a National Forest Policy in 1988 where it emphasized the need of people's participation in the management of forests. Specifically the policy urged the need for 'creating a massive people movement with the involvement of women, for achieving these objectives and to minimize pressure on existing forests.' In June 1990, the government of India formally unleashed a new system of forest management involving grass root institutions popularly known as 'Joint Forest Management' (JFM) (*see* **Social and Collaborative Forestry**: Joint and Collaborative Forest Management). The JFM is a tripartite body with the involvement of the Forest Department, local level institutions, and nongovernmental organizations (NGOs). The JFM characterizes a paradigm shift in forest management from a centralized management to decentralized management, from revenue orientation to resource orientation, from a production motive to a sustainability motive, from target orientation to process orientation, and from restricting people to working with people. By the year 2000, the JFM program had been launched in 22 states in India, covering an area of 10.24 million ha of forest (about 5.5% of the forested area) through 36 130 JFM committees. In the relatively short time of its existence, the JFM has had its impact in regressing the loss of forest cover in a few states such as West Bengal, Madhya Pradesh, and Andhra Pradesh. However, not all the states in the country have shown similar impacts of JFM. The failure of JFM is attributed often to the lack of coordination between state and members of a JFM initiative. More recently, JFM has been introduced in neighboring countries such as Nepal and Pakistan.

Community Managed Conservation Areas

In Brazil, as in many other tropical countries, a large number of indigenous communities continue to live within the forest where they are dependent on the forest resources for their livelihood. Declaration of protected areas and national parks in such countries have resulted in a serious social problem with either the displacement of the indigenous people or restriction of their use of the forest. Partly to address the social conflict and to maintain efforts to conserve the forest, the Brazilian government initiated the establishment of extractive reserves in the Amazon forest. Under this approach, rather than fence people away from the forest, the reserves permitted the people to manage the forest for their subsistence livelihoods, thereby providing incentives for conservation and sustainable management of the forest resources. Thus the extractive reserves have been broadly successful in preventing land clearance or logging. To date about 12 extractive reserves covering over 3 million ha have been established. However, extractive reserves have not always been successful in maintaining the balance desired between meeting the people's dependence and conserving the ecosystem. Close monitoring and reinforcement could perhaps make community managed conservation areas more effective for conservation than they actually are.

Community managed conservation areas might be highly relevant in regions that have very little forest under government control, as is the case in a number of South Pacific countries. The South Pacific Biodiversity program brought together local communities, NGOs, and governments in 14 countries in the south Pacific to conserve the biological diversity in what has been referred to as the community managed conservation area. The program provides for the sustainable use of the resources in these protected areas but ensuring that the important ecological features and processes are maintained.

Informal Model of Forest Management for Conservation: People's Movement

A number of informal people-based approaches for managing forest for conservation has been the cornerstone of conservation in many traditional cultures in the world. These approaches are essentially amorphous and have no formal structures. Often they have emerged in response to local community perceptions about how local natural resources were being exploited.

In India, there have been several important people-based movements that have made significant contributions to the way forests have been managed. One such illustration is the Chipko movement (chipko, to stick or embrace) initiated by the Bishnoi community of Rajasthan in the early eighteenth century. In this movement local people embraced trees, often at grave risk to their own lives, to prevent the trees from being felled by the King of Jodhpur (**Figure 9**). The movement has since spread to many districts of the Himalayas, in Uttar Pradesh, and Himachal Pradesh in the north, Karnataka in the south, and Bihar in the east, and to the Vindhyas in Central India, and is now realized as a popular people-led movement to conserve trees. Another notable people's movement, in the southern state of Kerala, India rescued a major evergreen forest, the Silent Valley, from being destroyed by a hydroelectric

Figure 9 Chipko movement in India (for details see text).

project. The valley was declared a national park in 1985. In Slovakia, an NGO, WOLF, has since 1993 been working to save natural forests that include large predators such as wolves. WOLF is predominantly managed by local tribes, each tribe adopting a mountain range to save the natural forest. Whether practiced in the Australian outback by the Aborigines or in Amazonia by native Indians, these movements have fought, often successfully, unscrupulous exploitation of forest resources by larger interests. Several such movements have, over time, gained sufficient strength and publicity that they have been later adopted into more formal approaches to forest management.

Conclusions and Implications

Prior to the major human settlements and advances tropical forests covered about 17 million km^2 of the earth's surface. Today, less than half of this remains. The forests lie in some of the most economically underdeveloped and heavily populated countries in the world. Consequently even these remnants face extreme pressures due to an increasing demand on the forest resources by the developing economies. It is feared that unless urgent measures are taken to conserve the remaining forest, not only will these forests be lost but there will also be an irreversible loss of the variety and performance of life functions on earth. Awareness of both threats and consequences has stimulated urgent efforts, initiated mostly at the beginning the twentieth century, to develop various approaches to managing forests in a manner that would conserve biological diversity and ecosystem processes. The establishment of protected areas has been central to these efforts, and now about 6.3% of the earth's land surface is under protection. While protected areas have their faults, there is an overriding consensus that they could be the last refugia for several scores of critically endangered species. Besides state-regulated protected areas, several semiformal approaches to managing forest for conservation also exist, such as sacred groves and people-inclusive forest management (e.g., joint forest management and community managed conservation areas). While the reach of these systems has been restricted, they have nevertheless been moderately successful in managing forest for conservation and local benefit in many developing countries. People-led movements have also been a powerful force in lobbying for improved management for conservation and sustainable development in countries such as India and Brazil, and have been precursors to some major conservation movements. It is believed that collectively the various models of conservation, from the very formal protected area networks to the informal but powerful people-led movements, will complement each other to avoid exploitative management in favor of sustainable management.

Further Reading

Bruner AG, Raymond EG, Rice RE, and da Fonseca GAB (2001) Effectiveness of parks in protecting tropical biodiversity. *Science* 291: 125–128.

Gadgil M and Guha R (1992) *This Fissured Land: An Ecological History of India*. New Delhi, India: Oxford University Press.

Hughes JD and Chandran MDS (1998) Scared groves around the earth: An overview. In: Ramakrishnan PS, Saxena KG, and Chandrashekara UM (eds) *Conserving the Sacred for Biodiversity Management*, pp. 69–85. New Delhi, India: Oxford and IBH Publishing Company Pvt. Ltd.

Hunter Jr ML (2002) *Fundamentals of Conservation Biology*. Massachusetts, MA: Blackwell Science.

Meffe GK and Carroll CR (1997) Conservation reserves in heterogeneous landscapes. In: *Principles of Conservation Biology*, pp. 305–343. Massachusetts, MA: Sinauer Associates, Inc.

Mittermeier RA, Myers N, Mittermeier GC, Ford H, and Myers N (2000) *Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*, pp. 33. Chicago, IL: University of Chicago Press.

Pullin AS (2002) *Conservation Biology*. Cambridge, UK: Cambridge University Press.

Ravindranath NH, Murali KS, and Malhotra KC (eds) (2000) *Joint Forest Management and Community Forestry in India. An Ecological and Institutional Assessment*. New Delhi, India: Oxford and IBH Publishing Company Pvt. Ltd.

Shafer CL (1990) *Nature Reserves: Island Theory and Conservation Practise*. Washington, DC: Smithsonian Institution Press.

Genetic Aspects of Air Pollution and Climate Change

D F Karnosky and R C Thakur, Michigan Technological University, Houghton, MI, USA

Introduction

The first incidences of air pollution impacts on the genetic constitution of forest tree populations were those documented near point sources of sulfur dioxide (SO_2), particulates, and heavy metals. Localized extinction of forests around these point sources was documented by ecologists in the past two centuries. In North America, the most spectacular of these areas were those surrounding ore smelters in Trail, British Columbia, Sudbury, Ontario, and Copper Basin, Tennessee. In Europe, the most dramatic areas included the Black Triangle area (of eastern Germany, Poland, and the then Czechoslovakia) which was largely due to soft coal burning in power plants and numerous situations where industrial facilities were located in valleys such that toxic emissions destroyed vegetation on the surrounding hillsides. With these early pollution problems, large areas of forests have simply been replaced by grasses or other tolerant vegetation.

Around the middle of the twentieth century, another type of air pollution, smog consisting of various photochemical oxidants, including nitrogen oxides (NO_X), ozone (O_3), and peroxyacetyl nitrate (PAN), began to impact forest tree populations. The first documented consequences of photochemical oxidant on forest tree populations occurred in the San Bernardino mountains where sensitive genotypes of ponderosa pine (*Pinus ponderosa*) began to die in large numbers, being replaced in the forest by more smog-tolerant species such as white fir (*Abies concolor*). Ozone downwind of major metropolitan areas has also been implicated in the loss of sensitive individuals in eastern white pine and trembling aspen in the eastern USA. In parts of the highly polluted Ohio Valley region in the eastern USA, sensitive genotypes of eastern white pine were virtually eliminated from the breeding populations between the mid-1950s and the mid-1960s due to deadly combinations of SO_2 and O_3. Since the 1980s, O_3 has been implicated in the loss of hundreds of thousands of pines in the mountains surrounding Mexico City, where O_3 levels are among the highest in the world.

Recently, the scientific community has realized that greenhouse gases of anthropogenic origin are building up in the earth's atmosphere (**Figure 1**) and that these gases are likely contributing to the trapping of heat near the earth's surface. As a result, there is a sharply rising trend in global mean temperatures (**Figure 2**). The increasing temperatures will likely eventually lead to changes in species-richness in a given area and changes in the range of many forest tree species.

In this article, we first discuss genetic aspects of air pollution effects on forests and then examine how the changing climate may impact the genetics of forest trees. Finally, we discuss some of the remaining knowledge gaps and research needs with

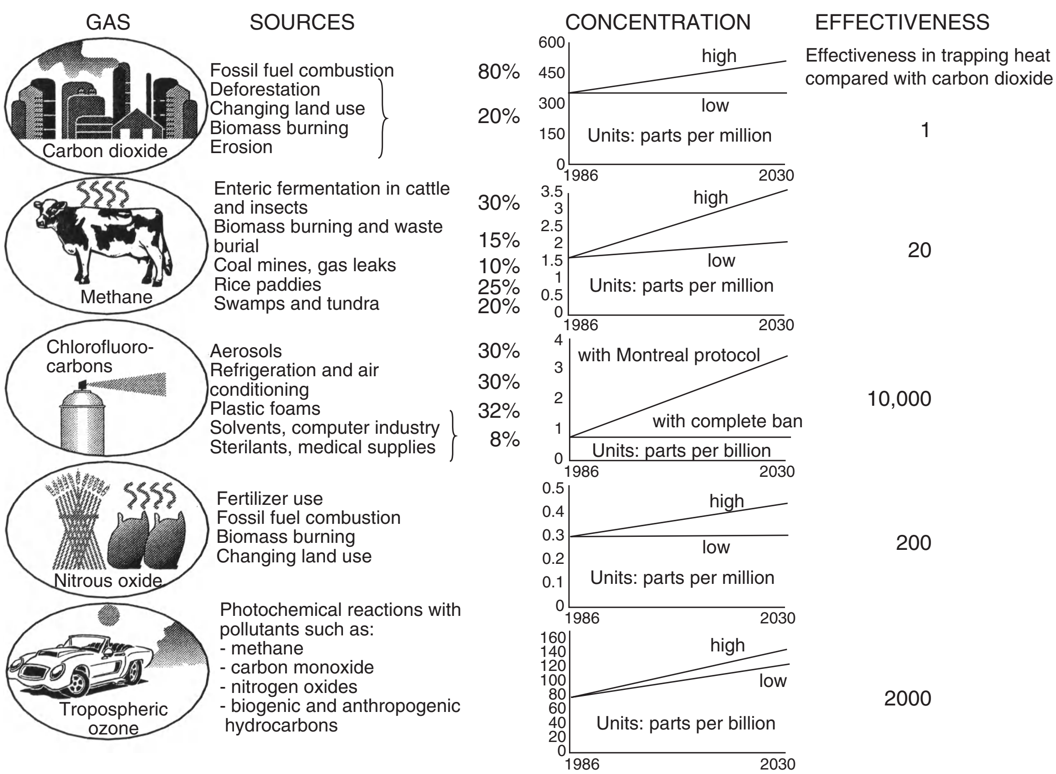


Figure 1 The major anthropogenic greenhouse gases. Reproduced with permission from Karnosky DF, Ceulemans R, Scarascia-Mugnozza GA, and Innes JL (2001) *The Impact of Carbon Dioxide and other Greenhouse Gases on Forest Ecosystems*. New York: CABI. Adapted from Milich (1999) Global *Environmental Change* 9: 179–201.

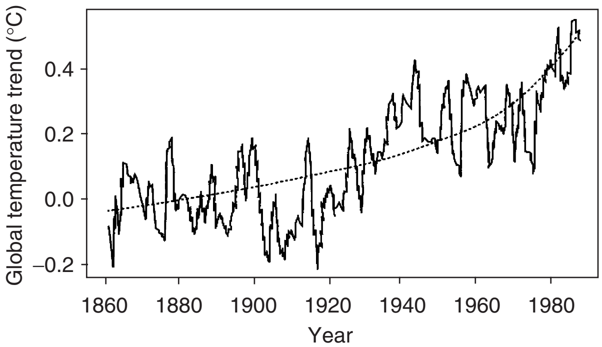


Figure 2 The Intergovernmental Panel on Climate Change (IPCC) global temperature record and a set of predicted temperatures. Reproduced with permission from Karnosky DF, Ceulemans R, Scarascia-Mugnozza GA, and Innes JL (2001) *The Impact of Carbon Dioxide and other Greenhouse Gases on Forest Ecosystems*. New York: CABI. Adapted from Bloomfield (1992) *Climate Change* 21: 1–16.

respect to genetic aspects of air pollution and climate change.

Genetic Aspects of Air Pollution

For air pollution to induce natural selection, there must be variation in air pollution sensitivity, the variation must be heritable, and the pollution must be a strong enough selection force to disadvantage sensitive trees severely. According to Anthony Bradshaw, who has studied natural selection in grasses growing in the presence of heavy metals, evolutionary population change takes place in three stages:

- Stage 1: elimination of the most sensitive genotypes
- Stage 2: elimination of all genotypes except the most tolerant (note: elimination of *all* forest tree genotypes, as has occurred in many point source pollutants, results in extinction, not evolution)
- Stage 3: interbreeding of the survivors to give even more resistant genotypes which are then further selected

The rate of selection is dependent on the severity of the pollutant stress, the type of reproduction (sexual or asexual reproduction), and the level of competition between genotypes (the more intense the competition between sensitive and tolerant trees, the faster the effects occur). Finally, air pollution-induced selection can take place at the level of differentiation in survival among individual trees (viability selection) or among pollen grains on a stigmatic surface (gametic selection).

In our laboratory, we have long studied the responses of forest trees to air pollution in an attempt to gain a better understanding of the potential for air pollution to impact natural selection. It is clear from these studies that there is tremendous variability in responses of forest trees to air pollution and this is manifested as differences between species, provenances, families within provenances, and tree-to-tree within families (**Figure 3**). Furthermore, we and others have shown that variable responses to air pollutants such as heavy metals, SO_2, and O_3, are highly heritable. We have also shown that the differences in responses to air pollution can directly affect the competitive ability of trees as air pollution can dramatically affect growth, as we demonstrated with trembling aspen affected by O_3 in controlled fumigation studies done in open-top chambers (**Figure 4**) and in field plantings under naturally elevated levels of O_3 (**Figure 5**). We have also shown that the effects of air pollution in the stage 1 of natural selection can occur very rapidly, as shown in **Figure 6**, where nearly 50% of the O_3-sensitive trembling aspen (*Populus tremuloides*) were eliminated from highly competitive close-spacing trials in a high-O_3 environment after only 5 years. Similarly, we have

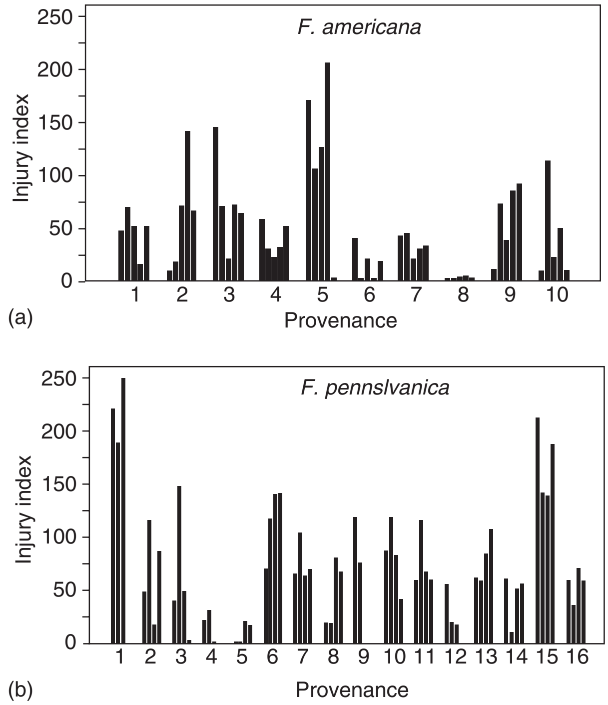


Figure 3 The average injury index for visible foliar injury after exposure of 1-year-old seedlings to 50 pphm ozone for 7.5 h. Each mean shown represents the average of five trees per family. There were either four or five half-sib families for each white ash (*Fraxinus americana*) provenance (geographic location) and either three or four families for each green ash (*F. pennsylvanica*). Reproduced with permission from the 1996 Air Quality Criteria for Ozone and Related Photochemical Oxidants. Washington, DC: US EPA Office of Resources and Development.

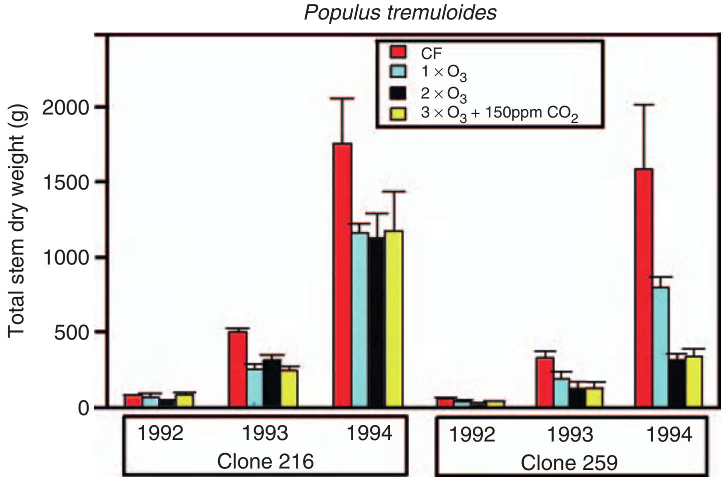


Figure 4 Total stem biomass per tree for an ozone (O_3)-tolerant (clone 216) and an O_3-sensitive (clone 259) trembling aspen (*Populus tremuloides*) clone exposed to charcoal-filtered (CF), ambient O_3 ($1 \times O_3$), twice ambient ($2 \times O_3$), or twice ambient $O_3 + CO_2$ (150 ppm over ambient) for three growing seasons in open-top chambers. The O_3-induced decreases in stem growth for the O_3-sensitive clone are particularly dramatic in year 3.

Figure 5 The effects of ambient air pollution on tree growth can be severe and is often variable due to genetic differences in sensitivity. Here is an example of three southern Wisconsin trembling aspen (*Populus tremuloides*) genotypes varying in ozone (O_3)-sensitivity in this trial in southern New York where ambient O_3 levels were quite high. The two tree plots represent 10-year-old sensitive (left), intermediate (middle), and tolerant (right) genotypes that grew at similar rates under low O_3 exposures.

documented a 10-fold increase in the mortality rate of O_3-sensitive eastern white pine trees (as compared to tolerant genotypes) in southern Wisconsin where ambient O_3 was moderately high. Thus, the evidence for stage 1 of natural selection occurring in natural forests is indisputable.

For forest trees, the final two stages of natural selection induced by air pollution are less well documented, with the exception of those populations surrounding severe point-source pollution where changes in genetic structure of polluted forest stands have been shown via studies of isozyme or molecular markers. For more subtle region-wide pollutants such as O_3, the evidence is less compelling that genetic change has occurred. Indirect evidence of these later stages of selection taking place has been presented by our laboratory in studies of 15 trembling aspen populations from across the USA. In a series of three studies, published in the late 1980s, we showed a strong negative correlation between the amount of visible foliar symptoms induced by O_3 and the maximum daily O_3 averages at the localities where the populations were collected (**Figure 7**). Additional studies are needed to verify

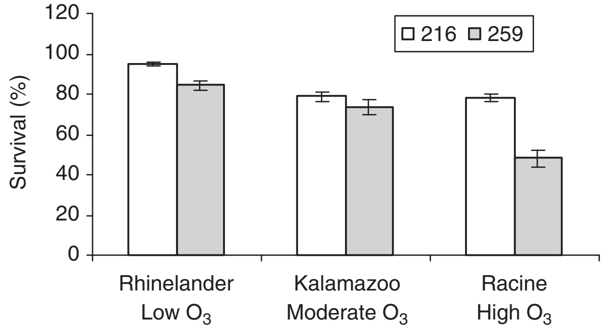


Figure 6 The rapid nature of ambient ozone (O_3) impacts on tree survival in highly competitive (tolerant and sensitive genotypes were intermixed at 0.5×0.5 m spacing) environments across a documented O_3 gradient. Survival at age 5 of two trembling aspen (*Populus tremuloides*) clones differing in O_3-tolerance (clone 216 = O_3-tolerant and clone 259 = O_3-sensitive). The three locations where this experiment was run included Rhinelander, WI = low O_3; Kalamazoo, MI = moderate O_3; and Kenosha, WI = high O_3.

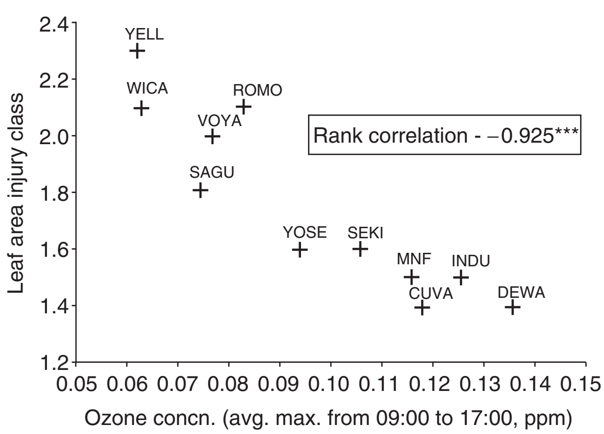


Figure 7 Scatter diagram illustrating the association between one measure of ambient ozone concentrations and one measure of foliar injury after an acute exposure to ozone for several populations of quaking aspen (*Populus tremuloides*). CUVA, Cuyahoga Valley National Recreation Area; DEWA, Delaware Water Gap National Recreation Area; INDU, Indiana Dunes National Lakeshore; MNF, Monongahela National Forest; ROMO, Rocky Mountains National Park; SAGU, Saguaro National Monument; SEKI, Sequoia National Park; VOYA, Voyageurs National Park; WICA, Wind Cave National Park; YELL, Yellowstone National Park; YOSE, Yosemite National Park. Reproduced with permission from Berrang PC, Karnosky DF, and Bennett JP (1991) Natural selection for ozone tolerance in *Populus tremuloides*: An evaluation of nationwide trends. *Canadian Journal of Forest Research* 21: 1091–1097.

that the genetic structure of these populations has changed. An intriguing question remaining is whether or not valuable unique genes or germplasm are being lost with the loss of the sensitive genotypes from the polluted populations.

Genetic Aspects of Climate Change

The rapid nature of the earth's changing climate has raised concerns for the adaptability of forest trees. Long-lived and stationary, forest trees are facing unprecedented changes in the levels of greenhouse gases (especially CO_2; see **Figure 1**) and in the temperature (**Figure 2**). The rapid rates of climatic change anticipated to occur in the near future, coupled with land use changes that impede gene flow, can be expected to disrupt the interplay of adaptation and migration. Implications of these changes for the genetic stability of forest tree populations are not yet fully understood. While ecologists have predicted large changes in the ranges of species over the next 100 years (**Figure 8**), geneticists counter that most tree species have rather large amounts of natural variation and that the changes may be more subtle than those modeled predictions. What is highly likely is that the northward shift of species ranges in the northern hemisphere will proceed with differing rhythms for various species. Species with limited genetic variability to start with, however, such as red pine (*Pinus resinosa*) and red spruce (*Picea rubens*) in North America and silver fir (*Abies alba*) in Europe, will be the first true test of how severe the competitive ability changes may become, how rapidly local populations will be lost, and how great the changes in species ranges may be.

Tree breeding and genetic selection have generally involved either plus tree selection followed by progeny testing or provenance testing followed by progeny testing of superior phenotypes. Then, seed orchards have been established and rogued (further selected on the basis of progeny test information) to provide the seed for the next generation. This process has continued with advanced generation selection and breeding in a few commercially important tree species. In all facets of these programs, selection is done based on the conditions prior to selection and for the most part these selections are not done on the basis of predicted pollution and climate scenarios that will be in place during the rotation of the commercial forest. Screening and selection of genotypes suitable for future pollution and climate scenarios are generally thought to be nearly impossible because of the complexity and cost of such programs. Thus, an alternative strategy in which a wider genetic base is maintained in our breeding population is essential for developing future forests. Maintaining large amounts of genetic diversity will increase the probability that adequate adaptability is maintained to meet rapidly changing environmental conditions.

Alternative strategies are also needed to insure that *in situ* and *ex situ* conservation methods such

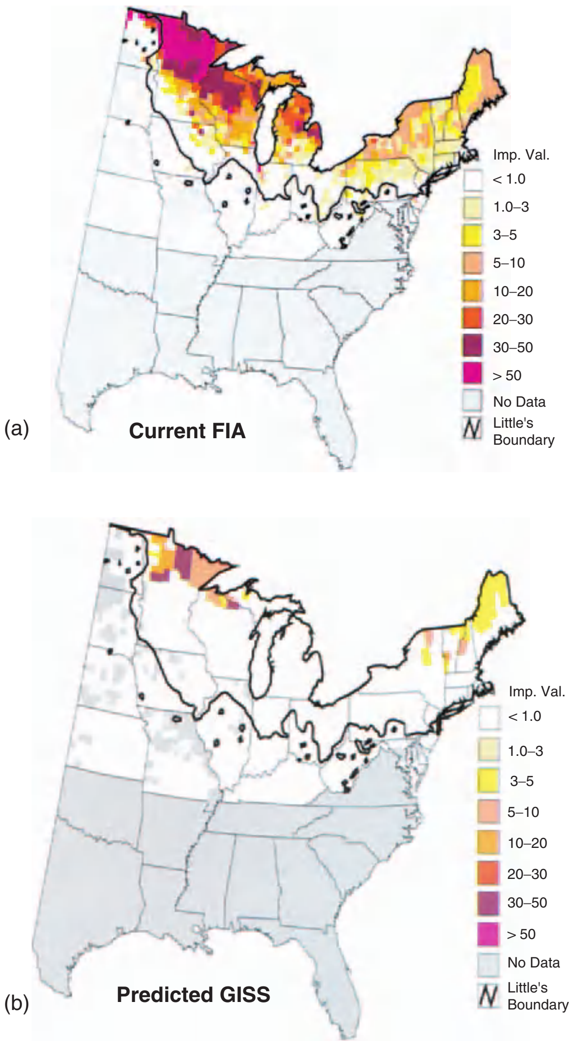


Figure 8 The projected impact of global warming on tree species richness and range is shown in these two figures. (a) Current range and importance values of trembling aspen (*Populus tremuloides*) versus the predicted range and importance value of the same species under a doubled-CO_2 climate (b). Adapted with permission from Iverson LR, Prasad AM, Hale BJ, and Kennedy Sutherland E (1999) *Atlas of Current and Potential Future Distributions of Common Trees of the Eastern United States*. USDA Forest Service Northeastern Research Station General Technical Report NE-265. FIA data are from USDA Forest Service's Forest Inventory and Analysis Program's predicted GISS is the prediction from the Goddard Institute of Space Studies general circulation model scenario.

as gene banks, clone banks, seed zones, or seed collection areas are maintained in several locations such that the changing pollution and/or climate scenarios will not result in the loss of such collections from single vulnerable test sites. Given the past several decades of 'laissez-faire' attitude towards traditional genetic field trials and field conservation efforts, this need to conserve forest genetic resources in multiple amounts may help genetics regain prominence amongst the forestry community.

Knowledge Gaps and Research Needs

Restoration of forests destroyed by severe air pollution (as in the region of the Black Triangle in Europe) remains a great challenge today, and there are currently no methods available to guide these restoration projects to recreate previous genetic diversity and genetic structure. Furthermore, reforestation under today's climate (light, temperatures, phenology, and moisture) and soil conditions (many former severely degraded areas by air pollution still have acidic soils or soils contaminated with heavy metals) may preclude simple replanting with single species. Furthermore, data may not be readily available as to what the stand structure, and genetic diversity were before the areas were affected by air pollution.

The questions of whether or not regional air pollutants such as O_3 have subtly affected the genetic structure of forest tree populations, and if rare alleles have been lost as sensitive genotypes are being lost, needs to be further studied. Recollections of previously sampled populations, as have been done in evolutionary studies of grasses, have been recommended to document selection over time. Also, intensive population sampling with newly developed molecular tools such as microsatellites, single nucleotide polymorphisms (SNPs), amplified fragment length polymorphisms, or restriction fragment length polymorphisms, could determine if population changes have occurred. Studies along sharp pollution gradients would also be useful in this argument.

Exploration of ways to induce more variability in genetically disparate species, such as red pine and white fir, could be beneficial in creating new opportunities for these species to adapt to future climate change. These could include studies of interspecific hybridization, intraspecific provenance hybridization, or insertion of stress tolerance genes isolated from other species via genetic engineering.

Understanding how climate change and related changes in greenhouse gases, such as CO_2 and O_3, will impact intra- and interspecific competition will help us better predict impacts of climate change on forest tree populations. Since these changes are rapid (from a historical viewpoint) but still long-term (from a research project duration viewpoint), long-term studies of population dynamics and competition will need to be done under realistic future climate scenarios. The extensive sets of provenance trials established in the twentieth century around the world should also prove useful in addressing questions related to adaptation to warming temperatures.

It is well known that trees grow at different rates and that they are also variable in how they allocate carbon to various above- and below-ground components. This information could be used to make genetic selections for trees to optimize carbon sequestration. Selections of trees with rapid growth rates, strong allocation to root systems, and inherent resistance to decay could be done for various environmental conditions in the major tree-growing regions of the world. Likely, such selections will include use of exotic species, hybrids of local and exotic species, or genetically engineered trees with altered carbon allocation patterns.

In contrast to long-term evolutionary trends for which local populations are well adapted, the rapid change in stresses of anthropogenic origin suggests that genetic management of forests will be essential. Methods to link tree breeding for utility benefits with gene conservation to facilitate sustainable forestry should be given a high priority. The importance of maintaining high levels of genetic diversity in breeding populations and in plantations cannot be overstated.

Recent development in understanding mechanisms of stress tolerance suggest a commonality of oxidative stress from diverse factors such as air pollutants, herbicides, temperature extremes, toxic salts, and drought. This finding may lead to an increased understanding of the antioxidant tolerance mechanisms and, eventually, to the possibility of selecting for stress tolerance. This could be particularly valuable for developing forest trees for unpredictable future stresses.

Air pollution, climate change, forest trees, natural selection, biodiversity, adaptation, trembling aspen, red pine, silver fir, tree breeding.

See also: **Biodiversity**: Plant Diversity in Forests. **Environment**: Environmental Impacts; Impacts of Air Pollution on Forest Ecosystems; Impacts of Elevated CO_2 and Climate Change. **Health and Protection**: Diagnosis, Monitoring and Evaluation. **Site-Specific Silviculture**: Silviculture in Polluted Areas. **Tree Physiology**: Forests, Tree Physiology and Climate.

Further Reading

Agrawal SB and Agrawal M (eds) (2000) *Environmental Pollution and Plant Responses*. Boca Raton, FL: Lewis.

Iverson LR, Prasad AM, Hale BJ, and Kennedy Sutherland E (1999) *Atlas of Current and Potential Future Distributions of Common Trees of the Eastern United States*. USDA Forest Service Northeastern Research Station General Technical Report no. NE-265. Washington, DC: US Government Printing Office.

Karnosky DF, Ceulemans R, Scarascia-Mugnozza GE, and Innes JL (2001) *The Impact of Carbon Dioxide and other Greenhouse Gases on Forest Ecosystems*. New York: CAB International.

Miller PR and McBride JR (1999) *Oxidant Air Pollutant Impacts in the Montane Forests of Southern California*. New York: Springer-Verlag.

Müller-Starck G and Schubert R (2001) *Genetic Response of Forest Systems to Changing Environmental Conditions*. Boston, MA: Kluwer Academic.

Saxe H, Cannell MGR, Johnson O, Ryan MG, and Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist* 149: 369–400.

Scholz F, Gregorius HR, and Rudin D (eds) (1989) *Genetic Effects of Air Pollutants in Forest Tree Populations*. Berlin: Springer-Verlag.

Szaro RC, Bytnerowicz A, and Oszlanyi J (2002) *Effects of Air Pollution on Forest Health and Biodiversity in Forests of the Carpathian Mountains*. Amsterdam: IOS Press.

Taylor GE Jr, Pitelka LF, and Clegg MT (eds) (1991) *Ecological Genetics and Air Pollution*. New York: Springer-Verlag.

Yunus M and Iqbol M (1996) *Plant Response to Air Pollution*. New York: John Wiley.

Molecular Biology of Forest Trees

R Meilan, Oregon State University, Corvallis, OR, USA

Introduction

Transformation and Regeneration

In order to genetically engineer a plant, one must be able to insert a gene into the genome of an individual plant cell and then cause that cell to differentiate into a whole plant. The former process is referred to as transformation; the latter, regeneration.

The most common way of transforming cells exploits the ability of *Agrobacterium tumefaciens*, the causative agent of a common plant disease known as ‘crown gall.’ *Agrobacterium* contains a closed-circular piece of double-stranded DNA called the tumor-inducing (Ti) plasmid. During infection, *Agrobacterium* inserts a segment of the Ti plasmid, called T-DNA (transferred DNA), into the plant’s nuclear genome. This T-DNA contains genes encoding enzymes that catalyze the synthesis of plant growth regulators (cytokinin and auxin) which together control cell proliferation. This results in the formation of a tumor, within which the bacterium resides. The T-DNA also contains genes encoding enzymes that catalyze the synthesis of unique amino acids that the plant cannot utilize, and that serve as a carbon source for the bacterium.

Agrobacterium does not select specific genes to be shuttled into the plant. The T-DNA is defined by specific border sequences; thus, any genes located between these borders will be transferred. Plant genetic engineers isolate the Ti plasmid, excise the genes responsible for pathogenesis, and replace them with genes of interest. A minimum of two genes generally is inserted between the T-DNA borders: the target gene (e.g., insect or disease resistance) and a selectable marker. After the modified plasmid is reinserted into *Agrobacterium*, a piece of plant tissue (explant) is co-cultivated in a suspension of bacterial cells containing this modified Ti plasmid. However, not all of the explant cells will be transformed by the bacterium.

Selection helps determine how successful transformation was. The most commonly used selectable marker gene is *NPTII*, which imparts resistance to kanamycin. Untransformed plant cells ordinarily die when exposed to this antibiotic. When co-cultivated explants are plated on a solid medium containing kanamycin, only cells transformed with *NPTII* survive. Because the selectable marker gene is directly linked to the gene of interest (transgene), it too should be present in the transformed cell.

Another DNA delivery system, biolistics, involves coating microscopic beads (usually gold or tungsten) with DNA. These beads are propelled at an explant, usually with a burst of compressed air as the driving force. Once inside the cell, DNA that sloughs off the bead can recombine with a plant chromosome. Biolistics is often less efficient than *Agrobacterium*-mediated transformation because of cellular damage from the impact of the beads, digestion of the transgene by cytosolic enzymes (nucleases), and the need for recombination. The selection process for cells transformed biolistically is as that described above.

Transformed cells that survive selection are used to regenerate a whole plant. The two main routes for *in vitro* regeneration are embryogenesis and organogenesis. In the former, cells are coaxed to differentiate into an embryo, similar to what is contained within a plant's seed. Organogenesis, on the other hand, is the process by which cells differentiate directly into specific organ types (e.g., shoots and roots). Both means of regeneration are done by successive transfers of the co-cultivated explants to media containing the proper type and concentration of plant growth regulators, mainly cytokinin and auxin. Varying the cytokinin : auxin ratio will result in callus formation, shoot organogenesis, or root initiation.

Recombinant DNA Techniques

The expression of a gene's coding sequence (i.e., transcription and processing to produce mRNA and translation of mRNA into protein) is carefully regulated by adjacent control sequences. Promoters are upstream elements that direct the timing, location, and extent of a gene's expression. Constitutive promoters allow for high levels of expression, in (nearly) all tissues, all of the time. The most commonly used constitutive promoter is derived from the cauliflower mosaic virus (CaMV) *35S* gene. Other promoters can be activated through treatment with a specific inductive agent, or may allow for tissue- and/or temporal-predominant expression. Enhancers are the portion of a promoter that can elevate a gene's expression level, and can act in *trans*. There are also downstream elements, terminators, which signal the end of transcription.

Once a gene is transcribed, its message undergoes processing. In some cases interspersed sequences, called introns, are cut out of the mRNA at well-defined sites. The remaining sequences, termed exons, are then spliced together.

It is possible to enzymatically reverse-transcribe single-stranded mRNA to reproduce the double-stranded DNA from which the message was derived. This product is called complementary DNA (cDNA). Complementary DNA does not contain introns that may have been present in the corresponding genomic DNA. A cDNA library is a collection of sequences from only those genes that were being actively transcribed at the time the mRNA was extracted. Partial sequence information derived from the cDNAs in a given library is called an expressed sequence tag (EST) library.

Restriction enzymes are proteins that catalyze the cleavage of DNA at very specific recognition sites, usually about four to eight base pairs in length. Another enzyme, called ligase, fuses the ends of DNA that have been cut by the same restriction enzyme. This pair of enzyme types allows molecular biologists to mix and match various coding sequences and promoters.

Reporter genes allow one to visualize a promoter's expression pattern. The most common reporter gene, β-glucuronidase (GUS), encodes an enzyme that catalyzes the conversion of a colorless substrate to an insoluble, blue-colored product that precipitates in cells expressing the gene encoding it.

Polymerase chain reaction (PCR) is a technique that allows for amplification of a specific piece of

DNA. Short pieces of DNA (usually about 15 to 30 nucleotides in length), referred to as primers, are designed to complement sites on opposite strands of the target DNA. These primers are mixed with a DNA sample containing the fragment to be amplified, along with a complete set of nucleotides (i.e., dATP, dCTP, dGTP, and dTTP) and thermostable DNA polymerase. The mixture is heated to 94°C for approximately 1 min to separate the two strands of DNA (denature). Subsequent cooling of the mixture allows complementary strands to anneal to each other; the optimal annealing temperature depends on the length and composition of the primer (usually about 55–60°C). Because the primer DNA is of a much higher concentration than the template, it is much more likely to find its partner. The mixture is then heated to a temperature that is optimal for the polymerase to extend the primers using the genomic DNA as a template (72°C). Successive rounds of denaturation, annealing, and elongation result in a geometric increase (up to 4×10^6 times in 25 cycles) in the accumulation of product. Reaction mixtures are contained in tubes that are inserted in the aluminum block of a thermocycler. This machine can rapidly heat and cool liquid that is circulated through the interior of the block, and has a microprocessor that can be programmed to maintain different temperatures for various lengths of time.

Nucleic acids (e.g., restricted genomic DNA, PCR-amplified product, RNA, etc.) can be separated via electrophoresis and visualized. A dilute ($\sim$0.8%), heated solution of agarose (a polysaccharide) is poured into a form and allowed to solidify (as a gel). A ‘comb’ is inserted into the solution before it cools to create depressions (wells) in the gel, where DNA samples can be loaded. A strong electrical current is passed through the gel matrix, allowing the nucleic acids (which are charged molecules) to be separated based on their molecular weights. A standard, containing a mixture of nucleic acid fragments of known size, is run in a parallel lane on the gel, for estimating the size of nucleic acid fragments contained within the sample. To visualize the separated DNA fragments, the gel is stained with a dye, such as ethidium bromide, which binds to nucleic acids and fluoresces an orange color under ultraviolet light.

Platforms for Studying Tree Biology

Marker-Aided Selection

Marker-aided selection (MAS) involves the identification of individuals based on the presence of DNA markers in offspring derived from parents whose genomes have already been mapped. DNA markers are usually random nucleotide sequences that do not encode a functional gene; they are frequently amplified via PCR and are visualized on a gel. The position of the markers on a chromosome is mapped by determining the frequency of their mutual recombination when haploid gametes are formed in a given individual. To accomplish this, one needs a pedigree (a population in which gamete contribution from specific individuals can be traced to their offspring). Target genetic traits, that show extremes in variation, can be identified in a segregating population at an early stage in plant growth, based on linked markers. Traits of interest that are measured on a quantitative (linear) scale are referred to as QTLs (quantitative trait loci). These traits are typically affected by more than one gene. Examples include wood density, stem form, and frost resistance.

The potential impact of MAS on traditional breeding is tremendous. Once breeders know which bands on the gels indicate extremes for the traits of interest, screening can be conducted at a very early age, and selected individuals can be clonally propagated. Conducting this work in a laboratory obviates the need for expensive field trials, and forest managers will realize the additional genetic gain soon after crossing the selections from the previous generation. Sexual reproduction following MAS is possible, but gains will be fewer and greatly delayed relative to the clonal propagation. This is because juvenile selections must reach maturity, and the planting stock will not be genetically identical to the parents. However, wide-scale adoption of MAS for tree improvement has not been realized. Various problems impede the application of MAS, including the lack of cost-effective, high-throughput marker systems and lack of linkage disequilibrium. The latter is said to occur when the observed frequencies of haplotypes (a set of closely linked genetic markers present on one chromosome, which tend to be inherited together) in a population do not agree with haplotype frequencies predicted by multiplying the frequency of individual genetic markers in each haplotype.

Gene-Tagging Methods

Because of the ease with which it can be transformed, poplar (*Populus*) is a convenient model system for discovering tree genes of potential commercial value. Using gene tagging, a new gene or regulatory element is inserted into the genome as a probe for determining the function or expression pattern of genes adjacent to the insertion site. With gene-trap tagging, a reporter gene (e.g., GUS) is used to visualize the expression pattern of a nearby gene (**Figure 1**). In another tagging method, activation tagging, a strong

Figure 1 Staining of a poplar gene-trap line. The blue color demonstrates that GUS expression was limited to the vascular tissue in this leaf. Photograph supplied by Andrew Groover, Institute of Forest Genetics, US Forestry Service, Davis, CA, USA.

enhancer that is effective some distance from a native promoter is randomly inserted in the genome. Elevated expression of the nearby gene may result in an aberrant phenotype. Alterations that yield desired phenotypic changes, such as early flowering, modifications in crown form, or root development, are then analyzed for the causative gene (**Figure 2**). Overexpression of some native genes (e.g., those affecting wood quality) may not give rise to a visually apparent change. In this case, other, high-throughput analyses are needed for screening a population of transgenics (see below).

Both gene-trapping and activation tagging are a form of 'gene discovery' because the genes identified may be functionally unknown. Nevertheless, the unique nature of the inserted sequences (tags) permits the affected gene to be easily identified and isolated.

Poplar Genome Sequence and Informatics

The US Department of Energy has committed $28 million to producing a 6 × draft sequence (on average, every gene is sequenced six times) for the entire *Populus* genome by the end of 2003. As a result,

Figure 2 A GA 2-oxidase (GA2ox) mutant isolated via activation tagging. The GA2ox gene encodes an enzyme that degrades biologically active forms of gibberellic acid, a plant growth regulator involved in controlling various aspects of plant growth and development (e.g., seed germination, flower initiation, fruit development, stem elongation, wood formation, leaf expansion). Mutant (left) and wild-type (right) plants are the same age and were grown under the same conditions. Photograph supplied by Victor Busov, Forest Science Department, Oregon State University, Corvallis, OR, USA.

poplar is only the third plant species for which the entire genome sequence is available.

To maximize its utility, a genomic sequence must be annotated. Genome annotation, one aspect of the rapidly evolving field of informatics, has two components. The first is structural, involving the identification of hypothetical genes, termed open reading frames (ORFs), in the DNA sequence using computational gene-discovery algorithms. The second component focuses on assigning function to the predicted genes by searching databases for genes of known function that have similar sequences. For complex eukaryotic genomes, the main problem lies in the structural component of annotation. In eukaryotic genomes, a gene is defined as a locus of cotranscribed exons, which may give rise to several splice variants and, hence, multiple protein products with multiple functions. The structural identification of genes depends heavily on the use of homologous cDNA/EST or protein sequences. Algorithms for coding-sequence recognition exhibit performance trade-offs between increasing sensitivity (ability to detect true positives) and decreasing selectivity (ability to exclude false positives). The identification of intron–exon boundaries and splice sites is of further importance. Genes not represented by homologous DNA or protein sequences must be identified by *de novo* methods, which remains a serious impediment to genome annotation (described below).

Transformation to Confirm Gene Functionality

Transformation is an important tool for analyzing gene functionality. Through constitutive or conditional up- or down-regulation (knock-in/knock-out, KI/KO) of a target gene, important information about its function and downstream targets can be obtained. To date, tree genetic engineering has largely been performed using strong constitutive promoters, the aim being to obtain maximum levels of expression and, consequently, maximal effect. Such a strategy may be useful for imparting certain commercial traits (e.g., insect resistance or herbicide tolerance), but is not practical when the goal is to alter the expression of an endogenous gene. In fact, numerous cases of gene silencing have resulted from this approach. Moreover, altering the expression of key genes, such as transcription factors or other regulators, may have lethal or at least strong negative effects on plant development. In the future, an important application of genetic engineering will be large-scale evaluation of gene function via KI/KO strategies. Without a reliable system for conditional transgene expression, it may be impossible to produce transgenic plants with altered expression of numerous genes vital to growth and development. It is imperative for the inducer to be highly specific to the target promoter and to lack phytotoxicity. The target promoter must also be tightly regulated (i.e., no 'leaky' expression), with high-level expression being conferred upon induction.

High-Throughput Analyses

Gene expression Microarray technology can be used to study the simultaneous expression patterns of thousands of genes (**Figure 3**). Here, unique sequences of DNA (either oligonucleotides or cDNA) sequences are anchored to a glass slide in neatly arrayed microscopic spots (the probe). Spotting is done using very fine needles and robotics. Messenger RNA (the target) is isolated from both control and treated plants; each RNA sample is labeled with a different color fluorescent dye. The labeled RNA is allowed to hybridize to its complementary single-stranded DNA probe before the microarray is scanned. A laser then excites each fluorescent dye at a specific wavelength, and emissions are captured digitally. The fluorescent images for the control and treated samples are superimposed and the resulting color of each spot reveals whether a given gene is differentially expressed in the two samples.

Chemical characterization If the forward genomics approaches described above do not result in a visual phenotype, one must have a way to quickly screen large populations of independent transgenic lines. Techniques have been developed for using near-infrared (NIR) spectra to obtain quantitative measurements of lignin, cellulose, other carbohydrates, and extractives from plants. The accuracy and precision of these techniques is equal to conventional chemical methods. Similar success has been reported with descriptions of physical properties (e.g., density, microfibril angle, modulus of rupture, and tensile stress), making it possible to use NIR data to infer mechanical properties of wood. Samples showing atypical NIR phenotypes can be further subjected to mass spectral analyses for more detailed insights into the biosynthetic networks that have been perturbed.

Applied Technology

Recent Progress

Trees have already been transformed with genes that impart a variety of commercially useful traits, including insect resistance (**Figures 4** and **5**), herbicide tolerance, modified lignin and cellulose, altered metabolism, phytoremediation, and hormone biosynthesis.

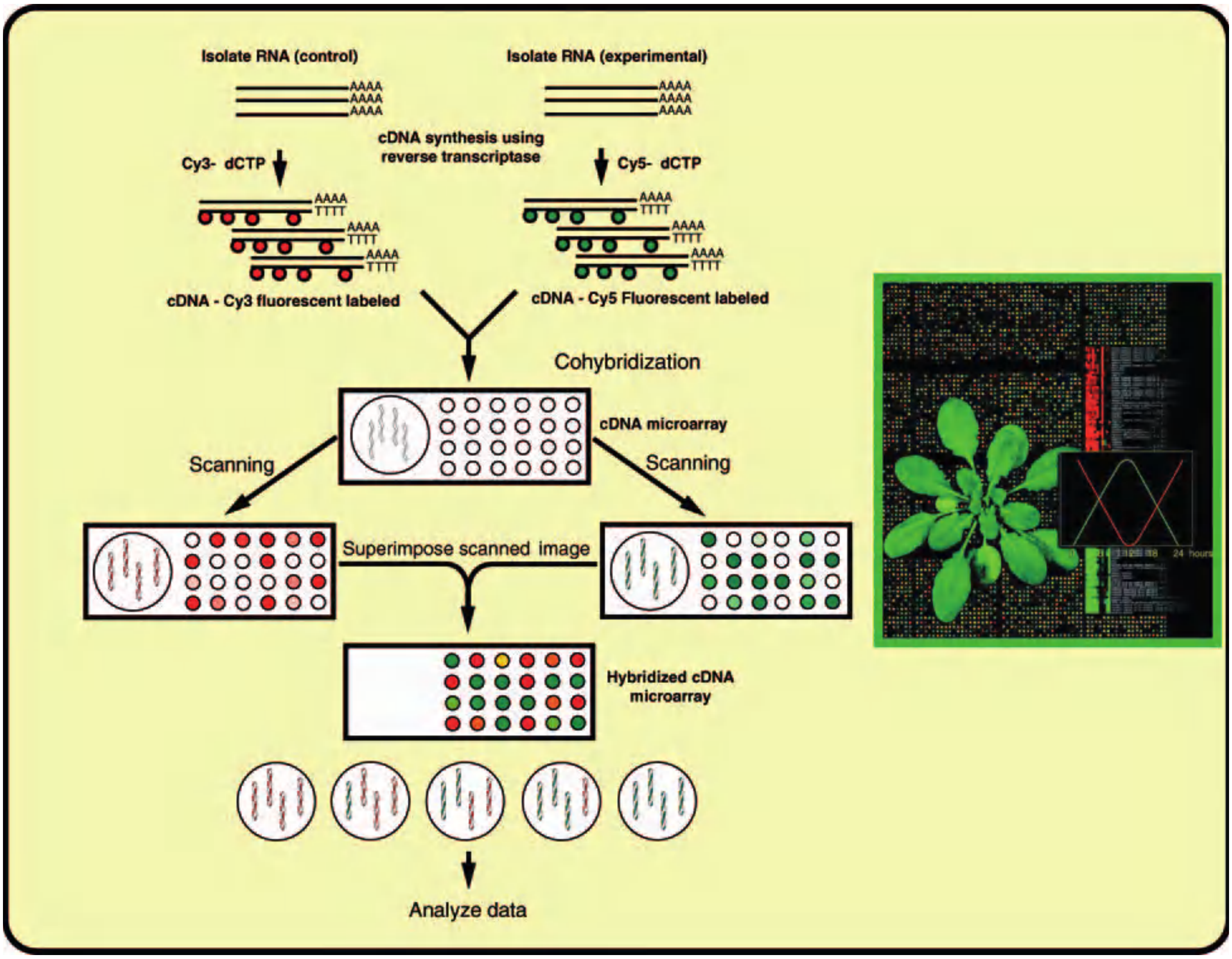


Figure 3 Experimental approach for labeling, hybridization, and scanning cDNA microarray. RNA is isolated (from control and experimental conditions) and labeled separately using two distinct fluorescent dyes (Cy3-dCTP and Cy5-dCTP) using reverse transcriptase. Both the labeled samples are cohybridized to the microarray. After hybridization and washing, the microarray is scanned using a confocal laser scanner at specific wavelengths, 543 nm (Cy3-dCTP) and 633 nm (Cy5-dCTP), respectively, for the two fluorescent dyes. The two fluorescent images are superimposed, and the data is analyzed for gene expression, using bioinformatics and image processing software. Fluorescent spots that are either red or green indicate the gene represented in the spot is expressed under one condition but not in the other. Spots carrying yellow/purple grades indicate that the gene represented in the spot is differentially expressed between the control and experimental conditions. Reproduced with permission from Rishi AS, Nelson ND, and Goyal A (2002) DNA microarrays: gene expression profiling in plants. *Reviews in Plant Biochemistry and Biotechnology* 1: 81–100. Arabidopsis Microarray insert reproduced with permission from Wisman and Ohlrogge (2000) *Plant Physiology* 124: 1468–1471.

Plants are now being used as bioreactors to produce recombinant proteins for commercial purposes in a rapidly emerging field of biotechnology known as 'molecular farming' (or 'biopharming'). However, recent incidents (e.g., StarLink and Prodigene) have stirred public uneasiness regarding the potential for contaminating the food supply with genetically modified crops that are expressing biologically active molecules. Therefore, the use of non-food crops, such as poplar or other tree species, may alleviate public and regulatory concerns about utilizing plants as 'factories' to produce anything from biodegradable plastics and industrial enzymes to antibodies and other pharmaceuticals. It is possible to effect the production of these compounds in transgenic trees, as a way of adding value to the crop. Transgenes can be placed under the control of an inducible, leaf-specific promoter so that there is no metabolic drag during the life of the plant, and so the transgene is not expressed in the bole of the tree.

Public Concern

Genetic engineering has been used to introduce novel, commercially valuable traits into a variety of agronomic crops. Although the potential benefit of these traits has also been demonstrated in transgenic trees, no such trees are currently being grown in the USA for commercial purposes.

Figure 4 Field-grown insect-resistant poplars. The tree depicted in the left-hand panel was transformed with the *Cry3A* gene from *Bacillus thuringiensis*. The tree on the right is a nontransgenic control. Damage is the result of feeding by larvae of the cottonwood leaf beetle (*Chrysomela scripta*).

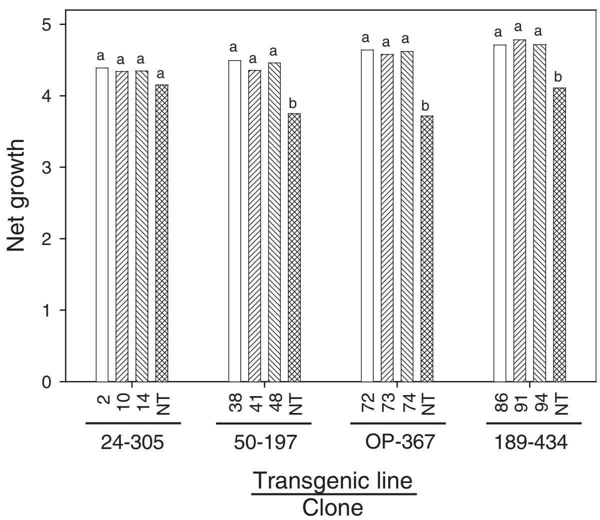


Figure 5 Growth of insect-resistant transgenic poplar trees. The first three bars in each cluster represent mean growth of 10 independent transgenic lines containing the *Cry3A* gene; black bars are for nontransformed controls (NT). Bars labeled with the same letter are not significantly different from each other. On average, nontransgenics grew 24% slower than the transgenic lines. Slower growth is presumably the result of having less photosynthetic capacity, as a result of insect feeding.

Agronomic crops generally are herbaceous annuals that are highly domesticated and have few, if any, wild relatives. Most tree plantations are established in close proximity to wild or feral relatives, increasing the probability of transgene spread. Thus, a major concern over the use of transgenic trees is the potential for extensive transgene dispersal through pollen and seeds. Because the issues surrounding the commercial deployment of transgenic woody perennials are more complex, federal regulatory agencies are now deciding what additional safeguards need to be put in place. Key areas of concern include: increased invasiveness, horizontal transfer, and development of resistance by the pest to the transgene product.

Flowering Control

Before transgenic trees can be grown for commercial purposes it is imperative to have a system for mitigating the spread of transgenes to interfertile wild relatives. Sterility is the most effective way of accomplishing this objective, as well as maintaining rapid growth. Normally, after trees undergo the transition to maturity, photosynthate is diverted away from vegetative growth and used to produce reproductive structures. Blocking flowering will likely result in preserving juvenile growth rates and preventing the formation of unwanted reproductive structures (e.g., seed pods, cotton, pollen, etc.). Finally, sterility will help curb genetic pollution. Trees such as poplar, which can be vegetatively propagated, are often grown in intensively managed plantations. In some cases, a single genotype is planted across thousands of acres. Because these trees are clonally propagated, all of their cells, including their pollen, contain exactly the same DNA. This monotypic pollen can travel considerable distances and fertilize flowers on compatible wild trees, which could affect genetic diversity in the wild. Flowering control has the potential to reduce the likelihood of this occurring.

Methods for Engineering Reproductive Sterility

One common way to engineer sterility is to ablate cells by expressing a cytotoxin gene in a tissue-specific manner. Floral promoters can be fused to one of a variety of cytotoxin genes that lead to rapid and early death of the cells within which the gene expressed. One of the more popular ways to engineer sterility in herbaceous plants employs an RNase gene, the product of which degrades messenger RNA.

A second way to genetically engineer flowering control is through the use of dominant negative mutations (DNMs). DNM genes encode mutant proteins that suppress the activity of coexisting wild-type proteins. Inhibition can occur by a variety of means, including formation of an inactive heterodimer, sequestration of protein cofactors, sequestration of metabolites, or stable binding to a DNA regulatory motif. Overexpression of floral regulatory genes that encode proteins with altered amino acid in the highly conserved domains can result in mutant floral phenotypes. Similar changes can also eliminate the encoded protein's ability to bind DNA. A potentially powerful alternative approach is to introduce a transgene encoding what is called a 'zinc finger' protein, which is specifically designed to block transcription of the target gene.

A third technique to control flowering involves gene silencing. In a variety of eukaryotic organisms, double-stranded RNA is an inducer of homology-dependent gene silencing; use of double-stranded RNA to induce silencing has been termed RNA interference. Studies in plants have shown that strong silencing can be achieved by introducing a transgene containing an inverted repeat of a sequence that corresponds to part of the transcribed region of the endogenous gene targeted for silencing. Such transgenes induce posttranscriptional gene silencing (PTGS) by triggering RNA degradation. Although this approach appears to provide a reliable means for engineering stable suppression of gene activity in plants, whether PTGS will be effective practically is uncertain, due in part to the ability of plant viruses to suppress PTGS. An alternative is to use a transgene containing an inverted repeat of a target gene's promoter region; this has been shown to induce *de novo* DNA methylation and transcriptional gene silencing (TGS). Unlike PTGS, TGS is not susceptible to viral suppression; however, it is unclear whether all endogenous plant promoters can be silenced by this method.

All of these approaches rely on the use of genes that control floral development, either through the use of floral-specific promoters or coding sequences with high homology to native genes that are targeted for suppression/silencing. In addition, flowering-time genes provide a means of advancing or retarding the onset of reproductive growth. The former can facilitate more rapid progress through conventional breeding; the latter can, depending on the rotation of the crop, serve as a transgene confinement strategy.

The Need for Transgene Stability

Stability of transgene expression is especially important for trees, which undergo numerous dormancy cycles and are often exposed to extreme environmental changes during their long lives. Unstable expression has taken on greater significance given recent reports that environmental changes and dormancy can trigger transgene silencing. Sexual reproduction may also affect the stability of transgene expression. To date, little evidence exists for somaclonal variation or transgene instability in poplar, but these characteristics will need to be evaluated over several years and in a variety of settings for any transgenic tree that is to be commercialized.

See also: **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species; Genetic Systems of Forest Trees. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Forest Genetics and Tree Breeding; Current and Future Signposts.

Further Reading

Alberts B, Bray D, Lewis J, *et al.* (1994) *Molecular Biology of the Cell*, 3rd edn. New York: Garland.

Burdon RD (2003) Genetically modified forest trees. *International Forestry Review* 5(1): 58–64.

Campbell MM, Brunner AM, Jones HM, and Strauss SH (2003) Forestry's fertile crescent: the application of biotechnology to forest trees. *Plant Biotechnology Journal* 1: 141–154.

Carson MJ and Walter C (2004) *Plantation Forest Biotechnology for the 21st Century*. Trivandrum, Kerala, India: Research Signpost Publishing.

Lewin B (2000) *Genes VII*. New York: Oxford University Press.

Rishi AS, Nelson ND, and Goyal A (2002) DNA microarrays: gene expression profiling in plants. *Reviews in Plant Biochemistry and Biotechnology* 1: 81–100.

Rishikesh B, Nilsson O, and Sandberg G (2003) Out of the woods: forest biotechnology enters the genomic era. *Current Opinion in Biotechnology* 14: 206–213.

Strauss SH and Bradshaw HD (2003) *The Bioengineered Forest: Challenges for Science and Society*. Washington, DC: RFF Press.

Strauss SH, DiFazio SP, and Meilan R (2001) Genetically modified poplars in context. *Forestry Chronicle* 77(2): 1–9.

Wullschleger SD, Tuskan GA, and DiFazio SP (2002) Genomics and the tree physiologist. *Tree Physiology* 22: 1273–1276.

Propagation Technology for Forest Trees

W J Libby, University of California Forest Products Laboratory, Berkeley, CA, USA

Introduction

There are six major kinds of propagules now available for the reproduction of forest trees: seeds, sprouts, grafts, cuttings, tissue-culture plantlets, and somatic embryos. Each has two or more subclasses, and each has increasingly understood advantages, disadvantages, and uses. For several of these kinds of propagule, the maturation state and physiological condition of the starting material can vary substantially, with important consequences. These two concepts are discussed in general and with respect to each kind of propagule. The terminology currently in use is not always clear, and is sometimes conflicting. Alternative terminology is noted where such confusion is common.

Some Terminology for Propagule Stages

With the exception of sprouts, each of the other five kinds of propagule has terminology associated with stages suitable for storage; its early intensive-care stage; and its stage as a propagule ready for outplanting in field conditions. The 'seedling–steckling–plantling–embling' parallel terminology for field-ready propagules was formally adopted at the 1983 Second Meeting of the International Conifer Tissue Culture Work Group in Federal Way, Washington, and by 1986 had been accepted by the Genetics and Tree-improvement Working Group of the Society of American Foresters. However, these terms have not been widely or uniformly adopted. These and other commonly used terms are summarized in **Table 1**.

Seeds

The most common form of propagule in natural forests, and for artificial regeneration of forests, has been and is the seed. Most forest-tree seeds result from sexual reproduction, and thus the seeds from a given tree differ genetically from their parent(s) and from each other, providing for diversity and ongoing evolution. A typical seed consists of one or more embryos; surrounding nutritive tissue, which also contributes various enzymes, hormones, and other growth regulators that influence development and germination; and enclosing seed-coat tissue. Given the right environmental conditions, the seed germinates. The germinant grows and develops through juvenile seedling and adolescent sapling stages to become a mature tree.

Natural Regeneration

In pre-Neolithic times, all forest regeneration was natural, with (usually) seeds regenerating extant forests and colonizing new areas without purposeful help from humans. Neolithic behavior began to impact many species of plants and animals several thousand years ago, as humans began domestication of those species and replaced hunting-and-gathering cultures with agriculture. Except for clearing forests for agriculture and housing, human Neolithic behavior was much later in impacting most forest-tree species. Substantial forest planting began barely a thousand years ago, and conscious domestication

Table 1 Terminology for storage and early development

Propagule Type	Storage stage	Intensive-care stage	Field-ready stage: Traditional	Field-ready stage: SAF[a]
Seeds	Seed	Germinant[b]	Seedling	Seedling
Grafts	Scion	Wrapped graft	Graft	Grafted plant
Cuttings				
Rooted	Cutting or hedge or stool	Rooted cutting	Cutting or plantling	Steckling
Unrooted	or mother plant	None[b]	Set or offset or cutting	Cutting
Tissue cultures	Culture	Plantlet	Plantling	Plantling
Somatic embryos				
Encapsulated embryos	Synthetic seed	Germinant	Somatic seedling	Somatic seedling
Naked embryos	Embryogenic tissue or dehydrated embryo	Germinant	Somatic seedling	Embling

[a] Terminology accepted by Society of American Foresters' (SAF) Genetics and Tree-improvement Working Group as of 1986.
[b] Unrooted cuttings set, and seeds scattered or planted, directly on the forest site have no controlled intensive-care stage but, for the first months after setting, scattering, or planting in the field, they are fragile until well rooted.

(often called 'tree improvement') did not become common until the second half of the twentieth century.

Natural regeneration remains typical and appropriate for most parks and reserves. It is also relied on in many harvested forests, and there the harvest practices may have large and sometimes unintended consequences. Species composition of the subsequent forest is strongly influenced by harvest practices, for example, clearcutting or selective harvesting favoring or disfavoring light-demanding or shade-tolerant species. Where some sort of selective harvest system is employed within a species, the parents that are left strongly influence the quality of that species in the subsequent forest. When the more useful trees are harvested (high-grading or creaming), the forest becomes decreasingly useful for later harvests. When the more useful trees are retained to become parents of succeeding generations, the usefulness of the forest for harvest may be increased in the long run at substantial short-term opportunity cost.

Artificial Regeneration

Artificial regeneration is employed to augment an extant forest, to replace the previous forest, or to establish a new forest. In some cases, seeds are scattered or planted directly on the intended site, but more commonly they are germinated in nurseries and seedlings are planted. As humans have increasingly employed artificial regeneration of forests, there has frequently been a progression from (1) collecting conveniently gathered seeds to (2) selecting the mothers (seed-parents), then (3) selecting both mothers and fathers (pollen-parents), then (4) testing to determine the better families, and finally (5) selecting the better offspring within tested families. Seeds have generally been employed in steps 1–4, while various clonal techniques are employed for step 5.

Most species have seeds that are relatively inexpensive to collect, handle, and store. However, nursery propagation is difficult for several forest species whose seeds are expensive to collect; and/or have very short storage lives; and/or have complicated requirements for germination; and/or germinate erratically over long periods of time.

Wild seeds During forestry's equivalent of the early Neolithic, wild seeds were generally collected near to where they would be used. While early data from seed-source (provenance) tests frequently indicate that nonlocal populations are outperforming local populations, longer-term studies often show that the locals are best over periods of several decades. As communication and transportation improved in the nineteenth and twentieth centuries, seeds were often collected at greater distances from their intended planting sites. This practice has frequently proved to be a serious or even disastrous mistake, as these nonlocal populations encountered environmental events, pests, and pathogens to which they were not well-adapted. Whether local or distant, seed collectors often collected from trees that were malformed, or had produced unusually abundant seeds, or had been felled in early thinning; in other words, from mother trees that had undesired qualities. In some forestry programs, those early-Neolithic practices still persist in the twenty-first century.

As the importance of the genetic quality of forest-tree seeds became understood, it became common practice to collect seeds from the better trees in natural stands and plantations. This was sometimes accomplished by felling the select trees during good seed-years, or by climbing them. In some programs, seed-production areas were designated in natural stands or plantations. In these, the quantity, weight, and germinative vigor of the seeds were improved by thinning, fertilizer use, and protection from seed-destroying pests. If the poorer trees were removed during thinning, the average genetic qualities of both the seed-parents and pollen-parents were upgraded.

Orchard seeds Genetic merit is further upgraded by concentrating selected parents in seed orchards. Seed quantity, weight, and germinative vigor are often increased by locating the orchards on warm, dry sites; fertilizer use; irrigation (or water deprivation); and pest exclusion. Genetic control is further increased by augmenting the pollen naturally delivered to the female organs with select pollen, and fully obtained by controlled pollination to produce pedigreed full-sib families. At this level, the parents have usually been further characterized and selected by testing of their progeny, and inbreeding can be avoided by mating unrelated parents (**Figures 1–6**).

Sprouts

Some forest-tree species naturally sprout at or near the root collar when the top is killed, from the stump when cut, or from roots. When applied on purpose, this regeneration technique is called coppicing (or pollarding if the stem is cut 2–3 m above ground). It results in maintaining many of the same (usually well-adapted) genotypes in the subsequent forest. Root-sprouting results in spreading the clone over short distances, and it can be stimulated by ripping the soil to cut up the root systems, or by otherwise damaging the roots.

Sprouts can also serve as good sources of cuttings or tissues for subsequent cloning to other sites. They are particularly effective because traits of the mature tree can be evaluated, and because the sprouts are usually at a juvenile or early adolescent maturation state.

Physiological Condition and Maturation State

A propagule's physiological condition depends on its supply of photosynthates and mineral nutrients, and on the interaction of its growth regulators (such as hormones and inhibitors) with its recent and current environment. The propagule's physiological condition strongly affects its performance during its growth and development. Physiological condition can be influenced to produce more juvenile-appearing or more mature-appearing propagules by the husbandry of the donor plants and during propagation.

Figure 1 *Pinus radiata* full-sib seedlings hedged to produce much larger numbers of cuttings of select full-sib families. The stecklings thus produced from this hedge-orchard will be almost fully juvenile by virtue of the hedges being maintained close to ground level. Courtesy of New Zealand Forest Research Institute.

While the maturation state of most germinating seeds is early juvenile, it is clear that the maturation state of graft scions, cuttings, and tissue-culture plantlets of many forest-tree species varies substantially and importantly. For most species, this variation is reasonably predictable by the chronological age of the donor plant and the part of the plant used as a cutting or tissue donor; most important is the current maturation state of the cutting or tissue when it is donated.

Maturation can be understood as a developmental genetic process, proceeding more or less continuously from embryonic through various juvenile, adolescent, and mature stages, to a late-mature stage when systems are likely to fail. Different parts of a large tree are typically at different maturation states, with the more juvenile (usually early adolescent) states being found low in the tree or in the roots, and the most mature occurring in the terminal meristem(s). One useful indicator of likely maturation state of the donated part is its cumulative distance along the stem from the position of the seedling's cotyledons. Thus, a propagator can influence the maturation state of propagules not only by choosing

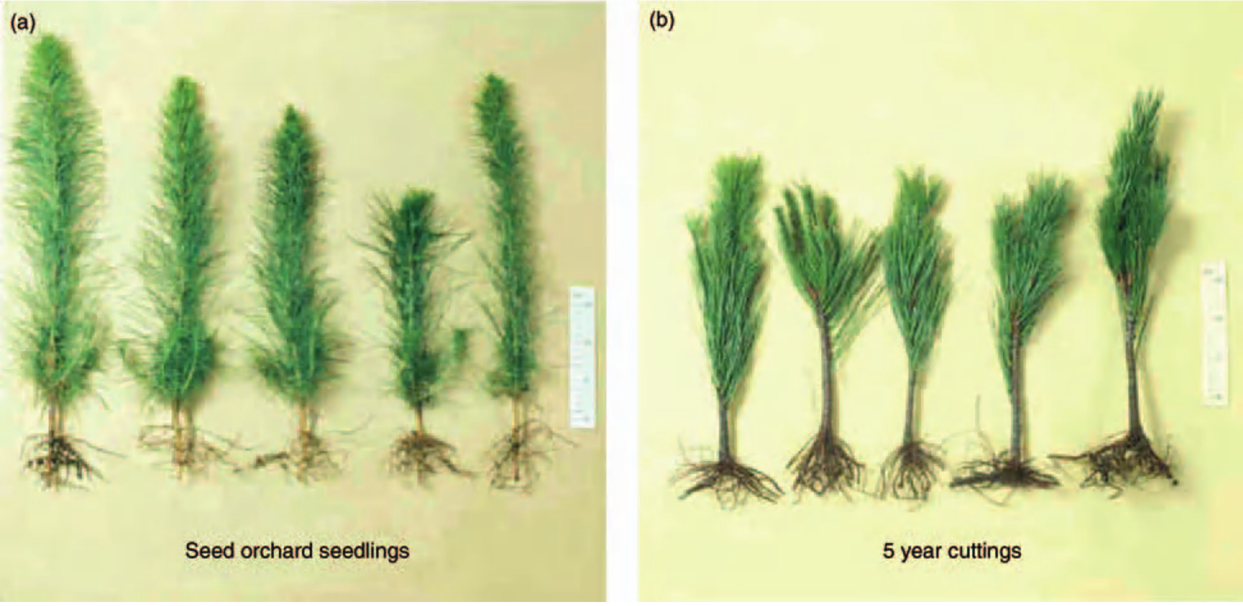


Figure 2 Propagules of *Pinus radiata*, 3 months after planting, comparing habit and vigor of (a) seedings with paler foliage and green apical tufts and (b) stecklings from 6-year-old trees with deeper green foliage and sealed buds (concealed by foliage). Courtesy of New Zealand Forest Research Institute.

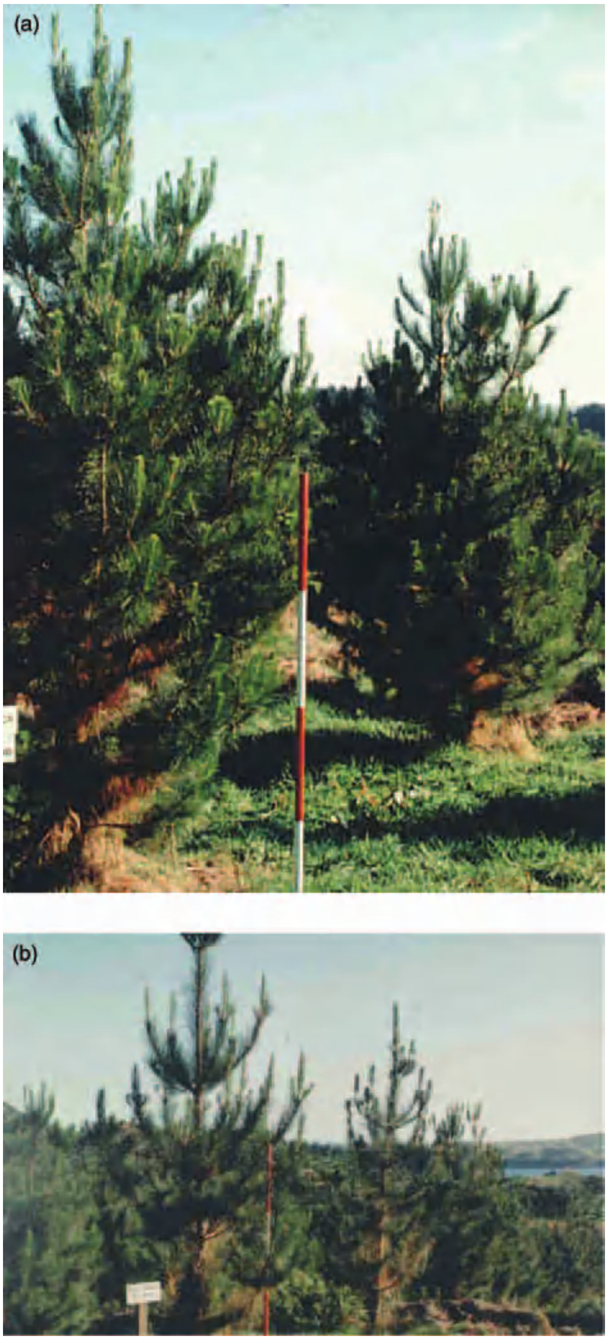


Figure 3 Contrast in *Pinus radiata* between (left) juvenile habit of seedling planting stock, with paler foliage and green apical tufts, and (right) stecklings (rooted cuttings) from 5-year-old trees with deeper green foliage and sealed buds (concealed by foliage). Stecklings from first-year seedlings or stool beds resemble the seedlings. Those taken from progressively older seedlings become more difficult and costly to produce, and make slower growth. Courtesy of New Zealand Forest Research Institute.

the chronological age of the donor plant or culture, but also by choosing the location on the donor plant to take the tissue or organ.

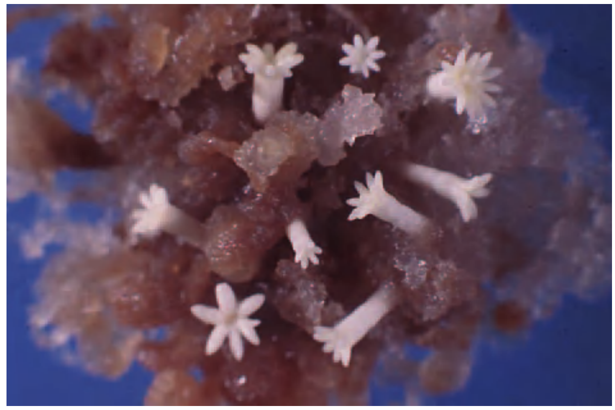


Figure 4 Mature embryos (white) of *Pinus radiata*, which have differentiated out of callus-like embryogenic tissue that developed from an excised embryo on culture medium. Courtesy of New Zealand Forest Research Institute.

Figure 5 Harvested somatic embryo shoots of *Pinus radiata*, transferred to a germination medium, where the hypocotyl and epicotyl elongate and develop green chlorophyll. Courtesy of New Zealand Forest Research Institute.

While the maturation of a clonal line can be slowed by techniques such as low-hedging of donor plants or rapid serial propagation, it is less clear whether the maturation state of tissue or other propagule material can be reversed. It is clear that elements of maturation affecting vegetative propagation proceed rapidly in some species (such as sugar pine, *Pinus lambertiana*) and are long persistent in the juvenile state in others (such as willows, *Salix*).

The effects of maturation state on the performance of propagules can be anticipated by considering the performance of the part of the tree whose terminal meristem is or was at that maturation state. Thus, in an example typical of many conifer species, a propagule produced at a mature maturation state

Figure 6 Somatic embryo shoots of *Pinus radiata* transferred into a rooting medium. In this variation of the somatic embryogenesis technique, the basal part of the hypocotyl initiates roots in a manner similar to that of shoots from organ culture. Following sufficient root development, the developing germinant then hardens off to become a field-ready embling. Courtesy of New Zealand Forest Research Institute.

will develop the lower-bole form, branch architecture, and thinner bark typical of the upper bole; the wood of its lower bole will have, for a given ring number from the pith, the longer tracheids, lower (steeper) microfibril angle, and lower specific gravity typical of upper-bole wood; and its growing shoots will have greater resistance to juvenile diseases, greater susceptibility to browsing, and will more quickly exhibit sexual competence.

Seedlings are normally juvenile when they germinate and their subsequent development is considered to be the norm. Several terms are associated with the concepts and effects of physiological condition and maturation state of other kinds of propagule, and they are most applicable to the scion portion of grafted plants, to cuttings and stecklings, and to a lesser extent to tissue cultures and plantlings. ‘Cyclophysis’ refers to the maturation state of the terminal meristem and the effects of that on propagation and subsequent development. ‘Topophysis’ has elements of cyclophysis, but adds an effect of the additional differentiation that occurs after lateral meristems are produced and grow into a branch hierarchy, plus the different physiological conditions of branches in different parts of the tree. ‘Periphysis,’ less used, refers to the effects of the operational environment of the donor plant on the physiological condition of the parts sampled from the donor. ‘Plagiotropism’ indicates that the main stem of the growing propagule develops at an angle and rather like a branch (often with bilateral symmetry), as contrasted to vertical, radially symmetric ‘orthotropic’ growth typical of seedlings and other juvenile propagules.

Grafts

Grafted plants, often simply called grafts, are compound organisms. In its simplest form, a grafted plant consists of a rootstock (which may be a clonal propagule or a seedling) and a scion, usually a twig or bud from the desired donor plant. Sometimes interstock stems from a third plant are grafted between the rootstock and the scion. The rootstock becomes the root system and sometimes the basal part of the bole, while the scion becomes the upper part of the tree. Many techniques are available for grafting, with a unifying principle of matching the cambium of the scion to the cambium of the rootstock to promote early fusion and healing.

Grafting is commonly used to produce highly uniform clones of fruit or nut trees, and for some forest-tree species to be planted in urban and amenity settings. However, it has not gained wide acceptance as a means of producing planting stock for forests. This is largely due to its higher cost, compared to seedlings, cuttings, and stecklings. It is also due to the frequent occurrence of incompatibility between the scion and the rootstock, which can result in sickening and then death of the grafted plant years or even decades after planting.

Rootstocks are generally of the same species as the scion, although successful grafts are advantageously made using scions of species different from the rootstock (for example, *Juglans regia* scions on *J. hindsii* rootstocks). Using seedling sibs of the grafted scions as rootstocks or rootstock clones selected for general compatibility is sometimes successful in reducing or eliminating a stock–scion incompatibility problem.

Seed Orchards and Breeding Orchards

Seed orchards and breeding orchards concentrate desired genotypes in one place for more effective production of improved planting stock. While some seed orchards and breeding orchards are established with stecklings or pedigreed seedlings, most employ grafts. Twigs that are sufficiently mature to be sexually competent are used as scions, thus usually producing pollen and/or seeds earlier and on smaller trees than if seedlings were used. Severe top-pruning, or dwarfing rootstocks, sometimes help keep the trees small for easier-controlled pollination and collection of seeds

Cuttings

Cuttings are usually twigs detached from the donor plant. In some species, stem sections, root sections, and/or sprouts can also serve as cuttings. In many tree species, the maturation state of the cutting is of great importance. Juvenile cuttings typically root easily and grow well, but mature cuttings root with difficulty, grow weakly, and often maintain branch form for several or even many years.

Unrooted Cuttings

In some species, such as willows (*Salix*) and poplars (*Populus*), it is common to plant unrooted dormant cuttings (sometimes called ‘sets’ or ‘offsets,’ terms commonly used when planting such dormant clonal propagules as onion bulbs, potato tubers, and gladioli corms) directly into the forest site. In some areas, poplar cuttings (poles) 6 m or more long are inserted into planting holes so that their bases reach reliable moisture, where they root and then grow. Some riparian species naturally reproduce when twigs broken off during flood conditions are partially buried downstream and root after the water recedes. Unrooted cuttings of upland species such as radiata pine (*Pinus radiata*) are sometimes planted in soils where young trees are prone to toppling. Given favorable conditions, a high percentage of such cuttings root on site and they are more windfirm than planted seedlings, stecklings, or plantlings on such sites.

Stecklings

There is confusion of terminology in practice and in the literature, with well-rooted propagules originating as cuttings also being called cuttings (Table 1). Nursery-produced well-rooted cuttings, called stecklings, are a common form of cloned propagule for many forest-tree species.

Either dormant or actively growing twigs, sprouts, or root sections may be taken as cuttings. The dormant cuttings may be stored for weeks or even months before setting, and they frequently suffer fewer pathogenic problems than do cuttings taken during the growing season. However, if pathogens are controlled, cuttings that were actively growing and are immediately set frequently root more quickly than do cuttings that are dormant when set. When the cuttings used are root sections, steckling production is fairly straightforward; it involves stimulating shoots to develop and grow from the root section, which also produces new roots.

In established clonal programs, donor plants are often maintained as low-pruned hedges, sometimes called ‘stool beds’ or ‘mother plants.’ A hedge orchard allows a large number of clones and variable numbers of donor plants per clone to be maintained and managed in a relatively small area, under conditions that produce cuttings in a physiological condition favorable for rooting and subsequent growth.

Depending on species and conditions, rooting of cuttings may be done in an outdoor nursery or in enclosed structures ranging from small cold-frames to elaborate greenhouses and growth chambers. Since a cutting has no roots, moisture loss must be reduced by high humidity or periodic misting. Root initiation can often be speeded and root system quality improved by application of auxins such as indole-acetic acid or analogs of that naturally occurring hormone. Stem-rotting pathogens must be avoided or controlled until roots develop and rapid growth resumes. For many species, the quality of the root system is important and can be improved in the nursery by root-pruning, by lifting and loosening the soil (wrenching), or by growing the recently rooted cutting in an appropriate container with internal structure that guides the developing roots. The rooted cutting becomes a field-ready steckling when it attains a size and physiological condition appropriate for outplanting. As with seedlings, nursery practice to foster the appropriate physiological condition often involves a change in fertilizer formulation, moisture stress, and cold soil, all of which combine to produce roots ready to resume active growth immediately following transplanting to the field.

Tissue Culture

‘Tissue culture’ is a generic term that includes *in vitro* growth and proliferation of relatively unorganized cells (cell culture), of callus (callus culture), of particular tissues, and of organized organs such as shoots or roots (organ culture). Organ culture is the form of tissue culture most commonly used to propagate forest trees.

Plantling Production

Cultures may be initiated using cells, tissues, or organs from various parts of the donor plant, including leaves, terminal meristems, stem sections, root sections, and excised embryos. The physical, nutrient, and growth-regulator composition of the culture media are crucial, as are the removal and subsequent exclusion of most or all fungi, bacteria, viruses, and other organisms that would thrive on the culture media and/or infect the growing tissue. Sterile procedures are followed in producing the culture media, preparing the culture containers, and during preparation and handling of the plant material as cultures are initiated and then multiplied.

A major advantage of tissue culture as a mass-propagation technique is the rapid exponential proliferation of material producing plantlets. Another major advantage is the ability to store small numbers of cultures from each clone in a slowly growing or dormant condition while the clones are being tested, and then rapidly multiply those clones that are selected. A problem with many species is that the cultures slowly mature, and/or physiologically degrade, thus changing the performance of the cultures and subsequent propagules.

Adventitious plantlets When cultures are grown as cells or callus tissue, and then shoots develop when the conditions and composition of the culture medium are changed, or if shoots develop from other than shoot meristems during organ culture, these shoots and the resulting plantlets that develop when they root are called 'adventitious.' Multiplication rates are generally very high in such cultures. However, there is some evidence that within-clone variation is also higher in such cultures, apparently resulting from higher mutation rates, lower ability to repair such mutations, and/or persistent (epigenetic) effects that are maintained within clonal sublines but not subsequently inherited following sexual reproduction. Other anomalies may occur when tissues developing on some different pathway incompletely change to become shoot meristems. Thus, there has been a shift away from these adventitious forms of tissue culture.

Axillary plantlets When cultures are initiated using explants including the terminal meristems of embryos or shoots, these meristems then continue to grow shoots of increasing length. These shoots are harvested, cut into stem sections, and the stem sections are used to initiate new cultures. The stem sections usually contain one or more suppressed meristems in the axils of their leaves and, upon release from the inhibition of hormones from the terminal meristem, these axillary meristems then initiate long-shoot growth. Extension growth of the shoot organs and production of new stem-section explants are repeated through several or many cycles. When the culture medium is formulated to stimulate root production instead of shoot growth, the rooted shoots are termed axillary plantlets.

Plantlet Care and Development

Whether axillary or adventitious, newly rooted plantlets are fragile and need intensive care. They must be slowly acclimatized to nonsterile ambient conditions. This is commonly done by moving the growing plantlets through a series of nonsterile environments with increasingly greater variation in temperature and humidity. When able to cope with ambient conditions, the plantlets are transferred to a normal greenhouse or open-air nursery, with nursery practices similar to those for rooted cuttings. When the plantlets reach a size and physiological condition suitable for outplanting, they are called plantlings. As with stecklings, the maturation state of the plantlings may not be fully juvenile, and their maturation state will affect their subsequent growth and development when outplanted.

Somatic Embryogenesis

It has recently become possible to produce embryos from somatic cells, rather than from fused gametes. Thus, the normal genetic recombination that results in no two zygotes being identical can be avoided, and clones can be produced by somatic embryogenesis. As of the early twenty-first century, somatic embryogenesis has become available technology for a few species, for example yellow poplar (*Liriodendron tulipifera*) and several species of spruce (*Picea*), while the techniques are proving to be difficult for several other species. Somatic embryogenesis has not yet been intensively attempted with most species of forest trees.

Explants appropriate for initiating embryo-producing (embryogenic) cultures are commonly obtained from tissues such as suspensor organs connecting normal zygotic (sexually produced) embryos to surrounding nutritive tissue. In some species, embryogenic tissue has also been induced in cultures of such things as pith tissue obtained from mature plants. This latter approach allows the substantial advantage of cloning from donors that have developed to an advanced maturation state, an advantage not available when cultures are initiated from embryonic tissues associated with (or part of) new embryos following sexual recombination.

As with organ culture, the embryogenic tissue proliferates rapidly, and very large numbers of embryos can be induced to develop with a change in culture conditions and media composition.

While it is relatively easy to advance the maturation state of a clonal line, a clonal line's maturation state has been difficult, if not impossible, to reduce. A major advantage of somatic embryogenesis is that embryogenic tissue can be cryogenically stored at very low temperature. Later, clonal propagation can be resumed at an embryonic maturation state when the clone has been adequately tested for confident deployment, or when it is needed for special or unusual purposes.

A second possible advantage is the insertion of foreign genes into the cells of embryogenic tissue, followed by identification and testing of the genetically engineered miniclones (lines that differ by only one or a few genes from otherwise identical lines of the original clone). The identified miniclones can be cryogenically stored, and those genetically modified

Table 2 Comparative advantages and 2003 status

	Seeds	*Grafts*	*Cuttings*	*Cultures*	*Embryogenesis*
Cost	Very low	Moderate	Low	High	Potentially low
Gain[a]	Modest	Modest	High	High	Very high
Lag[b]	Varies	Modest	Short	Modest	Modest
Rate[c]	Low	Modest	Modest	High	Very high
State[d]	Juvenile	Mature	Varies	Varies	Embryonic
R&D[e]	Advanced	Advanced	Advanced	Early	Very early

[a] Genetic gain attainable, given reasonable tree-improvement programs.
[b] Lag time from selection to substantial propagule production. Seed production following selection of parents varies from immediate to several decades.
[c] Multiplication rate once propagule production begins.
[d] Graft scions are likely to be used at a mature state, while cuttings and cultures may be initiated at early-juvenile to mid-adolescent maturation states, balancing advantages and disadvantages.
[e] The research and development status of the technology.

miniclones that prove to be acceptable can later be mass-produced.

Emblings

When embryo development is stimulated in embryogenic tissue, the embryos can be harvested and 'converted' (germinated) immediately, or they can be dehydrated, stored, and germinated later. In either case, these naked embryos need favorable conditions for their germination and early growth. As with plantlets, after the somatic embryo germinants have been acclimatized to ambient conditions, they can be grown in a normal greenhouse or outdoor nursery. When they reach a size and physiological condition suitable for outplanting, they are called emblings.

Somatic Seedlings

Harvested embryos can also be encapsulated. In this procedure, each embryo is surrounded with a gel containing nutrients and growth regulators, all contained within a hard coating. This coating can be color-coded, with clone name or number, organization logo, and other information printed on it. These synthetic seeds can be handled with the equipment and procedures well developed for seedling nurseries. Because the materials encapsulated with the embryos will affect their germination, growth, and development, it is useful to differentiate these propagules from those developing from naked somatic embryos. Thus, when field-ready, they are called 'somatic seedlings' rather than either emblings or seedlings.

Relative Properties and Status of Propagule Types

Table 2 summarizes some of the advantages and disadvantages of the various types of propagule discussed above.

See also: **Tree Breeding, Principles**: Conifer Breeding Principles and Processes; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tree Physiology**: Physiology of Vegetative Reproduction.

Further Reading

Ahuja MR (ed.) (1991) *Woody Plant Biotechnology*. New York: Plenum Press.
Ahuja MR and Libby WJ (eds) (1993) *Clonal Forestry*, vol. 1, *Genetics and Biotechnology*, vol. 2, *Conservation and Application*. Heidelberg, Germany: Springer-Verlag.
Bey M-N, Leroy M, and Verite S (eds) (1992) *Mass Production Technology for Genetically Improved Fast Growing Forest Tree Species*, vols. I, II and synthesis. Bordeaux, France: AFOCEL.
Bonga JM and Durzan DJ (eds) (1987) *Cell and Tissue Culture in Forestry*, vol. 1, *General Principles and Biotechnology*, vol. 2, *Specific Principles and Methods: Growth and Development*, vol. 3, *Case Histories: Gymnosperms, Angiosperms and Palms*. Dordrecht, The Netherlands: Martinus Nijhoff.
Diamond J (1999) *Guns, Germs, and Steel*. New York: W. W. Norton.
Dodd RS and Power AB (1988) Clarification of the term topophysis. *Silvae Genetica* 37: 14–15.
Hartmann HT, Kester DE, Davis FT Jr, and Geneve RL (1997) *Plant Propagation: Principles and Practices*. Upper Saddle River, NJ: Prentice Hall.
Jain SM, Gupta PK, and Newton RJ (1994) *Somatic Embryogenesis in Woody Plants*. Dordrecht, The Netherlands: Kluwer Academic.
Larsen CS (1956) *Genetics in Silviculture*. Edinburgh, UK: Oliver & Boyd.
Schopmeyer CS (ed.) (1974) *Seeds of Woody Plants in the United States*. US Department of Agriculture Handbook no. 450. Washington, DC: US Government Printing Office.
Wright JW (1976) *Introduction to Forest Genetics*. New York: Academic Press.
Zobel B and Talbert J (1984) *Applied Forest Tree Improvement*. Prospect Heights, IL: Waveland.

GEOGRAPHIC INFORMATION SYSTEMS *see* RESOURCE ASSESSMENT: Forest Change; Forest Resources; GIS and Remote Sensing; Regional and Global Forest Resource Assessments.

H

HARVESTING

Contents

Forest Operations in the Tropics, Reduced Impact Logging

R Heinrich and U Arzberger, Food and Agriculture Organization, Rome, Italy

Introduction

In recent years considerable efforts have been made in introducing improved forest harvesting practices to tropical forests to support sustainable forest management. However, only a small proportion of forests in the tropics is actually being managed on a sustainable basis. Environmental groups and, increasingly, the general public have called for refined harvesting systems and techniques so as to utilize wisely forest resources, thereby maintaining biodiversity and keeping forest stands intact in order to provide forest goods and services for the present as well as for future generations. The application of reduced impact logging (RIL) systems and techniques seems to have gained increasing importance in meeting environmental challenges and providing economic and social benefits.

Forest Operations in the Tropics

In tropical countries, harvesting operations are fundamentally different from those applied in temperate zones. Stand densities in temperate forests are considerably higher than in the tropics, generating much higher potentials for commercial timber volumes per hectare. There is less diversity of tree species in temperate zones, and the utilization of commercial tree species permits simplified forest operations. Due to the application of both selective and clear-cutting as well as the higher standing timber volumes per hectare, harvesting densities in general greatly exceed those in the tropics. Directional felling is easier to carry out in temperate zones due to the usually smaller-sized trees and crowns; and soil conditions are better for skidding operations. In spite of varying seasons, climatic conditions allow the appropriate implementation of harvesting operations throughout the whole year.

In the tropics, forest operations are generally more complex to organize and implement than in temperate zones. Natural forests in the tropics are characterized by a higher abundance of different species with many diverse sizes of timber and ample stand densities with only a few species of commercial interest. The harvestable wood volumes per hectare vary considerably depending on the occurrence of commercial tree species. The situations that most often complicate harvesting operations are the following:

- large trees with large crowns
- low carrying capacity and high vulnerability of forest soils
- extensive variety of timber sizes
- high precipitation rates, which often contribute to soil erosion
- lack of forest road and skid trail infrastructure
- long transport distances on poorly paved roads due to scarcity of appropriate road construction material.

Preharvest Planning

The main objectives of preharvest planning are to optimize harvesting operations and to minimize environmental impacts. A harvest plan should consist of a written description of the planned operation and a detailed topographic map of the harvesting operation area. Preharvest plans should also include information on harvestable tree species, as well as data on other factors to be taken into consideration in harvesting planning, such as soil and terrain conditions or existence of watercourses. Detailed information about specific working equipment and the workforce involved plus careful attention to the integration of local communities in the projected operation are additionally preconditions for well-planned harvesting operations.

Forest Road Engineering

The goal of forest road engineering is to provide reliable access to the forest for management purposes and for silvicultural and harvesting operations. It involves specifying design standards and field layout, followed by construction and maintenance of forest roads including setting of skid trails, location and layout of landings as well as constructing subsidiary structures, such as bridges and culverts.

Forest roads are unquestionably the most environmentally problematic feature of timber harvesting operations, since a major part of the total soil erosion can be attributed directly to them because of inadequate design and construction standards, as well as poor maintenance practices.

Tree Felling and Cutting

Tree felling and cutting includes all activities from felling the standing tree to its preparation into logs for wood extraction. These activities include the felling process itself, cutting off tree crowns and limbs, crosscutting stems into logs and sometimes debarking of logs.

In tropical regions, trees may be large and heavy with huge crowns and might be connected by strong vines to each other. They fall with a tremendous force which can uproot neighboring trees; and stems may shatter, bounce, and roll uncontrollably. Therefore felling operations are both the most hazardous part of harvesting operations for the labor force. They are also a major cause of damage to the forest stand and result in the generation of a large amount of wood waste.

Wood Extraction

Extraction of wood is the process of moving trees or logs from the felling site to a landing or roadside. Extraction practices can be distinguished by the system used and the harvesting equipment employed (**Table 1**). Regardless of the type of logging system used, extraction can inflict substantial damage on forest ecosystems.

In the tropics the most common method of wood extraction is the ground-skidding system. A conventional set of ground-skidding equipment consists of ground-dependent machines, which may consist of either crawler tractors, wheeled or tracked skidders, or a combination of them. They are generally equipped with winches.

The use of draft animals, such as elephants, oxen, horses, or water buffaloes, can be economically attractive, particularly in remote areas. They are often used by local communities in small-scale operations and in forest stands with smaller-sized trees.

Cable systems are a preferred method for wood extraction in hilly to steep terrain. With this method, logs are transported either partially (as in ground and high lead operations), where logs may drag on the ground causing soil disturbance, or fully suspended in the air (as in skyline operations). Ordinarily, the

Table 1 Advantages and disadvantages of different extraction systems

Extraction system	*Advantage*	*Disadvantage*
Ground skidding	Low cost extraction system Short training requirement Simple technology	Tendency to cause the greatest environmental problems High density of skid trails Limited by slope gradient and soil conditions
Draft animals	Low soil and stand damage Extremely narrow skidding paths Low investment and maintenance costs	Limited extraction distances Mostly limited to small timber sizes and small-scale operations
Cable	Low density of roads No skid trails Very low environmental impact when properly done	High investment costs Laborious assembly and disassembly of the cable system
Helicopter	High production rates Low density of forest roads Very low environmental impact	Very expensive Thorough planning and precise organization needed Extremely highly skilled team of workers needed
Manpower	Narrow skid trails Necessary equipment very simple Cheap	Hard and slow work Limited extraction distances

timber is transported by carriages which are moving on a cable. The power source – a winching machine, also called a yarder – is located either at the top or the lower station, depending on the type of system used.

Helicopter systems are the most productive as measured by cubic meters of timber produced per hour or day and yet are the most expensive wood extraction system. Helicopters are only used in difficult and steep terrain where high-value tree species are extracted and where intensive forest road development would be too expensive and not appropriate.

With the introduction of the crawler tractor, log skidding by manpower has almost disappeared in tropical Africa. However, it is still being used in Asia and in the Pacific region where it is called kuda-kuda. Short wooden wedges, driven into the sides of the log, give the men a hold to control and push the log lengthwise over wooden cross-skids. Skidding distances may exceed 1 km where there are no alternative methods of extraction.

Landing Operations

Work on landings include all activities in connection with sorting, storing, and preparing the extracted stems or logs for further transportation to the processing facility or any other final production destination. Landings are always connected to roads so as to provide access to the stored timber by transport vehicles.

Transport Operations

At present the most common form of log transport in the tropics is by means of logging trucks. In remote areas, however, often a combination of land and water transport is used: hauling timber from the landing to an embarkation point by trucks, where the journey is continued by water transport, using barges or rafts. In some rare cases, railways are an alternative means of transport.

Harvesting Intensity

Harvesting intensity is a decisive criterion that influences the degree of impact on forests. Generally the total standing timber volume may range from 50 to over 200 $m^3 ha^{-1}$ in the tropics. Harvesting intensity in tropical forests varies considerably between regions, countries, and even within countries. In Africa a low logging intensity forest operation is usually practiced with a mean extracted timber volume of 8–25 $m^3 ha^{-1}$. Medium and moderately high logging intensity operations as practiced in South America often reach 10–50 $m^3 ha^{-1}$ of harvested timber. In Asia and the Pacific region, logging intensity is higher than in the other two regions, reaching about 40–100 $m^3 ha^{-1}$.

Reduced Impact Logging

Definition of Reduced Impact Logging and Conventional Logging

Reduced impact logging (RIL) may be defined as an intensively planned and carefully controlled implementation of harvesting operations used in order to minimize impact on forest stands and soils, usually in cutting individually selected trees. In contrast to RIL, conventional logging systems are carried out without much concern about possible environmental impacts to the forest stand and soils and the sustainable utilization of forest products and services.

The aim of RIL is to introduce environmentally sound forest operations and to avoid negative impacts that could occur in conventional logging systems. Besides following the forest operation suggestions described above, other improvements can be obtained by applying RIL techniques in order to decrease impacts and increase benefits. The main characteristics of RIL are shown in **Table 2** and described below.

The idea behind RIL is not a new one. It is actually a collection of environmentally sound forest practices already used in some temperate and tropical forests. Techniques such as preharvest inventory, worker training, directional felling, prescribed skidding or advanced road construction are well-established practices in a number of countries. Additional practices specific to tropical forests are, for example, mapping of individual crop trees and preharvest cutting of vines.

Stand Entries at Predetermined Cutting Cycle

In order to provide sufficient time for the regeneration of remaining forest stands and to guarantee a sufficient amount of timber for future harvesting operations, a predetermined cutting cycle for stand entries should be defined and observed. This is a

Table 2 Main characteristics of reduced impact logging techniques

Stand entries at predetermined cutting cycle
Worker and supervisor training
Safety regulations
Favorable working conditions
Preharvest operational inventory, including tree marking and location mapping of potential crop trees
Vine cutting when required
Advanced road construction
Minimize extraction trails
Directional felling
Maximum utilization of all trees felled
Landings planned
Damage to residual stand minimized
Postharvest assessment
Rehabilitation of sites of negative impacts

major aim of sustainable forest management. A minimum interval has to be determined by silviculturists based on knowledge of local growth rates and an assessment of the degree of damage caused to the residual stand by the harvesting operation.

Worker and Supervisor Training

Forest workers are in many cases underpaid and poorly skilled. This fact results in negative environmental impacts and economic losses. Forest companies often involve local communities in the workforce for harvesting operations, because they are the only available workers in remote forest areas.

The implementation of training programs for logging and supervisory personnel at all levels is essential to improve the working conditions. Perhaps the lack of skilled workers is one of the main reasons why a successful application of RIL in tropical forests has failed to materialize on a large scale so far.

Safety Regulations

Training programs for workers, protective clothing, and properly serviced equipment contribute to significantly improved labor safety and health conditions. Safety has tended to be neglected due to economic difficulties. Accidents occur mainly during the felling process. Often, forest management does not know the real costs of accidents: many of the indirect costs resulting from inadequate safety regulations are difficult to determine, but they can be up to six times higher than the direct costs.

Favorable Working Conditions

Environmentally sound forest operations can only be carried out under favorable weather and soil conditions. Wet soils and heavy rainfall considerably hamper the use of ground-dependent machinery, and cause substantial soil disturbance and compaction. Preharvest plans need to consider alternative systems, should forest operations be hampered by weather, soil, and terrain conditions in a specific area.

Preharvest Operational Inventory

A preharvest operational inventory should estimate the timber volume and its distribution over the forest production unit as well as the number and the condition of potential crop trees. In tropical forests identification, marking, and mapping of each individual crop tree is essential to ensure efficient location of crop trees so as to increase the productivity of harvesting operations and to protect potential future crop trees.

Vine Cutting

Vine cutting, when required and properly implemented, can be an effective measure for improving the safety of the workforce during felling and for reducing crown damage to remaining trees. It generally should be done far enough in advance of felling to ensure that the vines have died and fully decomposed. Otherwise, safety may be compromised by vine cutting that has not been properly carried out.

Advanced Road Construction

The objective of advanced road construction is to minimize the clearing width, while at the same time ensuring that the width is adequate to permit the expected traffic to operate safely. In areas of high precipitation it is common to clear an area of forest alongside the road to allow sunlight to penetrate so that it can dry out the road surface after rainfall. The amount of roadside clearing can be reduced if appropriate drainage systems are used and properly maintained.

Minimizing Extraction Trails

In conventional skidding operations, uncontrolled driving to each harvestable tree or log due to the lack of skid trails can cause substantial soil disturbance and compaction. A system of skid trails, predetermined in the planning phase, should be adopted to minimize soil compaction by forest machines. Tracked and wheeled wood-extraction machines should stay on those skid trails. When using wheeled skidders the use of low-pressure and high-flotation tires further helps to minimize soil compaction.

Directional Felling

Directional felling is a specific tree-felling technique in which the direction of fall is determined by the operator prior to cutting. Where possible, trees should be felled in the direction of existing canopy gaps in order to reduce damage to nearby standing timber. In general, trees should be felled either towards or away from skid trails, preferably at an oblique angle to the skidding direction. Felling away from the skid trail will reduce problems for the extraction crew when tree crowns are large, whereas felling towards the skid trail can reduce the extraction distance substantially.

Maximum Utilization of Trees Felled

Most of the logging waste in forest operations occurs in both felling and cutting operations; some also occurs in skidding operations. Appropriate felling and cutting techniques include directional felling, cutting stumps low to the ground, and optimal crosscutting of stems into logs. Following RIL practices, such as mapping of felled trees and controlled skidding, wood waste due to lost logs very seldom occurs in skidding operations.

Landings

The location and design of landings should be done at the same time as road location and design. In many places, a small clearing at the side of the road is used for the landing rather than creating an entire landing structure.

Postharvest Assessment

Postharvest assessments can serve as an operational feedback for forest managers, technicians, and workers to determine the degree to which the objectives of RIL guidelines have been achieved, and to obtain information on how to improve forest operations in future. These include evaluation of stand and soil damages, as well as an assessment of costs and productivity of harvesting operations.

Minimizing Damage to the Residual Stand

Impacts on soil and forest stands arise inevitably from the use of heavy-duty machinery in forest operations. By following RIL practices and through proper implementation of harvesting operations, such damages can be minimized, thus leaving residual stands in better condition regarding future forest operations.

Rehabilitating Forests after Negative Impacts

Observation of the operating areas disturbed by roads, landings and skid trails, and also of the degree of soil disturbance, will provide an indication of whether rehabilitation is needed. If necessary, the areas with exposed soil should be revegetated with grass or other ground cover to prevent soil erosion. When harvesting only a few tree species, enrichment planting is often needed to guarantee diversity of species.

Benefits of RIL

Although a considerable number of studies on environmental impact assessment have already been carried out in tropical forests, many authorities have called for more comprehensive knowledge and information on the environmental, social, and economic benefits of forest operations. Unquestionably it has been proved that RIL significantly reduces damages to the remaining stand, soil, and watercourses. It has also been shown that RIL increases profitability on a larger scale, and considerably improves efficiency, recovery rates of timber, and safety standards for workers. Since higher recovery rates of felled timber generally can be achieved in RIL as compared to conventional logging systems, smaller areas of natural forest are subsequently affected by harvesting operations while at the same time the same amount of timber is recovered (**Table 3**).

RIL reduces the percentage of wood waste, thus increasing productivity and the economic return of operations. Minimized road length subsequently lowers maintenance and transportation costs, and contributes to a reduction in harvesting operation expenses, thus increasing financial benefits. Moreover, RIL has less impact on the residual stand and site, which enhances regeneration, allowing earlier re-entries with higher recovery rates in wood volume in m^3 in second cuts. However, overall costs for forest operations increase due to the expensive and comprehensive planning activities, which cost less in conventional logging systems. Overall, it is assumed that RIL practices are generally worthwhile (**Table 3**), but concerning specific financial benefits, the evidence of RIL experts is inconclusive.

Future Outlook

At present RIL is used by only a small number of forest companies and operators in the natural forests

Table 3 Mean values for various parameters in conventional and reduced impact logging systems obtained from examples in the scientific literature from the last 30 years

Parameter	*Unit*	*Conventional logging*	*Reduced impact logging*
Logging intensity	$m^3 ha^{-1}$	45	37
Logging intensity	trees ha^{-1}	8	8
Logging cycle	years	35	34
Costs			
Planning	\$US m^{-3}	1.44	1.72
Felling	\$US m^{-3}	0.60	1.16
Skidding	\$US m^{-3}	4.64	4.46
Damage			
Residual stand	% of residuals	49	29
Stand	trees/trees felled	22	9
Site	% of area	18	8
Canopy opening	% of area	25	16
Lost timber	% of removals	25	15
Utilization rate	% of felled timber	47	60

Source: Data compiled from ITTO (2001) *Tropical Forest Update*. http://www.itto.or.jp/newsletter/Newsletter.html and Killmann W, Bull GQ, Pulkki R, and Schwab O (2001) Does it cost or does it pay? *Tropical Forest Update* 11(2): http://www.itto.or.jp/newsletter/vlln2/index.html in the tropics. There are still many unknown aspects concerning RIL, and the major obstacle to the implementation of RIL is the common lack of knowledge about its benefits. The belief that RIL is more expensive is one of these obstacles.

Despite the research, data collection, and field studies that have been done so far, more effort needs to be dedicated to emphasizing the importance of RIL. Forest managers have expressed the need for research on a larger scale so as to provide reliable information concerning the benefits of RIL, especially the financial benefits. Comparative studies on RIL and conventional harvesting systems are necessary in order to acquire adequate data that would demonstrate, with examples, to forest companies and logging operators the numerous advantages of RIL. Consequent implementation of training programs for forest personnel at all levels and the availability of technical assistance are additional inducements for spreading the acceptance of RIL.

Through the application of RIL techniques, at least one source of negative impact on tropical forests from logging pressures could be partly reduced. Sustainable tropical forest management has to secure the existence and the continuity of the tropical forest ecosystems. RIL is a very important contribution to this end.

See also: **Environment**: Environmental Impacts. **Harvesting**: Forest Operations under Mountainous Conditions; Roading and Transport Operations. **Operations**: Logistics in Forest Operations. **Plantation Silviculture**: Sustainability of Forest Plantations. **Silviculture**: Natural Stand Regeneration. **Sustainable Forest Management**: Overview.

Further Reading

Durst PB (1999) *Code of Practice for Forest Harvesting in Asia-Pacific*. Bangkok: Food and Agriculture Organization of the United Nations, Regional Office for Asia and the Pacific.

Dykstra DP and Heinrich R (1996) *FAO Model Code of Forest Harvesting Practice*. Rome: Food and Agriculture Organization of the United Nations.

FAO (2001) *State of the World's Forests 2001*. Rome: Food and Agriculture Organization of the United Nations.

FAO (2003) *Forest Harvesting and Engineering Case Studies*. http://www.fao.org/forestry/FOP/FOPH/harvest/publ-e.stm.

Geist HJ and Lambin EF (2001) *What Drives Tropical Deforestation? A Meta-Analysis of Proximate and Underlying Causes of Deforestation Based on Subnational Case Study Evidence*, LUCC Report Series no. 4. Louvain, Belgium: Land-Use and Land-Cover Change International Project Office, University of Louvain.

Heinrich R (1997) Environmentally sound forest harvesting operations. In *Research on Environmentally Sound Forest Practices to Sustain Tropical Forests*, Proceedings of the FAO/IUFRO Satellite Meeting held in Tampere, Finland, 4–5 August 1995, pp. 1–7.

ITTO (2001) *Tropical Forest Update*. http://www.itto.or.jp/newsletter/Newsletter.html

Killmann W, Bull GQ, Pulkki R, and Schwab O (2001) Does it cost or does it pay? *Tropical Forest Update* 11(2): http://www.itto.or.jp/newsletter/vlln2/index.html

Harvesting of Thinnings

R Spinelli, National Council for Research – Timber and Tree Institute, Florence, Italy

Introduction

When thinning a forest, loggers operate under such peculiar conditions that special techniques and equipment are required. In principle, thinning teams face two main constraints: the low value of the harvest and the permanence of a residual stand that hinders machine movements. Of course, the impact of these factors largely depends on thinning type. The first thinning is most critical, because it yields very small trees and releases the densest residual stand. In contrast, the second and third thinnings are somewhat easier to implement: harvest trees are larger and may yield valuable products, while the residual stand is not excessively dense and offers more space for maneuvering. In fact, one often speaks of commercial thinning and precommercial thinning, according to whether the operation is sustainable from a commercial viewpoint or not. In precommercial thinning, the value of the harvest does not cover the overall harvesting cost, and the operation configures as a subsidized activity, performed with the aim of increasing future profit and improving forest stability. The first thinning is more likely to be conducted on a precommercial basis, whereas later thinning can offer some profit. At any rate, such profit is much inferior to that obtained from the final harvest, because the value of the harvest is lower and the harvesting cost higher – often twice as high.

Good Reasons for Thinning

Why thinning, then? There are several reasons. First, appropriate thinning allows released trees to grow healthier and larger than if they were left to compete with the removed trees, which increases the value of the final harvest. Second, by improving forest stability, thinning increases the chances for such a final harvest to occur in due time – and not be ruined by disease, windstorm, or fire. After thinning, released trees grow stronger and may better resist all kind of adversities, parasites and storms included. Furthermore, thinning implies the removal of any fuel build-up and decreases fire hazard, especially if the thinning breaks all 'fire ladders' – i.e., the dominated layer that connects the understory to the crowns of dominant trees, which may transform a litter fire into a catastrophic event.

These are 'strategic' benefits that accrue in the medium and long run. Other benefits have a more contingent nature, but at times they can be stronger motivators than any strategic goal, because they work in the short run – the here and now where we live. In general, any commercial thinning can be regarded as an anticipation of revenue that can be cashed in moments of need. Therefore, commercial thinning is a way to obtain quick cash when the business needs it. On a similar line, commercial thinning can help face demand peaks for certain products, or bridge age-class gaps in the available harvest: an intense thinning plan can supply pulp factories with significant amounts of pulpwood, if the volumes obtained from maturity cuts are not sufficient to cover the demand.

Whatever the reason for thinning, there are some crucial requirements that must be satisfied. First, it is imperative that the thinning improves the stand, or at least that it does not decrease its stability and value. This requirement stands even when the thinning is performed as a mere commercial operation, aimed at obtaining an anticipation of the projected revenue: no sound business would seek immediate cash at the expense of jeopardizing its capital base. Therefore, all thinning must be implemented in such a way that residual tree damage and soil disturbance are kept below the risk threshold, beyond which stand decline can be expected. Furthermore, as in any other economic activity, profit should be maximized – or losses kept to the absolute minimum – always within the limits allowed by sound forest practice. This is a very difficult task, since thinning is often a "borderline" activity from the financial viewpoint. Much research has been devoted to improving the economics of thinning, and more is in progress. Today, a number of alternative strategies are available to forest managers to apply a sound thinning plan effectively, while new machinery has been designed that can aid in the endeavor. Of course, the choice of any strategy and equipment must reckon with the working conditions typical for each case.

Working Method

Thinning crews can resort to any of the three classic working methods: shortwood, tree length, and full tree. The shortwood method implies delimbing and bucking felled trees at the stump site, before extraction. When applied to thinning, this method offers the great advantage of reducing the bulk of the wood being handled, which is particularly important when operating amidst a dense residual stand that hinders maneuvering. With the tree length method, felled trees are delimbed at the stump site, but they are bucked into logs only after they reach the landing. Therefore, they are extracted as full-length stems, which requires very careful planning if damage to the residual stand is to be kept within acceptable limits. Finally, harvesting by the full tree method implies extracting full trees to a landing, where they can be processed into a number of products. Here, handling is the most difficult, and the trade-off is in the total recovery of all available biomass – or the complete removal of dangerous fuel, depending on viewpoint.

In principle, the shortwood method is best applied to the second and third thinning, when removed trees have reached such a size to provide a few merchantable logs. In contrast, the full tree method seems ideally suited to the first thinning, which generally yields a crop of small trees that can hardly offer one good log. In this case, mass handling and whole-tree chipping are the most effective solutions (**Figure 1**).

The implementation of any harvesting method varies greatly with local conditions, and especially with the scale of the forest economy. Small-scale forestry and industrial forestry are two worlds apart, each with its own constraints and opportunities. In general, a business operating in a small-scale forestry environment enjoys better flexibility and is spared part

Figure 1 Moving on the corridors, a chip forwarder picks up whole-tree bunches, chips them on site, and takes the chip to a landing.

Figure 2 The integral harvester–forwarder is a new machine being introduced to thinning operations.

of the fierce global competition endured by the industrial company, but it also lacks the capital to acquire state-of-the-art technology. On the other hand, the industrial company can buy cutting-edge equipment, but it must deploy such equipment according to a very careful plan, if it wants to reach the efficiency required to match competition (**Figure 2**).

Translated into harvesting practice, this means that nonindustrial operations generally resort to low-productivity, low-investment equipment, such as the chainsaw and the adapted farm tractor (**Figure 3**). These two machines can be used to implement any of the harvesting methods described above. When applying the shortwood method, trees are felled, delimbed, and bucked with a chainsaw, and the logs are forwarded to the landing with a farm tractor, coupled to a dedicated forestry trailer. Tree-length and full-tree harvesting also rely on the chainsaw for felling–delimbing or felling respectively, while skidding can be performed by a farm tractor equipped with a log grapple or a forestry winch, depending on terrain conditions. As an alternative, extraction can be delegated to cheap second-hand skidders and forwarders, once industrial users have shifted to new, more productive models.

On the other hand, advanced mechanization is the pillar of industrial forestry operations. Here, the shortwood method is applied by the harvester–forwarder team, which is almost a symbol of Nordic forest technology. These two machines can carry out the whole task: the former felling, delimbing, and bucking the trees, the latter forwarding the logs to the landing and stacking them into neat piles. Although they work together, the two machines act independently with the advantage of simple logistics and easy planning. The alternative is to use a feller–buncher and a skidder to harvest full trees (**Figure 4**). These are cut and grouped in bunches with the feller–buncher, and dragged to the landing by a grapple

Figure 3 Felling with a frame-mounted chainsaw in a first thinning.

Figure 4 Compact feller–buncher in a late thinning.

skidder – or by a cable skidder, if terrain conditions prevent direct access to the bunches. Mechanized tree-length harvesting would require adding a delimber to this basic team, but this is comparatively rare. Today, most delimbers can also buck, and if one introduces such machines, then shortwood production is more likely to occur, which in turn will favor the adoption of the simpler harvester–forwarder team. On the other hand, one can always process the trees at the landing, which allows their tops and branches to be recovered for conversion into energy chips or mulch.

Whatever the system adopted, modern machinery is very expensive and can only be used if the value of their output will match their operating cost. When thinning, the value of the harvest is rather low: due to the limited size of removal trees, most thinning jobs only yield pulpwood and small sawlogs, which bear very low price-tags. Therefore, productivity must be high enough to compensate for the low value of the product. But this is difficult to achieve, because thinning does not offer favorable working conditions to mechanical equipment. In fact, productivity is proportional to the size of the harvested tree and to the ease with which the machine can move around, and we have just seen that thinning offers small-size trees and confined work space.

The Effect of Stem Size

Stem size governs the productivity of logging teams more than any other single factor (**Figure 5**). For each situation one may eventually identify a minimum stem size that makes harvesting economical: below such size, productivity does not reach the required level and the value of the harvest fails to match the machine's operating cost.

Stem size limits are particularly binding when harvesting shortwood, as today's harvesters can only treat one tree at a time. On the contrary, most feller–bunchers have accumulating capacity, so that they can cut more than one tree per cycle. This is crucial to compensating stem-size limitations. It is true that the time spent accumulating grows proportionally with the number of trees accumulated, but accumulation is only one stage of the felling cycle: the others – such as positioning the machine, moving the accumulation to the selected dump site, and dumping it to the ground – remain more or less constant, whatever the size of the accumulation. Therefore, even if the overall time consumption per cycle does grow with the number of trees accumulated in a cycle, its total value is always below the sum of the individual cycle times recorded if those trees were felled one at a time. That is why mass handling dampens the effect of decreasing stem size and allows its threshold value to be lowered. When harvesting with the shortwood method is no longer profitable, one may always resort to the full-tree method, which enjoys all the benefits of mass handling. The ultimate application of this concept is exemplified by whole-tree chipping, where tree bunches are fed to a chipper stationed at the landing. Under this scheme, trees are handled individually only when an accumulation is formed: this accomplished, they travel as a bunch through all the harvesting process. Whole-tree chipping is indeed the method of choice for early thinning, even though a low chip price occasionally drives loggers away from it.

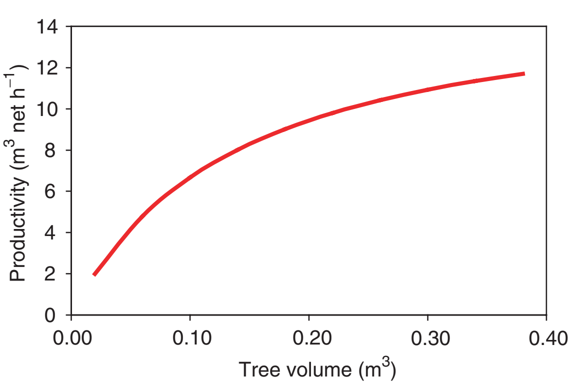


Figure 5 The effect of stem size on the productivity of a thinning harvester.

In fact, attempts have been made to develop shortwood harvesters capable of handling more than one tree per cycle. Results have been good, but not as conclusive as hoped. Some machines can really handle several trees per cycle, but the quality of processing often falls below the commercial standard, so that more development work is still needed.

Stem size limitations can also be tackled from another side, that of silviculture. Thinning is often conducted with the intent of facilitating natural selection: dominated trees are removed to leave more space for the dominant to grow. It is therefore no wonder that the size of the harvest trees so often falls below the economical threshold. Today, an increasing number of foresters support 'thinning from above' – a thinning concept that turns the conventional approach upside-down. They believe that if the small trees are healthy and well formed, they can be released with no prejudice to the future development of the forest. In turn, this allows the largest trees in the stand to be harvested, and this increases both the value of the harvest and the productivity of the harvesting teams. Several studies seem to indicate the viability of this thinning strategy, often dubbed as 'quality thinning.'

Manipulating Work Space

If stem size limitations can be partially solved through mass handling, other technical constraints must be faced in different ways. Confined work space is the second limiting factor that is peculiarly associated with thinning. The intensity of a thinning is determined by silvicultural considerations that integrate harvesting needs only to a limited extent. As a result, the total space available for maneuvering is a given value that loggers cannot alter too much, if they want to perform a good job: the density of the residual stand must reflect the growing conditions of the forest and guarantee its optimum future development.

However, if density remains a somewhat rigid parameter, spatial distribution may prove more flexible and it can be manipulated to a larger extent. From this consideration come the different thinning designs: row, row and selection, and group. These can all be regarded as adaptations to machine traffic of the original 'pure selection' design, which can be perfect from a silvicultural viewpoint, but gives results which are totally impractical for the harvesting crews. The ideal spacing job that leaves equally distant trees can only be applied to late thinning, when the density of the residual stand is so low that machines can sneak around leave-trees. Otherwise, one must open access corridors for machine traffic – removing entire tree rows in a geometric pattern. Selection thinning can be applied to the forest between two corridors (**Figure 6**). If all the work is conducted with mechanical equipment moving on the corridors, corridor spacing must not exceed twice the reach of the felling machines. If a larger spacing is adopted, trees must be felled towards the corridor using chainsaws, so that one may profit from the additional length of the stems. In this case, a processor can catch the felled trees by their tops and drag them to the corridor for processing. Corridor spacing can be increased even further if one is ready to take the felled trees to the corridors using a winch, a small tractor, or a draught animal. Moving corridors further apart is motivated by a desire to reduce the unproductive area represented by the corridors, which bear no trees. However, we have seen that increased corridor spacing often results in additional manual handling, and this can penalize industrial operations that must reach a high productivity if they are to remain profitable.

Figure 6 In early thinning, harvesters generally move along corridors, selectively thinning the stand on both sides.

Recently, compact harvesters have appeared that can move freely inside the stand, felling the trees and moving them to the corridors for extraction (**Figure 7**). They allow forest managers to increase corridor spacing without resorting to manual handling. However, the profitability of small-size thinning harvesters is questioned by many. Thinning harvesters can only handle thinning-size stems and lack the flexibility of large standard units, which can be deployed in both thinning and maturity cuts. Flexibility is an important asset in the logging business, where long-term planning is rare and a contractor can bid for a number of different jobs over a period of time. Furthermore, maturity cuts offer better profits than thinning, which is considered as a second choice by many. Today, the general trend is to acquire a standard harvester and adapt it to the occasional thinning jobs (**Figure 8**). In fact, it is the thinning that more often adapts to the harvester: moving from individual selection to group selection is another way to manipulate work space for

Figure 7 Dedicated thinning harvester in a row plantation.

Figure 8 Standard harvesters can be used in thinning operations as well as in maturity cuts.

Figure 9 Stem and soil damage in a badly managed thinning.

providing in-stand access to mechanical equipment. In addition, group selection contributes to increasing the size of harvest trees, with a similar effect to quality thinning. Group thinning also offers a number of silvicultural benefits, such as better resistance to wind and snow damage.

Managing the Impacts

For better or for worse, machines lend us extra power and increase our ability to impact the environment. In many cases, mechanized operations have indeed resulted in extensive environmental damage and there is a wealth of studies documenting the most common impacts. Large machines are especially prone to causing severe soil disturbance and widespread tree wounding, both of which can result in substantial yield losses (**Figure 9**). Worse than that, they can jeopardize the stability of the stand, making it more vulnerable to adversities: extensive tree wounding invites insect attacks, while soil disturbance can reduce tree stability and increase sensitivity to windblown.

Fortunately, mechanized thinning does not ordinarily result in extensive tree damage. Awareness of impact has informed the development of 'environmentally friendly' machinery: to some extent, the design of all forestry equipment produced today incorporates environmental concern, so that modern machinery generates increasingly less impact. As tolerance for impact keeps decreasing, manufacturers have to face the new trend in a proactive way. Some have transformed this constraint into a marketing tool, and they offer new machines that are specifically designed to create minimal disturbance. Compact shape, reduced size, and light weight are especially compatible with in-stand traffic, although not all opinions converge on its specific mode (**Figure 10**). Thinning harvesters can sneak between trees and

Figure 10 Specifically designed for thinning, this small forwarder can sneak into the residual stand without damaging the trees.

leave a very shallow footprint – to the point that the trails they tread are often known as 'ghost trails.' These machines exert a very low ground pressure: often below 50 kPa, which most soils can bear without suffering compaction. Experts suggest that such equipment should be allowed unrestrained circulation in the stand and not confined to corridors. The point they make is that such machines are so light that they hardly disturb the soil if they travel just once over the same spot. Confining the machine to predefined tracks would increase the number of passes over the same spot, thus forfeiting the benefit of low ground pressure. Of course, not all foresters agree on this matter, and the opportunity of allowing unrestrained stand traffic is still an open question.

Another feature of environmentally friendly mechanization is the use of biodegradable oils, especially hydraulic oil. Modern machines incorporate a good deal of hydraulics and carry large amounts of hydraulic oil. Leaks are very common and occur in a number of cases, including breakdowns and ordinary maintenance. The best way to

Figure 11 Self-leveling thinning harvester for steep-terrain operations.

prevent soil pollution is to use biodegradable oils. Much has been written on the performance of such oils, as well as on their real environmental compatibility – but nobody doubts that they are less harmful than mineral oils and perform almost as well. Their main drawback is a higher price and the fact that they occasionally cause allergic reactions in sensitive individuals.

Of course, 'environmentally friendly' technology is not the only way to reduce environmental impact. Operator training is crucial to low-impact silviculture, as well as to work safety and to the social promotion of forest labor. A number of studies have shown that the level of residual tree damage largely depends on operator skill and that this can be improved by appropriate training.

The availability of infrastructure is another requisite for effective, low-impact thinning. The case of mountain forests is typical (**Figure 11**). While experts highlight the environmental advantages of cable yarders, the lack of a suitable landing space often prevents the use of such equipment. In fact, the problem is general: fast technological progress implies that one often deals with obsolete infrastructures that need upgrading. Of course, such upgrading must follow appropriate rules to avoid generating more impact than the new technologies will avoid.

Concluding Remarks

Thinning has become one of the main preoccupations of forest managers, especially when artificially created forests are concerned. One assumes that the development of seminatural stands needs a certain amount of tending, which translates into a more or less intense thinning program. As thinning becomes increasingly expensive to implement, foresters worry about their ability to apply appropriate silviculture to their stands.

Any decisions about thinning revolve around three main considerations: (1) the cultural need for a thinning; (2) the economical performance of the operation; and (3) the possibility to mitigate its impact. Once the decision is taken, the logging manager will have to struggle against the low value of the harvest, the impact of limited stem size on machine productivity, and the constraints of restricted work space. Under these conditions the manager will try to make some profit or at least minimize losses.

A number of strategies are available to this end, in particular, selecting the most appropriate working method, employing the right equipment, and manipulating thinning design. The same strategies must be followed to keep the environmental impact within acceptable limits and make the operation a success.

See also: **Environment**: Environmental Impacts. **Harvesting**: Forest Operations under Mountainous Conditions. **Non-wood Products**: Energy from Wood. **Operations**: Forest Operations Management; Logistics in Forest Operations; Small-scale Forestry. **Plantation Silviculture**: Tending.

Further Reading

Anonymous (1997) *Proceedings of a Commercial Thinning Workshop*, October 17–18, 1996, Whitecourt, Alberta. Special report SR-122. Vancouver, BC: FERIC.

Bouvarel L and Kofman PD (1995) *Harvesting Early Thinnings Cost Effectively: The Present and the Future*. Hørsholm, Denmark: Danish Forest and Landscape Research Institute.

Brunberg B and Svenson G (1990) *Multi-tree Handling can Reduce First-Thinning Costs*. Uppsala, Sweden: Skogsarbeten.

Fröding A (1992) *Thinning Damage – A Study of 403 Stands in Sweden in 1988*. Institutionen för skogsteknik

Report no. 193. Uppsala, Sweden: Sveriges Lantbrukks-universitet.
Halloborg U, Bucht S, and Olaison S (1999) *A New Approach to Thinning: Integrated Off-ground Handling Reduces Damage and Increases Productivity*. Uppsala, Sweden: Skogsforsk results no. 23.
Hartsough B, Drews E, McNeel J, Durston T, and Stokes B (1997) Comparison of mechanized systems for thinning Ponderosa pine and mixed conifer stands. *Forest Products Journal* 47(11/12): 59–68.
Keane M and Kofman PD (1999) The thinning wood chain. In *Proceedings of a IUFRO Conference on Harvesting and Economics of Thinnings*. Dublin, Ireland: COFORD.
Kellogg L and Bettinger P (1994) Thinning productivity and cost for a mechanized cut-to-length system in the Northwest Pacific Coast Region of the USA. *Journal of Forest Engineering* 5: 43–53.
Lågeson H (1996) *Thinning from Below or Above? Implications on Operational Efficiency and Residual Stand*. Doctoral thesis. Umeå, Sweden: Swedish University of Agricultural Sciences.
McNeel J and Rutherford D (1994) Modeling harvester-forwarder system performance in a selection harvest. *Journal of Forest Engineering* 6: 7–14.
Puttock D and Richardson J (eds) (1998) *Wood Fuel from Early Thinning and Plantation Cleaning: An International Review*. Finnish Forest Research Institute. Research paper no. 667. Helsinki, Finland: Logging Industry Research Organization.
Raymond K and Moore T (1989) *Mechanized Processing and Extraction of Shortwood Thinning*. LIRO Reports, vol. 14, no. 5. Rotorua, New Zealand: TTS Institute.
Rieppo K and Pekkola P (2001) *Prospects for Using Harvester-Forwarders*. Työtehoseuran Metsätiedote no. 9.4 Helsinki, Finland: TTS Institute.
Siren M (1981) Stand damage in thinning operations. *Folia Forestalia* 474.
Sundberg U and Silversides CR (1988) *Operational Efficiency in Forestry*, vols I–II. Amsterdam, Holland: Kluwer Academic Publisher.

Roading and Transport Operations

A E Akay, Kahramanmaras Sutcu Imam University, Kahramanmaras, Turkey
J Sessions, Oregon State University, Corvallis, OR, USA

Introduction

Forest roads connect forested lands to primary roads to provide access for timber extraction and management, fish and wildlife habitat improvement, fire control, and recreational activities. Road location and design is a complex engineering problem involving economic and environmental requirements. Due to low traffic volumes, construction and maintenance costs are the largest components in the total cost of forest harvesting operations. Inadequate road construction and poor road maintenance have potential to cause more environmental damage than any other operation associated with forest management. Thus, forest roads must be located, designed, and constructed in such a way as to minimize construction and maintenance costs, satisfy geometric design specifications, and control environmental impacts.

Route Location

Road location is a cost optimization problem. The road location should achieve minimum total road cost, while protecting soil, water resources, and wildlife. The alignment should provide driver safety, reduce visual impacts, and improve the recreation potential of the forest. The systematic road location process consists of four phases: (1) office planning, (2) field reconnaissance, (3) selection of the final alignment, and (4) locating the alignment on the ground.

Office Planning

The first step involves study of the terrain using available data including topographical maps, air photo, orthophotos, digital elevation model (DEM), and soil and hydrologic reports. The designer studies the essential features of the land identifying the difficult places, such as swamps, rocky places, and steep or unstable slopes. The advantageous parts of the terrain, stream crossings suitable for bridges, saddles on ridges, suitable sites for curves, and gentle slopes, are also noted. If a logging plan is involved, the designer marks the suitable sites for log landings.

The road location must be economical for construction and feasible for hauling logs. The road should efficiently connect the main road to the secondary branches. At the end of this phase, the designer determines alternate feasible road corridors to be examined in the field reconnaissance. Office planning is the least expensive, yet the most important decisions of road design are made during this phase.

Field Reconnaissance

Each essential feature of the terrain (difficult and advantageous places) is examined in a detailed reconnaissance. To provide feedback for the earthwork operation, the designer should examine the terrain for limits of seasonal swamps, loose ground, rocky areas, and potential construction material. This phase is best done during the rainy season so that soil characteristics and the limits of wet places can be observed.

It is more convenient to start the fieldwork from the highest point of the road section to see the terrain easily by looking toward the bottom of the slope. In field reconnaissance, it is necessary to use appropriate survey instruments. At the end of field reconnaissance, one particular corridor is selected as the best corridor based on gradient, haul distance, ground condition, sources of road-building material, and stream crossing obstacles.

Selection of the Final Alignment

Following selection of the best corridor, the next step is to locate the final alignment. The party chief considers a number of strategies:

- On uniform terrain, building the road on a ridge minimizes the earthwork, provides good drainage, and reduces the number of culverts.
- On a side hill, keeping a constant gradient provides a balanced cut and fill section. If the side hill is steep, a full bench cross-section can be used to avoid overloading the slope below the road.
- In a valley, the route should be kept as low as possible, but above the floodplain. Proper choice of stream crossings and stream crossing angle minimizes bridge length.
- Cut bank heights should be kept low, because excessive earthwork increases construction and maintenance costs, increases potential for landslides, and requires special construction for drainage.

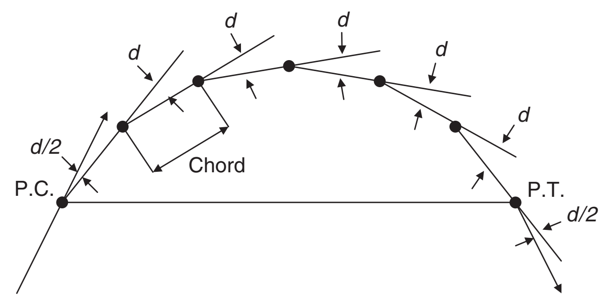
Laying Out the Alignment on the Ground

On uniform terrain the final location line is marked on the ground by centerline stakes with 15–20-m intervals. The road edges should be calculated on both sides from the centerline. On difficult and irregular terrain, the centerline and excavation and embankment limits should also be marked. The method for identifying the centerline and limits on a straight alignment varies with the method used for a horizontal curve.

On uniform terrain, a straight alignment is generally laid out by eye, using posts in three at a time. On uneven terrain, the grade line is carried forward in a series of incremental steps to preserve the gradient. The methods used for laying out a horizontal curve are aided using design tables. Several methods are used. The deflection angle method is described here. First, the deflection angle is defined, depending on the specified radius and a chord length (**Table 1**). Then, points on the curve are identified by turning chord deflections and pacing the chord distance (**Figure 1**). Several trials are generated from different starting points on the tangent, when a curve point of intersections is inaccessible.

Table 1 Deflection angles (in degree) for circular curves of various radii

Radius (m)	*Chord distance*		
	10 m	*15 m*	*20 m*
14	42	—	—
16	36	—	—
18	32	—	—
20	29	44	—
25	23	35	47
30	19	29	39
35	16	25	33
40	14	22	29
45	13	19	26
50	11	17	23
55	10	16	21
60	10	14	19
65	9	13	18
70	8	12	16
80	7	11	14
90	6	10	13
100	6	9	11
125	5	7	9
150	4	6	8
175	3	5	7
200	3	4	6



$$d = \frac{\text{Chord}}{\text{Radius}}\frac{180}{\pi}$$

Figure 1 Curve location using deflection angle (*d*) method. P.C., beginning point of curve; P.T., ending point of curve.

Cost Control in Forest Road Design

The total cost of a road section consists of the construction cost, maintenance cost, and transportation cost.

Construction and Maintenance Costs

Road construction and maintenance costs are generally calculated using the 'engineer's' method. In this method, quantities of required material used are estimated and then multiplied by the unit costs for the items (i.e., cost per meter, square meter, or cubic meter). The road construction cost is the total cost of the road construction activities: construction staking, clearing and grubbing, earthwork, drainage, surfacing, and seeding and mulching. The maintenance activities involve rock replacement, grading, culvert and ditch maintenance, and brush clearing. Detailed information regarding formulae and tables to calculate the costs of these activities can be obtained from the references given in the Further Reading section.

Transportation Costs

Transportation costs depend upon the traffic, cost of vehicle operation, and vehicle speed. Traffic volumes should consider the immediate and longer-term road use. Vehicle speed is a function of road width, alignment, gradient, surface type, and traffic volume.

Selection of Most Economical Road Standard

Forest road design involves simultaneous consideration of and trade-offs between construction costs, road maintenance, vehicle performance, and environmental effects. The trade-offs are not always obvious and vary depending upon local availability of construction materials, road standards, and topography. Based on these factors, the designer should be able to select the best road standard. It is important to know as much as possible about the future performance of a selected road standard so that adequate roads can be designed and built at minimum expense. If forest roads are planned for use during spring thaw conditions, road designers should take extra care in constructing the roads to reduce the road deformation.

Geometric Design Specifications

In order to ensure driver safety, smooth traffic, and efficient and economic movement of the trucks, the road alignment must satisfy certain geometric design specifications. The main elements of geometric design specifications are stopping sight distance, middle ordinate distance, vehicle off-tracking requirements, road gradient, horizontal curves, and vertical curves.

Stopping Sight Distance

The objective in determining the stopping sight distance (SSD) is to provide a sufficient sight distance for the drivers to safely stop their vehicles before reaching objects obstructing their forward motion. The SSD (in meters) for two-lane roads is computed in eqn [1]:

$$\mathrm{SSD} = \frac{V^2}{254(f \pm g)} + 0.278 V t_r \qquad (1)$$

where V is the design speed (km h^{-1}), t_r is perception/reaction time of the driver in seconds (generally 2.5 s), f is the coefficient of vehicle braking friction, and g is the road grade in decimal percent. On two-directional one-lane roads, the SSD is approximately twice the stopping distance for a two-lane road.

Middle Ordinate Distance

The middle ordinate distance must be visually clear, so that the available SSD is sufficient for the driver's line of sight (**Figure 2**). Experience has shown that a driver should be able to see from an eye height of 1070 mm and stop before hitting an object of 150 mm height at the mid-ordinate. On forest roads, 600 mm of object height at the middle ordinate point is generally used. Middle ordinate distance in meters is computed as follows:

$$M = R\left[1 - \cos\left(28.6\,\frac{\mathrm{SSD}}{R}\right)\right] \qquad (2)$$

where R is the radius of horizontal curve (in meters). It is a straightforward task to compute M, once the R and SSD have been determined.

Off-tracking

When traveling around the horizontal curve, the rear wheels of the vehicles do not track in the same path as the front wheels, which is called off-tracking. To accommodate the off-tracking of the rear wheels,

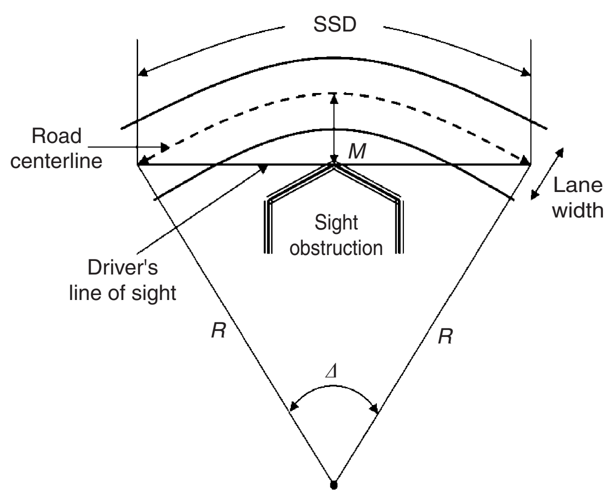


Figure 2 Middle ordinate distance (M) around a horizontal curve. SSD, stopping sight distance; R, radius; Δ, central angle of curve.

extra road width is required on the inside of the curve (**Figure 3**). The required curve widening depends on various factors such as vehicle dimensions, curve radius, and the central angle of the curve (Δ). To predict off-tracking (OT), an empirical method, providing the designers with quick, easy, and relatively accurate results, is generally employed.

$$\mathrm{OT} = (R - \sqrt{R^2 - L^2})[1 - e^{(-0.015\Delta\frac{R}{L}+0.216)}] \quad (3)$$

where L is computed for a stinger-steered trailer as:

$$L = \sqrt{L_1^2 - L_2^2 + L_3^2} \quad (4)$$

where L_1 is wheelbase of the tractor, L_2 is the length of the stinger measured from the middle of the tractor rear duals to the end of the stinger, and L_3 is bunk-to-bunk distance minus the length of the stinger. For a low boy or conventional trailer:

$$L = \sqrt{L_1^2 + L_2^2 + L_3^2} \quad (5)$$

where L_1 is wheelbase of the tractor, L_2 is the distance from the fifth wheel to the middle of the rear duals for the first trailer, and L_3 is the distance from the fifth wheel to the middle of the rear duals for the second trailer.

Road Gradient

Road gradient (%) is calculated in units of vertical rise divided by the horizontal distance. The minimum road gradient is limited by the minimum acceptable road grade to provide proper drainage. Having minimum 1–2% longitudinal gradient along the road section helps avoiding the ponding of water on the surface. The maximum road gradient is determined based on the design vehicle. A list of recommended truck gradients for low light trucks is shown in **Table 2**. Since trucks lose speed rapidly when climbing a grade, and ultimately reach an equilibrium speed, the vehicle performance should be taken into account to minimize overall transportation cost. In current vehicle performance models, the road alignment and surface type are taken as inputs, and alignment-specific results (ground speed, engine speed, gear shifting requirements, fuel consumption, and roundtrip time) are determined. Detailed information on these models can be obtained from the references in the Further Reading section.

Horizontal Curves

On low-volume forest roads, a circular horizontal curve is generally used to provide a transition between two tangents (**Figure 4**). To design a feasible horizontal curve, the designer considers the minimum curve radius, acceptable road grade on the horizontal curve, and minimum safe stopping distance.

Having high centers of gravity and narrow track width (the distance between the outside faces of the wheels at opposite ends of an axle), logging trucks may overturn due to an inadequate radius. Design

Table 2 Maximum road gradient (%) for various design speed and topography (Transportation Association of Canada)

Speed (km h^{-1})	*Rolling topography*	*Mountainous topography*
30	11	16
40	11	15
50	10	14
60	10	13
70	9	12
80	8	10

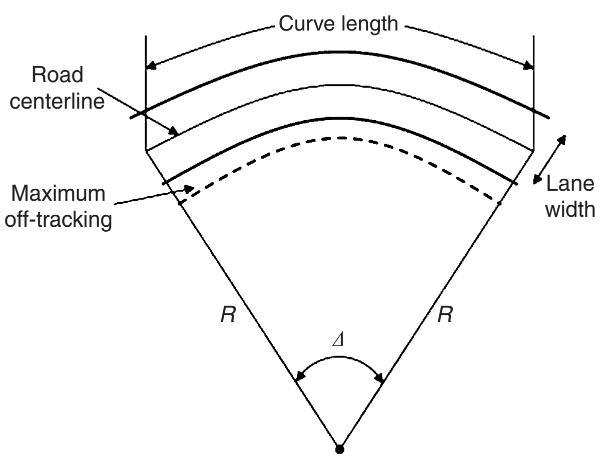


Figure 3 Maximum off-tracking on a horizontal curve. R, radius; Δ, central angle of curve.

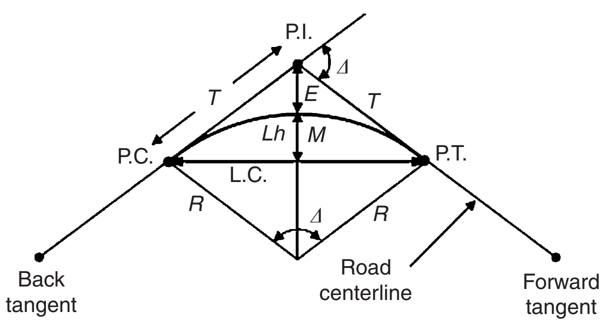


Figure 4 Geometry of a circular horizontal curve. P.I., point of intersection; P.C., beginning point of the curve; P.T., ending point of the curve; Lh, curve length; Δ, central angle; M, middle ordinate; R, radius; T, tangent distance; L.C., long chord; E, external distance. Equations: $Lh = \frac{\Delta\pi R}{180^\circ}$ $T = R\tan\frac{\Delta}{2}$ $L.C. = 2R\sin\frac{\Delta}{2}$ $E = T\tan\frac{\Delta}{4}$.

Table 3 Minimum radius for various vehicle speeds ($f_s = 0.15$, $e = 0$)

Speed (km h^{-1})	*Minimum radius (m)*
30	47
40	84
50	131
60	189
70	257
80	336

speed, lateral acceleration, and vehicle weight must be considered (**Table 3**).

The maximum gradient permitted on the horizontal curve should be kept lower than that on a tangent because: (1) off-tracking of the vehicle creates a higher 'effective' grade for both the truck and the trailer, (2) the truck incurs additional forces required to turn the tandem axles around the curve, and (3) the powered wheels may have unbalanced normal loads due to a combination of centrifugal force, super elevation, and angle of the trailer. The effects of these factors are increased as the radius decreases.

The safe stopping distance is computed using eqn [1] in which the limiting speed of the vehicle around the horizontal curve, V (in km h^{-1}), can be formulated considering vehicle weight, side friction force, centrifugal force, curve radius, side friction coefficient, and super elevation.

$$V = 11.27\sqrt{R(f_s + e)} \quad (6)$$

where f_s is the coefficient of side friction, R is the radius of horizontal curve in meters, and e (%) is the super elevation of the horizontal curve if it exists.

Vertical Curves

Forest road engineers customarily use parabolic vertical curves (**Figure 5**) with a constant rate of change of gradient, because: (1) they result in alignments comfortable to drive, (2) they are easy to lay out, and (3) the SSD is constant along the curve. The vertical curves should have a sufficient curve length to permit a log truck to pass a curve without bottoming out in the sag or breeching the crest and provides SSD.

In determining a feasible curve length, crest and sag vertical curves are considered separately based on the assumption that whether the curve length is greater or less than the SSD. Equations [7] and [8] indicate the formulation for length of the crest vertical curve in meters. If SSD is greater than the curve length (**Figure 6**):

$$Lv = 2SSD - \frac{200(\sqrt{h_1} + \sqrt{h_2})^2}{A^2} \quad (7)$$

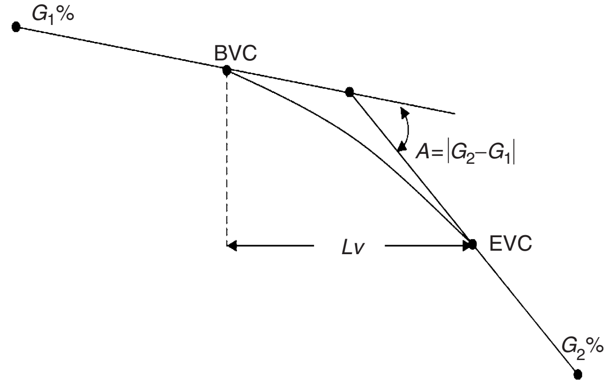


Figure 5 Geometry of a crest vertical curve (symmetrical). BVC, beginning point of the curve; EVC, ending point of the curve; Lv, curve length; G_1, initial tangent grade; G_2, final tangent grade; A, absolute difference between grades.

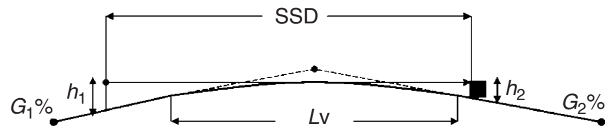


Figure 6 Stopping sight distance (SSD) is greater than the length of a vertical curve. G_1, initial tangent grade; G_2, final tangent grade; Lv, curve length; h_1, distance from road surface to level of driver's eye; h_2, height of object on road.

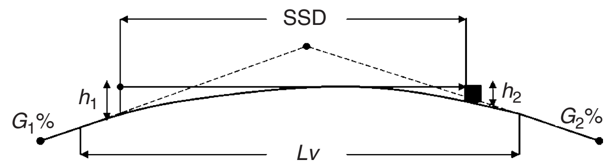


Figure 7 Stopping sight distance (SSD) is less than the length of a vertical curve. G_1, initial tangent grade; G_2, final tangent grade; Lv, curve length; h_1, distance from road surface to level of driver's eye; h_2, height of object on road.

where h_1 is the distance from road surface to level of the driver's eye, h_2 is the height of the object on road, and A is absolute value of the difference between gradients. If SSD is less than the curve length (**Figure 7**):

$$Lv = \frac{SSD^2 A}{200(\sqrt{h_1} + \sqrt{h_2})^2} \quad (8)$$

The length of a sag curve, for a required SSD, is formulated in eqns [9] and [10]. If SSD is greater than the curve length:

$$Lv = 2SSD - \frac{200(h_3 + SSD \tan \alpha)}{A} \quad (9)$$

where h_3 is the distance from road surface to level of the vehicle headlights and α is angle of the headlight beam above axis of the vehicle. If SSD is less than the curve length:

$$Lv = \frac{SSD^2 A}{200(h_3 + SSD \tan \alpha)} \qquad (10)$$

Forest Road Construction

Clearing and Grubbing

The road centerline, the cut and fill limits, and the clearing limit should be marked on the ground prior to clearing. The clearing limit is the width that the trees, stumps, and organic debris are to be cleared across the future roadway. The terminology of a forest road on a cut and fill type cross-section, which generally applies to most road types, is indicated in **Figure 8**.

The methods used for the clearing and grubbing should be consistent with good safety and environmental practices while keeping construction costs to a minimum. The hazardous snags and unsafe trees adjacent to the clearing limit should be felled and removed from within the road prism. Merchantable timber should be piled on the decking areas so as to not interfere with the construction of the road or turnouts. Unmerchantable material and stumps should be disposed of with care to prevent any hazard during the logging operation.

Earthwork

On gentle terrain, the bulldozer proceeds from both sides of the road to construct an embankment that will keep the road structure dry. In difficult terrain hydraulic excavators combined with advanced drilling and blasting technology are the best solutions both environmentally and economically. The features of the hydraulic excavator and advanced drilling and blasting technique in road construction are:

- The excavator operates by digging, swinging, and dumping of excavation.
- The excavator works from the fixed position and does not require additional road width for maneuvering.
- Using buckets and attachments increases the excavator's versatility to do ripping, trenching, loading, compacting, and hydraulic hammering.
- The high breakout force of the excavator reduces the need for blasting.
- The hydraulic drilling units attached to the excavator optimize blasting by performing vertical as well as horizontal drilling.
- Soft blasting techniques avoid loosening of fractured rock, and control the rock size.

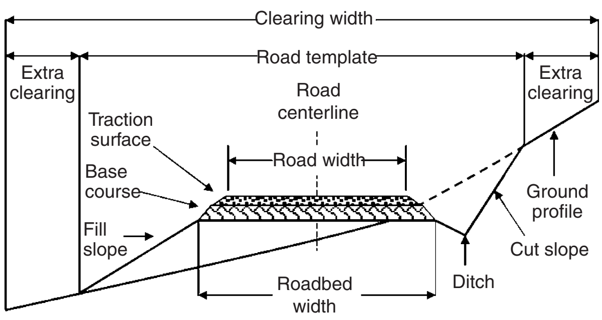


Figure 8 Road elements on the cross-section.

Building the desired cut and fill slope steepness is critical during the earthwork operation. If the operator constructs a steeper cut slope, this will require further excavation, increase construction cost, and may cause slope failure. Therefore, road cut and fill banks should be constructed to the slope angles that minimize slope failure and erosion. Cut and fill slopes are constructed depending on the available soil and rock types (**Table 4**).

Embankments are commonly used on stream drainages, swamps, flat ground, and are used as waste areas. The common methods used for embankment are: (1) end haul dumping where cut material is hauled to a fill area, and (2) side casting where cut material is pushed from a road cut to a close fill location. In both methods, material should be layer-placed and compacted to minimize future maintenance, soil erosion, and road failure. On deep fills and roads with heavy traffic, a mechanical roller can be used for effective compaction.

The economic distribution of cut and fill quantities in forest roads is traditionally determined using the mass diagram method. However, its capability is limited where soil characteristics vary along the roadway. To overcome the limitation of the mass diagram, linear programming has been used to plan the movement of earthwork during road construction.

Surfacing

Native-soil surfacing can be used when harvest operations are conducted during the dry season. However, road operations in the wet season require aggregate surfacing (crushed rock) to increase the strength of the

Table 4 Cut and fill slope types for various soil and rock types

Soil type	*Cut*	*Fill*
Common soil	1 : 1	1.5 : 1
Clayey soil	2 : 1–3 : 1	Not used
Solid rock	0.5 : 1	Not used
Fractured rock	0.75 : 1	1.25 : 1

forest road surface to support vehicle traffic (**Figure 8**). Aggregate surfacing also provides increased wheel traction and relatively smooth traveling surface that reduces the subsequent road maintenance, and extends the life of the subgrade by reducing road surface ruts and erosion. The rock size and the depth of the aggregate surfacing are determined based on the type of the subgrade soil along the roadway, road gradient, traffic density, season of road use, availability of the aggregate, and cost. A traction surface can be placed over the base rock to increase traction and to provide a smooth durable traveling surface.

The hardness, durability, wearability, and shape of the aggregate affect the quality of the road surfacing. The surfacing rock should be tested in the field in terms of its hardness, shape, and durability. If there is doubt regarding its compatibility, it should be directed to laboratory tests. The Los Angeles Abrasion Test is one of the standard laboratory tests that is used to examine the wearability of the rock.

On wet ground or soils that do not compact well, geotextile material is added on top of the subgrade to provide additional strength to the subgrade, keep soil moisture from surfacing, and prevent intermixing of soil and surface aggregate layer (**Figure 9**). This also reduces the depth of surface rock. The road engineer should determine the trade-off in terms of cost and effectiveness between reducing the rock depth and extra cost of laying down the geotextile. The best practice for using geotextiles involves:

- Spreading out the geotextile in short stages to allow rock placement to follow closely.
- Securing the top of the geotextile to avoid slippage.
- Placing the geotextile free of tears and wrinkles and join the rolls with overlapped joints.

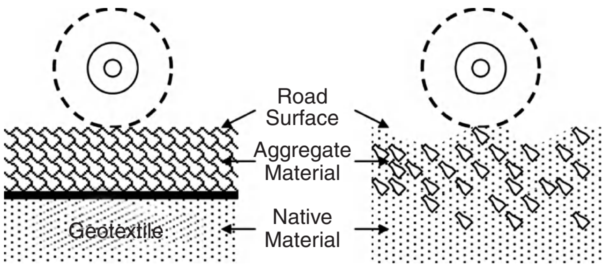


Figure 9 Geotextile material provides support and separation.

Drainage

When constructing a road, the road surface must be sloped to eliminate the tendency of surface runoff water to break up the road under heavy loads. There are three basic types of roadway templates (**Figure 10**):

- Crowned: half of the water is carried to the ditch and half to the outside shoulder.
- Insloped: water is carried to the ditch and ditch relief pipe culverts to the streams.
- Outsloped: road surface sheds runoff to the outside.

Ditched roads (crowned and insloped) require more excavation cost for the ditch and additional cost for relief culverts. Ditch water runoff should be intercepted periodically by relief culverts to carry roadway runoff from the ditch, transport it beneath the road, and discharge the water from the road (**Figure 11**). A catch basin is built in the ditch to channel the water from the ditch to the culvert inlet. Plastic relief culvert is widely used in forest roads because one person can handle plastic culvert installation and it is easy to cut to length for fabrication. The determination of culvert size depends on conditions of the precipitation, topography, soil, and vegetation types. Smaller diameter culverts

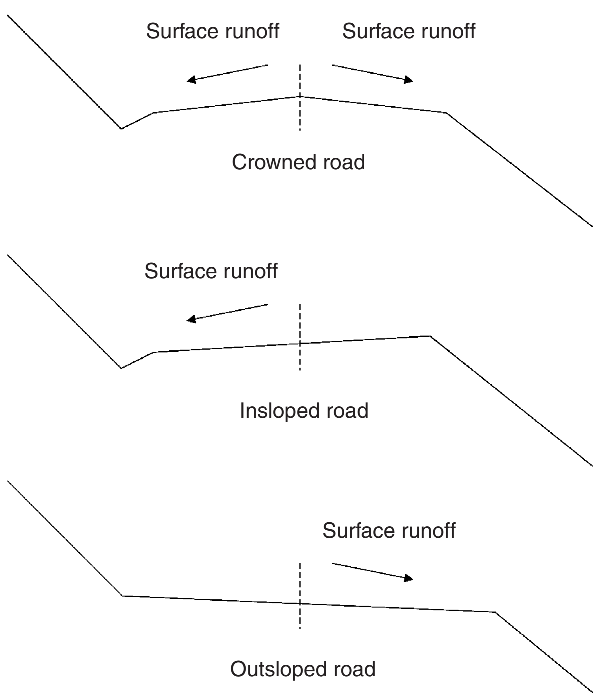


Figure 10 Ditched and outsloped roadway templates.

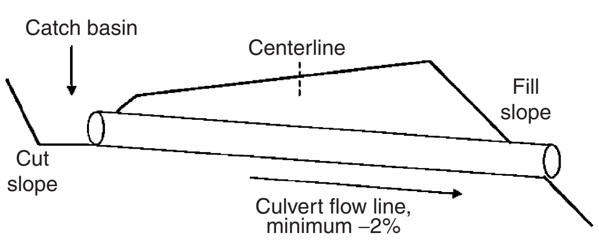


Figure 11 Geometry of a ditch relief culvert.

are inexpensive and easy to install. However, they are difficult to clean out and carry less water. Culvert spacing is generally determined based on its location on the hill, local rainfall intensity, soil erosion classes, road grade, and culvert size. Open-top culverts are also effective in controlling surface water. They offer land managers an alternative to crowning and ditching roadbeds for water control. The cost is comparable to that of a gravel broad-based dip. Installation of the culvert can be done manually or with the use of a small dozer. Open-top culverts must be cleaned regularly to remove sediment, gravel, and logging debris to allow normal function of structure.

Outsloped roads have reduced construction and maintenance costs and lessened environmental impacts due to their type of drainage. They also yield less erosion than a ditched road on the same location. Outsloped roads are not ideal for every condition. On wet or frozen surfaces, trucks slide to the outside of the roadway on steep grades. This lowers vehicle speed and in some conditions is unsafe. To enhance the effectiveness of outsloped roads, drain dips and water bars are used. Drain dips should be built considering adequate truck passage and road grade (2–8%). On road grades greater that 8%, water bars are often constructed to catch runoff water.

Seeding and Mulching

Bare cut and fill slopes, resulting from road construction on sloping terrain, increase soil erosion and stream sedimentation. Seeding and mulching can provide quick stabilization and enhance the beauty of the area. The best time for seeding is usually spring or autumn, but results will depend on local weather conditions. The seed mixture should be easy to plant, readily available, and adaptable to soil conditions (drainage, soil depth, aspect, drought tolerance, and climate conditions).

The use of mulch is considered to prevent erosion, keep seed on steeper slopes, reduce seedling mortality, and preserve soil moisture. Straw is the most commonly used mulch material. To increase the effectiveness of mulch, straw can be used in combination with other bank erosion control measures.

Forest Road Maintenance

Road maintenance protects the road investment, provides for safe and reliable vehicle operation, and controls environmental impacts. Road maintenance generally consists of road surface maintenance, roadway drainage maintenance, and ditch and culverts maintenance. Removing brush from both cut and upper fill slopes is also considered to maintain visibility.

Road Surface Maintenance

The forest road surface deforms under vehicle wheel loads and develops ruts over time if the subgrade is not constructed adequately. If the wheel load is excessive for the existing road surface conditions, shear failure occurs. Failure can also occur where the subgrade becomes saturated from standing water and the wheel load on this saturated subgrade causes damage. Ditches should be kept free of obstruction and ruts should be removed to avoid this type of damage. The forward and downward motion of wheels on the surface causes a corrugation called washboarding. To correct this, the surface rock should be reshaped to restore the camber of the road.

To decrease the road construction and maintenance costs, variable tire inflation technology is increasingly being considered for low speed operation. Central tire inflation (CTI) systems enable the driver to change and monitor the vehicle's individual tire pressures while driving. As tire pressure decreases, the tire footprint increases, primarily in the longitudinal direction. This reduces the stress applied to the road surface through a greater contact area and lower dynamic loads. Traction capability, related to tire contact length is also increased. Test studies have shown that reduction in stress reduces surface maintenance, sediment production, tire damage, and improves vehicle mobility, the ride quality, and traction on snow, ice, and loose sand.

Roadway Drainage Maintenance

Maintenance of the drainage system is also one of the key factors to preserve structural integrity and travel quality. Poor drainage can cause deterioration and weaken the road structure. To prevent this, rain and snowmelt must be quickly removed from the road surface before moisture soaks through the surface into the subgrade.

Ditch and Culvert Maintenance

Culvert maintenance involves removing debris, leaves, mud, and gravel from the culvert, the inlet, the outlet, and the catch basin. Plugged culverts cause significant ditch and roadbed erosion into the subgrade. To prevent catastrophic damage on the road, inspection and hand cleaning of culverts should be done during wet weather. Ditches should be kept free of obstructions with a shovel, a backhoe, motor grader, or loader. To stabilize the soil in ditches and to reduce the force of water, the ditch can be armored with rock, grass can be grown in the ditch bottom, and culverts should be installed at more frequent intervals.

Crossings Wetlands and Streams

Some of the planning and design considerations on wetland and stream crossings are:

- Limit the number, length and width of roads and skid trails.
- Locate roads outside riparian management zones except at stream crossings.
- Road fill must be bridged, culverted, or otherwise designed to prevent restriction of expected flood flows.
- Properly maintain road fill during and after road construction to prevent erosion.
- Correctly design, construct and maintain wetland road crossings to avoid disrupting the migration or movement of fish and other aquatic life.

Wetland Crossings

Wetland crossing methods include wood mats, wood panels, wood pallets, expanded metal grating, plastic roads, corduroy, and wood aggregate. Geotextiles can be also used to solve drainage problems in wetlands. Wood mats are individual cants or logs cabled together to make a single-layer crossing. Wood panels are constructed by nailing parallel wood planks to several perpendicular wood planks where the vehicle's tires will pass. Wood pallets are three-layered pallets similar to those used for shipping and storage, specifically designed to support traffic. They are easy to install, replace, and interconnect. Machine weight can be distributed over a broader area by placing a metal grating on top of a geotextile.

The grating is relatively light, inexpensive, and also it provides sufficient traction. Plastic roads, made of PVC and HDPE pipe mats, are portable, reusable, and provide lightweight corduroy type crossing. Using pipes generate a conduit for water to move through the crossing without further wetting the area. One method of building temporary roads across wetlands is the use of corduroy where brush and small logs are laid perpendicular or parallel to direction of travel. Nonwoven geotextile is recommended to separate the brush, logs, or mill slabs from the underlying soil. Wood aggregate (wood particles ranging in size from chips to chunks) can also be used as a fill material for crossing soft soils. Important advantages of using wood particles are they are relatively light and biodegradable. Geotextiles are used to provide subgrade restraint over areas of low bearing pressure. They are occasionally placed over buried corduroy to cross wet holes.

Stream Crossings

When the streams are shallow, inexpensive stream crossings can be constructed using drifts or fords (**Figure 12**). On shallow sandy rivers, stone-surfaced drifts are used when the fall is gentle. A higher-elevated concrete drift is used when the water flow is strong. Culvert drifts are also built in small rivers with heavy currents.

Open-bottom structures such as open-bottom arches and box culverts are also used for stream

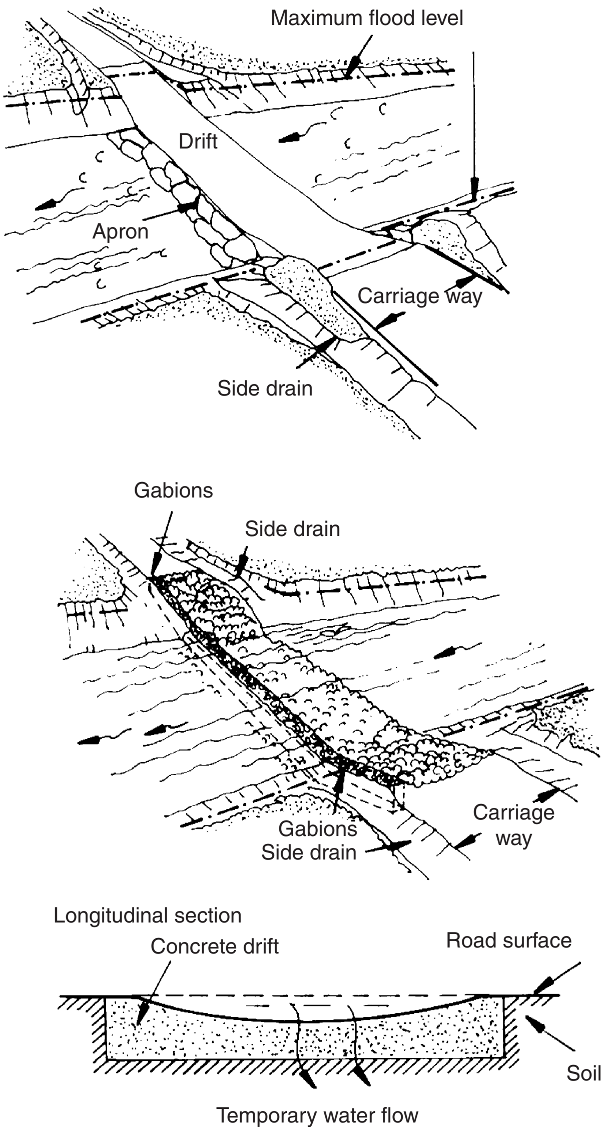


Figure 12 Examples of drifts. Reproduced with permission from Kantola M and Harstella P (1986) *Forest Harvesting Handbook on Appropriate Technology for Forest Operations in Developing Countries*. FTP Publication 19(2) pp. 79–81, National Board of Vocation Education of Finland.

Figure 13 Open-bottom Box Culvert. Courtesy of Big R Manufacturing.

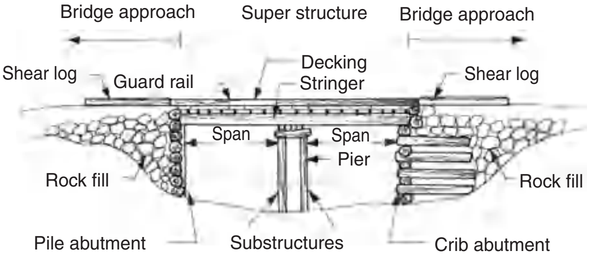


Figure 14 Log stringer bridge. Reproduced with permission from Kantola M and Harstella P (1986) *Forest Harvesting Handbook on Appropriate Technology for Forest Operations in Developing Countries*. FTP Publication 19(2) pp. 79–81, National Board of Vocation Education of Finland.

crossings. Their footings are installed on bedrock to prevent scouring (**Figure 13**). If they installed on an erodible foundation, the entire area should be ripraped between the footings. The size of the riprap material depends on water depth and flow velocity. Open-bottom culverts provide more natural conditions for fish passage than culverts.

Bridges must be built for deeper crossings. Construction cost of the bridges is high because they should be elevated sufficiently above maximum flood level, and be strong enough to carry the heavy traffic. When crossing a stream is inevitable, selecting the right structure is critical to ensure suitable and cost effective crossing, and minimum pollution of the stream.

Permanent bridges The most common type of permanent bridge is the stringer bridge where a deck is placed on top of the stringers to support the vehicle loads. Stringers can be logs, sawn timbers, and steel beams. Decking is placed perpendicular to the stringers and can consist of sawn lumber planks, timber deck panels, or concrete panels. Basic components of a log stringer bridge are indicated in **Figure 14**. The size of the stringer depends on the unsupported length of the span and loading. Stringers should be debarked, mortised, and anchored by wooden poles in the ground. The deck logs should be placed on the stringers perpendicularly, transversely, or diagonally.

Portable bridges When permanent access to a site is not needed, portable bridges are used and then removed after operations are finished. They have been used in military applications for many years, but use in forestry applications is more recent. In the past, the lower cost approaches to temporary stream crossings (log crossings, fords, and culverts) were used over portable bridges due to high initial cost of the bridges. However, these low-cost approaches frequently involve the use of large amount of fill in the stream crossing and may result in excessive erosion and sedimentation of the stream. Portable bridges cause less impact on water quality. Portable bridges can be made of steel or concrete panels and timber mats. A relatively new type of engineered design is the glulam bridge that can be moved from site to site relatively quickly and easily. To simplify the installation, the glulam panels are not connected to each other instead; they are set in place on site. Abutments to support the bridge ends are not required since the panels can be placed on a mud sill. The use of a portable bridge has been shown to be an environmentally sensitive method since it minimizes site disturbance and sedimentation in the stream.

Environmental Considerations

There are a number of actions that can be done during road construction and maintenance to protect the environment. Some of them are listed below:

- Earthwork operations should be scheduled for dry seasons.
- Steep grades should be avoided through soils that erode easily.
- Ditches and culverts should be constructed properly.
- Stream crossings should be located where minimum soil disturbance may occur.
- Stream crossing angles should be close to perpendicular.
- Seeding should be applied on cut banks and fill slopes to reduce erosion.
- Bridges and culverts should be constructed to handle the maximum water flow, and they should allow appropriate fish passage.
- Aggregate should be replaced to preserve structural integrity of the road.

- Grading and other maintenance activities, cleaning culverts and cleaning ditches, should be performed regularly.
- Excessive sediment delivered to streams has a dramatic effect on water quality and aquatic life; therefore, roads must be designed to minimize sediment production.
- The road segments with a high potential for delivering sediment can be identified using sediment prediction models.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Forest Operations under Mountainous Conditions; Wood Delivery. **Operations**: Forest Operations Management.

Further Reading

AASHTO (1990) *A Policy on Geometric Design of Highways and Streets*. Washington, DC: American Association of State Highway and Transportation Officials.

Akay AE (2003) *Minimizing Total Cost of Construction, Maintenance, and Transportation Costs with Computer-Aided Forest Road Design*. Thesis, Forest Engineering Department, Oregon State University, Corvallis, OR.

Douglas RA (1999) *Delivery, the Transportation of Raw Natural Products from Roadside to Mill*. Fredericton, Canada: University of New Brunswick.

FAO (1998) *A Manual for the Planning, Design, and Construction of Forest Roads in Steep Terrain*. Rome: Food and Agriculture Organization of the United Nations. Available online at http://www.fao.org/docrep/W8297E/W8297E00.htm

Hickerson T (1964) *Route Location and Design*. New York: McGraw-Hill.

Holmes D (1982) *Manual for Roads and Transportation*. Burnaby, Canada: British Columbia Institute of Technology.

Kantola M and Harstella P (1988) *Handbook on Appropriate Technology for Forestry Operations in Developing Countries*, Part 2, *Wood Transport and Construction*. Forestry Training Program Publication no. 19. Helsinki: National Board of Vocation Education of the Government of Finland.

Kramer BW (1993) *A Road Design Process for Low Volume Recreation and Resource Development Roads*. Corvallis, OR: Oregon State University.

Kramer BW (2001) *Forest Road Contracting, Construction, and Maintenance for Small Forest Woodland Owners*. Corvallis, OR: Oregon State University.

Pancel L (ed.) (1993) *Tropical Forestry Handbook*, vol. 2. Hamburg, Germany: Springer-Verlag.

Ritter M (1990) *Timber Bridges: Design, Construction, Inspection, and Maintenance*. Washington, DC: US Department of Agriculture.

Smith DM (1993) *Effects of Variable Tire Pressure on Road Surfacing*, vol. 2, *Analysis of Test Results*. US Army Corps of Engineers, Waterways Experiment Station. Prepared for the USDA Forest Service. Vicksburg, MI. Technical Report no. GL-93-20, p. 84.

Watts S (ed.) (1983) *Forestry Handbook for British Columbia*, 4th edn. Vancouver, Canada: University of British Columbia.

Wenger K (ed.) (1984) *Forestry Handbook*. New York: Society of American Foresters.

Wood Delivery

P M O Owende, Institute of Technology Blanchardstown, Dublin, Ireland

Introduction

Cost-efficient forest harvesting operations are key to economic timber production and overall competitiveness of the global wood production sector. Consequently, efforts have been made towards the enhancement of operational efficiency through:

1. Rationalization of forest harvesting techniques and work methods, including stand establishment, harvesting operations, wood delivery, ergonomic concerns, automation of machine functions, and the control of environmental impacts.
2. Improved wood supply logistics, including supply chain and information chain management, and harvesting and transport planning.
3. Maximization of raw material utilization including log value optimization, and use of unmerchantable material and forest residues as alternative fuel sources.
4. Development of the forest industry through customer focused production, quality control in the delivered wood, and work safety.

The efforts outlined above are aimed at the optimization of forest production on a sustainable basis. The rationalization of forest harvesting techniques and improvement of wood supply logistics can be implemented relatively quickly (i.e., over a short time span), hence wood delivery is a crucial issue in optimization of the entire wood supply chain. Wood delivery in the context of this article refers to the chain of operations related to the extraction and transport of different categories of timber and by-products of forest harvesting, including wood chips and forest residue materials that are used for energy. The forest residue is transported as compacted residue or slash logs.

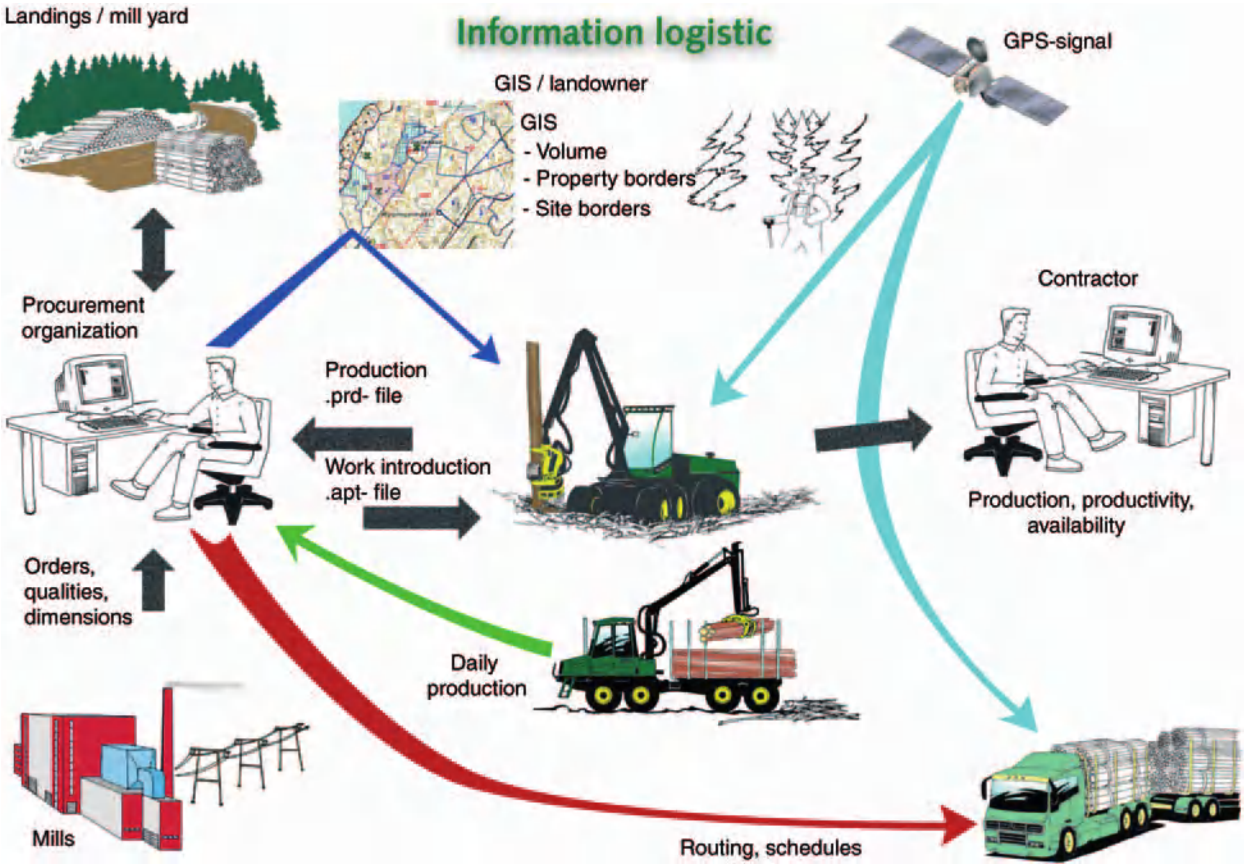


Figure 1 Spatial and production information flow/exchange in the logistics of wood delivery. Adapted with permission from Timberjack OY, Finland.

Mechanized wood harvesting systems consist of multiple operations (**Figure 1**), with a range of complex interactions. The overall efficiency of the operations may be optimized by integrating the individual operations for enhanced efficiency in wood production.

The salient requirements of the wood delivery logistics include:

- constant update of harvest plans
- real-time monitoring of production, machine productivity and availability assessments
- location of harvested material and delivery vehicles, delivery routing, and delivery schedules
- logical optimization techniques for individual processes, e.g., route optimization to minimize transportation cost.

For the illustrated linkages, it may be argued that there is need for a shared database for the different procurement organizations with common wood material sources, to allow for the exchange of raw material on the basis of dynamic production schedules.

Harvesting and Extraction

Harvesting systems are of primary importance in wood delivery for the following reasons:

1. Harvesting methods determine the mode of subsequent wood delivery systems used.
2. There is increasing emphasis on the use of combined harvesting and extraction systems to minimize soil disturbance and damage, e.g., the use of combined harvesting and extraction machines (see below).
3. Methods that are aimed at improving the cost-effectiveness of the wood supply chain, e.g., the delivery of forest residue (energy bundles) and wood chips are currently being redesigned to utilize the standard transportation vehicles used for wood delivery.

Harvesting Systems

Figures 2 through **6** show the five general classes of wood harvesting systems. The processes range from semimechanized to fully mechanized systems, and may be used in part, in whole, or in different suitable

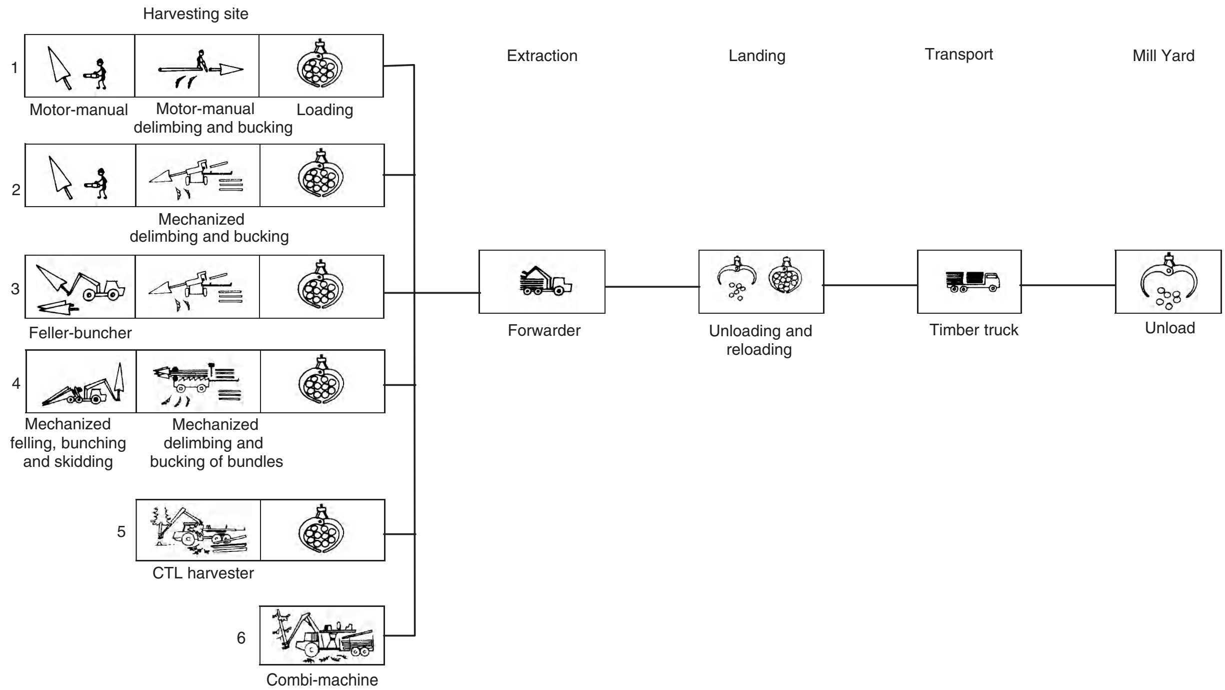


Figure 2 Cut-to-length (CTL) or assortment method of wood harvesting. Adapted with permission from Staaf KAG and Wiksten NA (1984) *Tree Harvesting Techniques*. Kluwer Academic Publishers, Dordrecht, The Netherlands: Martinus Nijhoff.

combinations (and sequence after tree felling) depending on the prevailing economic and socio-economic circumstances.

In the cut-to-length (CTL) or assortment system (**Figure 2**), the delimbing and bucking processes are carried out at the stump, and logs are forwarded over short distances to landings. This method is suitable where mills are far from the harvesting site. The system may be semimechanized, i.e., may use manual felling with chainsaws (also termed motor-manual), and manual delimbing, and bunching, or wholly mechanized with a CTL harvester for felling, delimbing, and bucking in a single operation. The full-pole system (**Figure 3**) may also be semimechanized (chainsaw felling, delimbing, and topping followed by skidding of stems) or fully mechanized (feller-buncher, skidder for in-forest transport, and processing with a stroke-delimber). In this system, the entire delimbed trunks or bucked logs are transported to mills.

In the whole-tree system (also called tree method), the un-delimbed trees are extracted for processing at landings (**Figure 4**). The concept is based on mass handling of tree stems, which compensates for the small tree sizes and enables cost-effective harvesting of coppice stands. Trees are bunched after felling to enhance the efficiency of subsequent handling.

Un-delimbed trees may also be separated into smaller stem sections and extracted for processing at the landings, followed by secondary transport as logs or tree parts, i.e., the tree-part system (**Figure 5**). In the chipping method (**Figure 6**), the harvested tree undergoes size-reduction into wood chips, in a process that may include debarking. The chipping may be done in the stand or after extraction of tree parts. The whole tree including the stumps may be chipped, but the presence of soil impurities makes quality control of wood chips difficult and expensive.

The full-pole and whole-tree methods are suitable for alpine, mountainous, and steep terrains, where they are typically combined with cable extraction systems. Whole-tree and tree-part methods are advantageous where the by-products of tree harvesting (limbs, tops, and sawdust) are valued for fuel. Due to the bulk nature of the material to be transported, they are deemed to be economic where harvesting sites are located in close proximity to the mills. Whereas CTL harvesting is popular in Europe, commercial whole-tree harvesting is common in North America.

Extraction Systems

Extraction refers to the phase of wood delivery in which whole trees, stems, or logs are moved to a major delivery point, either for further transport, or for secondary conversion, or both. Forwarders and skidders (**Figures 3** through **6**) are utilized in ground-based CTL and whole-tree harvesting systems, respectively. In comparison to skidders, forwarders allow for movement of larger loads, hence the density of the forest access road network may be

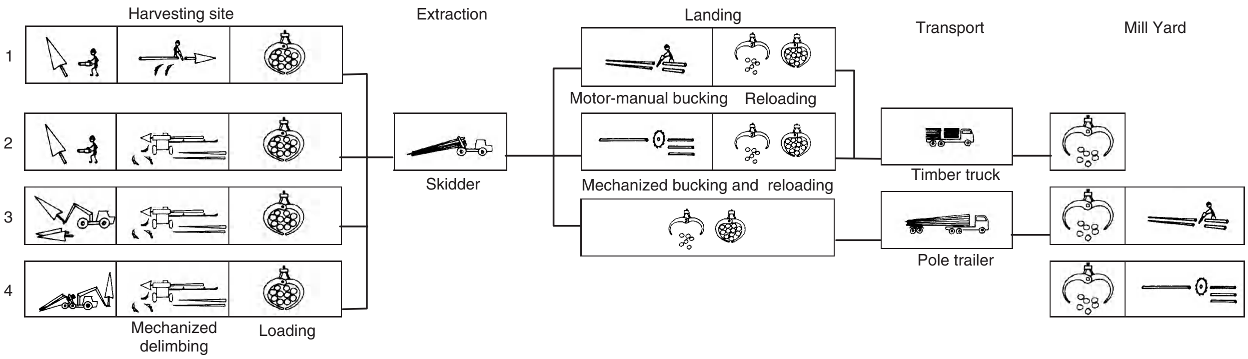


Figure 3 Full-pole method of wood harvesting. Adapted with permission from Staaf KAG and Wiksten NA (1984) *Tree Harvesting Techniques*. Kluwer Academic Publishers, Dordrecht, The Netherlands: Martinus Nijhoff.

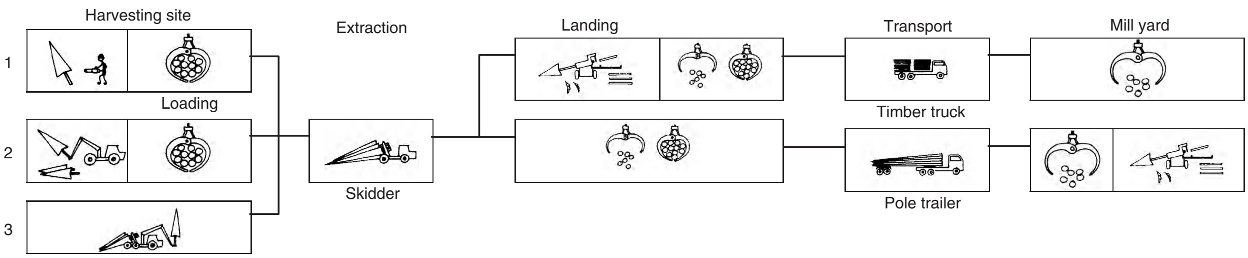


Figure 4 The processes in the whole-tree method of wood harvesting. Adapted with permission from Staaf KAG and Wiksten NA (1984) *Tree Harvesting Techniques*. Kluwer Academic Publishers, Dordrecht, The Netherlands: Martinus Nijhoff.

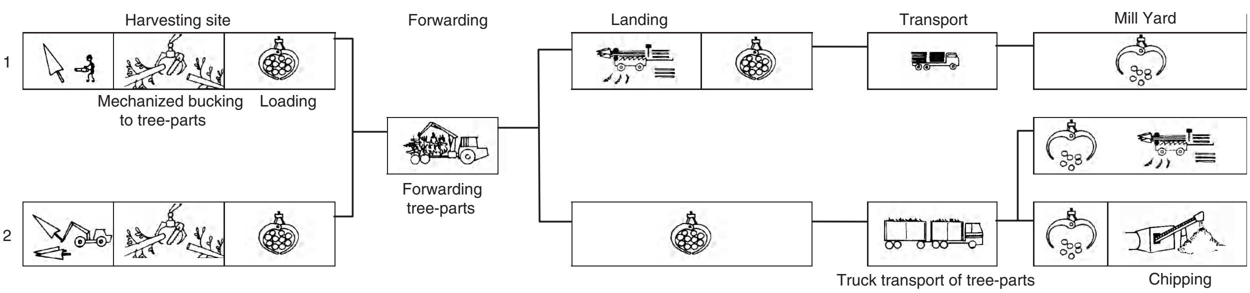


Figure 5 Processes in the tree-part method of wood harvesting. Adapted with permission from Staaf KAG and Wiksten NA (1984) *Tree Harvesting Techniques*. Kluwer Academic Publishers, Dordrecht, The Netherlands: Martinus Nijhoff.

reduced to minimize operation costs. They also cause less damage to the timber and residual tree in the harvesting of thinnings, since the logs are not dragged on the ground. Cable extraction is used in alpine conditions and on sensitive sites where there are limitations on machine flotation and mobility (*see* **Harvesting**: Forest Operations under Mountainous Conditions).

Environmental considerations in wood extraction are specifically aimed at minimizing disturbance and soil damage at the harvesting site. These include:

- soil disturbance, compaction and rutting due to machine traffic, which may impede the growth of residual trees in thinning operations, and also increase the potential for soil erosion and windthrow
- physical damage to residual trees and other vegetation on site, which may lead to loss of timber value and volume in subsequent harvests
- direct and indirect damage to streams and water pollution, e.g., introduction of spilled fuel and lubricants into streams and water sources in close proximity to the harvesting sites.

Soil disturbance and damage may be minimized by using brash, i.e., the portions of trees (stems or branches) with diameter below the minimum set for utilization (about 70 mm). Spreading of brash along the expected extraction routes during the harvesting process offers considerable support for subsequent machine traffic and can be very effective in minimizing rutting and soil damage (**Figure 7a, b**).

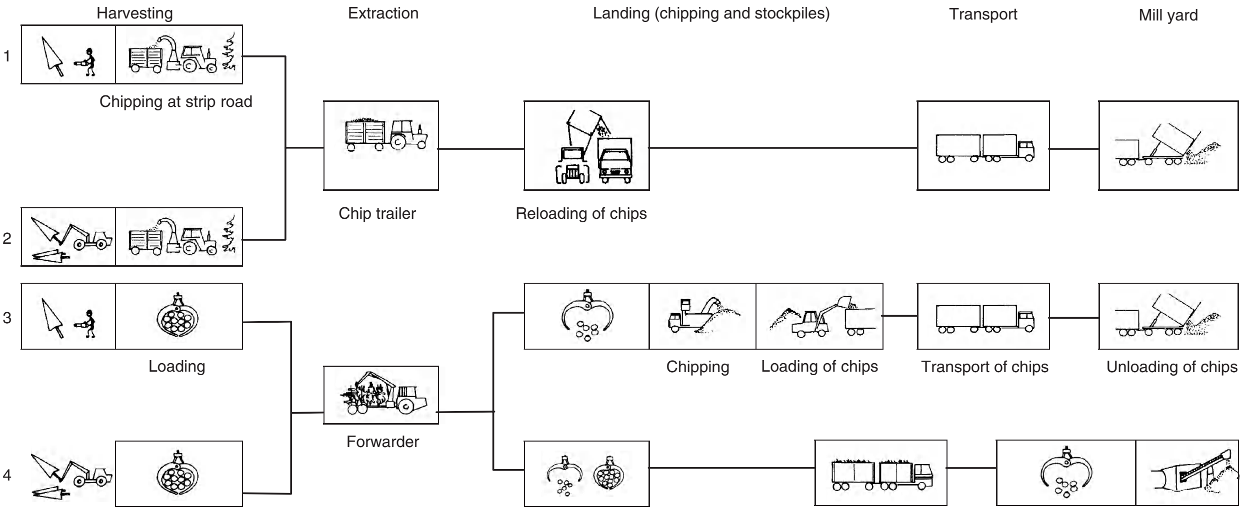


Figure 6 Processes in the chipping method of wood harvesting. Adapted with permission from Staaf KAG and Wiksten NA (1984) *Tree Harvesting Techniques*. Kluwer Academic Publishers, Dordrecht, The Netherlands: Martinus Nijhoff.

Low ground pressure machines are required for operation on soft ground such as on peat soils. Since wheeled forwarders as standard are unsuitable for the task, their nominal ground pressure may be reduced using band-tracks to enhance flotation (**Figure 7c**). When wheel slippage is limiting, wheel chains are used to enhance traction (**Figure 7d**). Alternative methods for minimizing damage on extremely sensitive harvesting sites have also been tested (**Figure 7e, f**). Site and timber quality limitations may necessitate a combined harvesting and extraction operation to limit the number of machine passes at a site (**Figure 8**). Aerial extraction using helicopters (heli-logging) or balloons (**Figure 9**) offers unique advantages for small clear-cuts (e.g., conservation sites), and may achieve specific visual impacts on difficult terrain such as wetlands and on steep slopes.

The importance of environmentally sensitive forest harvesting has a direct bearing on the efficiency of wood extraction operations. For example, in the CTL system, the forwarder is considered a higher environmental risk since the speed and size of its payload determines its productivity, whereas these also increase the risk of site damage. The need to control site disturbance and potential soil damage due to machine traffic and the enhancement of operation efficiency are the basis for terrain classification.

Terrain Classification

Terrain classification systems provide simple, uniform, and practical descriptions of site characteristics, and are primarily intended for:

- planning of wood harvesting, extraction, and silvicultural operations
- operations control, e.g., control of site damage
- evaluation and comparisons of mechanization options
- machine development and marketing plan
- harvesting contract negotiations.

The systems used in European countries (e.g., Ireland, the UK, and Scandinavia), the USA, and Canada are based on researched site descriptors, covering the three main factors that affect off-road machine mobility and performance. These are soil-bearing capacity, surface roughness, and ground slope or grade. On the basis of these factors, guidelines for suitable harvesting and extraction systems may be prescribed.

Ancillary Considerations in Harvesting and Extraction

It is recognized that even with the best planning and maintenance, main extraction routes in a harvesting site eventually degenerate through wear and tear. Some damage is also inevitable when the extraction is over long distances, and is more serious where brash supply is exhausted, or where there is a limited choice of routes. A limited flexibility in the choice of machines may also exacerbate site damage. However, since only a small proportion of the ground (about 10%) is covered by extraction machine trails, such damage may be remedied after the operation where it may be deemed necessary.

Periodic monitoring of harvesting operations should identify excessive site disturbance and damage, and allow for implementation of effective countermeasures. The following guidelines apply to harvester and forwarder routing:

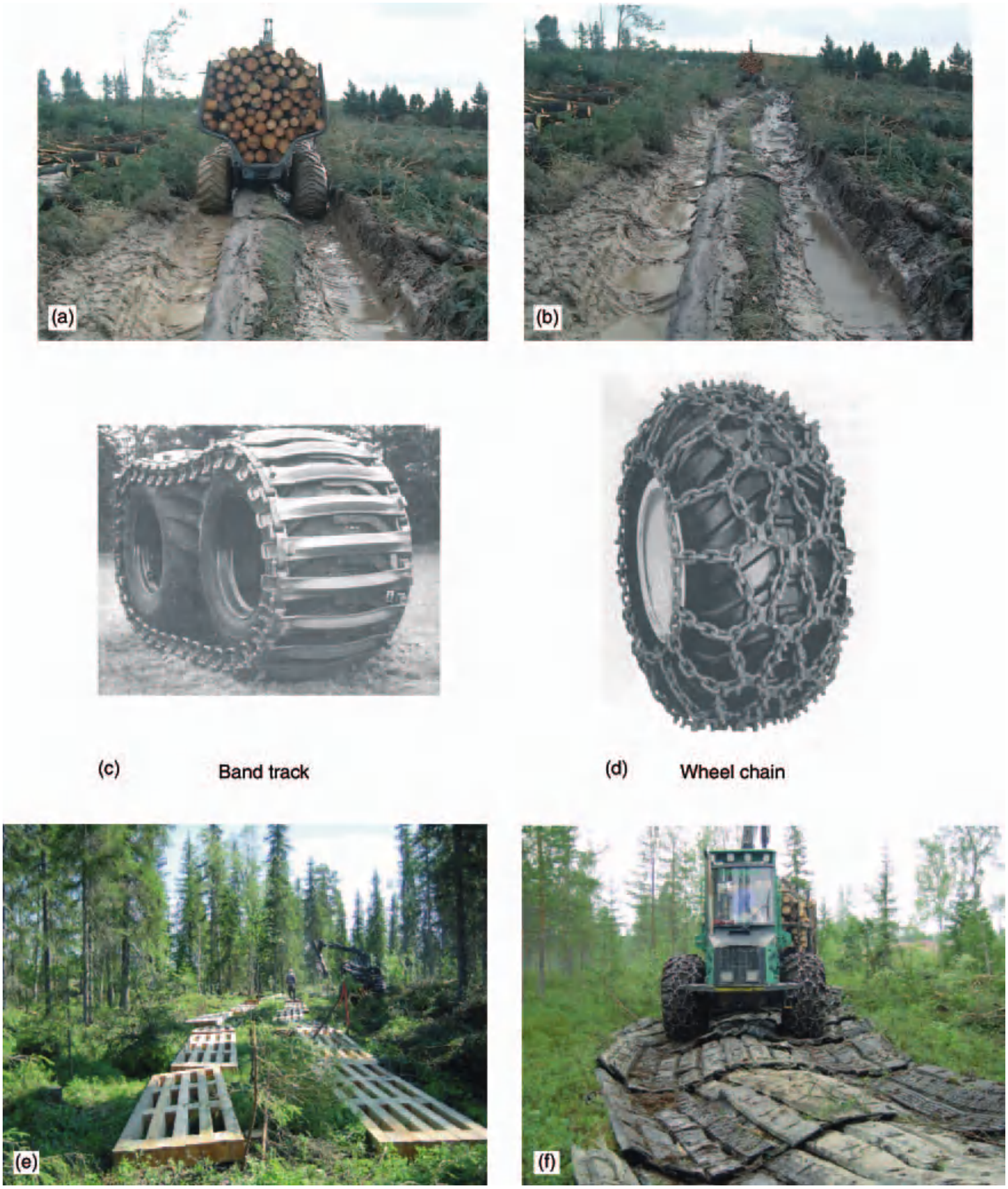


Figure 7 Illustration of (a) site damage by excessive rutting in cases of long extraction routes, and (b) laying of brash mat to minimize damage, and (c) machine band tracks and (d) wheel chains for enhancement of flotation and traction, respectively. Other possible mechanical strengthening of ground with (e) wooden platforms and (f) discarded tire mats may be applied, but the economic feasibility is a function of distance to be strengthened and volume of wood to be transported. Reproduced with permission from Forest Engineering Unit, University College Dublin; Clark Forestry Equipment UK; and Department of Forest Resource Management, University of Helsinki, respectively.

1. The use of partial forwarder payloads may be considered, but it invariably necessitates double-handling operations, and therefore increases the overall cost of extraction.
2. Adequate track reinforcement (with brash or other retrievable material), stream crossings, and embankment rolling should be provided in time and before the start of harvesting operations.
3. Sensitive sites that require the use of brash mats should be completed when the brash is still fresh and effective in the control of traffic-induced site damage. Delayed working should be avoided as it

Figure 8 A Combi-machine or HarWader for combined harvesting and extraction. Reproduced with permission from Partek Forest, Sweden.

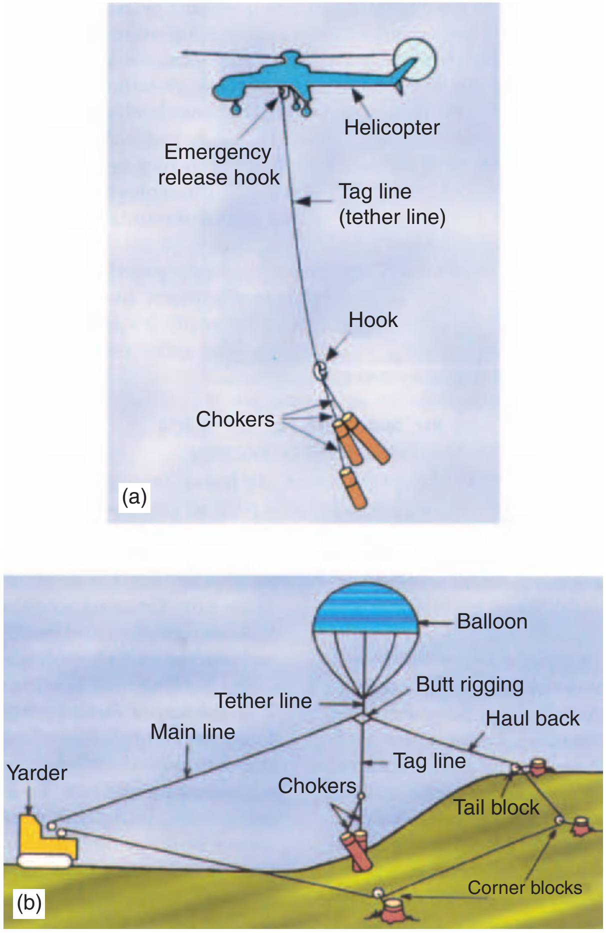


Figure 9 Illustration of aerial wood extraction: (a) using a helicopter (heli-logging) and (b) a balloon and cable system. Reproduced with permission from Food and Agriculture Organization of the United Nations Forestry Department, Rome.

allows the brash to dry and be degraded easily before the extraction is complete.
4. Route the extraction through corridors with adequate soil bearing capacity or with a good brash mat layer, while completely avoiding the sensitive spots or avoiding driving through them during the loaded trips.
5. Avoid uphill driving when loaded, and where possible, machine travel should be along the contours (rather than up–down) in areas that are prone to erosion.

Transportation

Profit is not realized in the production of timber and by-products until they are delivered to the mills, hence an efficient transportation system is of primary importance in forest harvesting. Transportation programs are drawn up on the basis of the source of wood, i.e., the mill's own forest, private forests, or imports. Ideally, the different options including road, rail, and waterways should be considered with respect to wood and by-product cost, and the production requirements and timetables at the mills or other delivery points. However, road transport can access remote harvesting sites, and also link the harvest sites to the rail systems and waterways, if such secondary transportation is required. **Figure 10** shows the characteristics of some of the vehicles used in road transportation of timber and wood chip.

Roads and Road Transport Regulations

Well-planned and well-managed roads are prerequisites for efficient wood delivery. Road classification determines the most appropriate haulage routes, hence, the economics of transportation. Road layout (viz. location, gradient, alignment, turning points, and haulage distance) can restrict the use of certain timber haulage rucks. Road quality (viz. surface condition such rutting, potholes, and roughness) also has a direct influence on the efficiency of wood delivery. For example, a weak, rutted, and potholed road or a rough road with poor alignment and steep grades increase the transportation cycle times. Road roughness is important since it excites dynamic behavior of trucks such that the associated loading is magnified to increase road damaging potential and to compromise driving safety. Other factors that influence road damage potential of haulage trucks include axle spacing and the load sharing characteristics, and the type of suspension systems. Therefore, wood delivery by road is carried out within strict limitations of axle loads and gross vehicle weights (**Table 1**). Ergonomic concerns with respect to increased vehicle vibrations (which affect operator comfort) may also impact on the efficiency of wood delivery.

Figure 10 Categories of machines and trucks used in wood delivery. Reproduced with permission from Forestry Contractors Association, UK, and Timberjack OY, Finland.

Environmental and Ancillary Considerations in Transportation

Damage to transportation routes constructed over naturally weak road substrata (e.g., organic soils) or those that are weakened by seasonal variations (e.g., the influence of spring thaw) present considerable limitations to wood delivery. Such damage imposes expensive repair and maintenance procedures, and therefore makes transportation a costly factor in the overall timber production process. Maintenance and repair costs for timber haulage trucks are also higher than the average for the transport industry in general, because of the rugged nature of the operating conditions and the heavy and bulky loads of wood.

It is well documented that reducing truck axle load decreases its road damaging potential exponentially. However, the economics of timber transportation necessitates a maximization of truck payload, so that wood delivery consignments need to be at about the maximum permitted truck axle and payloads (**Table 1**). The current operational practices aimed at enhancing the serviceability and minimizing the overall maintenance cost of wood delivery route networks include (1) the improvement of design standards for new roads and upgrading of weaker links in the delivery route networks; (2) use of road-friendly truck axle configurations and suspension systems (e.g., air suspension), and (3) the use of trucks with central tire inflation (CTI) systems which adjust tire pressures to suit actual environmental conditions.

Table 1 National axle load regulations for the OECD countries

Country	Maximum permitted loading on a single axle (kg)		Maximum permitted loading on tandem axle (kg)
	Driving	Carrying	
Australia	4 600–9 000		9 000–16 500
Austria	10 000	10 000	16 000
Belgium	13 000	10 000	20 000
Canada	4 500–10 000		16 000–20 000
Denmark	10 000	10 000	16 000
Finland	10 000	10 000	16 000
France	13 000	13 000	21 000
Germany	10 000	10 000	16 000
Ireland	10 500	10 170	11 500–20 340
Italy	12 000	12 000	19 000
Japan	10 000	—	20 000
Luxembourg	13 000	10 000	20 000
The Netherlands	10 000	10 000	18 000
Norway	10 000	10 000	16 000
Spain	13 000	13 000	21 000
Sweden	10 000	10 000	16 000
Switzerland	10 000–12 000		18 000
UK	9 000–10 000		16 000, 16 000–20 000, 34 000
USA	9 000	9 000	15 400

Machine Telemetrics and On-Board Electronics

Machine telemetrics refer to on-board electronic systems that are used for machine and harvesting process control, including measurement and optimization of stem cutting, communication equipment (voice and data), and navigation and route optimization functions. Other on-board electronic equipment include visual display screens, audio and visual warning and fault diagnostic systems, and weighing scales for determination of payloads.

Modern harvesters have on-board computer-based measurement and production data recording and monitoring systems. These can provide stem diameter, log length, and assortment categories, and the operator has options for production value optimization in response to market demand for specific wood assortments. Electronic files can be transmitted between different machines, for monitoring and control of production processes (**Figure 1**). Other peripheral devices that are necessary for data transfer (e.g., GSM connection, satellite navigation, and geographical information systems (GIS) maps), and route optimization systems based on global positioning systems (GPS) and GIS are also available.

Stem Optimization

Features of a typical harvester head are shown in **Figure 11**. The main components include the electromechanically actuated sawblade control, feed rollers and delimbing knives with adjustable grip pressures, and automatic vertical positioning of the head to minimize splitting which incurs quality loss. The systems also allow for easy monitoring of volume and assortments of the harvested wood. With the integrated measuring and control system, wood is processed to customer specifications at the stump, thereby enhancing the supply chain efficiency. Stem optimization also allow for tree processing on the basis of market price and product priority matrices. In fully integrated mechanized harvesting systems, real-time transfer of production data is possible between the harvester and the procurement station to meet dynamic customer specifications (**Figure 1**).

On-Board Weighing Scales

The transportation of timber (like all biological materials) under strict limitations of axle load and gross vehicle weights outlined in **Table 1** is exacting. Therefore there is a trend towards the use of on-board weighing devices on transportation trucks and on loading and unloading machines. Such devices are used to ensure that the payload and axle load comply with active road haulage load limits, and for economic reasons, also allow for the maximization of truck load capacity. On-board weighing systems include crane link weighing systems (which weigh and display individual grab weight; cumulative weight of a loading/unloading operation may also be displayed) and payload platform and axle overload indicators (weighing devices that can handle bulk loads such as logs and wood chips).

Routing of Extraction and Transport Operations

The aim of extraction routing is to minimize or avoid site disturbance and damage or degradation of a harvesting site. Spatial information in the form of base maps or when collated in a GIS may be used to demarcate harvesting sites on the basis of the most important factor, e.g., soil bearing capacity. This enables operators to identify areas that require special attention, e.g., precipices and crags, waterways, and swamps. However, site impact due to extraction routing is highly dependent on operator skills. Good understanding of inherent environmental constraints is therefore central to the control of site damage; operations on sensitive sites should be allocated to experienced operators.

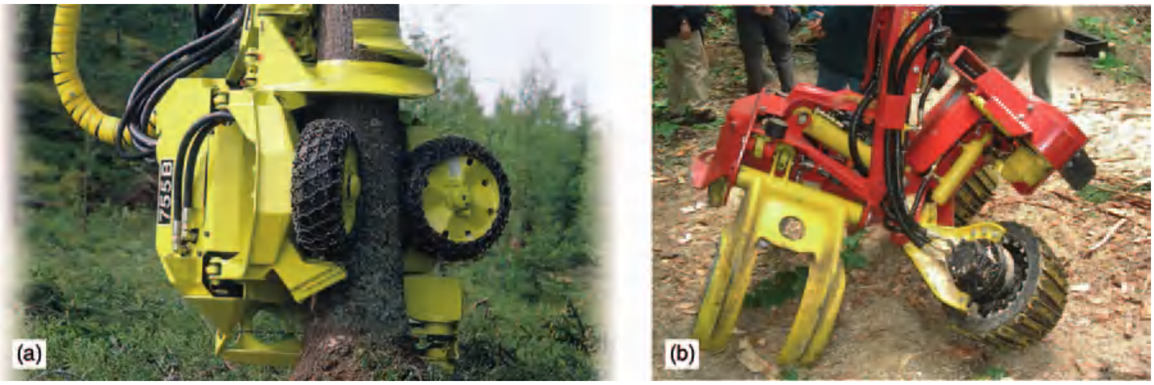


Figure 11 Single grip harvester head with (a) stem optimization capability and (b) a variance consisting of articulated delimbing knives and feed rollers for autonomous processing and loading capability. Reproduced with permission from Timberjack OY, Finland and Forest Engineering Unit, University College Dublin.

The main factors that are usually considered when selecting the location and cost-effective transportation routes include (1) route-dependent factors, such as the cost of road construction and maintenance, and the associated haulage costs, and (2) route-independent factors, including topography, soils, geography, and land use. When dealing with existing road networks for wood delivery, the former factor is most critical. Routing strategies associated with current networks must also address problems such as narrow road segments and bridges with load-carrying and vertical clearance restrictions. Other issues such as public safety and potential environmental pollution (emissions, noise, and transportation of hazardous materials) should be considered.

Site Harzards and Safety Issues in Wood Delivery

Hazards attached to wood delivery operations include:

- overhead power cables e.g., involved in the use of loading cranes mounted on high truck platforms
- poor site conditions and visibility
- operations in close proximity to tree felling areas or cable extraction corridors
- poor road and landing areas.

Such hazards require special considerations with regard to safety. For example, machine or vehicle operators should have appropriate protective outfits for tasks in loading/unloading, stacking, and securing of loads on trucks. Since they often work unsupervised in secluded and constantly changing environments, there is need to enhance their training in health and safety protocols on a regular basis.

Machine operators should also be aware of dangers of oil, fuel, and any chemical spillage. The risk of significant oil or chemical spillages is higher at the landings than elsewhere. Apart from acting as temporary timber storage areas for secondary transportation, landings also act as the end-points for the transportation cycles of both extraction machines and haulage trucks. They are also used for the delivery and storage of fuels, machine oils, chemicals, and spare parts, and may therefore be vulnerable to spills of oils and chemicals. All machines and trucks used should have kits for containing minor spills. The operators should also be trained in the protocols for dealing with major pollution incidences.

Monitoring of Performance of Wood Delivery Systems

Monitoring of components or whole wood delivery systems is essential for achieving optimum performance outcomes. The monitoring processes should include work analyses related to productivity in off-road and on-road transportation, and site impact assessments, with a view to identifying factors that may be improved through machine and process development or the enhancement of operator competence.

In-Process Assessments

These are systematic checks that are required during an operation. Since the site characteristics may be highly variable and obstacles may be obscured, machine operators are expected to make decisions on an ongoing basis. Prerouting assessment is important for the location of inherent obstacles in order to enhance efficiency in wood delivery. The importance of such assessment will be higher for unskilled operators. In-process assessments may also involve more advanced manual or machine telemetric system based time–motion studies to develop productivity functions. Time–motion study allows for objective and systematic examination of all factors which govern operational efficiency of a specified activity in order to effect improvement. With respect to forest machines, this may lead to improvements in harvesting procedures and planning for the necessary access locations during establishment of forest stands.

Post-Process Assessments

These are systematic checks that are required after an operation is completed. They are mainly geared to reverting a site to its original condition and to preventing secondary environmental degradation. For example, poor maintenance of access roads, extraction tracks, and landing areas may cause accelerated soil erosion and depreciation of water quality in the streams and water sources in the vicinity of a harvesting area, long after the operations are completed. Inadequate or poorly maintained roads incur high transportation costs. Therefore routine maintenance, rehabilitation, and upgrading of forest road networks should be implemented.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Forest Operations under Mountainous Conditions; Roading and Transport Operations. **Operations**: Ergonomics; Forest Operations Management; Logistics in Forest Operations.

Further Reading

Bradley A (1997) *The Effect of Reduced Tire Inflation Pressure on Road Damage: A Literature Review*. Forest Research Institute of Canada Special Report no. SR 123. City: Forestry Research Institute of Canada.

Dykstra PD and Heinrich R (1996) *FAO Model Code of Forest Harvesting Practice*. Rome: Food and Agriculture Organization.

Forest Service (2000) *Code of Best Forest Practice: Ireland*. Dublin: Forest Service, Department of the Marine and Natural Resources.

Lassila K (2002). *Ajouran Mekaaninen Vahvistaminen Puunkorjuussa Maaperävaurioiden Vähentämiseksi*. MSc Thesis, Department of Forest Resource Management, University of Helsinki.

Martin AM, Owende PMO, O'Mahony MJ, and Ward SM (2000) A timber extraction method based on pavement serviceability and forest inventory data. *Forest Science* 46(1): 76–85.

Martin AM, Owende PMO, Holden NM, Ward SM, and O'Mahony MJ (2001) Designation of timber extraction routes in a GIS using road maintenance cost data. *Forest Products Journal* 51(10): 32–38.

Nieuwenhuis M (2000) *Terminology of Forest Management: Terms and Definitions in English (Equivalent Terms in German, French, Spanish, Italian, Portuguese, Hungarian and Japanese)*. Vienna: IUFRO.

Owende PMO, Hartman AM, Ward SM, Gilchrist MD, and O'Mahony MJ (2001) Minimizing distress on flexible pavements using variable tire pressure. *Journal of Transportation Engineering* 127(3): 254–262.

Owende PMO, Lyons J, and Ward SM (2002) *Operations Protocol for Ecoefficient Wood Harvesting on Sensitive Forest Sites*. European Union 5th Framework Project (Quality of Life and Management of Living Resources) Contract no. QLK5-1999-00991 (1999–2002).

Roundwood Haulage Working Party (1996) *Code of PracticeRoad Haulage of Round Timber*. Dalfling, UK: Forest Contracting Association Ltd.

Sist P, Dykstra PD, and Fimbel R (1998) *Reduced Impact Logging Guidelines for Lowland and Hill Dipterocarp Forests in Indonesia*. CIFOR Occasional Paper no. 15. Situ Gede, Bogor, Indonesia: Center for International Forestry Research.

Staaf KAG and Wiksten NA (1984) *Tree Harvesting Techniques*. Dordrecht, The Netherlands: Martinus Nijhoff.

Forest Operations under Mountainous Conditions

H R Heinimann, Swiss Federal Institute of Technology, Zurich, Switzerland

Introduction

About 28% of the world's forests are located in mountainous areas, where forest management aims at simultaneously providing goods and welfare services while maintaining ecosystem functions at prudent, sustainable levels. Forest operations aims at delivering plans and operations that are technically feasible, economically viable, environmentally sound, and institutionally acceptable. To achieve this, there is a need to know best practices and to continuously improve them. Design, implementation, and control of forest operations for the specific conditions of mountainous areas are challenging due to difficult terrain conditions and high risks of adverse effects on environmental functions and values. Off-road transportation technology is the critical part of steep slope harvesting operations, and cable-based systems are often the backbone of harvesting systems. The main challenges for future developments probably are: the continuous improvement of practices and technologies for nontrafficable terrain, operationalization of environmental performance by quantifying the 'industrial metabolism' of operations, and development of both human resources and local capacity aspects of technology choices.

Significance and Characteristics of Mountain Forests

Mountain regions occupy about one-fourth of the earth's land surface (**Figure 1**). They are home to approximately one-tenth of the global population and provide goods and services to about half of humanity. Accordingly, they received particular attention in Agenda 21, endorsed at the United Nations Conference on Environment and Development (UNCED) in Rio in 1992. Chapter 13 of that document focuses on mountain regions, and states:

> Mountain environments are essential to the survival of the global ecosystem. Many of them are experiencing degradation in terms of accelerated soil erosion, landslides, and rapid loss of habitat and genetic diversity. Hence, proper management of mountain resources and socio-economic development of the people deserves immediate action.

The global mountain forest area covers about 9.1 million km^2, sharing about 8% of the global land area, and about 28% of the world's forests (**Figure 1**). One-half of the mountain forest area is located in temperate and boreal zones (west of North America, Europe, Far East), while the other half is located in subtropical and tropical regions (Central America, Eastern Andes of South America, continental and insular Southeast Asia, especially Borneo and Papua New Guinea). Mountain forests are fragile ecosystems, which are important for (1) the maintenance of life support services, (2) the supply of renewable resources (biomass, water), and (3) the provision of welfare services, such as mitigation of natural hazards, recreation, or intellectual stimulation.

While the supply of renewable resources, including fuelwood, timber, and other products, has been an important and familiar part of the economy, it has been less appreciated that natural ecosystems perform fundamental life support services (e.g., habitat, biodiversity, nutrient cycling, biogeochemical cycling, food-web functions). This array of services is generated by a complex interplay of natural cycles powered by solar energy and operating across a wide range of space and timescales.

The challenge is to develop land use policies and practices for mountain forests that will provide goods and welfare services simultaneously with maintaining ecosystem functions at prudent, sustainable levels. There is a need to incorporate major ecological considerations into silvicultural practices, e.g., imitating natural processes, reducing forest fragmentation, avoiding harvest in vulnerable areas, or restoring natural structural complexity to cutover sites.

Forest Operations in Context

Forest operations consist of all technical and administrative processes required to develop technical structures and facilities, to harvest timber, to prepare sites for regeneration, and to maintain and improve quality of forest ecosystems on a wide range of space and timescales. It aims at providing plans and operations that are:

- environmentally sound considering impacts on the natural and social environment and efficient use of natural resources including nonrenewable materials, renewable materials, water, energy, and space
- technically feasible considering the physical laws, engineering disciplines, and environmental aspects of the forest
- economically viable considering the cost and benefits of short- and long-range consequences
- institutionally acceptable considering the laws and regulations governing forest operations, landowner objectives, and social values.

The United Nations Environment Program UNEP has been promoting the concept of environmentally sound technologies (ESTs) to significantly improve environmental performance relative to other technologies. These technologies use resources in a sustainable manner, are less polluting, protect the environment, recycle more of their wastes and products, and handle all residual wastes in a more

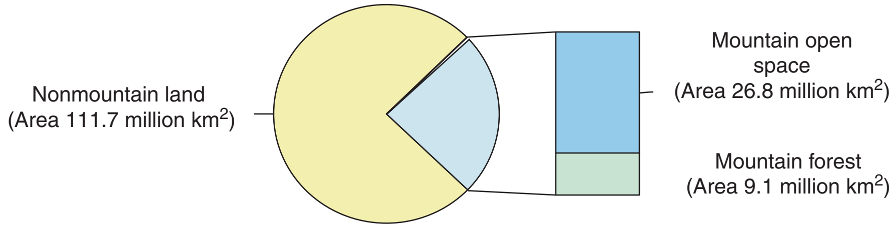


Figure 1 Proportions of the world's mountain forests.

environmentally acceptable way than the technologies for which they are substitutes. Additionally, they have to be compatible with nationally determined socioeconomic, cultural, and environmental priorities and development goals.

Forest operations technology aims at providing best practices that are the result of a continuous process of suiting harvesting practices to silvicultural regimes, and of improving economic and environmental performance. Best practices (BP) consist of strategies, activities, or approaches that have proven to be both effective and efficient.

Forest Operations Technology for Mountainous Terrain

Development and Deployment of Forest Operations Technologies

Accessibility is the most critical factor influencing feasibility of operations in mountainous terrain. Transportation consists of two phases, off-road and on-road, which are heavily dependent on each other. Four main concepts are available for facilitating off-road transportation: (1) ground vehicles moving on natural terrain, (2) ground vehicles moving on skid roads, (3) carriages moving on cable structures, and (4) aircrafts moving in the atmosphere (**Figure 2**). In nonmountainous terrain, off-road transportation is based on ground vehicles. System complexity increases with the effort to ensure off-road locomotion. Ground vehicles may move on a path over natural terrain or, if the terrain conditions become too complex, over geotechnical structures (skid roads). If terrain conditions become too difficult, cable structures enable the transport of partially or fully suspended loads over large distances overcoming various terrain obstacles. Aircraft-based technologies use the atmosphere as the medium for transport. Although at a high operational cost, helicopters have found a niche in transport for a number of site-specific situations when road costs are high, speed of operation is important, or fragile ground conditions exist.

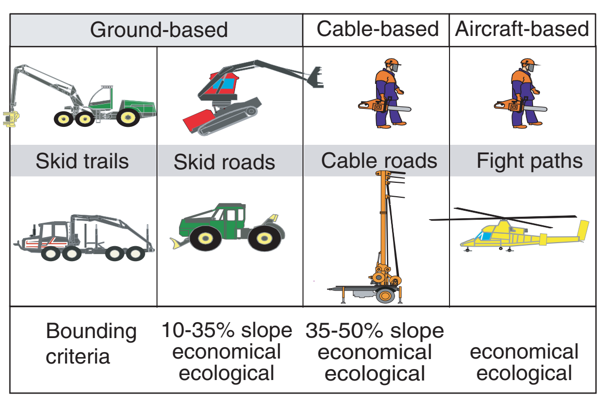


Figure 2 Basic harvesting system concepts. Off-road transportation technology is decisive for the layout of road networks and harvest units.

During the 1980s the engineering approach to developing road networks changed. It evolved from a technical task of cost minimization to a task that integrates technical processes with public involvement, environmental impact assessment, and public choice. At present, we are moving from an analysis–synthesis–evaluation design principle towards an engineering phase of algorithms and artificial intelligence. Availability of sophisticated computers, smart software, and digital terrain models are the backbone of future engineering work. The most advanced systems for the layout of both road networks and harvesting patterns are able to generate plans semi-automatically. Difference in the lifespans of on-road and off-road technologies is another problem becoming increasingly important. While the lifespan of roads is about 30–50 years, it has only been about 10–20 years for off-road technology. Therefore, a need to re-engineer forest road networks is emerging because off-road equipment has been altering its capabilities.

In trafficable terrain, ground vehicles are the basis for mechanized felling, processing, and transportation of trees. Mechanization of transportation progressed mainly in the 1960s and 1970s resulting in special machines like skidders, forwarders, or clambunk-skidders. Mechanization of felling and processing operations first took place in gentle terrain and slowly evolved on slopes. Beginning in the mid-1980s, manufacturers adapted tracked carriers for the special conditions of slopes. Being capable of processing trees mechanically in the stand increased the application of cut-to-length harvesting systems, first in thinning operations.

In nontrafficable terrain, cable yarders are the determinant technology of harvesting systems. Cable operations have been increasingly used in thinning operations, extracting small-size timber. This trend leads to emergence of smaller harvesters, and leaving systems developed for clear-cutting, such as high lead, grapple yarding, etc. The most advanced yarders make use of information technology to control speed, to move loads to pick-up locations, and to monitor the state of the system automatically.

Despite the options of sophisticated technology, biomechanical power (humans, animals) for felling, processing, and transportation is still important in many regions of the world, especially in developing countries. The dissemination of knowledge and the development of human resources in the forestry sectors is therefore an important issue to be emphasized in the future.

Cable Systems: The Backbone of Steep Slope Harvesting Systems

Cable yarding technology has a long tradition in Central Europe, in the Pacific Northwest of North America, and in Japan. In other regions of the world, it has been introduced only tentatively.

The basic structural model consists of a cable suspended between two points (**Figure 3**). A configuration is designated standing if the cable is fixed at support points A and B. A live line configuration has the cable fixed only at one support point B, with a mechanism to control the tensile force in the line at support point A. A running line configuration has a mechanism to control tensile forces at both support points (A, B). To make such a system operable, the two control mechanisms are integrated at the head end (A) while a pulley at the tail end diverts the tensile force. A difference between tensile forces is required to produce lift, and to move a load.

The simplest cable system configuration consists of an uphill yarding system (**Figure 4**). The load-supporting structure consists of (1) the skyline, (2) the head spar, (3) the tail spar, and (4) the anchors, which have to be designed and setup specifically for each cable corridor. The yarding process requires (5) a carriage moving on the skyline, (6) a mainline to pull the carriage, and (7) a mechanism to slackpull the mainline, to lift the load, to attach it to the carriage, and to release it at the landing. Gravity moves the carriage downhill to the location where a load is picked up. A mechanism clamps the carriage to the skyline, and the mainline is slackpulled manually to the position where chokers attach logs to it. The winch pulls in the mainline until the load attaches to the carriage and releases the clamp. The load then moves partially or fully suspended to the landing.

A downhill yarding configuration (**Figure 5**) requires additional lines and mechanisms. The yarding process requires – as for uphill yarding – (5) a carriage moving on the skyline, (6) a mainline to pull the carriage, and (7) a mechanism to slackpull the mainline, to lift the load, to attach it to the carriage, and to release it at the landing. A haulback line (8) moves the carriage uphill to the location where a load is picked up. A mechanism clamps the carriage to the skyline, and the mainline is slackpulled mechanically to the position where chokers attach logs to it. There are several slackpulling mechanisms available: driving a sheave by the yarder's slackpulling line, by an electromechanical engine, by a fuel engine, or by a hydraulic pump. The winch pulls the mainline in until the load attaches to the carriage and releases the clamp. The load then moves partially or fully suspended to the landing, simultaneously controlled by the mainline and the haulback line.

Operational efficiency depends far more upon rational organization of work processes than upon equipment capabilities, or workers' skills. It is therefore important to understand the essence of the workflow organization of cable-based harvesting systems. A harvesting system is designated 'tree length' if the conversion of trees to logs is done after the extraction operation at the landing or at mill site. This means that only felling is done at the stump site, either motor-manually or using steep slope feller-bunchers. Directional felling and bunching affect productivity positively. Several trees are chokered to a single load, which is attached to the mainline and extracted by a

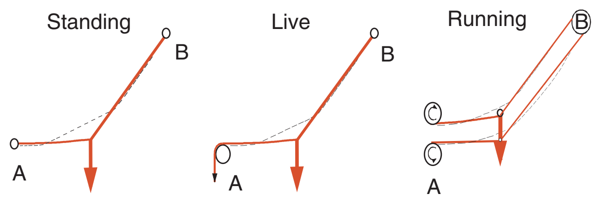


Figure 3 Types of load-supporting cable structures.

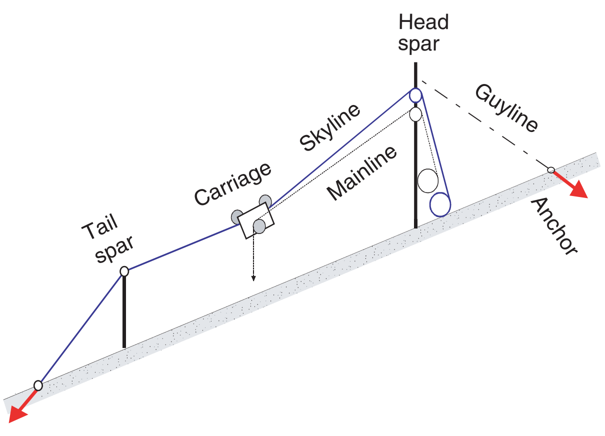


Figure 4 Components of a skyline yarding systems for uphill yarding.

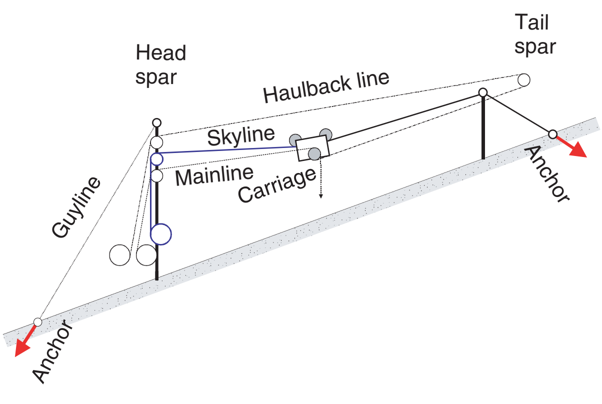


Figure 5 Components of a skyline yarding system for downhill yarding.

cable yarder to the landing. At the landing, the following operations have to be done: releasing the load, limbing, bucking, and piling. These operations may be mechanized by using an excavator with a stroke-delimber, which is common in North America. In Central Europe, a boom with an attached processor head is integrated into the yarder. A standard crew consists of one or two choker setters, one yarder operator, one processor operator, and one chaser. In countries with high labor cost, such as Central Europe, rationalization efforts have led to automated systems which can be operated by a two-man crew: one choker setter and one yarder operator. The yarder moves the load automatically from the stump to the landing and the empty carriage from the landing to the stump site. The yarder operator therefore gains additional time which can be used to process trees to logs while the carriage is moving automatically. Such a system requires radio-control of the yarder. Future developments aim to introduce bucking-to-value and bucking-to-order procedures as they are implemented in the Nordic wheeled harvester systems.

A harvesting system is designated cut-to-length (CTL) if the conversion of trees to logs is done at the stump site before the extraction operation. Felling, limbing, and bucking are all done at the stump site. Motor-manual systems use workers equipped with chainsaws. Mechanized systems are based on steep slope harvesters with the capacity to level the swing table. Several logs are chokered to a single load which is attached to the mainline and extracted partially or fully suspended by a cable yarder to the landing. A grapple attached to a boom handles the logs and piles them. In North America, an excavator-based loader usually does this operation, whereas in Central Europe the boom is integrated into the yarder. A standard crew is of the same size as for tree-length harvesting, and the minimal crew size consists of two, one choker setter and one yarder operator. As in tree-length harvesting, a crew size of only two requires radio-control of the yarder and the carriage. CTL systems may be used in both thinning and clear-felling operations. However, CTL cable yarding is best to minimize damage to residual trees in thinning operations.

Improving Operational Efficiency

Production economics investigates the interactions of factors of production with the output of production. It is only possible to develop empirical models with a limited range of validity due to the complexity of harvesting systems. Forest operations research has been analyzing and developing productivity models, which are the basis for estimating production rates (e.g., production rate in m^3 per productive system hour), and for optimizing systems' performance. The professional literature reports many of those studies. However, comparability is limited due to different standards of study layout, of timber volume measurement, and of time units. Another problem is that the number of different harvesting systems has reached a variety that demands too much effort when using traditional study methods. Future research will therefore have to concentrate on families of technologies (harvesters, forwarders, yarders, etc.), and on real-time gathering of operational data using sensors and data loggers. Optimization has been another field of forest operations research. Problems are often so complex that the use of traditional techniques of operations research, such as linear programming, needs excessive computing time or is even impossible. Advances in heuristic techniques open new possibilities to optimization, offering a broad area of future research.

Minimizing Environmental and Social Impacts

Since the 1970s, public awareness of environmental concerns has steadily increased. The UNCED conference adopted the concept of sustainable development as a programmatic goal for future development. However, there has been much debate on how to transfer this concept to the level of operations and harvesting systems. Risk analysis is one approach of studying the impacts of specific processes on safeguard objects. In forest operations the relevant safeguard objects are: (1) watersheds, (2) sites, (3) human beings, and (4) natural resources. Human activities affect these safeguard objects in different ways and on different scales of space and time.

Watersheds

Land use activities such as road network construction and harvesting regimes may have adverse effects on watershed processes. Research on erosion and sedimentation processes is complex and needs large-scale spatial data sets of a few critical variables to develop better understanding. Hypotheses postulate that channel networks integrate the cumulative effects of geotechnical and topographical variability, climatic triggering events (rainstorms, fires), and management regimes (roading, harvesting). Road erosion and identification of landslide trigger sites are problems that can be immediately remedied by considering rules of drainage, and roadway design. Imperviousness is an indicator for cumulative impacts at the watershed scale, which can be easily measured at all scales of development, as the percentage of area that is not 'green.' Current research converges toward a common conclusion:

that it is extremely difficult to maintain integrity of catchment processes when development exceeds 10–15% impervious cover. There seems to be a strong relationship between imperviousness and runoff, water quality, stream warming, stream biodiversity, and other dimensions of aquatic quality.

Site Disturbance

Harvesting activities such as off-road traffic and felling cause several site disturbances. Research has been concentrating on long-lasting effects, such as soil erosion and soil compaction. One aim is to understand the behavior of the vehicle–soil interaction and to provide threshold values to limit possible damages to an acceptable level. Mechanical behavior of soil depends on its water content. One strategy to limit soil disturbances is to avoid traffic whenever the water content approaches the limit of liquidity, or even exceeds it. Another approach is to minimize the actions at the wheel–soil interface by using low-ground-pressure tires. A third strategy is to limit traffic on fixed transportation lines (skid trails). Although progress has been made to reduce site disturbances, there are still many unsolved questions.

Health and Safety

Forest work may have impacts on health and safety of the workforce. Forestry is one of the sectors with the highest accident rates often resulting in heavy injuries or even death. Research investigates stress–strain processes of different systems, as a basis for system improvement and development. The International Labour Office (ILO) offers information on occupational health and safety, ergonomics, etc. A recent code of practice aims to protect workers from hazards in forestry work and to prevent or reduce the incidence of occupational illness or injury. It is intended to help countries and enterprises that have no forestry-specific regulations, but there are also useful ideas for those with well-developed prevention strategies. The available body of knowledge is considerable. The problem is how to disseminate it and how to apply the basic rules in firms and enterprises.

Life Cycle Assessment

Manufacturing processes are using energy and materials and releasing wastes to the environment. Life cycle assessment (LCA) has become an important tool to assess those energy and material uses and releases to the environment. It forms part of the novel orientation in environmental management, moving away from 'end of pipe' to 'begin of pipe' approaches. In forestry, use of LCA methodology has just started recently; therefore only preliminary results are available. The LCA framework is an important step to shift environmental issues from 'good feeling' to hard facts, and to establish a set of operational performance indicators (OPIs), as proposed by international standards on environmental performance (ISO 14031).

Prospects for the Future

We are looking back on a phase of development that has been dominated by environmental and institutional issues. Many people therefore misjudged the significance of technology and engineering sciences, and their role for sustainable development. There is a considerable body of knowledge on forest operations technology, even for sensitive mountainous areas. Improving the understanding of natural processes and their interactions with land use activities is important. However, dissemination of available knowledge and the development of human resources are probably more important, first in mountainous areas where the risk of degradation is high. The forest operations community will continue to improve the technical systems of forestry. The main challenges for future research and development will probably be:

- the shift to a process focus, considering all technical and administrative processes along a whole value chain of production (business re-engineering focus)
- active collaboration in the process of improving and developing the institutional framework (adaptation of policy instruments such as auditing, scientific based environmental standards, etc.)
- planning procedures based on algorithmic knowledge and spatial databases
- operationalization of environmental issues, following the emerging discipline of industrial ecology (quantification of the 'industrial metabolism') using and improving tools such as LCA or substance flow analysis (SFA)
- expansion of the concept of operational efficiency considering the 'eco-efficiency' approach proposed by the World Business Council for Sustainable Development
- development of human resources on all levels of forestry, taking into account future organizational concepts (virtual organizations, network-based structures) and new job profiles (novel training methods, new wage models, teamwork, promotion by performance)
- use of a mechatronic's paradigm of development, providing some 'intelligent behavior' to future machines and systems (sensing devices, control systems, etc.).

Sustainable development of mountain areas depends on recycling of resources rather than their extraction and eventual discard following use, and on turning from 'end-of-pipe' thinking to forward-looking approaches to product and process design. There is a big potential for this shift in thinking to develop sustainable management practices for mountain forest ecosystems.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Roading and Transport Operations. **Hydrology**: Snow and Avalanche Control; Soil Erosion Control. **Operations**: Forest Operations Management; Logistics in Forest Operations. **Site-Specific Silviculture**: Silviculture in Mountain Forests.

Further Reading

Aber J, Christensen N, Fernondez I, *et al*. (2000) *Applying Ecological Principles to Management of the U.S. National Forests*. Washington, DC: Ecological Society of America.

Heinimann HR (1999) Ground-based harvesting technologies for steep slopes. In: *International Mountain Logging and 10th Pacific Northwest Skyline Symposium,* 28 March–1 April 1999, Corvallis, pp. 1–19. Corvallis, OR: Oregon State University.

Heinimann HR (2000) Forest operations under mountainous conditions. In: Price MF and Butt N (eds) *Forests in Sustainable Mountain Development: A State of Knowledge Report for 2000*, pp. 224–230. Wallingford, UK: CAB International.

ISO (1999) *Environmental Management: Environmental Performance Evaluation – Guidelines*. Geneva, Switzerland: International Standards Organization.

Konuma J-I and Shibata J-I (1976) Cable logging systems in Japan. *Bulletin of the Government Forest Experiment Station* 283: 117–174. (in Japanese)

Price MF and Butt N (eds) (2000) *Forests in Sustainable Mountain Development: A State of Knowledge Report for 2000*. IUFRO Task Force on Forests in Sustainable Mountain Development, Wallingford, UK: CAB International.

Samset I (1985) *Winch and Cable Systems*. Dordrecht, The Netherlands: Martinus Nijhoff.

Schueler TR (2000) The importance of imperviousness. In: Schueler TR and Holland HK (eds) *The Practice of Watershed Protection*, pp. 100–111. Ellicott City, MD: Center for Watershed Protection.

UN (1992) *Managing Fragile Ecosystems: Sustainable Mountain Development*. Report of the United Nations Conference on Environment and Development, Rio de Janeiro, 3–14 June 1992. Available online at http://www.un.org/esa/sustdev/documents/agenda21/english/agenda21chapter13.htm

HEALTH AND PROTECTION

Contents

Diagnosis, Monitoring and Evaluation

M Ferretti, LINNÆA ambiente, Florence, Italy

Introduction

Over the last 30 years forest health became a popular issue together with the concern about acid rain, air pollution, and climate change. Terms like forest decline, and the German 'Waldsterben' (forest death) and 'Neuartigen Waldschäden' (new type of forest damage) became frequent in scientific literature as well as in popular media. This concern resulted in an unprecedent effort to study and monitor forest health. Since then the situation has evolved and now forest health diagnosis and monitoring is relevant to a much broader area of interest, including recent (e.g., climate fluctuation and change, biodiversity, sustainable resource management) and 'traditional' issues (e.g., pests, diseases, forest fire). Broadly, forest health diagnosis, monitoring, and evaluation aims to identify forest health problems, track forest health status through time and identify its relationship with environmental (biotic and abiotic) factors. It embraces a variety of activities and involves several topics and scientific disciplines. Forest health diagnosis, monitoring and evaluation is addressed here in terms of (1) definitions, factors affecting forest health and most known forest health declines in the world, (2) methods of diagnosis, monitoring, and evaluation, and (3) relevance and applications.

Forest Health

Importance of Definitions and Concepts

The definition of forest health is important as it provides guidance for the operational steps of the monitoring, e.g., the choice of the most suitable indicators (see below). A problem is that forest health still lacks a consensual definition. In most cases, definitions are based on the expectations of particular interest groups: a person interested in commercial timber (e.g., the owner of a pine plantation) would have a 'utilitarian' perspective (wood production), while a natural reserve manager would consider a more 'ecological' approach, taking into account, the wildlife, the preservation of species and habitat diversity, and the ecological processes. According to the approach, definitions may refer to different entities (individual trees, the stand, the forests, or the entire forest ecosystem) and consider different indicators (e.g., from injury to individual trees to the incidence and severity of pests, diseases, and mortality rates, presence and abundance of exotic species, growth rate, specific and structural diversity, fluxes of energy and chemicals from the atmosphere, and change in soil properties). This has clear operational consequences for the design of a monitoring program. Recent definitions of forest health as well as the criteria and indicators for sustainable forest management (SFM) consider key words such as 'long-term sustainability,' 'resilience,' 'maintenance' of 'ecosystems structure and functions,' 'multiple benefits and products.' Overall, this suggests that the health of individual trees is somewhat different from the health of the forest: although the detection of individual unhealthy trees is important as they may be signaling the occurrence of problems that may become serious in the future, it is important to consider that death of trees is as important as birth and growth to the vitality of forests. Thus, a healthy forest ecosystem may include unhealthy or dead trees. This means that forest health is no longer thought to be a property relevant to individual trees and stands but to forest ecosystems. In the remainder of this article the emphasis will be on forest and forest ecosystem health rather than on tree health, although reference to tree health will be made under specific chapters.

Factors affecting Forest Health

The health of forests can be subjected to many stressors (**Figure 1**) that may affect individual trees as well as the entire ecosystem.

Recognizing the stressor(s) of concern and its expected mechanism of action and pathways is important as it may help considerably the choice of the indicators to be adopted for monitoring. Natural and anthropogenic factors may act as stressors, singly and/or in combination. In addition, anthropogenic factors may substantially alter the occurrence and severity of natural ones. The role of the various stressors may change, and – according to the situation – the same factor may have a different role at a different time in the sequel of steps of a progressive or reversible decline. For example, air pollution is known to cause direct damage and even death of forest trees at very high concentrations. At low concentration, however, air pollutants may just weaken the resistance of forest trees to insect attacks; in this case a subsequent attack of an insect may cause the death of the trees that were already weakened by the exposure to pollutants. Emphasis on the interaction between different factors and on their ordering according to the peculiar site condition is also a convenient framework to identify the scenario of concern and to proceed toward a diagnosis.

Forest Declines

Instances of poor forest health have been documented worldwide. **Tables 1** and **2** report the best-known ones. Reports are almost always based on the evidence of the decline of forest trees and cover a wide array of ecological situations and forest species. Declines can occur as natural processes and as a result of anthropogenic activity.

Natural forest declines Natural forest declines (**Table 1**) include those related to the action, singly or in combination, of 'traditional' factors (e.g., pests, diseases, climate perturbations, nutrient disturbances, vegetation successional dynamics, and competition). Natural forest declines may involve individual trees of a given species at a certain site, an individual species throughout its range or within an ecosystem, and multiple species. In many cases, the cause of the decline is not obvious as there are complex interactions that need careful examination according to clear diagnostic criteria (see below).

Human-induced forest declines Different human activities may affect the health of forest ecosystems: fire and mismanagement are probably the most obvious ones. However, much work on forest decline concentrated on atmospheric pollution. Traditionally, a distinction is made between the decline of forest trees around pollution sources and those declines for which the effects of nonacute, background pollution level are advocated.

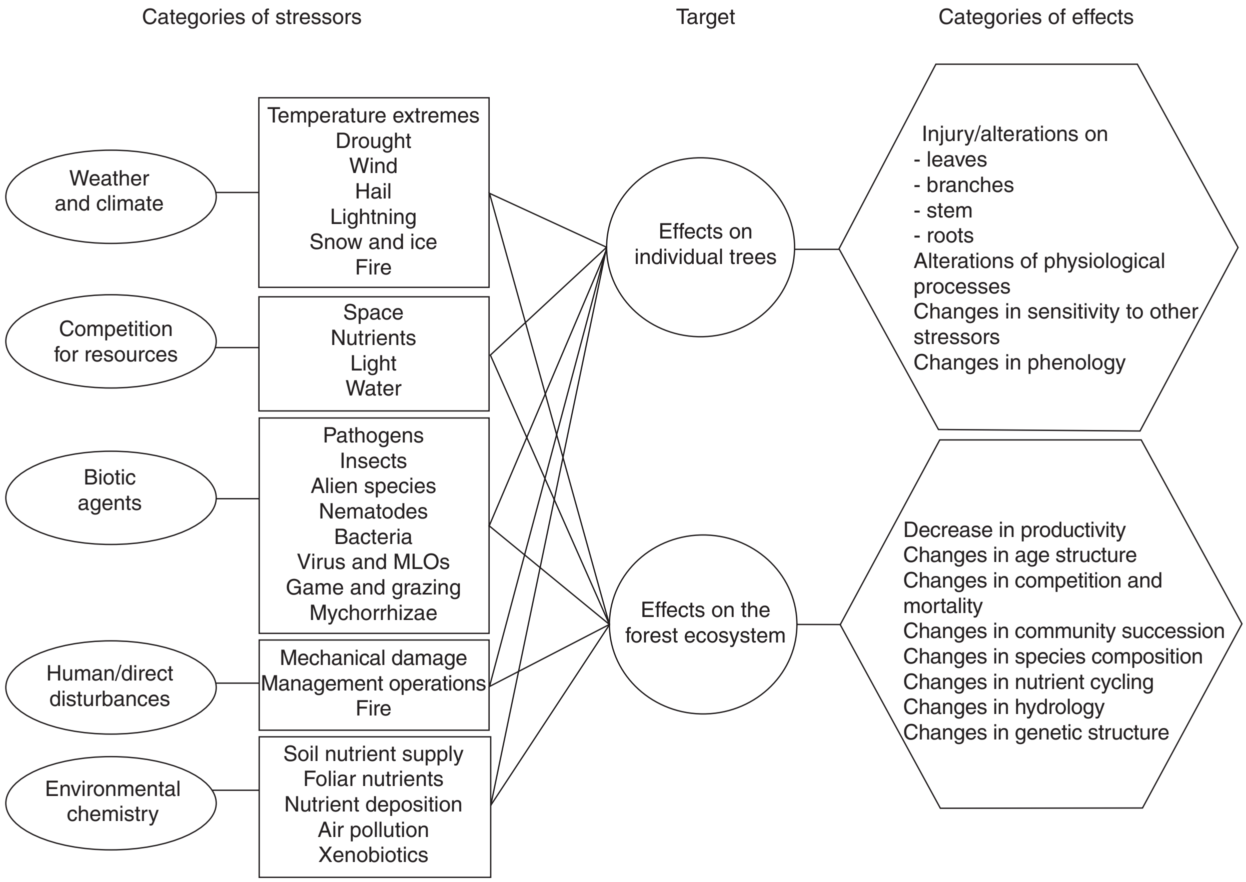


Figure 1 Stressors that may affect forest trees and ecosystems causing various effects. MLOs, mycoplasma-like organisms. Compiled on the basis of Committee on Biological Markers of Air Pollution Damage in Trees (1989) *Biological Markers of Air Pollution Stress and Damage in Forests*. Washington, DC: National Academy Press.

Declines around pollution sources Declines around pollution sources usually involve a distinct spatial pattern, with the most damaged areas being located close to the pollution source. Here, acute foliar injuries are almost always present; they are caused by concentration of pollutants that are directly toxic to plants. As the distance from the source increases, chronic injury and/or indirect effects may occur. The best-known cases of declines around pollution sources for which conclusive studies have been reported are shown in **Table 2**. Tree mortality and/or damage have also been reported around sources of pollution in Europe (Arc Valley, Maurienne, France; Øvre Årdal, Norway; Leanachan Forest, Fort William, Scotland, UK) and evidence for other cases in the Kola Peninsula of China, Korea, and the former USSR is emerging.

Forest declines and regional air pollution Well-documented cases of regional forest decline that can be attributable to air pollution are limited (**Table 2**). This reflects the inherent complexity of research into cause and effect; with few exceptions, at the regional scale the concentration and deposition of air pollutants is usually not enough to cause direct injury to the trees; rather, secondary effects (e.g., soil mediated) can occur, but they usually are less obvious and involve a suite of other factors. Examples of regional effects of air pollutants include the effects of ozone (O_3) on the decline of *Abies religiosa* (Desierto de Los Leones, Mexico) and on the pines (mostly *Pinus jeffreyi* and *P. ponderosa*) in the western USA. In Europe, the damage to Norway spruce (*Picea abies*) in the area between the northern Czech Republic, south Poland, and southeast Germany due to sulfur dioxide (SO_2) is the most widely known example. In several other cases, air pollution was suspected to be involved but evidences were not conclusive.

Methods in Forest Health Diagnosis, Monitoring, and Evaluation

Diagnosis

Identifying whether the forest of concern is healthy or not and, if unhealthy, what could be the cause of

Table 1 Cases of tree and forest declines

Geographic area	*Region/country*	*Species/forest*	*Early record*
Africa	Benin	*Casuarina equisetifolia*	—
	Botswana, Zambia, Zimbabwe	*Pterocarpus angolensis*	1950s
	Gambia River	Assorted species in mangrove forests	—
	Côte d'Ivoire	*Terminalia ivorensis*	1970
	Sahel	*Azadiracta indica*	1990
	South Africa	*Ocotea bullata*	—
	South Africa	*Pinus radiata*	—
	Sudan	*Acacia nilotica*	1930
	Uganda	Assorted species	1984
	Tanzania	*Pinus patula*	—
Asia	Bangladesh	*Heritiera fomes*	1915
	Bhutan	*Abies densa*	1980
	China	*Pinus massoniana*	—
	China	*Pinus armandi*	—
	India	*Shorea robusta*	1907
	Japan	*Cryptomeria japonica*	1970
	Japan	*Abies veitchii, A. mariesii*	—
	Sri Lanka	*Calophyllum* sp., *Syzigium* sp.	1978
	Sri Lanka	Assorted species in montane rainforest	1978
Europe	All regions	*Quercus* spp.	1739
	All regions	Various species	1980s
	Central and Southern Europe	*Abies alba*	1810
	South and Central Sweden	*Pinus sylvestris*	1980s
	South and Central Sweden, Central Europe	Norway spruce	1889
	Spain, France, Germany, Switzerland, Italy	*Fagus sylvatica*	—
Latin America and the Caribbean	Argentina	*Austrocedrus chilensis*	1948
	Argentina	*Nothofagus* (forests)	—
	Brazil: Minas Gerais, Rio Doce valley	*Eucalyptus* spp.	1974
	Chile	*Pinus radiata*	—
	Chile	*Nothofagus dombeyi*	—
	Chile	*Nothofagus* spp.	—
	Colombia	*Quercus humboldtii*	—
	Colombia	*Eucalyptus globulus*	—
	Galápagos Islands, Ecuador	*Scalesia pedunculata*	1930s
	Mexico	*Abies religiosa*	1981
	Mexico	*Pinus hartwegii*	1981
	Peru	*Eucalyptus globulus*	1983
	Uruguay	*Celtis spinosa*, *Eucalyptus* spp., *Quercus* spp., *Satia buxifolia*, *Schinus* spp.	1990
North America	'Inland empire'	*Pinus monticola*	1927
	Alaska	*Chamaecyparis nootkatensis*	1880
	Eastern Canada and northeast USA	*Betula* spp.	1930
	Eastern Canada and northeast USA	*Acer saccharum*	1970s
	East USA	*Quercus* spp.	1900
	East USA	*Fagus grandifolia*	—
	East USA	*Picea rubens*	1970s
	East USA	*Abies balsamea*	—
	Northeast USA and Canada	*Fraxinus pennsylvanica*	1930s
	South California	*Pinus ponderosa*	1950s
	South California	*Pinus jeffreyii*	1950s
	Southern USA	*Pinus echinata*	1930
Pacific region	Australia	*Eucalyptus marginata*	1920
	Australia	*Eucalyptus* spp.	—
	Australia, New Zealand	*Pinus radiata*	1966
	Hawaii	*Metrosideros polymorpha*	1970s
	Hawaii	*Acacia koa*	1970s
	New Zealand	*Nothofagus* spp.	1950
	New Zealand	*Metrosideros* spp., *Weinmannia racemosa*	1920
	New Zealand	*Cordyline australis*	1980
	Norfolk Islands	*Araucaria heterophylla*	1970
	Papua New Guinea	*Nothofagus* spp.	—

Table 1 Continued

Geographic area	*Region/country*	*Species/forest*	*Early record*
	Queensland	*Avicennia marina*	—
	Tasmania	*Eucalyptus delegatensis*	1960s
	Tasmania	*Eucalyptus obliqua*	1960s
	Tasmania	*Eucalyptus regnans*	1960s
	Tasmania	*Eucalyptus nitida*	1960s

Source: Data from Ciesla WM and Donabauer E (1994) *Decline and Dieback of Trees and Forests*: *A Global Overview*. Rome: Food and Agriculture Organization; Innes JL (1993) *Forest Health: Its Assessment and Status*. Wallingford, UK: CAB International.

Table 2 Cases of tree and forest declines related to air pollution

Type	*Geographical area*	*Site/region/country*	*Species or forest type involved*
Decline and dieback around pollution sources	Europe	The Rhone valley, Switzerland	*Pinus sylvestris*, *Abies alba*
		San Rossore, Pisa, Italy	*Pinus pinea*
	North America	Copper Basin, Tennessee, USA	*Mixed hardwood forest*
		Redford, Virginia, USA	*Pine forest*
		Spokane-Mead, Washington, USA	*Pinus ponderosa*
		Sudbury, Ontario, Canada	Various vegetation types
Declines related to regional air pollution	Europe	East Germany – North Czech Republic – South Poland	*Norway spruce*
	Latin America	Desierto de Los Leones, Mexico	*Abies religiosa*
	North America	Western USA	*Pinus jeffreyi*
			Pinus ponderosa
			Various other species
Declines with unclear relation to air pollution	Europe	Central and South Europe	*Abies alba*
		Greece	*Abies cepha lonica*
		Southwest Sardinia, Italy	*Pinus pinea*
		North and central Europe	*Picea abies*
		North and central Europe	*Pinus sylvestris*
		The Netherlands	*Pinus sylvestris*, *Pseudostuga menziesii*
	North America	Eastern USA and Canada	*Pinus strobus*
			Fraxinus nigra
			Fraxinus americana
			Betula papyrifera
			Acer saccharum
			various hardwoods
			Pinus sp.
			Abies balsamea
			Picea rubens
			Abies fraseri
		Southeastern USA	*Pinus taeda*
			Pinus echinata
			Pinus elliottii

Source: Data from Innes JL (1993) *Forest Health*: *Its Assessment and Status*. Wallingford, UK: CAB International.

the observed unhealthy condition can be a difficult task. Acute injury on trees is easy to diagnose; on the other hand, nonacute, subtle effects on trees and/or ecosystems can be difficult either to identify in the field or to ascribe to a particular cause. In many cases, different factors may interact (see **Figure 1**); depending on the case, an accurate diagnosis needs careful examination of the various potential causal agents and the use of diagnostic criteria and tests.

Diagnostic criteria Several criteria have been developed that can provide a convenient framework for cause-and-effect research and for diagnostic purposes (**Table 3**). These criteria are based upon traditional human and plant pathology and have been developed further to take into account the complexity of certain situations. For example, the criterion of strong correlation implies that both cause and effects can be identified and measured and this is not always

Table 3 Diagnostic criteria for forest health diagnosis

Koch (1876)	*Committee on Biological Markers of Air Pollution Damage in Trees (1989)*	*Schlaepfer (1992)*
The infecting agent must be present in all patients showing symptoms of disease	Strong correlation	Detection and definition of the problem
The infecting agent must be isolated from the patient	Plausibility of mechanism	Description of magnitude, dynamics, and variability of the phenomenon
The infecting agent must produce the disease under controlled laboratory condition	Responsiveness or experimental replication	Detection of associations in space and time between the symptoms and the hypothetical causes
	Temporality	Experimental reproduction of the observed symptoms
	Weight of evidence	Explanation of mechanism
		Validation of the models

Source: Data from Koch R (1876) Untersuchung über Bacterien, V. Die Aetiologie der Milzbrand-Krankheit, begründet auf die Entwicklungsgeschichte des Bacillus anthractis. *Beitrage zur Biologie Pflanzen* 2: 277–310; Committee on Biological Markers of Air Pollution Damage in Trees (1989) *Biological Markers of Air Pollution Stress and Damage in Forests*. Washington, DC: National Academy Press; Schlaepfer R (1992) *Forest Vegetation and Acidification*: *A Critical Review*. In: Schneider T (ed.) *Acidification Research*: *Evaluation and Policy Applications*, pp. 27–44. Amsterdam, The Netherlands: Elsevier.

possible: the physiologically active dose of an air pollutant (the fraction of the pollutant present in the atmosphere that enters the plant through the stomata) cannot be measured as a routine procedure e.g., during large-scale monitoring. In addition, one must consider that correlation does not necessarily mean causation, and this is the reason for which the other criteria in **Table 3** need to be considered.

Diagnostic procedure for individual trees While a forest is more than the sum of the trees present, the diagnosis at individual tree level remains important for different situations, including commercial plantations and recreational forests. Individual tree diagnosis is supported by a number of textbooks that provide useful identification keys, practical examples, pictorial atlases as well as the approach for a sound diagnostic procedure. Tree-related diagnosis is also related to pathology and entomology (*see* **Entomology**: Bark Beetles; Foliage Feeders in Temperate and Boreal Forests; Sapsuckers. **Pathology**: Diseases affecting Exotic Plantation Species; Diseases of Forest Trees). A suitable diagnostic procedure involves the collection of preliminary information (species identification, site condition, recent tree history) and close examination of the case in hand. A careful examination of the aerial parts of the trees is essential to identify and describe the symptoms and injuries together with the location in relation to existing knowledge about the species being considered. If the case in hand matches the known description, confirmatory evidence is sought and – if found – the diagnosis is achieved, its reliability being dependent on the weight of evidence. If the case in hand does not match existing knowledge, or if no confirmatory evidence is found, additional investigations have to be considered which may involve destructive sampling. In some cases the problem may remain unexplained either because the damage is too old or the evidence is insufficient for a diagnosis.

Diagnostic tests Besides the above criteria and procedure, careful diagnosis may involve the use of diagnostic tests. Biochemical, physiological, and morphological tests are available (see the section on 'Indicators'). With few exceptions, diagnostic tools involve complex sampling procedures and laboratory analysis and can be expensive. This may limit their applicability at the large scale.

Monitoring

Definition Monitoring is a general term to identify a type of study that can be applied to several environmental resources. Monitoring can be defined as 'the systematic observations of parameters related to a specific problem, designed to provide information on the characteristics of the problem and their changes with time.' Emphasis should be placed on the connection between the monitoring and the management of the resource being considered, e.g., the monitoring is carried out to track the progress toward a management objective. The management action can be understood at local level (e.g., thinnings) or at the large scale (e.g., political negotiations to decrease pollutant deposition). Note that the emphasis on management objectives forces the monitoring designer (1) to obtain an unambiguous definition of forest health from stakeholders and (2) to establish clear conceptual and/or mechanistic models to link forest health as defined and the expected management action. These are important as effective monitoring can only be based on explicit assessment and measurement endpoints.

Two important characteristics of monitoring are its time dimension and its nature of routine, systematic and organized activity. This implies monitoring should be based on a careful design, which has to cover a series of issues (**Table 4**).

Monitoring approaches Monitoring can be carried out to obtain information about the status and trend in the spatial and temporal development of forest health over a defined spatial and temporal domain, and for cause-and-effect investigations. Forest health monitoring can be of value also in the framework of before-and-after studies but in this case it needs to be placed in the context of an experimental design.

Status and trend (extensive studies) In general, the assessment and monitoring for status and trend of forest health is carried out on regional populations of forests, with regions being small (e.g., local, subnational scale) or large (e.g., national, international scale). At the stand level, assessment of status and trend can be necessary for economically important forests and it was carried out for example in commercial pine plantations in the southeastern USA, and *Acer saccharum* forests (syrup production) in southeast Canada and the northeastern USA. In such cases, careful diagnostic approaches and specific indicators are essential. At the large scale, status and trend investigations usually concentrate on a few, easy to measure, low-cost, and sometime simplistic indicators that are measured at many sites by trained observers. However, as many observers are needed for this type of survey, their skill in forest pathology and entomology may be not always high, and – together with the indicators used and the limited time available for site visits – this can have consequences for the quality of the results. In many cases, a careful diagnosis cannot be carried out, and causes of poor forest health may remain unexplained unless the observed phenomenon is very obvious. This clearly indicates that – in most cases – large-scale monitoring programs have a role as detection monitoring, to identify problems to be investigated in more detail at a later stage. In this respect, integration between a survey approach (e.g., terrestrial and aerial surveys) and extensive and intensive studies can provide a number of benefits for detecting, diagnosing, and monitoring health problems. Status and trend surveys must allow inferences on a statistical basis. False-positive (Type I) and false-negative (Type II) errors as well as sufficient precision of the estimates of population parameters must be considered, and a statistically based sampling design is essential to ensure the success of status and trend monitoring.

Cause-and-effect (intensive studies) Cause-and-effect investigations aim to establish a relationship between stressors(s) and response(s). In the field stressors are difficult to isolate from other factors that need to be accounted for. For this reason, cause-and-effect investigations require data about a number of variables, usually referred to as stressor (independent variables, or predictors, in a statistical model), response (dependent variables), and intermediate (covariates) variables. Cause-and-effect investigations can be very expensive and usually are carried out on a limited number of selected sites. In general, sites for intensive studies are selected purposively, according to the hypothesis being tested and/or the scenario of concern (e.g., plots along gradients of pollution, age, or succession). Under some circumstances, plots can be installed as case studies: this can occur to study the effects of extreme/catastrophic events that may offer the chance for studies otherwise impossible. Although sites for cause-and-effect studies are selected on a preferential basis (thus prohibiting statistical inference), observations and measurements within sites should always be based on a sampling design.

Indicators of forest health An indicator is a characteristic that can be measured or assessed to estimate status and trends of the target environmental resource. A number of indicators can be used in forest health monitoring and the choice of the most suited ones depends on the problem being examined, the available resources, the available expertise, and the

Table 4 Design issues for a forest health monitoring program

Design issue	*Areas of concern*
Definition of the scientific problem	Users' needs and clear questions for the designers
Sampling design	Formal definition of nature, iteration, selection, and number of (sub)samples; inferences
Quality assurance	Standard methods with known performances; data reproducibility and consistency
Field and laboratory work (when needed)	Safe procedures and logistics
Data management/analysis/reporting	Proper data management, accessibility, data analysis and reporting

ecological, spatial, and temporal coverage of the investigation. Indicators can be considered according to their nature (e.g., stress, response), ecosystem compartment (e.g., atmosphere, vegetation, soil), platform used (terrestrial, aerial, satellite), and method of detection (from visual assessment in the field to biochemical analysis in the laboratory). An overview of indicators most frequently adopted in forest health monitoring programs is given in **Table 5**.

It is notable that **Table 5** does not cover the zoological component of the ecosystem which is important but which is very seldomly covered in forest health monitoring. This reflects both the 'old,' tree-oriented, concept of forest health and the difference between the spatial scales used in typical forest studies (mostly based on a plot size of less than 1 ha) and those needed for e.g., bird investigations (typically more than 30 ha). Recent emphasis on

Table 5 Most common indicator categories and measurement methods

Area	*Compartment*	*Indicator category*	*Type of measurement*
Atmosphere	Air	Meteorological parameters	Instruments in the field
		Concentration of chemicals	Instruments in the field
	Wet deposition	Quantity	Instruments in the field
		Concentration of chemicals	Instruments in the field and laboratory
	Dry deposition	Quantity	Instruments in the field and laboratory
		Concentration of chemicals	Instruments in the field and laboratory
Vegetation	Trees	Species	Direct observation
		Abundance	Direct observation, inventory, remote sensing
		Diameter at breast height	Direct measurement
		Height	Direct measurement
		Tree rings	Measurement in laboratory
		Crown condition	Direct observation, remote sensing
		Chemical indicators	Instruments in laboratory
		Biochemical indicators	Instruments in laboratory
		Physiological indicators	Instruments in the field and laboratory
		Physical indicators	Instruments in the field and laboratory
		Stem condition	Direct observation
		Root condition	Instruments in the field and laboratory
		Litter fall, quantity and chemistry	Instruments in the field and laboratory
	Herbs, shrubs	Species	Direct observation
		Abundance	Direct observation
		Chemical indicators	Instruments in laboratory
		Biochemical indicators	Instruments in laboratory
	Ferns, lichens, mosses	Species	Direct observation
		Abundance	Direct observation
		Chemical indicators	Instruments in laboratory
	Fungi	Species	Direct observation
		Abundance	Direct observation
		Chemical indicators	Instruments in laboratory
Soil	Solid phase	Physical properties	Instruments in the field and laboratory
		Chemical indicators	Instruments in the field and laboratory
		Biological activity	Instruments in the field and laboratory
	Soil water	Physical properties	Instruments in the field and laboratory
		Chemical indicators	Instruments in the field and laboratory
		Biological activity	Instruments in the field and laboratory
Water	Groundwater	Chemical indicators	Instruments in the field and laboratory
	Runoff water	Chemical indicators	Instruments in the field and laboratory
	Lakes	Chemical indicators	Instruments in the field and laboratory
		Biological indicators	Instruments in the field and laboratory
	Streams	Chemical indicators	Instruments in the field and laboratory
		Biological indicators	Instruments in the field and laboratory
		Biological activity	Instruments in the field and laboratory

Source: Data from Innes JL (1993) *Forest Health*: *Its Assessment and Status*. Wallingford, UK: CAB International; Bundesforschungsanstalt für Forst – und Holzwirtshaft (ed.) (1998) *Manual on Methods and Criteria for Harmonized Sampling*, *Assessment*, *Monitoring and Analysis of the Effects of Air Pollution on Forests*. Hamburg, Germany: BFH; D'Eon SP, Magasi LP, Lachance D, and DesRoches P (1994) *Canada's National Forest Health Monitoring Plot Network*: *Manual on Plot Establishment and Monitoring*. Petawawa, Canada: Canadian Forest Services; Olson RK, Binkley D, and Böhm M (eds) (1992) *The Response of Western Forests to Air Pollution*. Ecological Studies no. 97. Berlin: Springer-Verlag; Tallent-Halsell NG (1994) *Forest Health Monitoring 1994*: *Field Methods Guide*. EPA/620/R-94/027. Washington, DC: US Environmental Protection Agency.

forest ecosystem health and the role of biodiversity to promote sustainable forest management has led to a reconsideration of this approach, and now soil biota, rodents, birds, butterflies, and small and large mammals are increasingly considered.

Terrestrial investigations

1. Visual indicators of tree condition consider the appearance of plant organs, in general foliage, reproductive structures, branches (often as a single unit, the crown), and stem. The roots are usually difficult to examine as routine indicators, but are of interest in in-depth cause-and-effect research. The examination of the various organs usually considers the frequency and intensity of symptoms as well as their cause, when possible. In the case of reproductive structures, the timing and abundance of flowering and fruiting are important. **Table 6** reports a list of indicators used in forest health surveys in Europe and North America. Since visual indicators are based on visual estimates they are prone to observer bias, and this needs to be taken into account with adequate Quality Assurance programs (see below).
2. Quantitative measurements of leaf/needle biomass and needle retention can include systematic collection of litter by litter traps, direct measurement of leaf area index (LAI), the identification of needle traces from branches and stems, and the analysis of digital images of crown condition. All these methods are useful as they provide objective data respectively on primary productivity, past needle retention, and crown condition. However,

Table 6 Indicators of tree condition considered in forest health monitoring programs in North America and Europe

Canada ARNEWS	*US FHM*	*Europe: UN/ECE ICP Forests*	
		Level I	*Level II*
Abiotic foliage symptoms – level	Catastrophic mortality	Crown defoliation	Crown defoliation
Abiotic foliage symptoms – type	Crown density	Crown discoloration	Crown defoliation type
Bare top height	Crown diameter	Damage category	Crown discoloration – age foliage affected
Crown closure	Crown dieback		Crown discoloration – color
Crown condition	Damage category (type)		Crown discoloration – location
Current foliage missing	Damage location		Crown discoloration – nature
Diameter at breast height	Damage severity		Crown discoloration – type
Dominance	Damage/cause of death		Crown morphology
Foliage damage – disease	Diameter at breast height		Crown shading
Foliage damage – insects	Foliage transparency		Damage to leaves/needles – extent
Height to top of live crown	Height		Damage to leaves/needles – type
Height to base of live crown	Live crown ratio		Damage to the branches – location
Needle retention	Social class		Damage to the branches – type
Seed	Tree age		Damage to the stem – location
Stem form	Tree age at diameter at breast height		Damage to the stem – type
Storm damage			Deformation of foliage – extent
Total height	Tree history		Deformation of foliage – type
Woody tissue damage – disease			Diameter at breast height
Woody tissue damage – insects			Dieback/shoot death – extent
Wood tissue damage – other			Dieback/shoot death – type
			Epiphytes
			Flowering
			Foliage size
			Foliage transparency
			Fruiting
			Height
			Removals and mortality
			Social class

ARNEWS, Acid Rain National Early Warning System; FHM, Forest Health Monitoring.
Source: Data from Innes JL (1993) *Forest Health: Its Assessment and Status*. Wallingford, UK: CAB International; Bundesforschungsanstalt für Forst – und Holzwirtshaft (ed.) (1998) *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*. Hamburg, Germany: BFH; D'Eon SP, Magasi LP, Lachance D, and DesRoches P (1994) *Canada's National Forest Health Monitoring Plot Network: Manual on Plot Establishment and Monitoring*. Petawawa, Canada: Canadian Forest Services; Olson RK, Binkley D, and Böhm M (eds) (1992) *The Response of Western Forests to Air Pollution*. Ecological Studies no. 97. Berlin: Springer-Verlag; Tallent-Halsell NG (1994) *Forest Health Monitoring 1994: Field Methods Guide*. EPA/620/R-94/027. Washington, DC: US Environmental Protection Agency.

their application is usually limited at intensively monitored sites because of technical and operational difficulties and costs.

3. A number of nonvisual indicators are available to assess tree health (**Table 7**). Most of them require time and appropriate equipment and can hardly be incorporated in large-scale surveys. Rather, many of them are attractive for intensive studies and cause-and-effect research.
4. Indicators for ecosystem-level health assessment. Ecosystem-level health assessment goes beyond the health of individual components: individual trees may die from insect attack but the ecosystem can still be healthy. The reverse is also true: for example, nitrogen deposition may substantially affect the nutrient balance of the system. This may affect species composition and diversity, population and community dynamics, herbivores' behavior, soil biota, soil water, and runoff quality without necessarily killing trees. In general terms, health assessment at the ecosystem level needs to consider resilience, vigor, and organization of the ecosystem as well as the presence of stressors that may exceed the tolerance limit of the system (see below). Resilience, vigor, and organization can be interpreted in operational terms as diversity, integrity of the physical, biotic, and trophic networks, productivity, equilibrium between demand and supply of essential resources, resistance to catastrophic change, and ability to recover. Also, the occurrence of endangered species has to be considered. To measure these characteristics, a number of proxies have been adopted, most of them being already listed in **Table 5**. Indicators such as birds and various other groups of taxa (e.g., rodents, small and large mammals) would be a useful complement. References and methods for ecosystem-level studies and monitoring are available, covering carbon and energy dynamics (above-and belowground primary production estimation from global to local levels), nutrient and water dynamics, and manipulative experiments.

Remote sensing Remote sensing is mostly based on analysis of imagery that can be collected from aircraft or from satellites; it includes aerial photographs, airborne or spaceborne multispectral scanner recordings, and radar recordings. Applications can be relevant at a variety of spatial scales, from local ($>1:25\,000$) to global ($<1:2\,50\,000$). It is important to acknowledge that different scales require different platforms and sensors: for example, satellites NOAA-AVHHR are the most used at the global scale, while sensors like the Landsat Thematic Mapper (TM), SPOT HRV/Xs, and IRS-1C/LISS are used at the regional scale. However, technical progress is rapid in this respect.

Remote sensing by aerial photographs can provide valuable information concerning yellowing, crown density, and mortality. In this respect, color-infrared (CIR) imagery is believed to provide more useful information than black-and-white imagery, although

Table 7 Possible nonvisual indicators of tree condition

Morphology and histology	*Biochemistry*	*Physiology*
Cellular structure	Biochemical substances	Photosynthesis
Foliage surface properties	Myo-inositol	Respiration
Tree rings	Detoxification systems	Transport and allocation of photosynthate
	Peroxidase activity	Assimilate level
	Superoxide dismutase	Assimilate transport
	α-Tocopherol	Transpiration
	Ascorbic acid	
	Glutathione	
	Enzyme and amino acids	
	Arginine, hystadine, tryptophan, and putrescine	
	Glutamic acid, aspartic acid, glutamine, and asparagine	
	Adenine nucleotides and pyridine nucleotides	
	pH of foliar substances	
	Fatty acid composition	
	Protoplast composition	
	Electrical conductance	
	Foliar pigment concentration	
	Mineral nutrition	
	Tree ring chemistry	
	Needle wax chemistry	

Source: Data from Innes JL (1993) *Forest Health: Its Assessment and Status*. Wallingford, UK: CAB International.

it seems less valuable when damage differentiation is not clear. A more sophisticated and expensive technique is based on multispectral imagery; it is based on the spectral characteristics of the green vegetation (pigment absorption in 0.4–0.7 μm range) whose changes can be related to changes in chlorophyll-*b* content. In the past, the resolution of satellite imagery was insufficient to detect the condition of individual trees, and applications were mostly useful to provide information about insect and fungal problems over large forest areas. However, recent technical progress and the use in combination of geographic information systems (GIS) and Landsat TM data make it possible to identify site susceptibility to insect attacks as well as to detect attacks on individual trees. An example is the identification of mountain pine beetle (*Dendroctonus ponderosae*) attacks on lodgepole pine (*Pinus contorta* var. *murrayana*) in various districts of British Columbia, Canada. These data are used to inform forest management and this is a valuable advance. Remote sensing and its application to forest monitoring are undergoing rapid evolution. Applications are now available in many fields related to forest health, including forest biodiversity, structural parameters, productivity, and carbon and chemical content of the foliage. For example, studies of ecosystem gross and net primary production (GPP and NPP, respectively) at the global scale received great benefits from recently improved remote sensing from the Earth Observing System. Implications for estimates of forest growth, seasonal dynamics of CO_2 balance for global carbon cycles studies and thus for important political and economic questions are obvious. From the monitoring point of view, advantages of using imagery include the opportunity to keep a permanent record of the forest under investigation and the possibility of adapting the sampling design and the sample size for imagery-based studies according to the investigation being undertaken. Disadvantages include the impossibility of making a careful diagnosis, and the difficulty of recognizing detailed symptoms and obvious damaging agents; in addition, assessment is made using a coarser method. Subjectivity is not completely solved, although it does not seem to be a major problem since images taken at different years can be rescored by the same interpreter.

Quality assurance An important part of any monitoring programme is quality assurance (QA). QA is a key issue for investigations aiming to generate representative results at the large scale (national, international) and in the long term, as it aims to improve the consistency, reliability, and cost-effectiveness of the program through time. QA is a systematic, formally organized series of activities that defines the way in which tasks are to be performed to ensure an expressed level of quality. The QA program ensures (1) proper design of the monitoring and its documentation, (2) the preparation, use, and documentation of standard operating procedures (SOPs), (3) the training of field crews, ring tests between laboratories, calibration and control phases, and (4) the formal, statistical evaluation of data quality.

Data management Data management (i.e., storage, evaluation, accessibility) is an increasingly important issue and can even determine the success or the failure of the monitoring program; it should be carefully planned at the early stage of the monitoring design. A data management plan should be prepared with details about (1) needs and goals, (2) available computer resources (hardware, software, protection, maintenance), (3) data resources (nonspatial data and GIS resources, data load, data standards, database design and file formats, metadata), (4) human resources, (5) data management strategies (data acquisition, QA/quality control data maintenance, legacy data, data security, data archives and storage, data applications, data dissemination), and (6) implementation.

Evaluation

Evaluation approaches and limitations Evaluation of data generated by forest health monitoring is usually driven by the monitoring approach adopted, the technique used, and the indicator adopted. Usually, data are evaluated in order to identify spatial and/or temporal trends and/or to identify cause-and-effect relationships. Data analysis is subjected to the nature and properties of the data (determined by the sampling design adopted, the metric of the indicator used, and by the frequency distribution of the observations), the comparability of the data (both in space and time) and by the reference adopted, i.e., the definition of what is to be considered 'healthy' or 'normal.' While the data issues can be managed from a technical point of view, the question about 'health' thresholds is controversial. For example, the classification adopted by the UN/ECE program in Europe identifies 25% crown defoliation as a threshold for damage. The 25% threshold was set to indicate a sort of 'no – return' limit, i.e., a tree whose defoliation exceeded that limit would have no chance to recover. This is now demonstrated to be untrue and cases of rapid recovery have been reported.

Uncertainty in health thresholds occurs because stressors may affect forests with different intensity and frequency. For example, herbivores are usually present on the foliage of trees. Yet their action affects the health of the trees only when they exceed some tolerance limit. Therefore, a first information need is to know this limit. In addition, tolerance limits may be exceeded cyclically and this can be seen as an integral part of the ecosystem dynamics. Thus, a second information need is to know the historical frequency of the insect infestation. It implies that an indicator of forest health has a range of natural and historical variation: if such a range is known, then it would be possible to establish thresholds that can be used as diagnostic tools. Recognizing the inherent variation of the potential stressor has a clear importance for evaluating the health of a given forest.

Evaluation methods Evaluation methods include various statistical and geostatistical approaches and are subjected to the same data limitations reported for the evaluation approach. Several references exist that may help in making decisions about most appropriate statistical analysis. When status and trend monitoring is concerned, data processing should provide summaries of descriptive statistics (e.g., totals, descriptors of central tendency, descriptors of frequency distribution), estimates of population parameters (e.g., estimates of population means, totals, and proportions), comparison between two subsequent sampling occasions (with statistical tests), and comparison between sites/group of sites (with statistical tests). It is important to remember that both parametric and nonparametric statistics need sampling to be based on random elements. Similarly, decisions about the most suitable statistical test should be based on the metric of the indicator used and the frequency distribution of the observations. Association and relationship between indicators can be explored by means of various univariate and multivariate statistical analyses. In the case of large-scale, long-term monitoring the use of models to incorporate the effects of covariates (e.g., the age of the trees or the effect of difference in methods) and for mapping purposes is essential.

In the case of cause-and-effect monitoring, relationships between indicators of for example, tree condition and indicator of stress (e.g., drought indices, pollutant deposition) are usually investigated by means of various multivariate techniques (e.g., discriminant analysis, ordination techniques, factor analysis, multiple regression). Recent work has focused on multiple regression techniques that may allow the quantification of the proportion of the variance of a response (dependent) variable (e.g., tree crown defoliation) explained by various predictors (independent variables).

Relevance and Applications of Forest Health Monitoring

Relevance

Forest health monitoring programs have potential in many respects. While they were started in relation to air pollution and within that framework as a contribution to international conventions and legal mandates, now the area for application is much broader. A first advance was to place more emphasis on traditional damaging agents. More recently, forest health monitoring has been included in program related to issues such as biodiversity, carbon sequestration, long-term ecological research, and international processes dealing with SFM and long-term resource management. For the above reasons, forest health diagnosis, monitoring, and evaluation is an area of concern for politicians, decision-makers, resource managers, and scientists as well as for the public. In this perspective, progress towards integration between monitoring networks with different topics (e.g., freshwater and forests) and scale of interests (local, regional, global) can provide a considerable added value.

Forest Health Monitoring Programs

Forest health monitoring is carried out at a variety of geographical scales, from local to international. Initial development occurred in Europe and North America, where comprehensive monitoring programs were developed (**Table 8**).

Monitoring Results: Examples

The data collected by monitoring programs provided insight into different topics. Examples may include the documentation of (1) changes in tree condition, (2) the incidence of pests on forest health, and (3) the role of various natural and anthropogenic factors that may affect forest health.

Changes in tree condition The collection of data about tree condition in Europe revealed that complex patterns could occur both in space and time. The development of the condition of trees varies with the species and the region being considered. **Figure 2** shows an example related to Scots pine (*Pinus sylvestris*) in Europe. As with many environmental variables, the frequency of trees with more than 25% defoliation changes through time; it fluctuates in the Mediterranean region (rapid increase and decrease), while the trend is different for the North Atlantic

Table 8 Forest monitoring programs in Europe and North America

Program feature	*Europe EC and UN/ECE ICP Forests*	*North America*	
		Canada ARNEWS	*USA FHM*
Aims	To monitor the effects of anthropogenic factors (in particular air pollution) and natural stress factors on the condition and development of forest ecosystems in Europe and to contribute to a better understanding of cause-effect relationships in forest ecosystem functioning in various parts of Europe	Early recognition of air pollution damage to Canada's forests and to monitor changes in forest vegetation and soils caused by pollutants	Determine the status, changes, and trends in indicators of forest condition on annual basis
Structure	Different monitoring intensity levels: Level I (less intensive) Level II (more intensive)	Connected with other terrestrial survey	Different monitoring intensity levels (Detection Monitoring – DM: less intensive; Intensive Site Ecosystem Monitoring – ISEM: more intensive). Connected with aerial and other terrestrial survey.
Plot selection	Systematic grid (Level I); purposive (Level II)	Purposive	Systematic grid (DM); Purposive (ISEM)
No. of plots	C. 5900 Level I; C. 850 Level II	150	C. 4000 (DM); 21 (ISEM)
Coverage	30 countries	National	National (C. 34 conterminous USA plus Alaska)
Started in	1986 (Level I); 1995 (Level II)	1984	1990 (DM)

Source: Data from Bundesforschungsanstalt für Forst- und Holzwirtshaft (ed.) (1998) *Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests*. Hamburg, Germany: BFH; McLaughlin S and Percy K (1999) Forest health in North America: some perspectives on actual and potential roles of climate and air pollution. In: Sheppard LJ and Cape JN (eds) (1999) *Forest Growth Responses to the Pollution Climate of the 21st Century*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

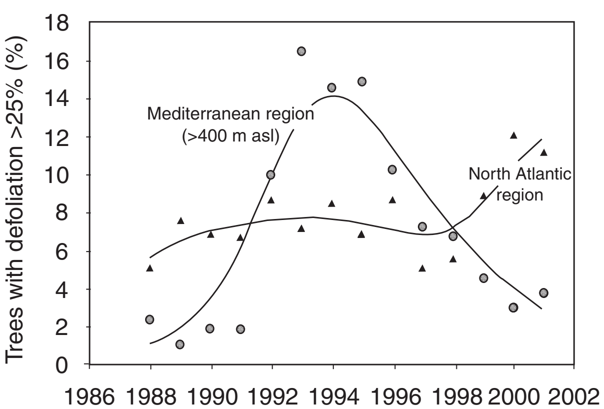


Figure 2 Frequency of Scots pine (*Pinus sylvestris*) trees considered damaged (defoliation over 25%) over the period 1988–2001. Based on data by EC and UN/ECE (2002) *Forest Condition in Europe. Results of the 2002 Large-scale Survey*. Geneva and Brussels: UNECE and EC.

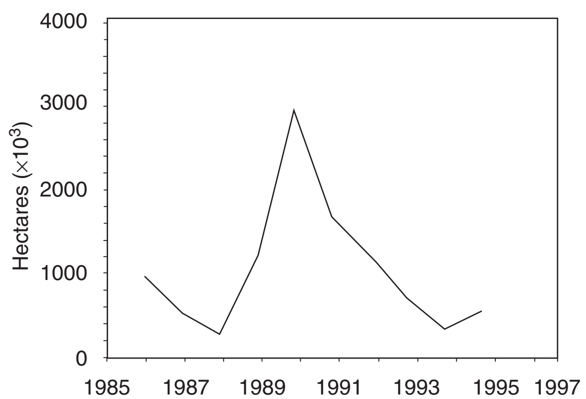


Figure 3 Area with aerially detected defoliation by gypsy moth (*Lymantria dispar*) in the USA over the period 1986–1995. Based on data by Forest Insect and Disease Condition in the US Report 1986–1995.

region, where an increase of defoliated trees was obvious only in the years 2000–2001. The interpretation of this as a directional trend needs caution, as the previous example clearly shows that it may be reversed in a few years.

Assuming that data are comparable through time and space, the data in **Figure 2** confirmed that no general decline in the health of forest was occurring: rather, the dynamics seem to be specific for individual species at certain sites or group of sites.

Incidence of pests The changes in the severity of an insect's action is exemplified by the aerial survey in the USA (**Figure 3**) which shows remarkable

Table 9 Significant predictors of defoliation and foliar concentration of nitrogen (N) and sulfur (S) in *Picea abies* and *Fagus sylvatica* in Europe

Predictor	*Response*					
	Defoliation		*Foliar N concentration*		*Foliar S concentration*	
	Picea abies	Fagus sylvatica	Picea abies	Fagus sylvatica	Picea abies	Fagus sylvatica
Soil type	–					
Stand age	+	+	–		–	
Altitude			+		+	
Precipitation	–			+		+
Air temperature		–				
Deposition of nitrogen	–		+		n.e.	n.e.
Deposition of sulfur	+		n.e.	n.e.	+	+

+, Positve correlation; –, negative correlation. n.e., not examined.
Source: Data from EC-UN/ECE (2000) *Intensive Monitoring of Forest Ecosystems in Europe*. Brussels: UN/ECE.

variation in gypsy moth (*Lymantria dispar*) defoliation over the period 1986–1995.

Role of various natural and anthropogenic factors Data collected at the intensive monitoring sites in Europe indicate that, at many plots, the present deposition of acidifying compounds may exceed the critical load for the impact on soil; excess occurs at 45%, 65%, and 80% of sites for pine (mostly Scots pine, $n = 57$), spruce (mostly *Picea abies*, $n = 96$), and beech (mostly *Fagus sylvatica*, $n = 42$). However, the statistical studies carried out so far have confirmed that natural factors have the major role in determining forest condition at the sites concerned. Statistically significant effects of nitrogen and sulfur deposition were also detected although their role is less clear in size and direction (**Table 9**).

See also: **Biodiversity**: Biodiversity in Forests; Endangered Species of Trees. **Environment**: Impacts of Air Pollution on Forest Ecosystems; Impacts of Elevated CO_2 and Climate Change. **Experimental Methods and Analysis**: Design, Performance and Evaluation of Experiments; Statistical Methods (Mathematics and Computers). **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Hydrology**: Impacts of Forest Management on Water Quality. **Inventory**: Forest Inventory and Monitoring; Large-scale Forest Inventory and Scenario Modeling. **Resource Assessment**: GIS and Remote Sensing; **Sustainable Forest Management**: Overview; **Tree Physiology**: Mycorrhizae; Nutritional Physiology of Trees; Stress.

Further Reading

Ciesla WM and Donabauer E (1994) *Decline and Dieback of Trees and Forests: A Global Overview*. Rome: Food and Agriculture Organization.

Edmonds RL, Agee JK, and Gara RI (2000) *Forest Health and Protection*. Boston, MA: McGraw-Hill.

Elzinga CL, Salzer DW, Willoughby JW, and Gibbs JP (2001) *Monitoring Plant and Animal Populations*. Oxford, UK: Blackwell Science.

Huettl R F, and Mueller-Dombois D (eds) (1993). *Forest Decline in the Atlantic and Pacific Regions*. Berlin: Springer-Verlag.

Innes JL (1993) *Forest Health: Its Assessment and Status*. Wallingford, UK: CAB International.

Innes JL and Haron AH (eds) (2000) *Air Pollution and the Forests of Developing and Rapidly Industrializing Countries*. IUFRO Research Series no. 4. Wallingford, UK: CAB International.

Innes JL and Oleksyn J (eds) (2000) *Forest Dynamics in Heavily Polluted Regions*. IUFRO Research Series no. 1. Wallingford, UK: CAB International.

Manion PD and Lachance D (eds) (1992) *Forest Decline Concepts*. St Paul, MN: American Phytopathological Society.

Olson RK, Binkley D, and Böhm M (eds) (1992) *The Response of Western Forests to Air Pollution*. Ecological Studies no. 97. Berlin: Springer-Verlag.

Pankhurst CE, Doube BM, and Gupta VVSR (1997) *Biological Indicators of Soil Health*. Wallingford, UK: CAB International.

Sala OE, Jackson RB, Mooney HA, and Howarth RW (eds) (2000) *Methods in Ecosystem Science*. New York: Springer-Verlag.

Schlaepfer R (ed) (1993) *Long Term Implications of Climate Change and Air Pollution on Forest Ecosystems*. Progress report of the IUFRO Task Force 'Forest, Climate Change and Air Pollution.' Vienna: IUFRO.

Sheppard LJ and Cape JN (eds) (1999) *Forest Growth Responses to the Pollution Climate of the 21st Century*. Water, Air, and Soil Pollution no. 116. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Spellerberg IF (1994) *Monitoring Ecological Change*. Cambridge, UK: Cambridge University Press.

Spiecker H, Mielikäinen K, Köhl M, and Skovsgaard JP (eds) (1996) *Growth Trends in European Forests*. European Forest Institute Research Report no. 5. Berlin: Springer-Verlag.

Strouts RG and Winter TG (1994) *Diagnosis of Ill-Health in Trees*. London: HMSO.
Wulder MA, and Franklin SE (eds) (2003) *Remote Sensing of Forest Environments: Concepts and Case Studies*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Biochemical and Physiological Aspects

R Ceulemans, University of Antwerp, Wilrijk, Belgium

Introduction

Forest ecosystems fulfill various functions with economic, social, and ecological significance. They also form habitat for various species of plants and animals. However, forest ecosystems are exposed to serious threats from attacks by parasites and diseases, from air pollution, fires, and climatic changes. As forests are sensitive ecosystems, they are susceptible to these disturbances, whether caused by biotic or abiotic influences. These biotic and abiotic influences could be of natural origin (such as fires, insect or pathogen attacks, and species invasion) or anthropogenically caused (such as air and soil pollution, global climatic changes, and fragmentation). In this article some physiological and biochemical aspects of tree responses and forest health will be reviewed. The contribution is focused on air pollution (in particular ozone) and climate change (in particular elevated atmospheric CO_2 concentrations) and how these relate to forest health. These two issues provide a good basis for understanding the links between biochemistry and physiology and forest health. So, the contribution is restricted to these two stress factors as they are used as examples of how trees respond to external stresses.

With regard to air pollution, various atmospheric pollutants might affect tree growth and forest health such as nitrogen dioxide (NO_2), nitrogen oxides (NO_x), ozone (O_3), sulfur dioxide (SO_2), hydrofluoride (HF_6), and hydrocarbons (such as CH_4). Air pollution can change the physical and chemical environment of forest trees. Pollutant stresses, as well as competitional, climatic and biological stresses, have important implications for forest growth and ecosystem succession because they provide forces that favor some genotypes, affect others adversely, and eliminate sensitive species that lack genetic diversity. Pollutant stresses in a forest ecosystem are superimposed upon and interact with the naturally occurring stresses that trees are already experiencing. These additional stresses can accelerate the processes of change already underway within ecosystems.

Forests and the human uses of forests and forest products have an impact on greenhouse gas concentrations in the atmosphere. There is a feedback from the climate system where forests are affected by the changes in climate, and the chemical composition of the atmosphere. Forest ecosystems and wood-based products also have the ability to sequester atmospheric CO_2 and thus offer an opportunity to mitigate climate change. However, this balance must be correctly understood, quantified, and modeled if we wish to assess the potential of forests to regulate sudden climatic changes, to improve the reliability predictions, and to reduce the uncertainty of the consequences of climatic change on forest health and forest ecosystems. As photosynthesis is the key process that all autotrophic organisms (trees, green plants, and algae) use to exchange mass and energy with the environment, this process will first be briefly reviewed.

Photosynthesis and the Importance of Nitrogen

Photosynthesis is the principal process to perform two essential transformation processes – on the one hand the conversion of high-quantity solar energy into high-quality chemically fixed energy, and on the other hand the conversion of simple inorganic molecules (CO_2, H_2O) into more complex organic molecules (sugars and carbohydrates). The harvestable product of a tree, generally the stem, depends not only on photosynthetic carbon uptake by the foliage, but also on respiration of the various organs and carbon investments into renewable organs (leaves, fine roots) and generally nonharvested organs (branches and large roots). Consequently, there is no obvious relationship between photosynthesis and wood production. A fast-growing tree generally needs high photosynthesis, but the reverse is not necessarily true. When growth is related to total net photosynthesis integrated over the entire growing season and the total light intercepting leaf area, positive relations are generally obtained. However, photosynthesis remains the principal physiological process that also closely reflects the response of a tree to abiotic or biotic disturbances.

Abiotic factors such as light, temperature, CO_2 concentration, vapor pressure deficit, and nutrient status, but also air pollution, climatic changes, and drought, have a major effect on net photosynthesis, and thus on tree growth and productivity. All environmental conditions that tend to reduce the photosynthetic rate (including low light, low temperature, low nutrient availability, and high air pollution levels) reduce the photosynthetic carbon gain. Plant water status and ozone level, for example, influence the carbon relations of a tree at the gas exchange and growth levels. Low nutrient uptake reduces the amount of nutrients available for incorporation into new living biomass. In particular, a shortage of phosphorus and nitrogen severely affects the photosynthetic capacity. In addition, the partitioning of carbohydrates will favor construction of a larger root biomass for nutrient uptake. All tree species appear to have a large degree of adaptability to the climatic conditions of their habitat at the photosynthesis level.

Nitrogen is required by trees (and all other plants) in large amounts. To a large extent, it governs the use of phosphorus, potassium, sulfur, and other nutrients. Approximately 75% of the nitrogen in a plant leaf is required for the photosynthetic machinery. In natural ecosystems, such as most forests, nitrogen is usually a growth-limiting factor. In mature forests, however, nitrogen demand can be low. Changes in the nitrogen supply of an ecosystem can have a considerable impact on its nutrient balance. Nitrogen saturation can mean that some other resource such as carbon, phosphorus or water, for example, rather than nitrogen, becomes the growth-limiting factor. There are pronounced differences in nitrogen content and in photosynthetic capacity per unit of nitrogen among tree leaves grown under different conditions of light (both quantity and quality), of soil nutrient content, and of atmospheric composition (CO_2 level, ozone concentration). Specific leaf area (i.e., the ratio of leaf area to leaf dry mass), nitrogen content, and photosynthetic quantum efficiency differ significantly among leaves grown under these various conditions.

Tree Responses to Air Pollution

General Effects of Air Pollution on Forest Health

The degree to which vital tree functions are affected by pollutants and the extent to which visible damage can be detected depend on many factors, both biotic and abiotic. The most important of these factors are the species, age, growth form, developmental phase, and general vigor of the plant, climatic and edaphic conditions, but also the chemical nature, concentration, time, and duration of action of the different pollutants. Air pollutants can act on trees in both chronic and acute ways. In several cases the effects of pollution are proportional to the product of the concentration of the air pollutants and the duration of exposure, but the relationship is only linear over a certain range. The lower limit of this range is set by the concentration threshold, below which there are no observable changes, even after prolonged exposure to pollution. At the upper limit of the range, i.e., when a certain high concentration is exceeded, even very brief exposures cause damage. The effect of pollutants also depends on the time of day when their concentrations are highest. Peak concentrations of atmospheric pollutions occurring before noon, when the stomata are usually fully open, are more harmful than if they occur during the night. On the other hand, if the trees have only been exposed to toxic fumigations (e.g., photooxidants) for a few hours during the day, the night can be a time for recovery.

The symptoms of damage are varied and usually nonspecific. The same pollutant may generate quite different effects in different species and, on the other hand, the same symptom may be produced by several different pollutants. The nature and intensity of damage caused by individual pollutants are modified by all other simultaneously active environmental and stress factors. Trees subjected to pollution suffer greater damage from drought and frost than healthy trees. Criteria for early warning of incipient pollution damage are: disturbances in photosynthesis and modified response of stomata, accumulation of pollutants in the tree, reduction of buffering capacity of tissues, reduced or enhanced activity of enzymes, appearance of stress hormones (especially ethylene), and increase or decrease of respiration activity. However, in order to evaluate a stress situation, conclusions cannot be drawn from certain symptoms alone, but response patterns based on more than one criterion should rather be considered.

Acute damages appear as erosions of epicuticular waxes on the surface of leaves or needles, e.g., as a consequence of acid effects; other acute damages due to toxic effects are chlorophyll leaching, discoloration of leaves, necrosis of tissue, dieback of shoots, or dying of the whole plant. Generally, damage of this kind only occurs in the immediate vicinity of the pollution source. Spatially restricted forest damage caused by inputs of high concentrations of sulfur dioxide (SO_2) and halogenides in the vicinity of smelting works and industrial plants is well known. On a larger scale, a decline in growth vigor and severe damage were observed in spruce forests of central Europe at the beginning of the 1970s. Supposedly, the far-reaching air pollution of sulfuric gases and the associated soil acidification due to depositions in those days were the main cause of the damage. Chronic damage leads to reduced productivity and defective fertility (e.g., pollen sterility). In trees, growth, especially cambial growth, decreases. Based on changes in the structure of the wood and on the analysis of annual tree rings, the progressive pollution injury can be tracked and dated. As a particular example the physiological and biochemical responses of trees to one specific air pollutant (ozone) will be reviewed and summarized.

The Impact of Ozone

Ozone (O_3) is formed by photodissociation of molar oxygen and by electrical discharges. Like other air pollutants, ozone can act on trees in both chronic and acute ways. In the latter case, episodes of short duration (e.g., half an hour) and rather high O_3 concentration (100 to above $200\,nl\,l^{-1}$) may cause sudden and irreversible, physiological and macroscopic injury. The proposed initial event is membrane destruction. Depending on the location and climate, such O_3 episodes may be rare events. However, at many sites in the northern hemisphere, the mean seasonal O_3 exposure over a long period is significantly enhanced above the preindustrial level. This type of ozone impact is termed chronic. Tree responses to chronic exposure can distinctly differ from those to acute impact, even though the accumulating O_3 doses may be similar. Contrasting with acute effects, responses to chronic impact may reflect acclimatization, i.e., metabolic regulation, to ozone stress, including enhanced defense and repair capacities, but also endogenous burst induction. Also, such effects may eventually become irreversible. Under most field scenarios, chronic rather than acute ozone regimes appear to be ecologically meaningful for the long-term development of trees. Therefore, experiments that have employed acute O_3 regimes may have little relevance for interpreting plant performance, in particular of long-lived plants, like trees, under the prevailing chronic ozone scenarios of given field sites.

There is evidence that ozone after passage through the stomata rapidly decomposes into secondary oxidative derivatives which themselves can be injurious to the metabolism and structure of leaves so that the concentration of ozone approaches zero in the intercellular space of the leaf mesophyll (**Figure 1**). The decay of ozone into reactive derivatives, unless already occurring during the diffusive influx process, largely occurs in the mesophyll apoplast which contains antioxidants like ascorbate that form the first line in oxidant defense. To the extent that O_3 or its derivatives reach the plasmalemma, they may link to receptors that can initiate oxidative burst reactions and programmed cell death, leading to local necroses as a means against spreading injury. Such defenses are mediated at the gene level through molecular signal chains, including the oxidative ozone derivatives, ethylene formation, as well as salicylic or jasmonic acid. As ozone hardly reaches the chloroplasts, molecular signaling is also suggested to induce the decline of chloroplasts (loss of pigments and Rubisco activity). The mechanistic nature of the receptors and signal chains has only partly been unraveled to date; however, it appears that the primary defense against O_3 is rather similar at the cellular level to responses elicited by biotic agents.

Physiological and Biochemical Defense Mechanisms

After an exposure to air pollutants such as ozone, reactive oxygen species (ROS) are primarily formed within the apoplastic fluid of tree leaves. This first reaction is similar for other external stressors (including enhanced ultraviolet B radiation and salinity stress). Most probably the antioxidative capacity within the apoplast of exposed leaves is of significant importance in determining the resistance of trees to air pollution. Therefore forest researchers, and in particular tree modelers, are eager to introduce this parameter in models describing the real ozone flux, for example. However, the apoplastic antioxidative capacity should be considered with caution as it is not entirely clear what the best parameter is to estimate this antioxidative capacity. Many apoplastic antioxidants in relation to ozone and other air pollutants have been reported in the literature and ascorbate has been mentioned the most in this regard. Indeed, experiments have indicated high reaction constants between ascorbate and, e.g., ozone, ROS and other radicals, but its relative antioxidative capacity *in vivo* is still largely unknown. Moreover, the decay of ozone through a direct reaction with cell wall ascorbate is not sufficient to explain the different degrees of ozone sensitivity of different tree species.

The capacity to scavenge ROS has been assigned to a wide variety of molecules other than ascorbate. Examples of low-molecular antioxidants are phenolics (such as ferulic acid, caffeic acid, catechol, syringic acid, and *p*-coumaric acid), polyamines, diketogulonate, and glutathione. The involvement of phenolic compounds in the sensitivity of poplar (*Populus*) to ozone has clearly been demonstrated: after a single pulse exposure of a resistant poplar clone there was a marked increase of phenolic compounds. Phenolics are present in the apoplastic fluid and play an important role in lignin biosynthesis. Lignin is a complex macromolecule that originates from the oxidative polymerization of cinnamyl alcohols as the principal monomeric units. The question remains: how efficient are phenolic acids, compared to ascorbate, in scavenging ROS? Generally, this question remains

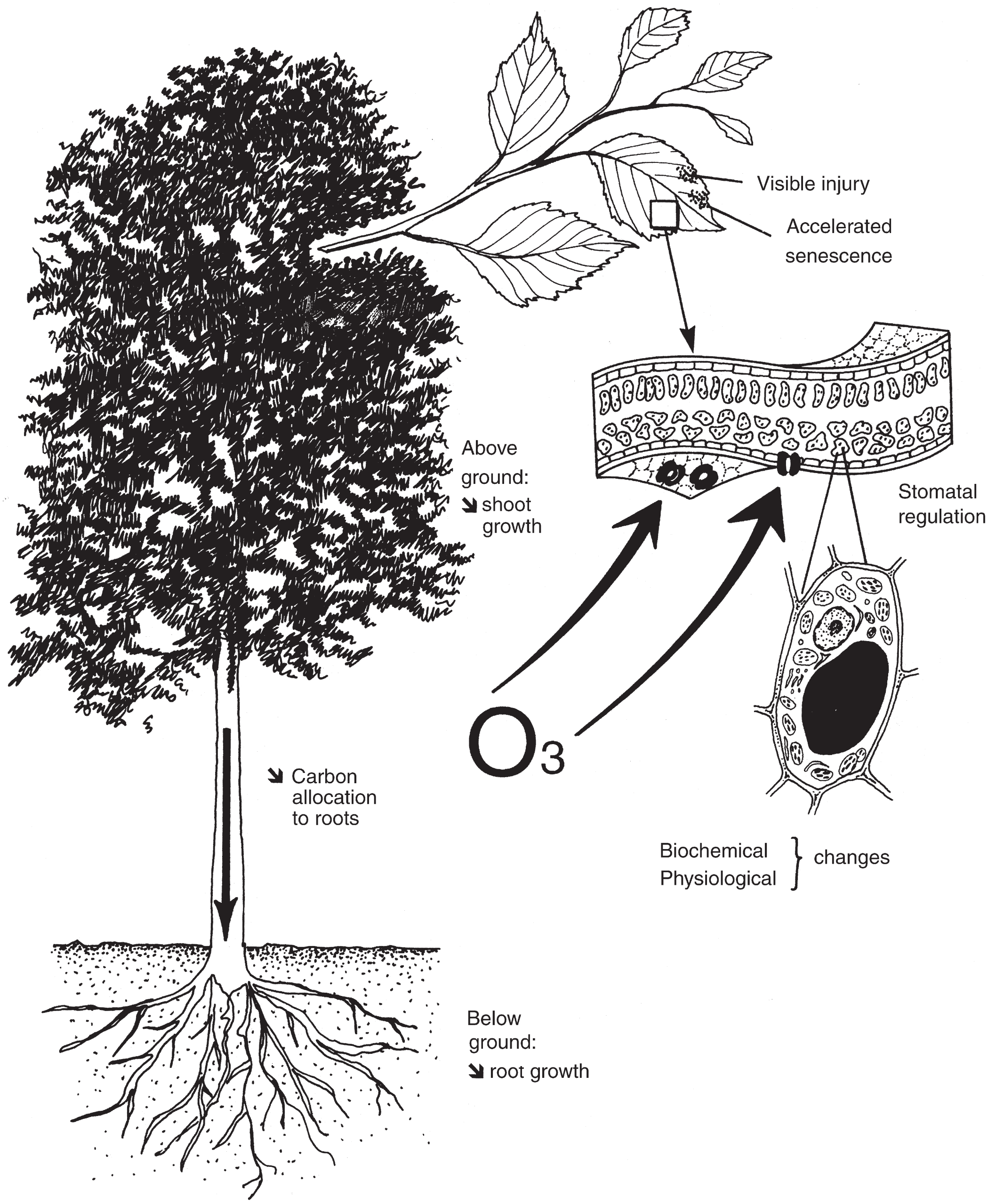


Figure 1 Schematic diagram of the impact of tropospheric ozone (O_3) on different physiological and biochemical processes at various hierarchical levels of organization. Ozone that enters the leaf through the stomatal pores alters different physiological and biochemical processes inside the leaf and the cells, but also affects a range of other functions and structures. *Environmental Pollution and Plant Responses* by Bortier K, Ceulemans R, and De Temmerman L. Copyright 1999 by CRC Press Inc. Reproduced with permission of CRC Press Inc.

unanswered, but a few naturally occurring components seem to have larger instantaneous antioxidative power than ascorbate (e.g., diketogulonate, ferulic acid, *p*-coumaric acid, gallic acid, resveratol, and quercetin). Because electronic transfer can take place between ascorbate and other antioxidants (e.g., phenolic acids), possible synergistic effects should be further considered in the future.

Climate Change Effects on Forest Trees

Role of Forests in the Global Carbon Cycle

In terms of carbon storage and cycling, forests represent the most important vegetation type on the earth. Although forests cover around 30% of the land area of the globe, they accomplish a disproportionately large part of the terrestrial bioproductivity

(65%), i.e., forests fix worldwide more or less 25 Gt of carbon per year. By their perennial character and longevity, forest ecosystems contain 80–90% of the above-ground plant carbon and 60–70% of the soil carbon on the globe. As such, they contain over 60% of the carbon stored in the terrestrial biosphere. So, forest ecosystems make up a stock of nearly 500 Gt of carbon in their biomass and a stock of nearly 700 Gt of carbon in the necromass, essentially under the form of organic matter in the soil. This impressive mass illustrates the buffering role that ecosystems can play in view of the additional carbon flux generated by the use of fossil fuels, by deforestation, and by changing land use. Apart from their significant role in the development of rural areas, forests have a major value for nature conservation, play an important role in preserving the environment, and represent a critical controlling factor of the hydrological cycle. However, forests are also key elements of the carbon cycle and represent significant carbon sinks.

The net carbon exchange of terrestrial ecosystems is the result of a delicate balance between uptake (photosynthesis) and losses (respiration and decomposition), and shows a strong diurnal, seasonal, and interannual variability. Under stable conditions, during daytime the net ecosystem flux is dominated by photosynthesis, while during the night, and for deciduous ecosystems in leafless periods, the system loses carbon by respiration. The total amount of carbohydrates produced in a forest canopy by photosynthetic carbon fixation is the gross primary productivity (GPP). Part of the produced carbohydrates is lost through autotrophic leaf respiration, while the rest is allocated from the leaves to other (tree) organs where it can be used for the construction of biomass or for metabolism and then respired as CO_2. The total amount of carbon incorporated in the biomass is the net primary productivity (NPP). The present atmospheric concentration of CO_2 limits the ability of forest trees to fix carbon. As tree photosynthesis is highly sensitive to atmospheric CO_2 and as NPP is strongly related to net photosynthesis, a stimulating effect of elevated CO_2 on NPP might be expected, provided that nutrient conditions are not limiting.

Tree Responses to Elevated Atmospheric CO_2

Because of the dependence of photosynthetic carbon fixation on the atmospheric CO_2 concentration, any increase in CO_2 tends to enhance the rate of assimilation and therefore plant growth. The reason why net photosynthesis may be enhanced is related to a number of factors connected to the characteristics of the primary carboxylating enzyme (i.e., Rubisco). Woody plants, when exposed to elevated CO_2 for varying periods of time, show not only stimulated photosynthesis, but also increased growth rate and biomass accumulation. Experiments on field-grown trees suggest a continued and consistent stimulation of photosynthesis of almost 40–60% for a doubling of the atmospheric CO_2 concentration and there is little evidence of a long-term loss of sensitivity to CO_2 that has been suggested by earlier experiments with tree seedlings in pots. Such an increase in photosynthesis translates into a 38% and 63% average increase in the biomass of coniferous and deciduous species, respectively. The relative effect of CO_2 on above-ground dry mass of field-grown trees is, however, highly variable and larger than that on seedlings or young saplings. Despite the importance of respiration to a tree's carbon budget, no strong scientific consensus has yet emerged concerning the potential direct or acclimation response of woody plant respiration to CO_2 enrichment. Effects of CO_2 concentration on static measures of response are often confounded with the acceleration of ontogeny observed in elevated CO_2.

A more robust and informative measure of tree growth in field experiments is the annual increment in wood mass per unit leaf area, which increases on average by 27% in elevated CO_2. There is no support for the conclusion from many studies of seedlings that root-to-shoot ratio is increased by elevated CO_2; the production of fine roots may be enhanced, but it is not clear that this response would persist in a forest. In general, nitrogen shortages are easily induced by accelerated growth in elevated CO_2, which could cause lower concentrations of nitrogen in leaves. Lower foliar nitrogen concentrations in CO_2-enriched trees result in larger attacks by herbivorous insects, an important contributor to fluxes of carbon and nitrogen in forest ecosystems. Experimental observations of lower nitrogen in leaves of trees grown in elevated CO_2 led to the suggestion that the behavior of herbivores feeding on those leaves is indeed affected. Although CO_2 effects on herbivory could have important ramifications for forest health, forest productivity, and nutrient cycling, there is not yet any framework for integrating the experimental observations with the population dynamics of the insect, as would be necessary for an assessment of the impact on ecosystem productivity.

Various climate models predict an increase in CO_2 emissions in the atmosphere and, simultaneously, an increase in the earth's temperature. Much of what we know about the contemporary global carbon budget has been learned from careful observations of the atmospheric CO_2 mixing ratio and the $^{13}C/^{12}C$ isotope ratio, interpreted with global circulation models. From these studies we have learned: (1) that about one-third of the annual input of CO_2 to the atmosphere from fossil fuel combustion and deforestation is taken up by the terrestrial biosphere; and (2) that a significant portion of the net uptake of CO_2 occurs at mid-latitudes of the northern hemisphere and that, in particular, north temperate terrestrial ecoystems (mainly forests) are implicated as a large sink. The method of stable isotope ratios combined with global circulation models provides the necessary global and continental scale perspectives for carbon balance calculations, but their use in addressing small temporal and spatial changes in the carbon balance is rather limited.

Over the last 200 years the flora of the earth has experienced a 28% rise in CO_2 concentration, having been progressively adapted to a CO_2-poor atmosphere for 20–30 million years. If current anthropogenic CO_2 emissions are not reduced and the rate of deforestation not slowed down, plants growing in the year 2040 will be exposed to around 500 ppmv CO_2, in contrast to the current levels of around 358 ppmv. The extent to which terrestrial ecosystems act as carbon sinks to buffer the increase in atmospheric CO_2 concentration (through enhanced NPP) is uncertain. However, the importance of forests and their interactions with climate are considerable, since trees account for nearly 65% of the terrestrial atmospheric CO_2 fixation. Their long life and large dimensions make them a considerable sink on carbon store on the earth. Evidence that past increases have directly affected trees is limited. Tree ring analysis and surveys of leaf chemical composition of leaves of herbarium specimens of 1750 AD revealed some important changes; the study of plant communities growing close to natural CO_2 sources has recently provided interesting and relevant information.

Actions to Monitor and Protect Forest Health

Worldwide actions have been and are being undertaken both to monitor and protect forest health. For example, European Community (EC) action has been developed over the years in cooperation with International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP) and in line with objectives formulated in ministerial conferences on the protection of forests in Europe and the United Nations Conference on Environment and Development (UNCED, Rio de Janeiro, 1992). In January 2003 a proposal for a European Parliament and Council regulation (2003/C 20 E/10) was presented for the establishment of a new EC scheme on the monitoring of forests and environmental interactions to protect EC forests. The protection of forest ecosystems is a major concern to the EC. The main objective of the EC action is to contribute towards the protection of forest ecosystems in the EC by monitoring the conditions of these ecosystems. The EU and its member states are committed to the protection of forests and to the sustainable management of forests in all relevant pan-European and international processes related to forests. Forest ecosystem conditions, changes of these conditions, the reaction of forest ecosystems to environmental stress, and the effects of policies can only be traced by means of monitoring. Changes in forest ecosystem condition as well as the reasons for these changes may be recognized at an early stage, thereby allowing the adoption of timely and appropriate measures. The monitoring of air pollution and global change effects on forests will be carried out on a systematic network of observation points, which covers the whole Community, and a network of intensive monitoring plots. The systematic network provides representative information on forest conditions and changes. Intensive monitoring in selected plots allows for indepth monitoring activities in order to observe ecosystem processes. The intensive monitoring plots and the monitoring on the systematic network of points thus complement each other.

See also: **Environment**: Impacts of Air Pollution on Forest Ecosystems; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Health and Protection**: Integrated Pest Management Principles. **Tree Physiology**: A Whole Tree Perspective; Forests, Tree Physiology and Climate; Nutritional Physiology of Trees; Physiology and Silviculture; Stress.

Further Reading

Agrawal SB and Agrawal M (2000) *Environmental Pollution and Plant Responses*. Boca Raton, FL: Lewis CRC Publishers.

Alscher RG and Wellburn AR (1994) *Plant Responses to the Gaseous Environment. Molecular, Metabolic and Physiological Aspects*. London: Chapman & Hall.

De Temmerman L, Vandermeiren K, D'Haese D, *et al.* (2002) Ozone effects on trees, where uptake and detoxification meet. *Dendrobiology* 47: 9–19.

Ehleringer JR and Field CB (1993) *Scaling Physiological Processes: Leaf To Globe*. San Diego, CA: Academic Press.

Karnosky DF, Ceulemans R, Scarascia-Mugnozza GE, and Innes JL (2001) *The Impact of Carbon Dioxide and other Greenhouse Gases on Forest Ecosystems*. Wallingford, UK: CAB International.

Matyssek R and Sandermann H (2003) Impact of ozone on trees: an ecophysiological perspective. *Progress in Botany* 64: 349–404.

Mohren GMJ, Kramer K, and Sabate S (eds) (1997) *Impacts of Global Change on Tree Physiology and Forest Ecosystems*. Dordrecht, The Netherlands: Kluwer Academic.

Norby RJ, Wullschleger SD, Gunderson CA, Johnson DW, and Ceulemans R (1999) Tree responses to rising CO_2 in field experiments: implications for the future forest. *Plant, Cell and Environment* 22: 683–714.

Roy J, Saugier B, and Mooney HA (2001) *Terrestrial Global Productivity*. San Diego, CA: Academic Press.

Sanderman H, Wellburn AR, and Heath RL (eds) (1997) *Forest Decline and Ozone. A Comparison of Controlled Chamber and Field Experiments*. Berlin: Springer-Verlag.

Valentini R (ed.) (2003) *Fluxes of Carbon, Water and Energy of European Forests*. Berlin: Springer-Verlag.

Yunus M and Iqbal M (eds) (1996) *Plant Responses to Air Pollution*. Chichester, UK: John Wiley.

Integrated Pest Management Principles

M R Speight, University of Oxford, Oxford, UK
H F Evans, Forestry Commission, Farnham, UK

Introduction

Integrated pest management (IPM) has a variety of definitions, but its philosophy is simple. For a particular crop–pest interaction, one or more appropriate pest management tactics are combined into a package which minimizes costs and environmental impacts, whilst maximizing yields and net profits. Its two bedrock foundations are prevention and monitoring, i.e., strive to avoid pest problems at the outset, but keep a watch on the crop in case something significant goes wrong. IPM is a concept which is now widespread through all types of crop production, and it is increasingly the goal of any grower who loses yield, both quantity and quality, to damaging organisms such as weeds and nematodes, pathogens, and insects. As a practical crop protection solution, IPM is far from universal – it is often difficult, indeed sometimes impossible, to produce a viable IPM package. Problems which arise to curtail the full implementation of IPM include pest dynamics, host-plant and climate interactions, the practicalities of crop production, and very often, the socioeconomic conditions prevalent in the region of interest.

Forestry covers a very broad range of crop production tactics, from small-scale village forestry or agroforestry to huge plantations, either artificial or, at least initially, naturally occurring. Countries practicing forest management range from small, subsistence, isolated economies with little or no infrastructure to deliver education, specialist advice or spare cash to implement modern pest management protocols, to highly developed first-world countries to whom all the benefits of science and technology are theoretically available. Trees are grown from the furthest north and south temperate regions of the world to the equator, and from below sea-level to thousands of meters above sea-level. The trees themselves may be indigenous, native species growing in natural conditions to which they have evolved, or alternatively, they may be complete exotics with not even members of the family growing as natives in the locale, planted on sites which bear little or no relation to the conditions to which these trees evolved thousands of miles away. Nevertheless, many forestry practices and their associated pests and diseases have basic similarities, principles, and interactions, wherever in the world they occur.

In this section, insect pests will be discussed, but it must be borne in mind that many of the principles and indeed examples presented have a great deal of relevance to other forest pest situations, fungal diseases in particular. In fact, the modern approach to forest pest management is frequently not to target particular pests or diseases at the outset, but instead to employ the concept of general plant health and thus consider the widest range of symptoms and their underlying causes for tree decline and debilitation.

Insect Pests and Their Impacts

It is extremely helpful to consider trees as but one part in a complex ecology which has evolved over millions of years. Other crucial members of this association are at one end of the spectrum the environment in which the tree is growing (soil, climate, altitude), and at the other end, insects and diseases which utilize the tree for food or living space (or usually both). These herbivores themselves often have their own enemies in the form of predators, parasites, and pathogens, and the forester is simply one of these competitors for the resources which the tree provides. Unfortunately, this competition is very one-sided, especially in economic terms, since foresters cannot tolerate much, if any, resource removal by others – pests and diseases have to be defeated.

Paramount in this war to defeat the competition is the concept of impact. The actual harm done to a tree by an insect is frequently very difficult to assess. Heavy leaf loss may not be extreme when averaged over the life of the tree, especially when the trees are grown for many decades, whereas boring in the

Table 1 Pest types – defoliators

Insect groups
Larvae of moths (Lepidoptera) and sawflies (Hymenoptera), nymphs or larvae, and adults of grasshoppers (Orthoptera) and beetles (Coleoptera)
Activity
Leaves can be eaten partially or entirely, or the epidermises between the veins removed (skeletonization or leaf mining)
Primary impact
Main impact involves the removal of photosynthetic area, with a very wide range of deleterious effects. These include shoot, stem, and root growth loss, reductions in height and volume increment, reduction or cessation of flowering or seed set. Growth losses may be temporary, such that the tree reflushes foliage after an isolated defoliation event and growth returns to normal, or after extended and repeated bouts of defoliation, the tree dies. Actual impact losses are often impossible to quantify economically
Secondary impact
Tree vigor is considerably reduced and natural defenses against herbivores diminished, resulting in attacks by secondary pests such as boring Lepidoptera or Coleoptera. Trees can be killed in a short time by ring barking or girdling
Main examples
Teak defoliator moth, *Hyblaea puera* (India, South Asia, Southeast Asia), nun moth, *Lymantria monacha* (Eastern Europe), pine sawfly, *Neodiprion sertifer* (Western Europe)
See **Figures 1** and **2**

Figure 1 *Hyblaea* defoliation. From Speight and Wylie (2000) *Insect Pests in Tropical Forestry*. Reproduced with permission from CABI.

shoots or wood may not be a cause for concern if the tree can still survive and produce a marketable product. In particular, if pest management tactics have a financial implication (and they usually do), then, in order to calculate a realistic cost/benefit analysis, it is crucial to have some quantitative notion

Figure 2 Pine sawfly.

Table 2 Pest types – sap-feeders

Insect groups
Nymphs and adults of bugs (Hemiptera, especially Homoptera; aphids, psyllids, scale insects, mealybugs)
Activity
Removal of phloem or, less commonly, xylem sap or plant cell contents using piercing mouthparts from leaves, shoots, stems, or roots. Note that sucking is a common misnomer for many sap-feeders–relatively high internal plant pressure negates the need to suck
Primary impact
Removal of primary production synthates and organic nitrogenous compounds from the tree and hence a significant reduction in yield resulting in the same losses as defoliation. There may also be direct loss of foliage arising from a wound reaction to injection of saliva by the feeding insect
Secondary impact
Local or widespread leaf mortality and loss, with same consequences as chewing defoliation. Shoot and stem feeding also causes bark necrosis and damage, allowing invasion of inner tissues by pathogens such as fungi
Main examples
Cypress aphid, *Cinara* spp. (South and East Africa), Leucaena psyllid, *Heteropsylla cubana* (pan-tropical), spruce aphid, *Elatobium abietinum* (Western Europe)
See **Figures 3** and **4**

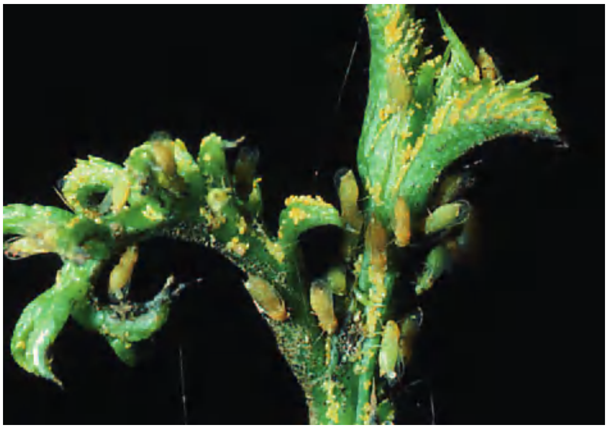


Figure 3 Leucaena psyllid.

Figure 4 Spruce aphid. Reproduced with permission from Speight MR, Hunter MD, and Watt AD (1999) *Ecology of insects: Concepts and Applications*. Blackwell Publishing.

of how much economic damage is being done to see if control, if possible at all, is cheaper. In forest situations in particular, this knowledge is frequently lacking or at least inadequate, and many countries now have active research programs involving long-

Table 3 Pest types – shoot-borers

Insect groups	Larvae of moths (Lepidoptera – Tortricidae, Pyralidae; shoot-borers, tip moths) and larvae and adults of beetles (Coleoptera – Scolytidae – shoot beetles)
Activity	Tunneling inside growing shoots, usually leaders followed by secondaries. Tunnels become larger and more elongated as the insect grows and develops
Primary impact	Death of attacked shoot, followed by cessation of growth in very young trees, or the new dominance of one or more secondary shoots in older saplings. Trees become distorted, bushy, and dead-headed
Secondary impact	Production of straight, non-forked logs prevented. Expected dominant height not achieved
Main examples	Mahogany shoot-borer, *Hypsipyla* spp. (pan-tropical), pine shoot moth, *Rhyacionia* spp. (Southeast Asia, North and Central America, Western Europe), pine shoot beetle, *Tomicus piniperda* (Western Europe)
See **Figures 5** and **6**	

term monitoring to provide impact data related to pest density. As might be expected, such data are only likely to be available for a minority of tree/insect associations, and then mainly in developed countries.

Insects which have evolved to utilize tree resources can be split into several distinct types. The major types are sap feeders, defoliators, bark feeders, shoot borers, bark borers, wood borers, and root feeders. The methods which they employ to exploit tree resources, and the tactics available to foresters to defeat them, vary according to their behavior and ecology. **Tables 1–7** present the main characteristics of these types of pests, together with examples of some major forest pests from each category.

Reasons for Outbreaks

The IPM of forest insects must be considered to be a preventive technique first and foremost. For ecological, economic, technological, and social reasons, it is frequently impossible to control a pest outbreak or eradicate a damaging species even locally once the damage has begun, and so it is vital to grow trees, whether at a local agroforestry level or in an industrial plantation, in ways that reduce the probability of serious pest incidence. The first stage in this preventive strategy involves developing a sound knowledge of why insect pest outbreaks occur. Armed with this knowledge, foresters and economists can, if they choose, grow trees using methods which avoid such occurrences. Of course, it may be that a tactic which is well known to increase the likelihood of pest (and disease) problems, such as intense monocultures, is essential to sound silvicultural practice, and hence

Figure 5 (a) Shoot moth damage. (b) Shoot moth larva.

cannot be avoided. **Table 8** considers tree health and its decline, as major predisposing factors to insect and disease outbreaks, whilst **Table 9** itemizes forest management tactics known to exacerbate pest problems for even healthy trees. Note that various items in both tables are interlinked and overlap; **Figure 15** provides a flowchart which attempts to link various aspects of tropical forestry which can result in pest problems.

Some of the factors presented in the tables will be considered in more detail here.

Tree Species Resistance and Site Matching

Of all the predisposing or avoidable problems mentioned in these tables, two related items stand out as fundamental to promoting and preserving tree health and reducing pest or disease attack. These are: (1) tree species and site-matching (essentially environmental); and (2) the use of resistant or nonsusceptible tree species or genotypes (essentially genetic). Put simply, even if a tree which is genetically resistant to an insect or a fungus is chosen, it may still be rendered prone to attacks by planting it in a place where the soils and/or climate are unsuitable. On the other hand, if a susceptible tree species or genotype has to be used for sound economic reasons, then planting it in a habitat where its health and vigor will be optimal may enable resulting pest problems to be tolerated. The type of pest also has an influence here. Sap-feeders and stem, shoot, or bark borers seem to be particularly influenced by tree stress or lack of vigor in the host, whereas defoliators are less predictable. Defoliators may be deterred, however, if a tree genotype is basically disliked or rejected by a potential pest, irrespective of where it is planted.

Figure 6 Pine shoot beetle damage.

Table 4 Pest types – bark feeders

Insect groups
Larvae of moths (Lepidoptera – Cossidae and Indarbelidae), termites (Isoptera), adult weevils (Coleoptera – Curculionidae)
Activity
Larvae or adults feed on bark material, excavating shallow tunnels which may reach to the inner layers. Broad, irregular patches of bark can be excavated. Young trees may have bark stripped completely
Primary impact
Local bark necrosis; girdling and death of young transplants in the case of weevils. Most visual activity of termites such as earthen tunnels up trees from the soil is not life-threatening; only dead bark or wounds are targeted
Main examples
Subterranean termites (e.g., *Odontotermes*) (Asia-Pacific), pine weevil, *Hylobius abietis* (Western Europe)
See **Figures 7** and **8**

Figure 7 Termite galleries.

Figure 8 (a) *Hylobius abietis* (b) *Hylobius* damage.

A final problem may concern long-term changes to the environment, wherein host-plant or mortality factors which normally reduce outbreaks to tolerable levels break down, rendering a crop much more difficult to grow economically. One example involves the green spruce aphid, *Elatobium abietinum*, in the UK, where the incidence of cold snaps in late winter is the only significant mechanism for checking

Table 5 Pest types – bark-borers

Insect groups	Larvae and adults of beetles (Coleoptera – Scolytidae, Platypodidae, Cerambycidae, Buprestidae; bark beetles, ambrosia beetles, longhorn beetles, flathead borers)
Activity	Adults lay eggs on bark surface or in maternal galleries excavated in the bark at the parenchyma/sapwood surface. Larvae ramify through inner bark in usually solitary tunnels which expand as the larvae grow. Pupation occurs at the end of the tunnel or within the wood and new adults emerge through characteristically shaped holes in bark. Nonvigorous trees are more likely to be attacked
Primary impact	Species-specific patterns of engraving of galleries on sapwood which, if extensive, causes ringbarking (girdling of tree and hence death). Dead trees then become breeding sites for more beetles of the same or different species
Secondary impact	Production of large numbers of new-generation adults that may overcome defenses in even healthy trees (mass outbreak). Note that attack by secondary pests can be indicative of general tree decline and ill-health, linked to climate or site mismatches, pathogens, soil conditions, overcrowding, and so on
Main examples	Acacia longhorn beetle, *Xystrocera festiva* (Southeast Asia), eucalyptus longhorn, *Phoracantha semipunctata* (pan-tropical, Mediterranean), European spruce bark beetle, *Ips typographus* (continental Europe), southern pine beetle, *Dendroctonus frontalis* (USA)
See **Figures 9–11**	

population upsurges. Warmer winters, for whatever climatic reason, are now allowing the pest to cause much more damage to the widely planted but genetically susceptible Sitka spruce.

One example which encompasses both environmental and genetic factors involves the eucalyptus longhorn beetle, *Phoracantha semipunctata* (Coleoptera : Cerambycidae). This species is a native of Australia, but has now spread to most parts of the tropical, semitropical, and warm temperate parts of the world where eucalyptus is grown, including Asia, Africa, southern Europe, and the USA. Adult female beetles seek out trees whose bark moisture contents are reduced – larvae cannot survive in hosts with high bark moisture. Some commercial species of eucalypt such as *Eucalyptus grandis* are known to be drought-intolerant, in that they grow poorly on dry soils and should therefore be inappropriate for planting on arid sites in low-rainfall conditions or at or near the tops of slopes, and so on. Such tree species seem to exhibit low bark moistures in general, and although they may be able to withstand attacks by *Phoracantha* in relatively high rainfall areas, in drier conditions the beetle larvae thrive under the bark, killing large numbers of trees. The logical approach to the prevention of this pest is (1) to plant *Eucalyptus* species which are naturally drought-tolerant; and (2) if drought-intolerant ones are required for silvicultural reasons, only put them on sites with moist soils in climates without a prolonged dry season.

Figure 9 (a) *Xystrocera* larva. (b) *Xystrocera* damage.

Figure 10 Bark beetle larvae. From Speight and Wylie (2000) *Insect Pests in Tropical Forestry*. Reproduced with permission from CABI.

Figure 11 *Ips* galleries.

Pest Reservoirs

Even when relatively resistant tree genotypes are to be utilized, and the sites in which they are to be planted are essentially suitable for them, it is possible to increase pest risks. In the case of pine shoot moth outbreaks in Southeast Asia, it was clear that the most serious damage to tropical pines caused by the tunneling larvae of *Dioryctria* and *Rhyacionia* species occurred when the young plantations were established in close proximity (literally mere tens of meters) to naturally occurring stands of indigenous *Pinus* species. The latter trees were relatively lightly attacked by the pest, but the insects quickly discovered the exotic trees, which were not only more suitable but also planted in large, even-aged stands on very poor soils. The resulting damage to leading shoots caused a reduction in expected dominant height at 10 years old of 25+ m down to a non-economic 5–6 m at the same age.

Trees of the same species within the same stands can also act as pest reservoirs, especially when

Table 6 Pest types – wood-borers

Insect groups
Larvae of moths (Lepidoptera – Hepialidae, Cossidae (goat and swift moths)), larvae of woodwasps (Hymenoptera – Siricidae); larvae of beetles (Coleoptera – Cerambycidae (longhorn beetles), Buprestidae (flathead borers)), termites (Isoptera)

Activity
Larvae tunnel from the outside, frequently leaving a telltale wound or exudation point on the bark surface. Tunnels extend either within the surface timber, or in the center of the heartwood

Primary impact
Serious degrade of timber. Note that, in most cases, the tree itself remains healthy, only the economic value is degraded. With termite attack, ingress is normally only through previous physical damage such as pruning wounds, or after primary fungal infection. Almost all woodwasp and beetle attack is secondary, following tree stress

Main examples
Beehole borer, *Xyleutes ceramica* (South Asia, Southeast Asia), woodwasp, *Sirex noctilio* (Europe, New Zealand, Australia), pine sawyers, *Monochamus* spp. (worldwide in temperate forests)

See **Figures 12** and **13**

Figure 12 Woodwasp.

Figure 13 Xyleutes larvae.

outbreaks are, initially at least, localized to small pockets of damage or death. These small pockets provide new colonists which spread into the surrounding forests, causing much more widespread and serious damage. One example of this involves the mountain pine beetle, *Dendroctonus ponderosae,* in the USA and Canada. Larvae feed and grow under the bark of lodgepole pine trees; when they are sufficiently abundant, their tunneling ring barks (girdles) the host tree which dies, providing, incidentally, ideal breeding sites for a large number of

Table 7 Pest types – root-feeders

Insect groups
Termites (Isoptera), larvae of beetles (Coleoptera – Scarabaeidae (white grubs or chafers), Curculionidae (vine weevils)), larvae of moths (Lepidoptera – Noctuidae (cutworms))
Activity
Roots of very young transplants most frequently eaten whole or have bark removed. Some tree genera such as *Eucalyptus* are more susceptible than others
Primary impact
Small trees wilt, die back, and die soon after planting, particular problems in forest nurseries
Secondary impact
Older trees may be attacked following root deformation or damage earlier in life (as in nursery handling)
Main examples
Subterranean termite, *Coptotermes curvignathus* (Asia-Pacific), white or curl grub, *Lepidiota* spp. (Australia), vine weevil, *Otiorhynchus sulcatus* (Europe)
See **Figure 14**

Figure 14 Root termite damage. From Speight and Wylie (2000) *Insect Pests in Tropical Forestry*. Reproduced with the permission from CABI.

secondary pests. Low-level (endemic) populations of mountain pine beetle persist in one or two stressed trees per stand until numbers build up sufficiently to

Table 8 Reasons for insect pest outbreaks – tree health decline

Attack by a primary pest
Damage at nursery stage
Dry soil
Infection by a primary pathogen
Natural disasters (fire, drought, wind)
Old age
Overcrowding
Poor soil
Waterlogged soil
Wrong site/species matching

Table 9 Reasons for insect outbreaks – detrimental management tactics

Damage during growth (e.g., pruning or brashing)
Introduction of exotic pests by travel and trade
Mishandling in nursery
Monocultures
Planting near to pest reservoirs in older and/or natural stands
Poor match between tree and site/climate leading to tree stress
Provision of pest reservoirs in thinnings or logs
Underthinning
Use of susceptible species or genotype

overcome the resistance of healthier, large-diameter trees in the vicinity. Outbreaks then ensue as groups of infested trees form bigger patches until most of the stand is infested and all the trees are killed.

Handling Damage

There are various stages in the growth of a forest crop when hands-on intervention is called for. This can start in the nursery, continue into young plantations, and still be prevalent as far as harvest and beyond. For example, it is very easy to damage the roots of nursery stock by rapid and rough transplanting. Root curling is a common problem which, whilst not serious enough at the outset to prevent vigorous young trees establishing in a plantation, can lead to early root decline, secondary pest attack, and tree death, as in the case of *Acacia mangium* in Sabah. Pruning and brashing are frequently called for as the young forest grows, and untrained or careless actions can provide ideal sites for the ingress of insects such as termites, and other problems such as fungal pathogens. Later, stands need thinning to reduce competition between trees. Certainly, the maintenance of tree vigor by thinning is a significant factor in reducing susceptibility to pests, but it is important not to leave thinned timber lying within stands or even in adjacent log piles, for fear of new pests breeding and proliferating in the debris. Examples include the massive increase in bark beetles, especially the highly damaging spruce bark beetle, *Ips typographus,* in Europe after wind storms. In such cases the wind-felled trees act as breeding resources for pioneer beetles that build up to sufficient numbers to attack and kill the remaining healthy standing trees. Forest hygiene is, therefore, another form of preventive pest control. Finally, when the trees are eventually harvested, damage to remaining trees by logging or skidding damage must be avoided, and log piles must not remain for any length of time close to younger plantations. Felling only when a market is ready to receive the produce can avoid the risk of mass outbreaks of pests such as bark beetles and longhorns.

Practices which increase the risk of pest outbreaks can be avoided under the general heading of ecological (or silvicultural) control, which is summarized in **Figure 16**.

Interventionist Management Tactics

Prevention is thus much better than cure, but is unfortunately not entirely dependable. As mentioned above, defoliators in particular are less influenced by attempts to grow the healthiest trees, and various ‘risky’ strategies such as growing monocultures of exotic tree species on poor soils may be unavoidable logistically and economically. Appropriate management tactics differ for different types of insect pest, and actual ‘hands-on’ control of insects and indeed diseases is often not a viable option. However, recourse may be made to more interventionist tactics if available. These may either be in the form of longer-term, semipermanent control using natural enemies of pests in biological control, or the short sharp tactic of employing various types of pesticides, biological or chemical, in response to an acute outbreak.

Inspection and Quarantine

Almost all countries in the world take part in some form of trade in trees, timber, and/or wood products. The movement of such material from one region of the world to another, especially across international borders, is an ideal way of spreading forest pests. There are classic examples of forest pests being introduced deliberately into new countries, such as the gypsy moth, *Lymantria dispar*, into the USA from Europe in the 1880s to form a new silk industry, but **Table 10** shows some examples of pests introduced by accident. Hence, a vital part of IPM for forest insect pests these days is a routine but efficient system of inspection at docks and harbors to prevent such imports, to quarantine infested material, and to seek out and destroy imports already arrived and potentially dangerous.

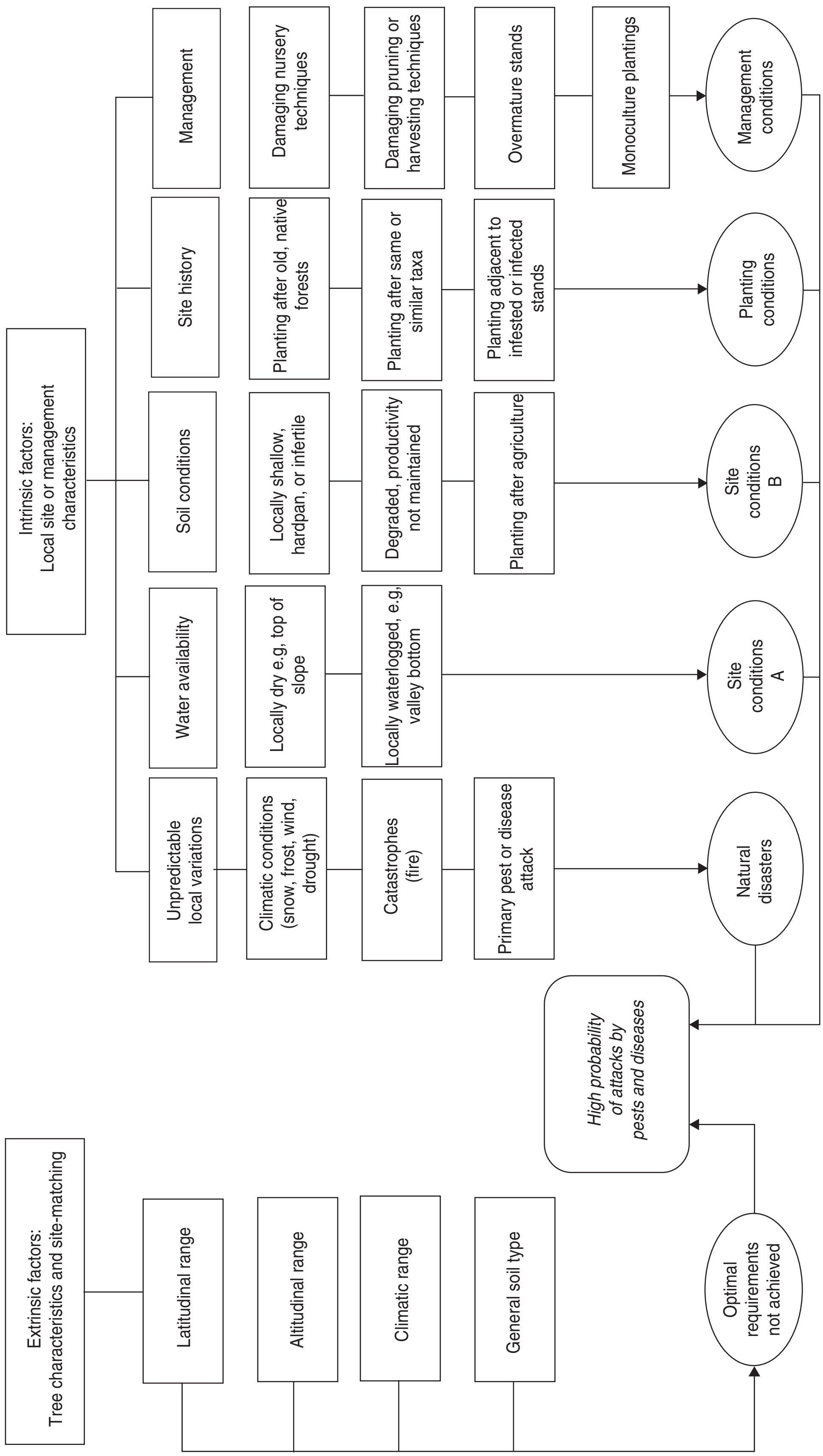


Figure 15 Factors which increase the risk of trees being attacked by pests and diseases.

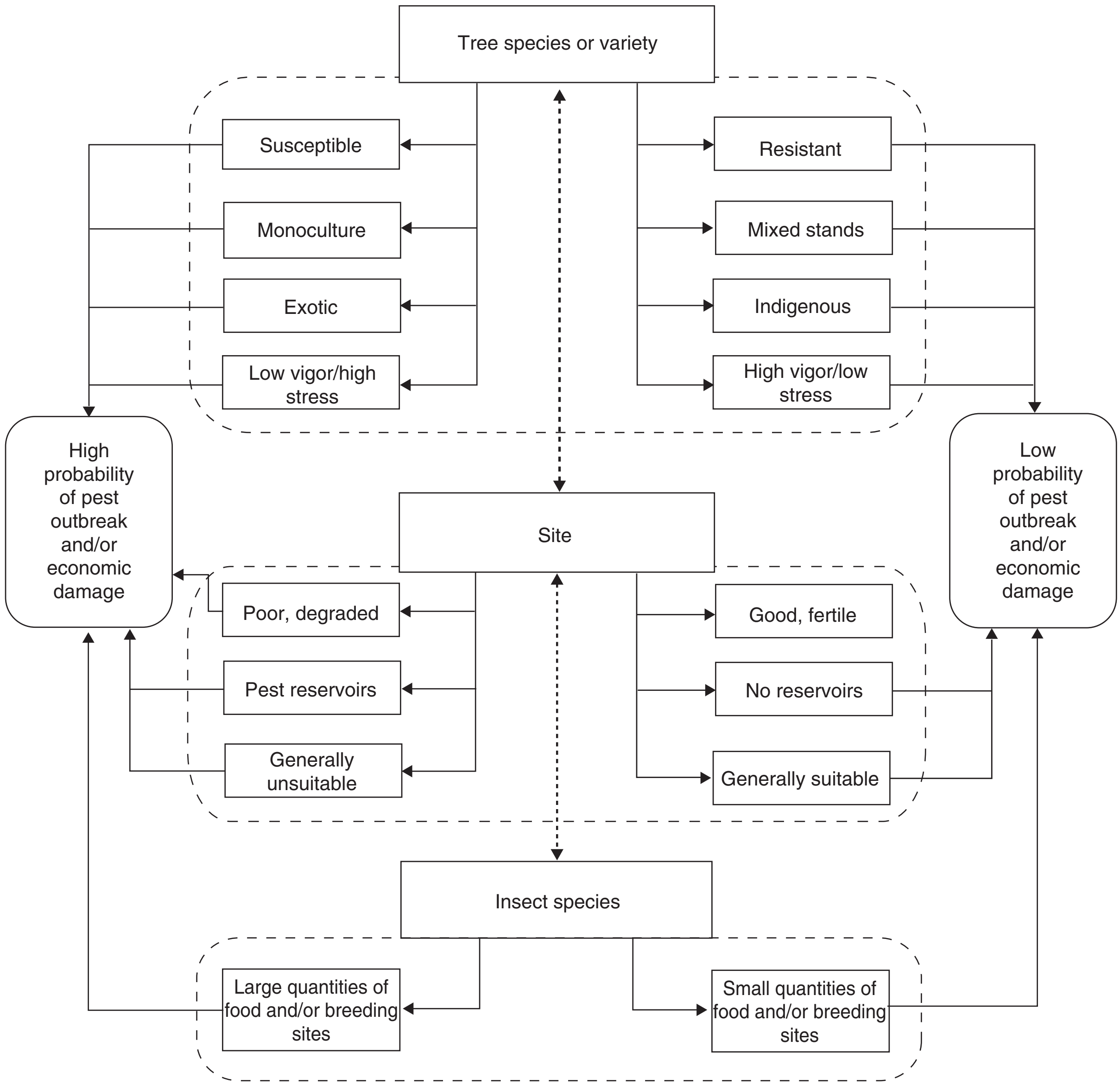


Figure 16 General flowchart depicting the 'rights and wrongs' of ecological control.

Table 10 Examples of forest pests introduced from one country to another

Pest	*From*	*To*	*Method*
Gypsy moth (*Lymantria dispar*)	Europe	USA	Egg masses on wheels and chassis of returning army trucks
Bark beetles (Scolytidae)	South Africa	St Helena	Bark beetles in the timber of food packing cases
Asian longhorn beetle (*Anoplophora glabripennis*)	Asia	USA	Larvae carried in solid wood palettes and crates
Spruce bark beetle (*Ips typographus*)	Continental Europe	UK	Adults in packing, bark, debris, 'wainy edge' on saw timber
Termites (Isoptera)	Asia	New Zealand	In processed timber products such as chopsticks
Pine woolly aphid (*Pineus pini*)	Australia	South Africa	On imported pine seedlings
Eucalyptus snout weevil (*Gonipterus scutellatus*)	Australia	USA	Aircraft stowaways
European pine woodwasp (*Sirex noctilio*)	Europe	Australia	Larvae inside miscellaneous wood and timber material

Biological Control

In theory, the use of natural enemies of forest insect pests to regulate their numbers below a level where damage is economically important is a very useful strategy. Predators such as birds, small mammals, and especially other insects seem to consume large numbers of lepidopteran larvae or aphids, whilst more host species-specific parasites (parasitoids) in the insect orders Hymenoptera and Diptera can reduce the densities of pests considerably. The problem, however is that in many cases this reduction in percentage mortality is insufficient either to prevent significant damage or to reduce existing outbreaks sufficiently. Put very simply, the reasons behind the outbreak where clearly the pest is being very successful for one reason or another tend to outweigh the ability of the enemies to make serious inroads into the pest population until most of the pest's food, such as foliage, has disappeared. By then, of course, it is too late for pest management to prevent significant losses. In the case of forestry, unlike many situations in agriculture and horticulture, there are relatively few pest management success stories for biological control using predators or parasitoids of insect pests. Major limitations include the sheer size of forest stands, the fact that many pests are concealed in bark wood or soil, and that many forest pest outbreaks occur because the odds are stacked in favor of the pests, as indicated earlier. However, **Table 11** shows some examples where at least partial success has been achieved.

Biological control in forest pest management has a better track record when considering the potential of insect pathogens. Bacteria, nematodes, viruses, and fungi have all been shown to have real success in pest management in other types of crop production, and for certain groups of forest pests, the defoliators in particular and possibly some of the shoot-borers and stem-feeders, pathogens show promise. **Table 12** summarizes the various types of pathogen, and shows how they are or may be employed. The most widespread pathogen at the moment is *Bacillus thuringiensis*, which is used in much the same way as a conventional insecticide. Major forest areas in North America, for example, are routinely sprayed from aircraft with *B. thuringiensis*, targeting pests such as gypsy moth, *Lymantria dispar,* and, in particular, spruce budworm, *Choristoneura fumiferana*. For the future, nematodes are showing a great deal of promise for the control of pests such as root

Table 11 Insect enemies as biological control agents in forestry

Enemy type	*Pest insect*	*Country*	*Biological control*
Predator	Great spruce bark beetle (*Dendroctonus micans*)	UK	Specific predatory beetle, *Rhizophagus grandis*, introduced from continental Europe; success in 5–10 years
Predators and parasitoids	Golden mealybug (*Nipaecoccus aurilanatus*)	Australia	Severe damage to hoop, bunya, and kauri pines reduced by a combination of 10 or so indigenous natural enemies
Parasitoid	Web-spinning larch sawfly (*Cephalcia lariciphila*)	UK	Fortuitous appearance of *Olesicampe monticola* in UK; success in 3–5 years
Parasitoid	Cypress aphid (*Cinara* spp.)	East Africa	*Pauesia juniperorum* released and dispersed over large areas of Kenya and Malawi; significant reductions in pest damage predicted

Table 12 Insect pathogens as pest control agents

Pathogen	*Pests*	*Limitations*
Fungi, e.g., *Metarhizium*, *Beauveria Entomophthora*	Pine shoot-borers, termites, white grubs (scarab larvae), defoliating Lepidoptera	Moist conditions required; concealed pests may not encounter spores
Bacteria, e.g., *Bacillus thuringiensis*	Defoliating Lepidoptera, some Coleoptera	Bacterial toxins must be ingested (eaten); some commercial formulations are relatively expensive; nonpersistent; no proliferation in environment; application problems
Nematodes, e.g., *Steinernema*, *Heterorhabditis*, *Deladenus*	Root- and stem-feeding weevils; woodwasps	Relatively slow to contact pest larvae under bark; bulk production and application problems
Viruses, e.g., nucleopolyhedroviruses (NPVs)	Defoliating Lepidoptera and sawflies (Hymenoptera)	Viruses must be ingested (eaten); host-specificity means cross-infectivity unlikely; application problems; time lag before killing pests

and collar weevils, and great potential has been shown in the use of viruses. The nucleopolyhedrovirus (NPV) of the teak defoliator moth, *Hyblaea puera,* in southern India is the best example so far of pathogens in the control of tropical forest pests. NPVs are usually extremely species-specific, have enormous multiplication rates, and can persist in a stable forest environment for long periods of time. The remaining problems to their commercial adoption center around their production prior to application, the efficient timing and application of the pathogens, and the ability to respond rapidly to new and geographically isolated pest outbreaks.

Chemical Control

There are basically two types of chemicals with potential in the management of insect pests in forestry; insecticides and pheromones.

It is simplest to state that the use of insecticides in all but a very small minority of cases of forest pest problems is impossible, for economic, technological, and environmental reasons. The only occasions when they may be useful are in the nursery, or just at planting out when they may be used as dips or soil granules on occasion to protect young transplants from root- or stem-feeding insects such as termites, grasshoppers, or weevils. In a nursery, the major dilemma of a manager is when not to spray. It is very tempting to take action at the first sign of an insect or fungus in a forest nursery, especially if the person involved is responsible to a higher authority for the production of large numbers of healthy transplants. Caution has to be advised. Most observations of defoliation in a nursery are ephemeral and localized. In the vast majority of cases, a strategy of doing nothing will undoubtedly save money and reduce pollution of everything from silk farms to fish farms. However, more confidence can be gained by effective monitoring against known economic injury levels defined by a threshold population size for a given sampling effort.

The chemical treatment of growing plantations is extremely problematic, and only in the most severe cases should spraying be contemplated, even when the most advanced technological standards are available. These days, the whole concept of interventionist IPM is based on monitoring and prediction, so that if aerial applications of pesticides are called for, they are over a very small area with specific targets and timing. The technology for application is vital, ideally using atomizers producing optimal droplet sizes in a spray cloud (controlled droplet application: CDA) and hence minimizing the volume of chemical used (ultralow-volume: ULV). Most important is the type of insecticidal compound employed. Many developed countries have ever more stringent legislation preventing the use of older insecticides which have been employed effectively for generations, and those which remain tend, for political more than ecological reasons, to be the most specific and environmentally ‘friendly.’ Hence in Europe, for example, one of the most widely used insecticides for the control of defoliating Lepidoptera is diflubenzuron (Dimilin), not a poison at all, but instead a chemical which kills insects by interfering with chitin formation and thus effectively prevents larval pests molting to the next lifestage. This increases the relative specificity because it is only those organisms with chitin (invertebrates, mainly insects) that could possibly be susceptible.

Pheromones are used extensively for monitoring insect pest populations, but they have also had limited success in a technique known as mating disruption or confusion. In this technique, synthetic analogs of species-specific sex-attractant pheromones are uniformly released over large areas of forest from various types of dispenser. Male moths attempting to locate the point-source attractiveness of females lose the ability to find mates, resulting in far fewer eggs laid and hence significantly reduced pest populations. Field trials show that even shoot-dwellers, such as the pine shoot-borer *Eucosma sononama*, can be effectively controlled, and the potential for the technique for other more serious borers such as pine shoot moths (*Rhyacionia* spp.) and mahogany shoot-borers (*Hypsipyla* spp.) needs to be investigated.

Table 13 Monitoring systems for forest insect pests

Pest	*Country*	*Monitoring technique*
Pine looper moth (*Bupalus piniaria*)	UK	Count pupae in soil under canopies in winter to determine high-risk sites; eggs counted only in these sites in early summer
Five-spined bark beetle (*Ips grandicollis*)	Australia	Pheromone traps baited with synthetic pheromones to determine spread and arrival in new areas
Southern pine beetle (*Dendroctonus frontalis*)	USA	Aerial surveys to detect browning leaves in canopies, mid to late summer
Douglas fir tussock moth (*Orgyia pseudotsugae*)	USA	Pheromone delta traps catch male adults, known relationship between number of males in traps and later larval densities
Nun moth (*Lymantria monacha*)	Eastern Europe	Pheromone traps to determine the period of peak flight, monitor incidence of swarming moths during the period (walk-and-watch method)

Monitoring and Prediction

Using the appropriate chemical or biological tactic in the right place at the right time without wasting labor and money, whilst still achieving successful control, is an IPM juggling act. Perhaps the most fundamental feature of IPM compared with conventional pest management tactics is the reliance on some form of monitoring procedure to tell the forester whether or not he or she can expect to have a pest problem in the future. Hence the luxury of IPM is the decision to take no action, safe in the knowledge that nothing economically serious is going to happen. It is crucial to note that no monitoring system can be regarded as reliable without impact assessments, risk or hazard ratings, and a knowledge of threshold densities (numbers of the lifestage counted above which significant pest damage can be expected). Various techniques, some more laborious than others, are used in forestry as monitoring systems, and **Table 13** shows some examples.

Conclusions

An IPM 'toolbox' may be imagined which contains all the elements of pest management discussed above. These include preventive systems such as site choice and species matching, as well as interventionist tactics such as chemical and biological control. Underpinning these tactics is a sound and reliable monitoring system with which management decisions can be made. Clearly, not all specific forest pest situations will require each of these tactics, and so the 'toolbox' concept can be applied whereby the various components appropriate to a particular problem (and its solution) can be used, leaving the rest for a different scenario.

See also: **Entomology**: Bark Beetles; Defoliators; Foliage Feeders in Temperate and Boreal Forests; Population Dynamics of Forest Insects; Sapsuckers. **Health and Protection**: Integrated Pest Management Practices. **Pathology**: Insect Associated Tree Diseases.

Further Reading

Speight MR, Hunter MD, and Watt AD (1999) *Ecology of Insects: Concepts and Applications*. Oxford, UK: Blackwell.
Speight MR and Wylie FR (2001) *Insect pests in tropical forestry*. Wallingford, UK: CABI.

Integrated Pest Management Practices

H F Evans, Forestry Commission, Farnham, UK
M R Speight, University of Oxford, Oxford, UK

Published by Elsevier Ltd., 2004

Introduction

The principles of integrated pest management (IPM) (*see* **Health and Protection**: Integrated Pest Management Principles) require a comprehensive knowledge of the reasons for pest outbreaks and, further, an understanding of which processes can be manipulated to reduce the severity of any outbreaks. While the concepts of IPM are intuitively sound, the practical implementation of those concepts to reach a successful conclusion is not always so easily achieved. In fact, case studies to illustrate IPM successes in forestry are relatively few if a strict definition of 'integrated' is adopted, such that there is a requirement for a multifaceted approach across a range of disciplines. In reality, although there are multiple variables to contend with, management will tend to rely on one or two key elements to achieve pest reduction.

This article deals with case studies that have been selected to illustrate the principles of IPM in practice and also to illustrate how those principles are applicable in both temperate and tropical forest systems. In providing these case studies, it is clear that not all groups of insect pests can be included and, therefore, some emphasis is based initially on discussion of management tactics in a wider sense, followed by the specific case studies.

Options in Integrated Pest Management

Traditional pest management tends to rely on one or, occasionally, a low number of options for reducing the damage caused by a particular organism. Choices are driven by the economic threshold that can be tolerated and by how quickly the pest population must be reduced below the economic threshold. In some cases, there is little choice but to use direct intervention methods based on chemical pesticides and this is an option within an IPM strategy. However, the key advantage of IPM is assessment of a range of options and the choice of a combination of these to achieve pest reduction. IPM therefore requires a disciplined approach to decision making, taking account of the individual and combined effects of a range of options. Ideally, the choices will also be dynamic in that the strategies employed will change and evolve with the changing densities of the target pest. **Figure 1** illustrates a range of the steps required to develop IPM in forestry and distinguishes two complementary approaches to management, namely prevention and cure.

Although the actions involved in achieving these ends may be similar, the ultimate aim will be to develop prevention so that long-term, sustainable population management can be achieved. In reality, there is usually a balance between prevention and

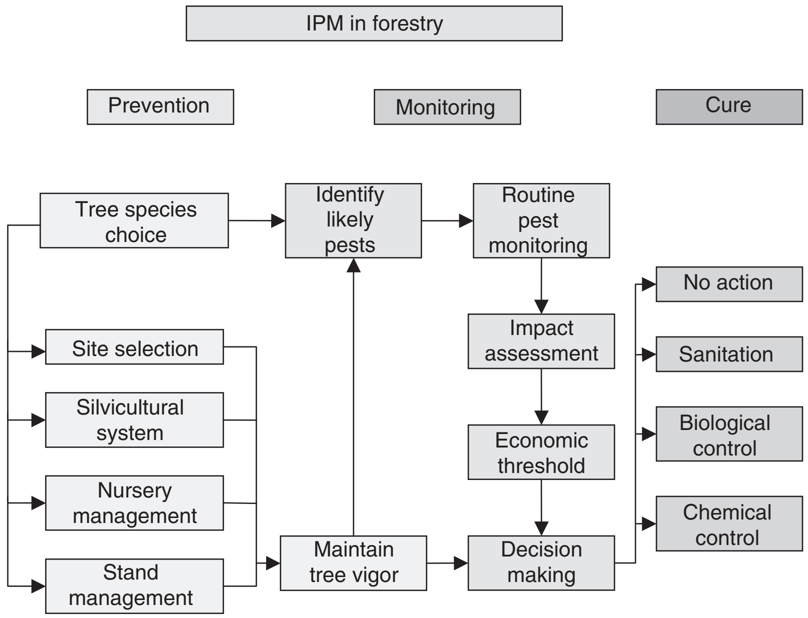


Figure 1 Schematic representation of the key components of integrated pest management in forestry.

cure, both of which depend on the quality of the monitoring and decision making components of the IPM system. Emphasis on maintaining tree vigor as a baseline component of an IPM system goes a long way towards achieving both prevention and, if there is an existing problem, cure.

General Management Tactics in Relation to the Feeding Strategies of Pest Insects

Insects are often classified according to the sites that are damaged during the life cycle. The majority of cases relate to the immature, larval, or nymphal stages of the particular pests. In part, this is determined by the processes employed by the adult pests to select suitable egg-laying sites that will lead to the highest likelihood of successful survival by their progeny. Consequently, the tactics employed to manage pests will be tailored to the types of feeding strategy by a given pest species. This is illustrated in **Figure 2**, which shows the four main categories of insect feeding strategy and some of the tactics employed to either prevent (a primary IPM strategy) or cure the problem.

Bark Feeders and Wood Borers

This group of pests is dominated by beetles (Coleoptera) but there are also significant representatives in the wood wasps (Hymenoptera) and moths (Lepidoptera). In the majority of cases the life cycle includes a period of feeding in the cambial layer of the inner bark which may occupy some or all of the larval feeding phase of the pest. Wood borers include an additional period during which the pest feeds in the sapwood or, occasionally, in the heartwood. Some, such as the wood wasps (in the hymenopteran family Siricidae) oviposit directly in the sapwood using a long ovipositor capable of boring into the wood.

The nature of these pests means that they spend the majority of their cycle in well-protected situations under the bark or in the wood itself. This makes it impractical or impossible to employ insecticides, although the use of systemic insecticides (those taken up by the roots of the plant) is being employed to attempt eradication of the Asian longhorn beetle (*Anoplophora glabripennis*) in the USA. An IPM approach, therefore, concentrates on understanding the nature of the interaction with the host tree and making use of the natural defenses of trees to prevent successful attacks. Thus **Figure 2** concentrates on prevention by matching trees to the site both in terms of tree species and of the mixtures and ages of trees that are present on site. There is considerable variation in the susceptibility of tree species and of the seed origins of particular species in relation to the ability of bark and wood borers to successfully attack trees. Defenses are usually manifested in aspects such as the nature and quantity of resins/sap produced (poisonous and sticky), bark thickness, presence of inedible stone cells (lignified tissue) and poor nutritional value. Healthy, vigorous trees have increased levels of defensive traits and it is possible, over the long term, to select or breed tree species with improved resistance to insect attack. Usually, however, we only realize how effective these defenses are when trees are damaged or stressed in some way and

MANAGEMENT TACTICS – BARK FEEDERS AND BORERS

PREVENTION
- Match tree species to site
- Avoid soil aridity or waterlogging
- Avoid overmaturity
- Avoid root damage in nursery
- Avoid log piles, etc. near stands
- Avoid pruning/brashing/extraction damage

CURE
- Injection with systemic insecticide for high-value trees
- Remove infested material from site before re-emergence of pest
- Change tree species mix/age structure to favor less susceptible species/age

MANAGEMENT TACTICS – DEFOLIATORS

PREVENTION
- Avoid preferred tree mixtures
- Avoid highly susceptible provenances

CURE
- *Nurseries* – local spray of insecticide only when serious leaf loss is observed
- *Plantations* – plant less susceptible species/provenances
- change tree species mix/age structure to favor less susceptible species/age
- Apply microbial insecticides
- Use mating disruption to reduce breeding success

MANAGEMENT TACTICS – SAP FEEDERS

PREVENTION
- Avoid nonvigorous trees (see BORERS)
- NB – prophylactic spraying in nurseries should **not** be carried out
- Avoid highly susceptible provenances

CURE
- *Nurseries* – local spray of insecticide only when serious leaf loss is observed
- *Plantations* – plant less susceptible species/provenances

MANAGEMENT TACTICS – ROOT FEEDERS

PREVENTION
- *Nurseries* – Avoid root damage
- *Plantations* – Reduce availability of breeding resources for weevils
- – Encourage alternative non-crop food sources
- – Incorporation of insecticide granules in planting hole if termite losses are high

CURE
- *Nurseries* – Soil drench of insecticide for white grubs, cutworms if losses serious
- *Plantations* – plant less susceptible species/provenances

Figure 2 Management tactics for the four main categories of pest feeding strategy.

then become highly vulnerable to attack. For example, wind not only destroys trees directly but also weakens standing trees to make them more vulnerable to attack by bark and wood boring beetles. Fluctuations of the eight-toothed spruce bark beetle *Ips typographus* in European spruce forests tend to be linked to episodes of tree stress that allow the beetle to build up in weakened trees before commencing attacks on the remaining living trees. Wind damage in France in the early part of the twenty-first century not only resulted in massive destruction from the wind itself but also ongoing destruction from the enormous populations of *I. typographus* that built up on the weakened and freshly killed trees. This has knock-on effects that are not confined to the area where the problems occurred initially. *Ips typographus* can be moved in wood with bark still present to other areas of the world where it is not native, thus posing a threat to those countries; this tends to increase during an episode such as that just experienced in France.

Prevention is, therefore, a practical proposition in relation to ensuring that trees are as healthy and vigorous as possible. Cure is also feasible, although this tends to require rapid action to prevent the pest populations from building up to epidemic proportions. A simple 6-week rule is used in many countries, including the UK; felled or damaged wood must be removed from site within 6 weeks of origin. This strategy acknowledges that the trees will be attacked rapidly but, by removing them quickly before the beetles are able to complete a full generation, the numbers of emerging adults on site is reduced significantly. Of course, the material taken off site must be processed quickly to prevent the movement of the pest to a new location.

In the longer term, restructuring of a forest may offer the ultimate management tool to keep bark and wood boring beetles within acceptable damage thresholds (this will be discussed in more detail in relation to the mountain pine beetle, *Dendroctonus ponderosae*, later in this chapter). However, the general principles are based on knowledge of the factors that encourage epidemic beetle populations. In the cases of bark beetles, this is often linked to the stocking densities and ages of the trees in a forest. For some beetles, high stocking densities, contiguous presence of trees, and an even age structure will be favored; this is the case for *I. typographus*, which sustains high populations in large contiguous forest blocks. Other beetles tend to attack older, overmature trees that offer thicker bark and tend to be less vigorous than younger trees. This is the case for mountain pine beetle and other *Dendroctonus* species.

The above examples are concerned with beetles that attack and kill living trees. However, economic damage can also be suffered as a result of secondary effects of bark and wood boring beetles. This is manifested in staining of wood as a result of fungi introduced by the beetles during attack and also the opening of the wood surface to colonization by saprophytic fungi and other organisms in the environment. This is generally a cosmetic degrade in that, provided the wood is harvested within a few months of attack, there is no loss of structural value but the wood tends to be downgraded because of its visual degradation. Wood borers also cause loss of value as a result of downgrading of wood quality resulting from presence of grub holes in the wood, often accompanied by fungal staining. In most cases, unless the attack is particularly severe, there is no significant loss in timber strength. The 6-week rule is effective against these organisms, although the introduction of staining fungi at the time of beetle attack and oviposition makes it difficult to prevent this form of degrade. General forest hygiene can help, but this has to be balanced against the desire, in relation to enhancing biodiversity, to retain deadwood in forests.

Defoliators

As the name suggests, defoliators damage trees as a result of feeding on the leaves. Their effects on the tree can range from cosmetic through to complete defoliation and death. Severity varies with the type of tree being attacked and on the time of year, relative to the growth cycle of the tree, when the attack occurs. For example, in temperate conifer forests the degree of damage and tree mortality is dependent on whether the pest attacks soon after bud burst and on whether it restricts its feeding to the older foliage or includes the current year's growth as well. In Britain the introduced lodgepole pine, *Pinus contorta*, is attacked by a range of defoliators that are normally associated with the native Scots pine, *P. sylvestris*. The European pine sawfly, *Neodiprion sertifer*, attacks older foliage on young trees and can completely strip that resource from the tree, leading to significant loss of tree growth. However, because it does not attack the current growth, trees normally survive even repeated episodes of defoliation. By contrast, attacks by pine beauty moth, *Panolis flammea*, include both the current foliage and, later, the older foliage and can lead to extensive tree mortality. Both the sawfly and the moth are sensitive to the seed origin of the lodgepole pine and this can be exploited, at least in part, to reduce the severity of attacks. More northerly provenances, particularly Alaskan origins, tend to have much higher levels of tolerance. Restructuring of the forest is also effective, particularly against pine beauty moth. In this case, switching to Scots pine results in lower levels of attack, partially linked to tree quality but mainly due to the greater presence of natural enemies associated with Scots pine. Thus an integrated approach would be to increase the proportion of Scots pine in a forest block and to include open spaces and an uneven age structure to attract and retain natural enemies, particularly small mammals that feed on the overwintering pupae in soil. Direct intervention is also feasible for most forest defoliators, with the preference being for application of microbial pesticides of which *Bacillus thuringiensis* (*Bt*) is the dominant agent. This has been used extensively in both Europe and North America and in an unusual case, for complete eradication of an imported moth (white marked tussock moth, *Orgyia thyellina*) in an urban situation in Auckland, New Zealand. *Bt* is the agent of choice for gypsy moth (*Lymantria dispar*) in Europe and North America, for spruce budworm (*Choristoneura fumiferana*) in North America, and for nun moth (*Lymantria monacha*) in Europe. It is normally applied from the air and, increasingly, is applied using sophisticated spray technology that enables effective targeting and minimal loss to non-target areas. It is relatively specific in its action and is regarded as environmentally sound. Even more specific microbial agents are found among the baculoviruses that tend to be monospecific or restricted to a few species within given genera. They have proved effective against both temperate (e.g., pine beauty moth, pine sawfly, gypsy moth) and tropical (e.g., teak defoliator moth, *Hyblaea puera* – see case study) pests. In all cases, precise timing to deliver the agent to the most susceptible larval stages is essential to ensure the highest mortality and most rapid kill. The drawbacks of using baculoviruses relate, ironically, mainly to their high specificity so that each pest requires a specific facility to produce the virus, usually *in vivo*. However, the environmental benefits are very high and, in some cases (e.g., pine sawfly) the virus can maintain natural epizootics once introduced and, therefore, reduce or eliminate the necessity for multiple applications.

Sap Feeders

Sap feeders are predominantly in the order Hemiptera, which includes adelgids, aphids, cicadas, leafhoppers, plant bugs, plant hoppers, psyllids, scale insects, and whiteflies. Both the adult and immature (nymphs) stages feed on sap by inserting their specialized sucking mouthparts (stylets) into the phloem or sometimes xylem (in the case of cicadas) of virtually any part of the tree but predominantly buds, leaves, or in some cases, bark. Damage can be severe and can occasionally lead to tree death. In most cases the trees survive but there may be secondary effects in making the trees vulnerable to attack by other pests and in the production of honeydew, a sweet waste product that is then colonized by fungi such as sooty molds. This can be both unsightly and further restrict tree growth by reducing photosynthesis due to coverage or remaining foliage.

IPM of sap feeders is similar to bark feeders and borers in that trees that are nonvigorous are more vulnerable to attack and, therefore, should be avoided. Similarly, there are large variations in the genetic susceptibility of trees to attack and careful selection of tree species, seed origins, and mixtures should help to reduce the severity of infestation. It is not practical to consider use of insecticides in plantation forests both because of the environmental impacts but also because of the rapid recolonization that tends to take place that would tend to require reapplication at relatively frequent intervals. However, sap feeders are also problems in nurseries and, in these situations, it is possible to consider emergency applications of insecticides to supplement any other measures such as encouragement of natural enemies and use of vigorous, more resistant species and seed origins.

Root Feeders

By their very nature as feeders in a hidden environment, this category of pest tends to be less studied, particularly from the point of view of delivering IPM through detailed knowledge of the factors leading to pest outbreaks. Within this group there has been most emphasis on pests at the nursery stage of production, where both the impacts and identities of the pests are easier to record and develop strategies for management. In temperate areas, root damage tends to be linked to beetle or lepidopteran larvae in the main. Weevils, especially in the genus *Otiorhynchus* (the vine weevil, *O. sulcatus*, being the best-known European example) and chafers, including the genera *Melolontha* and *Phyllopertha*, tend to be the most damaging. Cutworms in the lepidopteran family Noctuidae are also serious pests in that the larvae are soil dwelling and can browse both on the root collar and on the plant itself. Other pests include bibionid flies in the genus *Bibio* and nematodes, especially *Dolichorhynchus* spp. Tropical pests in this category include termites and white grubs (Coleoptera: Scarabaeidae).

Impacts in plantations can be serious but, not surprisingly, the cause can be overlooked because of the cryptic nature of the niche occupied by the pests. Young plants can be affected by the majority of pests associated with forest nurseries, with the addition of some root dwelling aphids, gall wasps, and bark beetles. In such situations, the key to success is reducing breeding resources for the pests as well as intervention using chemical or microbial pesticides in extreme cases. However, there has been relatively little work on this group of pests and it is likely that their impacts are often not recorded or underestimated.

Case Studies

Within the large array of forest pests in both temperate and tropical forests, there has been relatively little development of IPM from first principles (*see* **Health and Protection**: Integrated Pest Management Principles). However, it is possible to illustrate how approaches that fulfil the aims of IPM have evolved for selected temperate and tropical pests. We have, therefore, selected examples from temperate and tropical forestry to cover only two of the main feeding strategies discussed earlier, i.e., bark feeders/wood borers and defoliators.

Great Spruce Bark Beetle, *Dendroctonus micans* (Coleoptera: Scolytidae)

This is a serious pest of spruce throughout its range in Eurasia (**Figure 3**). However, as indicated in **Table 1**, the beetle can be managed successfully using IPM principles, with particular emphasis on early detection and introduction of the specific predatory beetle, *Rhizophagus grandis* (Coleoptera: Rhizophagidae) (**Figure 4**).

Great spruce bark beetle is somewhat unusual in its attack strategy compared with some of the more damaging, aggressive bark beetles that are also in the

Figure 3 Adult great spruce bark beetle, *Dendroctonus micans*. Photograph courtesy of Forestry Commission Research Agency.

Table 1 IPM of great spruce bark beetle, *Dendroctonus micans*

Great spruce bark beetle, Dendroctonus micans	*Life cycle*	*Pest status and characteristics*	*Risk factors*	*Integrated pest management*
A dangerous pest of spruce trees in northern temperate forests from Asia to western Europe. It attacks living spruce trees causing damage to the main stem and large branches and can kill trees during outbreaks.	Depending on location and average temperatures, the beetle has a life cycle that lasts from 12 to 24 months. Generations are not synchronized and eggs, larvae, pupae, or adults can be found at any time of the year. Females excavate an egg gallery in the living bark, each laying up to 350 eggs. Larvae feed communally, responding to a larval aggregation pheromone, which is a mechanism to enable them to withstand the sticky and toxic resins produced by the tree as a defense against attack.	Regarded as a serious pest of spruce in newly colonized forests and in forests where trees are particularly vulnerable to attack. It is a solitary bark beetle that completes its life cycle in living trees without the need for mass attack to overcome tree defenses. There is no adult aggregation pheromone or associated symbiotic fungi to overcome tree defenses.	Overmature, stressed, or damaged trees are more vulnerable to attack, but even apparently fully healthy trees can be colonized successfully. Trees planted on unsuitable soil types are particularly vulnerable to attack, e.g., Sitka spruce planted on relatively sandy soil in Denmark were attacked and killed by great spruce bark beetle.	1. Surveys to detect infestations, especially during early colonization in previously uninfested forests. This is particularly important in forests geographically isolated from known infestations and which may not have been colonized by the specific predator *Rhizophagus grandis*. 2. Selective felling to reduce or remove incipient populations in a newly infested forest or to reduce expanding populations in forests lacking *R. grandis*. Felling concentrates on removal of overmature or damaged/stressed trees, but avoiding further damage to remaining trees. 3. Restriction of timber movement to reduce the likelihood of infested timber being moved to uninfested forests. This applies particularly to those regions where *D. micans* is a new incursion (e.g., Great Britain, Massif Central in France) and where active management to contain outbreaks is being carried out. 4. Biological control using the specific predatory beetle *R. grandis*. This is a natural associate of *D. micans* throughout the majority of its Eurasian range. However, new incursions of the bark beetle will tend not to have the predator present and mass rearing and release strategies have been developed. The predator has been successfully introduced to the Georgian Republic, southeast France, Great Britain, and Turkey and is a key component of an IPM system.

genus *Dendroctonus* (see mountain pine beetle below). Females mate with males in the same brood chamber prior to emergence as mature adults. This, combined with the very high bias towards females in each generation (as high as 40 : 1 female : male), means that each female is immediately capable of attacking a host tree without recourse to attracting a male. In addition, the beetle is very well adapted to withstanding the copious resin flow that is characteristic of wounded spruce trees. It is not, therefore, necessary for the beetle to use mass attack strategies to establish a successful brood, nor does it require the added factor of an associated fungus to help overcome tree defenses. Thus, it is a relatively solitary bark beetle in which each female can establish a successful colony. This may, at least partially, explain why it has been able to expand its range westward into previously unattacked regions of Europe; it has established in the Georgian Republic, southeast France, Turkey, and Great Britain during the latter half of the twentieth century.

IPM strategies that have been adopted across Europe have included surveys to establish the extent of new infestations and then, dependent on the extent of the infestations, a number of options for management. In some cases, sanitation felling, including complete removal of forest blocks, has been carried out. This tactic reduces population pressure on remaining uninfested trees and, depending on the timing within the normal rotation of the crop, may

Figure 4 Larvae of the specific predator, *Rhizophagus grandis*, feeding on larvae of their prey, *Dendroctonus micans*. The predators feed gregariously and leave the empty husk of their prey behind before moving on to the next prey item. Photograph courtesy of Forestry Commission Research Agency.

only have a small impact on revenue achieved. However, in areas where both timber products and ground stabilization are management aims, early felling is not a viable option. In some cases, particularly in Great Britain, discovery of new infestations has been early enough to establish a containment regime such that movement of felled timber from known infested areas is regulated so that only wood that has been debarked is approved for transportation to uninfested parts of the country. The latter, under European Union rules, has been designated a Protected Zone and, at least in Great Britain, appears to have successfully restricted long-distance dispersal of the pest for the 21 years since the strategy was adopted. Natural spread, by beetle flight, still takes place, however, and this has been at a rate of 3–5 km per annum in the British outbreak. As part of the IPM strategy, a peripheral zone survey has been carried out annually and this has both quantified natural spread and also enabled new pioneer populations of the beetle to be managed by a combination of selective felling and further introductions of the predator *R. grandis*.

The cornerstone of an IPM approach to great spruce bark beetle is rearing and release of *R. grandis*. This predator is specific to *D. micans* and has been released with great success in all the new infested areas in Western Europe. In Great Britain, a program of releases was initiated in 1985 and has continued annually since then by concentrating on new infestations found on the periphery or in new areas remote from the main infested zone. For example, a completely new infestation was found in Kent, well to the east of the known infested area and this has also been successfully treated with *R. grandis*.

Overall, the combined strategy for great spruce bark beetle has been remarkably successful in all locations where predator-based IPM approach has been adopted. In relation to other bark beetles, this example is unique in that silvicultural management is not the main component of an IPM approach. This contrast is well illustrated by the mountain pine beetle example discussed below.

Mountain Pine Beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae)

Mountain pine beetle is one of the complex of *Dendroctonus* species that affects conifer forests in North America. Within the current range of the pest in western North America, it is regarded as one of the most destructive, with particularly heavy attacks and tree mortality being observed on lodgepole pine, although other pines are affected to a lesser extent.

By contrast to the European relative *D. micans* discussed above, this species adopts an aggressive attack strategy that relies both on weight of numbers and on an associated fungus to overcome the resin defenses of living trees. Low-level populations of the beetle are maintained by opportunistic breeding in weakened and dying trees, brought about through a range of biotic and abiotic factors. For example, wind or fire damage can reduce tree defenses sufficiently for even small populations of the beetle to build up. These populations may be large enough to become aggressive and to mass-attack living trees in the vicinity, leading to further attacks in a positive feedback loop. This can result in enormous population increases and spread of the pest over large areas.

Extensive research into the factors that lead to population outbreaks has been carried out, culminating in a sophisticated decision support system based on sound IPM principles. This can be accessed on-line from the Pacific Forestry Centre in British Columbia, Canada which offers a range of mountain pine beetle planning tools, including an excellent risk rating computer program. The key elements are described in **Table 2**. It appears from the information gathered on the pest, that the problem is partially man-made in that there has been a tendency for retention of older age classes of trees, by a combination of avoidance during felling and through implementation of fire suppression programs. Stand age is one of the key elements of the stand susceptibility index (SSI), which is made up of the following components:

$$\mathrm{SSI} = A \times D \times P \times L$$

where A is stand age, D is stand density, P is percentage of susceptible pine, expressed as basal area, and L is location (latitude, longitude, elevation).

The factors are described briefly in **Table 2** but, as a general rule of thumb, trees greater than 80 years

Table 2 IPM of mountain pine beetle, *Dendroctonus ponderosae*

Mountain pine beetle, Dendroctonus ponderosae	*Life cycle*	*Pest status and characteristics*	*Risk factors*	*Integrated pest management*
The most destructive pest of mature lodgepole pine trees in western North America. Western white pine and ponderosa pine can also be attacked. Outbreaks develop rapidly and can result in very large areas of trees being killed within a relatively short time period. It mainly attacks living, older, large-diameter trees (overmature), with initial attacks in stressed, unhealthy trees.	Over most of its range, mountain pine beetle has a 1-year life cycle, although this may extend to 2 years at high altitudes and in the northern part of its range. Larvae overwinter and recommence feeding in the spring to pupate and emerge as adults in mid to late July. Adults range in size from 3.5 to 6.5 mm. Initial attacks are by females that bore into the bark and, once established, produce an aggregation pheromone that, initially, attracts females then males. Mating occurs under the bark, after which the females bore vertical egg galleries in which eggs are laid in niches on the sides; up to 75 eggs are laid per gallery, but females can produce up to 260 eggs. Eggs hatch quickly and larvae feed at right angles to the axis of the egg gallery. They feed until winter, usually reaching 2nd or 3rd instar.	A highly destructive bark beetle that initially attacks weakened trees, but then uses mass-attack strategies to overcome apparently healthy trees. The beetle carries a blue-stain fungus that also contributes to overcoming tree defenses and, combined with larval feeding in the cambium, can lead to tree death. Losses arising from attack by the beetle can be enormous; during the period 1997–2002 an area of 9 million ha was affected in British Columbia, leading to losses of 108 million m^3.	Risk rating systems have been developed for mountain pine beetle. These offer the prospect of managing outbreaks by reducing the risk factors. The key factors are: 1. Stand age. Beetles prefer older trees which are less resistant and, being bigger, are easier to locate. 2. Stand density. Beetles prefer moderate densities which offer suitable bark thickness and only moderate tree defenses. Microclimate is favorable to the beetles. 3. Percent susceptible pine (basal area). Beetles prefer large trees with thicker bark and well-developed phloem that provides protection and ample breeding resources. Higher stand densities reduce searching time for new host trees. 4. Location factor. Beetles are more successful when temperatures support a 1-year life cycle. This factor is driven by latitude, longitude, and elevation.	1. Stand susceptibility index. A product of the four risk factors. This is a component of the mountain pine beetle decision support system which uses susceptibility ratings for longer-term forest management. A computer model has been developed to aid this process and is freely available from Natural Resources Canada. 2. Risk index. Beetle pressure is a function of the size and proximity of beetle populations to the stand being assessed for management. This is based on the relative size (small, medium, or large) of the beetle infestation within 3 km of the stand at risk. This information is then used in a lookup table for distance to the nearest infestation to derive a beetle pressure index. Together with the stand susceptibility index, this is combined to give an overall risk index between 0 and 100. 3. Reduction of stand risk through IPM. Stand susceptibility can ~be altered through silvicultural management, with the aim being to break up large, homogeneous stands predominantly composed of large highly susceptible trees. This requires selective felling to thin 'from above' thus lowering average age, size, and stand densities towards an acceptable susceptibility index. Beetle pressure is not so easily managed but includes factors such as sanitation logging and debarking, fell and burn, or possibly insecticide use.

old and stand densities from 751 to 1500 stems ha^{-1} are intrinsically the most susceptible. Combined with the proportion of pines with diameters >15 cm, but especially >40 cm, and a factor to reflect temperatures calculated from an equation for longitude, latitude, and elevation, an overall SSI from 0 to 100 can be calculated, with 100 being the most susceptible. Further assessment of risk includes a beetle pressure index (B) derived from lookup tables for size of infestation (small, medium, or large) and distance from the nearest infestation, ranging from within the stand to >4 km away. A value of $B=1$ indicates a large infestation within the stand, whereas a value of $B=0.06$ represents a small infestation >4 km from the stand.

Prior assessment of risk is a key tool in longer-term management of the threat posed by mountain pine beetle. Prevention can be achieved by working towards a reduction in the SSI towards a nonsignificant value. This can be achieved by controlling the stocking density in young stands as part of planning for future protection. In older stands, SSI reduction can be achieved by specific thinning, particularly of larger diameter, older trees combined with felling to reduce the proportions of pine within stands. Naturally, care must be taken in restructuring stands to avoid 'high-grading,' which could leave only inferior trees that have lower silvicultural and environmental values and be more vulnerable to abiotic factors such as wind and snow damage. Careful management of stands to reduce stem densities below $750\,\mathrm{ha}^{-1}$ can still achieve an acceptable SSI and leave sufficient larger, old pines for biodiversity interest.

If it is not possible to prevent beetle build-up, then a number of direct measures can be employed to manage and reduce the beetle outbreaks. These include rapid removal of infested material to prevent re-emergence of the pest. Fell and burn, treatment with insecticides, mechanical debarking, and sanitation felling can all achieve these ends, although they can be difficult logistically. Use of semiochemicals to attract beetles to trap trees or to traps placed away from the potential host trees has also been employed, with some success.

Pine Beauty Moth, *Panolis flammea* (Lepidoptera: Noctuidae)

Pine beauty moth has a long history as a pest of Scots pine, *Pinus sylvestris*, in continental Europe where it has periodically resulted in severe defoliation and tree mortality. By contrast, the moth is not regarded as a pest on Scots pine in Great Britain, where it remains at low levels on this tree species throughout the country. The appearance of large, outbreak populations of *Panolis flammea* on the exotic north American lodgepole pine, *Pinus contorta*, in Scotland during the 1970s was, therefore, a surprise. However, it also illustrates, in a converse way, one of the key principles of an IPM approach to pest suppression because the planting of an exotic tree species on marginal sites presented the moth with a situation in which key factors preventing population build-up were absent (**Table 3**). Specifically, trees were planted on deep, poorly-drained peat soils that provided ideal conditions for overwinter survival of the pupal stage and were also relatively impoverished with regard to presence of natural enemies.

The moth outbreaks were worse on deep peat sites over moine schist underlying rocks and, within the seed origins of lodgepole pine, were more serious on southerly provenances. This combination of high suitability as a larval food source and the enhanced overwinter survival led to rapid population increases that outstripped the available food supply in some forests, leading to a population crash but only after the host trees had been killed. Research into monitoring methods and aiming also to establish the economic threshold for lethal attack, indicated that when densities of pupae, determined by pupal surveys carried out during the winter months, exceeded $15\,\mathrm{m}^{-2}$, tree mortality was likely. Further assessment of risk was carried out by egg surveys on trees in the same vicinity as the pupal surveys. When densities exceeded 600 eggs per tree, lethal damage was very likely and decisions on direct intervention had to be made. Surveys using the sex attractant pheromone of pine beauty moth provided useful corroborative data of population trends, but were not accurate enough or sufficiently in advance of egg hatch to allow control operations to be organized.

Early work on direct control of the moth concentrated on low-volume aerial application of the chemical insecticide fenitrothion. Although this was generally effective, considerable effort was put into finding more effective application technology, such that ultra-low-volume controlled droplet application is now the only method used for aerial application in Britain. This methodology employs spinning disc or spinning cage technology to deliver droplets within a relatively narrow range of sizes and which are captured by the target canopy zone with an efficiency exceeding 90%. Intervention has been carried out several times in Scotland, mainly using the insect growth regulator diflubenzuron delivered at volumes of $1\text{–}4\,\mathrm{l\,ha}^{-1}$. Tests with baculoviruses also proved effective, although the registration for the viral agent in Britain has lapsed.

In the longer term, management of pine beauty moth is likely to include choice of tree species and avoidance of particularly susceptible soil types. Mixtures of lodgepole pine with other conifer species will provide partial reductions in susceptibility, particularly when Scots pine, with a higher level of associated natural enemies present, is planted in mixture. Avoidance of highly susceptible provenances will also reduce the likelihood of lethal populations developing.

Teak Defoliator Moth, *Hyblaea puera* (Lepidoptera: Hyblaeidae)

Teak defoliator moth is the most important of a number of moths associated with teak and other trees and shrubs in the Orient and Australasia (**Table 4**). It is characterized by very rapid development, leading to multiple generations each year, depending on the average temperatures at a particular location. Although generations overlap at a regional scale,

Table 3 IPM of pine beauty moth, *Panolis flammea*

Pine beauty moth, Panolis flammea	*Life cycle*	*Pest status and characteristics*	*Risk factors*	*Integrated pest management*
A pest of older Scots pine in continental Europe and, although present at low levels on Scots pine throughout Great Britain, has become a pest of the introduced North American lodgepole pine (*Pinus contorta*) in Scotland. Extensive outbreaks can lead to tree mortality, especially on deep peat sites.	The moth has a singe generation per year which commences with adult emergence in the spring, usually in March or early April, followed by oviposition up to May. Egg hatch occurs by around mid-May, after which larval feeding commences in the current year's foliage. Later instars (3rd to 5th instar) feed on older foliage so that large moth densities can result in complete defoliation. Larvae drop to the forest floor to pupate in July and remain in the litter–soil interface until the following spring. Females produce a sex pheromone to attract the males.	Although pine beauty moth is a periodic and serious pest on Scots pine in Europe, with records of major outbreaks in Germany, Finland, Norway, and Sweden, it is innocuous on this tree species in Great Britain. Outbreaks leading to extensive tree mortality were noted on lodgepole pine in Scotland during the 1970s and have recurred periodically at 7–8-year intervals since that time.	In Britain the main risk factors are tree species and site type. 1. Tree species. As indicated above, outbreaks have been confined to lodgepole pine, which also shows considerable variation in susceptibility to infestation depending on seed origin. Thus, more southerly origins, such as Skeena River and South Coastal are more suitable hosts than northernly origins, such as Alaskan or North Coastal. This applies both to female choice for egg laying and to subsequent larval performance on the foliage. The low severity of attacks on Scots pine in Britain is linked to the greater action of natural enemies and the lower survival of pupae below Scots pine canopies. 2. Site type. Sites with deep, waterlogged peat soils support greater populations than other soil types, especially over the underlying rock type called moine schist. Although the trees themselves are not intrinsically more suitable, it appears that the underlying soil type is more suitable for pupal survival over winter.	1. Monitoring and economic thresholds. Monitoring of pupal numbers or adults in pheromone traps provides information on population cycles and also a threshold for possible direct control measures. Pupal densities of $>15\,\mathrm{m}^{-2}$ are likely to result in severe defoliation or tree death. If this threshold is exceeded, egg surveys are carried out to determine whether populations have exceeded the threshold for damage on a local basis; the threshold is >600 eggs per tree. 2. Reduction of stand risk. Planting of Scots pine as a replacement for lodgepole pine will reduce risk considerably. If sites are not suitable for direct planting with Scots pine, then a mixture of lodgepole pine with Sitka spruce may reduce risk, but this is not sufficient to eliminate the likelihood of lethal attack. Selection of northerly seed origins of lodgepole pine is also a positive measure to reduce risk. 3. Direct intervention. If the economic threshold is exceeded, then direct intervention may be the only option to prevent tree mortality. The targets for intervention are the 1st and 2nd instar larvae and, therefore, timing of spray application to coincide with 95% egg hatch is a core part of pesticide application. Currently the only insecticide that is employed is the insect growth regulator diflubenzuron. Promising results have also been obtained in application of a baculovirus. In both cases, the use of sophisticated ultra-low-volume controlled droplet application systems ensures that sprays reach the target area in the top one-third of the tree, with little contamination of nontarget areas.

each population has a discrete center in which all the stages from egg, through larvae and pupae to emergent adults are well synchronized. Repeat attacks on the same trees are uncommon because moth populations migrate *en masse* to new locations.

Management of teak defoliator moth is dependent on early detection of infestations if any direct intervention is being contemplated. Remote sensing has not been developed and, therefore, surveys tend to be based on visual assessments by trained survey teams searching for early stages of defoliation. There has been some success in using light traps, particularly solar powered versions that facilitate sensing in remote locations without local power supplies.

Table 4 IPM of teak defoliator moth, *Hyblaea puera*

Teak defoliator moth, Hyblaea puera	*Life cycle*	*Pest status and characteristics*	*Risk factors*	*Integrated pest management*
A serious pest of teak trees (*Tectona grandis*) in India, Myanmar, Sri Lanka, Java, Papua New Guinea, Northern Queensland, Solomon Islands, West Indies, and East and South Africa. Although the moth causes extensive defoliation, trees are not usually killed but serious losses of growth increment have been recorded, especially in younger plantation teak. Attacks take place during the growth period of teak in the monsoon season and follow the northward progression of monsoons.	The moth has a very short life cycle, which can be completed in as few as 19 days but could extend to 36 days, depending on temperature. This can result in up to 14 generations per year. Each generation commences with swarming of the adults and migration to suitable host trees where they lay their eggs, singly on the under surface, on young leaves (i.e., tender leaves). Eggs hatch quickly and the young larvae feed initially on the under surface and later within a leaf flap cut by the larva at the leaf edge. Larvae pass through five instars and then drop to the ground to pupate. Emergence of adults is followed by mass migration to another site suitable for a further generation. This migratory behavior is not fully understood and makes it difficult to predict where the next infestation is likely to occur.	Loss of growth is the main negative characteristic of this pest. Up to 44% loss of volume increment has been recorded in young plantations up to 9 years old, while an overall loss of 13% volume has been quoted for the crop to rotation age at 60 years. The migratory characteristics of the adults and the very rapid development from egg through larvae to pupae make it very difficult to predict when or where the next outbreak is likely to occur.	There is a complex of factors that affects the likelihood of outbreaks occurring at both the local and the regional scales. 1. Flushing of teak. Teak does not grow during the dry season, although it will do so if availability of water is sufficient, as has been demonstrated in intensive plantation systems with drip irrigation. In natural and plantation forests, flushing of teak is coincident with the onset of monsoon rains and, therefore, breeding resources are regionally determined by the northward extension of the monsoon each year. 2. Proximity of alternative host plants. The moths are known to spend the dry season on food plants in the natural forest, of which 29 species have been recorded. Adult moths also rest on the foliage of non-food understory plants. It is thought that populations move from the natural forest to teak plantations when teak flushes in the spring. 3. Wind and migration. Mass migration of moths is linked to local wind conditions so that some sites, with well-defined wind directions, tend to have localized intense outbreaks while others where wind is more diffuse have distributed infestations.	1. Monitoring and economic thresholds. The migratory nature of teak defoliator moth makes it difficult to monitor the arrival of new populations for management decisions on direct intervention. Ground spotting using teams of trained observers has been employed in India with some success. This relies on rapid determination of infestations and the feeding back of information to managers. However, this is not a routine process. Use of light traps has also been studied and provides some promise for future monitoring. 2. Reduction of stand risk. It is known that some varieties and species of teak have early flushing, which could render them less susceptible to attack, e.g., varieties, known as 'Teli' ('oily') flush at least 1 month earlier than normal teak and appear to escape infestation. 3. Direct intervention. Although the moth is susceptible to a variety of chemical insecticides, most effort in India has concentrated on assessing the potential of microbial agents. Great advances have been made in isolation, production, and application of a naturally occurring baculovirus. Success in application of this agent depends on early detection of newly established populations.

Development of a full IPM system is in its infancy but work at the Kerala Forest Research Institute has thrown light on both population dynamics, migratory behavior of the adults and, with scientists from the Forestry Commission Research Agency, use of naturally sourced baculovirus applied using ultra-low-volume controlled droplet application technology. In this sense, there are interesting parallels to the management of pine beauty moth in Scotland, despite the enormous differences in generation times of the two moth species. Application of baculovirus in antievaporant oil formulations, but without any additional protection against ultraviolet light, has proved to be effective against 3rd instar larvae on standing teak trees. The targeting of this larval stage provides a longer window of opportunity for application and also takes account of the movement of the larvae over the leaf surfaces, which increases the likelihood of encountering lethal dosages of virus. On the basis of the results obtained in field testing, a virus production facility has been constructed by the Kerala Forest Research Institute to develop further the use of baculovirus as a key component of IPM of this important pest. Further work is needed to solve the difficult problem of development of an effective monitoring and tracking system for migratory moth populations. Remote sensing and use of geographical information systems (GIS) interfaces and predictive models offer prospects for success in the future, the principles of which will be applicable to other moths with rapid generation times and dispersal between generations.

Mahogany Shoot Borer, *Hypsipyla* spp. (Lepidoptera: Pyralidae)

This complex of moths poses the single most important threat to the commercial production of mahogany timber anywhere in the world. Apart from on a handful of isolated Pacific Islands, such as Fiji, all members of the mahogany group (Swietenoidea) within the Meliaceae are attacked the world over. Tree genera include *Swietenia* and *Cedrela*, indigenous to Central America, *Khaya* from Africa, and *Toona* from Australasia, and all are attacked to a lesser or greater extent both naturally, and especially when grown in plantations. The taxonomy of the moth is obscure. For at least 100 years, book after book has reported the existence of merely two species, *Hypsipyla grandella* in the New World, and *H. robusta* in the Old World (all the way from West Africa to the Solomon Islands). Unlike the spread of certain tropical forest pests from a recognized point of origin (see *Phoracantha semipunctata*, below), *Hypsipyla* is likely to be indigenous throughout its global range, and hence there are undoubtedly numerous genetically distinct populations that are likely to represent a number of species in relatively local areas. This is clear from the varied activities which *Hypsipyla* species can be found exhibiting; though shoot boring is the only direct economic damage, larvae indistinguishable from each other can be found attacking the bark, shoots, fruit, and flowers at various stages of development on the same tree (**Figure 5**). Such a varied but as yet unquantified genetic diversity has vital implications for general insect ecology, host–tree interactions, and of course pest management.

Figure 5 Larva of *Hypsipyla* attacking a shoot on a mahogany tree.

Figure 6 A mahogany tree distorted into a forked shape after being attacked by *Hypsipyla* larvae.

The economic damage is centered around the larva's tunneling up and down the leading shoot of trees up to 4 years or so old. The leader then distorts and/or dies, with the result that the young tree becomes bent, forked, or otherwise misshapen (**Figure 6**). Marketable high-value mahogany must consist of a straight, single stem for at least the first 4 m of height, and since this height is usually reached within 4 years or even less in most species in most locations, the key to the IPM of *Hypsipyla* is to prevent larval attack from the nursery stage until this age or height is reached. After that, any further damage to the tree is not economically significant, though mature trees may act as reservoirs of pests which are then available to attack individual young trees or whole new plantations in the vicinity. Despite this seemingly easy goal, realizing this aim has proved to be hugely intractable over at least 50 years of trying. This type of insect is a classically low-density pest, in that it takes only one larva per tree to destroy any economic value; tolerance of even a low pest density is not possible in any but a small minority of situations where trees such as *Khaya*

Table 5 IPM of mahogany shoot borer, *Hypsipyla* spp.

Mahogany shoot borer, Hypsipyla *spp.*	*Life cycle*	*Pest status and characteristics*	*Risk factors*	*Integrated pest management*
A pest of many species of tropical mahoganies of such magnitude as to preclude the commercial and sustainable production of high-quality timber in almost all countries throughout Central and South America, Africa, southern and southeast Asia, and Australasia. Effective IPM programs would have huge economic significance for many tropical countries.	Eggs are usually laid singly on the upper leaves or shoots of young trees from the nursery stage onwards. The hatching larva soon tunnels into a leading shoot, constructing a tunnel which may eventually extend for 10 cm or more. Copious sap and resin exudes from an entrance hole somewhere along the length of the tunnel, which binds together boring dust and frass produced by the larva into an easily recognizable orange or brown mass. Pupation usually takes place inside the tunnel. The whole life cycle takes 1 to 2 months, depending on tree species and climatic conditions, and single trees may harbor several larvae at different stages of development.	The leading shoot usually dies and several buds are produced near or around the damaged tip. One or more of the resulting laterals become dominant. An unblemished stem of at least 4 m is required, which takes a minimum of 3 or 4 years to achieve with most host trees, but attacked trees routinely end up stunted, dwarfed, bent, or forked, any of which renders them economically valueless. Prevention of larval establishment in tunnels in the shoots is vital, since the probability of killing larvae once inside before appreciable shoot damage occurs is very low. The natural ecology of the genus in tropical forests is essentially unknown.	Risks vary from country to country and tree species to tree species. 1. Tree species. A large number of species within the Swietenoidea are attacked, and reliable genetic resistance has been hard to find. Host species exotic to a particular country may be less attacked by the indigenous borer populations than native species. Some tree species are better able to tolerate shoot attacks and grow straight subsequently than others. 2. Age. Trees of all ages may be attacked. Individuals between 6 months and 3 years old seem to be most heavily attacked, but this is linked to site and tree species. If a tree can be grown pest-free for the first 4 years of life, direct pest management is no longer required. 3. Site type. Trees growing on dry or conversely clay soils are more likely to be attacked. Soil aridity or waterlogging both increase attacks. Well-drained but moist soils in high rainfall areas show fewest attacks. Sites at the bottom of valleys appear to support fewer forked trees resulting from borer attack as compared with those on slopes or at the tops of hills. 4. Planting conditions. Trees planted in the open with no overhead shade suffer most attacks, and individuals in these locations may suffer most repeated attacks. However, trees in the open grow most rapidly, but they may be attacked when taller and older than those in shade. Trees in the shade of other vegetation, whether natural or	Much more detailed information is required about the pest's natural ecology and host–plant interactions. Various IPM components based on risk averse tactics may however be attempted. 1. Tree resistance and choice of species. Exotic species or those with the ability to grow straight after an attack may be preferable, especially those showing strong apical dominance. Fast growth especially for the first 3 years is very important. 2. Choice of planting site. Shady conditions should produce a higher percentage of unattacked trees, though they will grow more slowly. This growth rate may be improved if moisture is available. In some situations, this may be the only way to produce a few marketable individuals. Dry or waterlogged sites must be avoided. Line or enrichment planting may be preferable to plantations. 3. Biological control. Predators, parasitoids, and even pathogens are likely to be inadequate for the prevention of attack, or to remove the pest when it has established. 4. Chemical control: insecticides. Routine and regular contact poisons may prevent attack for the crucial first few years, but it is highly debatable whether or not such tactics are economically or environmentally viable. Systemic insecticides from soil-applied formulations are not sufficiently effective. 5. Chemical control: pheromones, etc. Producing the appropriate cocktail of synthetic sex-attractant pheromones has so far proved impossible. Suitable compounds derived either from a sex-attractant, or possibly from tree fruit and flower volatiles, for monitoring and/or mating disruption, have potential in theory.

Table 5 Continued

Mahogany shoot borer, Hypsipyla *spp.*	*Life cycle*	*Pest status and characteristics*	*Risk factors*	*Integrated pest management*
			seminatural forest or an early cash or tree crop, grow more slowly but show a higher percentage of nonattacked individuals, and if attacked at all, very seldom more than once. The chance of recovery to a straight stem after attack is higher with plants growing in shade. 5. Location. New plantings of individual trees or whole plantations, in the vicinity of older plantations, or natural forest which contains members of the Meliaceae, are more likely to be attacked. Extreme isolation will remove high risks for a while.	6. Sanitation and pruning. When a small proportion of trees in a stand are attacked, complete removal and destruction may be tolerable, at the early stages of establishment at least. When more than one lateral shoot becomes dominant after an attack on an otherwise vigorous tree, pruning of all but one shoot may eventually produce an acceptable tree (especially *Khaya*).

anthotheca in Mozambique appear to be able to regrow a straight stem after recovery from certain types of attack.

IPM of *Hypsipyla* species has yet to be achieved commercially (**Table 5**). If and when commercially viable tactics are devised, they are likely to be relatively specific to certain geographical locations or individual tree species. A single solution which works over all the tropics is unlikely to be practical, though some general tactics may be fundamental to all IPM programs.

Eucalyptus Longhorn Beetle, *Phoracantha semipunctata* (Coleoptera: Cerambycidae)

Phoracantha semipunctata is a native of Australia which began to spread throughout the world wherever eucalypts were grown from the early 1900s onwards. It is now firmly established almost everywhere, from South and Central America (including parts of the southern USA), through Africa and parts of Asia, and into various countries of the Mediterranean region. All species of *Eucalyptus* may be attacked, as well as other members of the same plant family (Myrtaceae), but some species, such as the widely planted *E. grandis*, seem to be particularly prone to attack (**Table 6**). The key to which host species are most preferred is undoubtedly linked to their ability to withstand arid conditions – *Phoracantha* is a classic 'secondary' pest where the host tree has to be stressed in some way before colonization can be successful. Essentially, the more drought-intolerant a species, the more likely it is to be attacked by *Phoracantha* as soon as soil conditions lose moisture. This is a particular problem for regions with dry seasons where water stress for trees is an annual event.

Adults mate on the bark of suitable host trees, and the eggs hatch into larvae which burrow under the bark and feed and grow between the inner bark and the sapwood surface (**Figure 7**), in much the same way as the bark beetles described earlier in this section. As the larvae grow, and especially when multiple attacks occur in one stem, ring-barking or girdling of the infested trees occurs, and the host dies. Final instar larvae tunnel into the wood and pupate in chambers prior to emerging through characteristically flattened or oval-shaped exit holes. The links between drought-stress and insect success are complex, but seem to be associated with the facts that young larvae have difficulty tunneling into trees with active sap flow. Once established under the bark, there is a further problem for them in that trees with high bark moisture in well-irrigated sites support little or no larval survival. Protection is, therefore, supremely simple – never plant drought-intolerant eucalyptus species in regions or sites where the soils may dry out.

Conclusions

IPM as an approach to sustainable forest pest management has many attractions. In particular, it is a knowledge-based system that involves development of a deep understanding of underlying processes. We have placed the emphasis on prevention of pest outbreaks so that planning for pest management

Table 6 IPM of eucalyptus longhorn beetle, *Phoracantha semipunctata*

Eucalyptus longhorn, Phoracantha semipunctata	*Life cycle*	*Pest status and characteristics*	*Risk factors*	*Integrated pest management*
A very significant mortality factor for many species of *Eucalyptus* planted virtually anywhere in the world, but only if the trees are significantly influenced by dry or arid soil conditions. Vigorous trees in normal moisture conditions should be resistant.	The whole life cycle takes between 2 and 12 months, depending on the climate. Between 10 and 100 eggs are laid in bark crevices (coarser-barked species of *Eucalyptus* enable beetle eggs to be better protected from predation and parasitism). Larvae hatch after 2 weeks or so and colonize the inner bark/sapwood interface where they can feed and grow for several months. Tunnels are typically flattened and filled with tightly packed frass. Pupation in the wood itself may last 10 days. Adult lifespans may reach 90 days or more, giving the pest ample opportunity to seek out the flowers of healthy trees for energy, and then new suitable, stressed, host trees over a large area of territory. The most significant mortality factor seems to be competition for food and space in overcrowded larval populations; the effects of natural enemies are not so important if host conditions are suitable for the pest.	The species is secondary; vigorous, nonstressed trees are not at risk. Infested trees are typified by thin crowns, yellowing leaves or considerable leaf fall. Patches of bark may be loose and easily stripped off to reveal larval tunnels and the insects themselves. Older attacks are identified by the exit holes of newly emerged adults. The numbers of trees killed in a stand or a plantation varies considerably. The beetle is only a minor pest in Australia (though recently it has become more serious in Queensland), but in other countries, where both beetle and tree are exotic, mortalities can reach over 40%.	1. Tree species. The most susceptible species of *Eucalyptus* include *E. globulus*, *grandis*, *nitens*, *saligna*, and *tereticornis;* more resistant ones include *E. camaldulensis*, *cladycalyx*, and *sideroxylon*. It is important to note that some of the most susceptible species are also the most desirable from a silvicultural perspective. 2. Age. Once trees reach a size at which the bark is thick enough to support the tunneling of beetle larvae, attacks can be expected. Eucalypts on rapid growth sites will reach such a stage within a very few years. 3. Site type and planting conditions. Dry soils, arid conditions, seasonal droughts, etc., coupled with eucalypt species that are inherently drought-intolerant, are in high-hazard categories. Even planting in localities where soil aridity is not usually a problem can be risky, so that individual trees on the tops of ridges in shallow sandy soils can be expected to be at high risk of attack. 4. Forest management. Log piles or larger thinnings and brashings allowed to remain in forest stands may easily provide the pest populations with the resources to initiate successful breeding and then to move on to attack even temporarily stressed adjacent trees. Similarly, trees allowed to remain in the plantations beyond their optimal harvesting age (overmature trees) also pose a threat by providing breeding material for *Phoracantha*.	1. Tree health care. The promotion of tree health and vigor by strict adherence to the risk 'rules' above will virtually guarantee that *Phoracantha* is not a problem. However, the provision of sickly, drought-stressed trees is an accident waiting to happen. Cure, once the trees have been attacked, is almost impossible. 2. Tree species choice. Avoid all susceptible species wherever possible. Highly desirable growth or timber characteristics are only useful if the trees survive to reach harvestable age and size. 3. Stand sanitation. Remove or process all potential sources of adult beetles, such as infested trees (young and overmature), log piles, thinnings, unbarked cut logs, etc. 4. Biological control. Both egg and larval parasitoids of *Phoracantha* are known, and vigorous research programs are being pursued, in California for example, to promote biological control. So far, natural enemy impact has not reached levels where mortality is reduced commercially in high-risk situations.

is included from the outset of any forest operations, from planting to harvesting. Although success in pest reduction can be achieved at any stage of the crop, the options available tend to diminish as the crop matures. For example, choice of less susceptible tree species or provenances is only an option that can be controlled fully during the establishment phase of a crop. Thereafter, adjustment to the balance of species, ages, sizes, and spacings of trees are viable options, provided that the processes employed to adjust the variables are understood. In this respect, the case study on mountain pine beetle provides a

Figure 7 Larvae of *Phorocantha semipunctata* and the damage they cause to eucalyptus bark.

good example of effective use of detailed biological and silvicultural information in offering options for both prevention and cure. Of course, it may not be possible to put the choices into practice in all cases, either for economic or for logistic reasons and, therefore, a high element of flexibility is needed to implement successful IPM.

The increasing trend to reduce the use of chemical pesticides provides further impetus to strengthen knowledge-based management systems, although no options should be ruled out until all variables have been considered and their consequences assessed. IPM is, therefore, not a quick-fix solution to pest management, but can provide sustainable long-term pest prevention or suppression with only limited recourse to repeated intervention, particularly with chemical pesticides. We can expect it to be an increasing part of forest pest management in the future.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Bark Beetles; Foliage Feeders in Temperate and Boreal Forests; Population Dynamics of Forest Insects; Sapsuckers. **Health and Protection**: Integrated Pest Management Principles.

Further Reading

Evans HF (2001) Biological interactions and disturbance: Invertebrates. In: Evans J (ed.) *The Forests Handbook. Volume 1. An Overview of Forest Science*, pp. 128–153. Oxford, UK: Blackwell.

Evans HF (2001) Management of pest threats. In: Evans J (ed.) *The Forest Handbook. Volume 2. Applying Forests Science for Sustainable Management*, pp. 172–201. Oxford, UK: Blackwell.

Evans HF, Straw NA, and Watt AD (2002) Climate change: Implications for forest insect pests. In: Broadmeadow MSJ (ed.) *Climate Change: Impacts on UK Forests*, pp. 99–108. Edinburgh, UK: Forestry Commission Bulletin 125.

Kogan M (1998) Integrated pest management: Historical perspectives and contemporary developments. *Annual Review of Entomology* 43: 243–270.

Pacific Forestry Centre (2004) http://www.pfc.cfs.nrcan.gc.ca/entomology/mpb/index_e.html

Speight MR, Hunter MD, and Watt AD (1999) *Ecology of Insects: Concepts and Applications*. pp. 1–350. Oxford, UK: Blackwell Science Ltd.

Speight MR and Wylie FR (2001) *Insect Pests in Tropical Forestry*, pp. 1–307. Wallingford, UK: CABI.

Tatchell GM (1997) Microbial insecticides and IPM: current and future opportunities for the use of biopesticides. In: Evans HF (ed.) *Microbial Insecticides: Novelty or Necessity?*, pp. 191–200. Farnham, UK: British Crop Protection Council.

Watt AD, Stork NE, and Hunter MD (eds) (1997) *Forests and Insects*, pp. 1–406. London, UK: Chapman & Hall.

Watt AD, Newton AC, and Cornelius JP (2001) Resistance in mahoganies to *Hypsipyla* species – a basis for integrated pest management. In: Floyd RB and Hauxwell C (eds) *Hypsipyla shoot borers in Meliaceae. Proceedings of an International Workshop held at Kandy, Sri Lanka, 20–23 August 1996*, pp. 89–95. Canberra, Australia: ACIAR.

Williams DW, Long RP, Wargo PM, and Liebhold AM (2000) Effects of climate change on forest insect and disease outbreaks. In: Mickler RA, Birdsey RA, and Hom J (eds) *Responses of Northern U.S. Forests to Environmental Change. Ecological Studies 139*, pp. 455–494. New York: Springer-Verlag.

Forest Fires (Prediction, Prevention, Preparedness and Suppression)

M Jurvélius, Forestry Department, FAO, Rome, Italy

Introduction

The problems and negative impacts associated with large-scale uncontrolled forest fires have increased worldwide over the past two decades. Globally an estimated 300–400 million hectares of forests and woodlands burn annually, emitting an estimated 9.2 billion tonnes of greenhouse gases; however, fire is a vital and natural part of some forest ecosystems, and a multitude of plants and tree species have become fire-dependent. In the early 1990s global changes had reached proportions that led to the global meeting in Rio de Janeiro (Earth Summit, 1992). Changes in the global fire dynamic and an increase in weather disturbances like El Niño have now created a growing awareness that fires are a major threat to many forests and their biodiversity therein, directly contributing to the climate change process.

In particular, tropical rainforests which were thought to be resistant to fires are now experiencing large-scale fires because of unsuitable silvicultural management practices. Globally 95% of all fires originate from various human activities; therefore these activities can be predicted and to some degree prevented well in advance. The difficulty lies in predicting and minimizing the impacts of the remaining 5% of all fires which are mostly caused by lightning.

There is therefore a need to develop proactive fire management strategies aiming at preventing fires from happening, i.e., allowing for the use of fire in useful or 'good' fires, but preventing destructive or bad fires (wildfires) from starting.

Fire preparedness includes a variety of activities with the aim of improving the capabilities to react in case of fire (reactive fire management strategies). Fire preparedness may have a totally different connotation depending on the country concerned.

Fire suppression or firefighting is the procedure or activity of mitigating the results of fire that already has started.

The fire itself consists of three separate components (oxygen, heat, and fuel) which are joined together. If any one of these components is removed, a fire will die.

The last step in extinguishing a fire is called mopping up, which ensures that the fire is dead and can no longer spread. After the fire is removed, the first silvicultural aspects can start, with the aim of rehabilitating the burned forest.

Background to Fire Management

The problems and negative impacts associated with large-scale uncontrolled forest fires have increased worldwide over the past two decades. By far the worst forest fires in recent times, in an economic sense, occurred between 2000 and 2003 in Australia and in the USA. However, the worst fires from an environmental, ecological, and climatological point of view took place between 1997 and 1998 when millions of hectares burned and smoke blanketed large regions of the Amazon basin, Central America, Mexico, and South-East Asia. Estimates suggested that these fires had an adverse impact on as much as 20 million hectares of forests worldwide, contributing to an estimated 13–40% of annual global carbon emission of fossil fuels, primarily through the burning of deep peat soils in South-East Asia. (Peat is a renewable natural resource which will start to replenish once the water table level of the burned area is returned to the level preceding the drainage.)

Global Warming

Contributors to the increase in global warming are found in deforestation, in shifting cultivation and land use changes which normally account for 20% of annual global carbon dioxide emissions.

Globally an estimated 300–400 million hectares of forests and woodlands burn annually, emitting an estimated 9.2 billion tonnes of greenhouse gases; however, fire is a vital and natural part of some forest ecosystems, and a multitude of plants and tree species have become fire-dependent over the last 15 000 years, due to human-induced fires.

Historical Use of Fire

Fire has been a part of the natural landscape for millions of years, forming these landscapes long before human beings arrived. The use of fire by hominids is thought to be 1.5 million years old. During the early period of human use of fire, fire was mainly developed to protect humans; later, fire was refined into a formidable weapon in hunting by perfecting techniques of prescribed or controlled burning. The Aborigines of Australia have skillfully been using controlled burning in northern Australia over an annual area of 30 million ha for more than 40 000 years to maintain the health and vigor of certain ecosystems, to produce seeds, to hunt, for signaling, and for warmth.

Expansion of the Concept of Fire Management

There is a growing awareness that fire needs to be managed at an ecosystem level. Forest fire management is a narrower concept, referring to the management of fires confined to forest areas; however, the majority of fires which currently destroy forests are caused by fires outside forests that spread into forests. Restricting fire management activities to forests is one reason why fire has become an escalating problem and a strong threat to present efforts in sustainable natural resource management.

Global Changes

The increasing global problem of wildfires (fires burning out of control) was first recognized in the early 1970s, when rapid population growth was experienced throughout the developing world; wildfires started to destroy forest vegetation and biomass, resulting in considerable soil erosion by wind and water.

Previously, fire had been used in shifting cultivation, with people frequently moving from one site to another, allowing for fallow periods between cultivations. However, due to population growth, this was no longer possible, and people developed semipermanent agriculture, coupled with traditional annual burning. In parts of Africa, the fire cycle was reduced from once every 10 years to an annual event. Most ecosystems, despite being adapted to fire, could no longer be sustained due to the drastic changes in fire frequency. Fire-adapted ecosystems have adapted to 'fire regimes' that are spaced out over a period of many years to allow for natural regeneration of the forest. If no fire occurs in these ecosystems, then many woody species do not regenerate, and frequent fires can destroy regeneration.

Fire and Food Security

In the savanna ecosystem, where 50% of all global fires occur, the importance of managing fires primarily centers on food security for local people rather than on the traditional concern to protect forest resources in the form of timber and wood products. The hundreds of millions of people living in this environment are traditionally called farmers, and yet they are using hundreds of different non-wood forest products (NWFP) for their daily survival, particularly in the poorest households.

Any uncontrolled fire occurring in this forest environment immediately results in local food shortage. The above areas, where forests are providing a large share of the local food, are largely devoid of global forest as well as fire data (**Figure 1**).

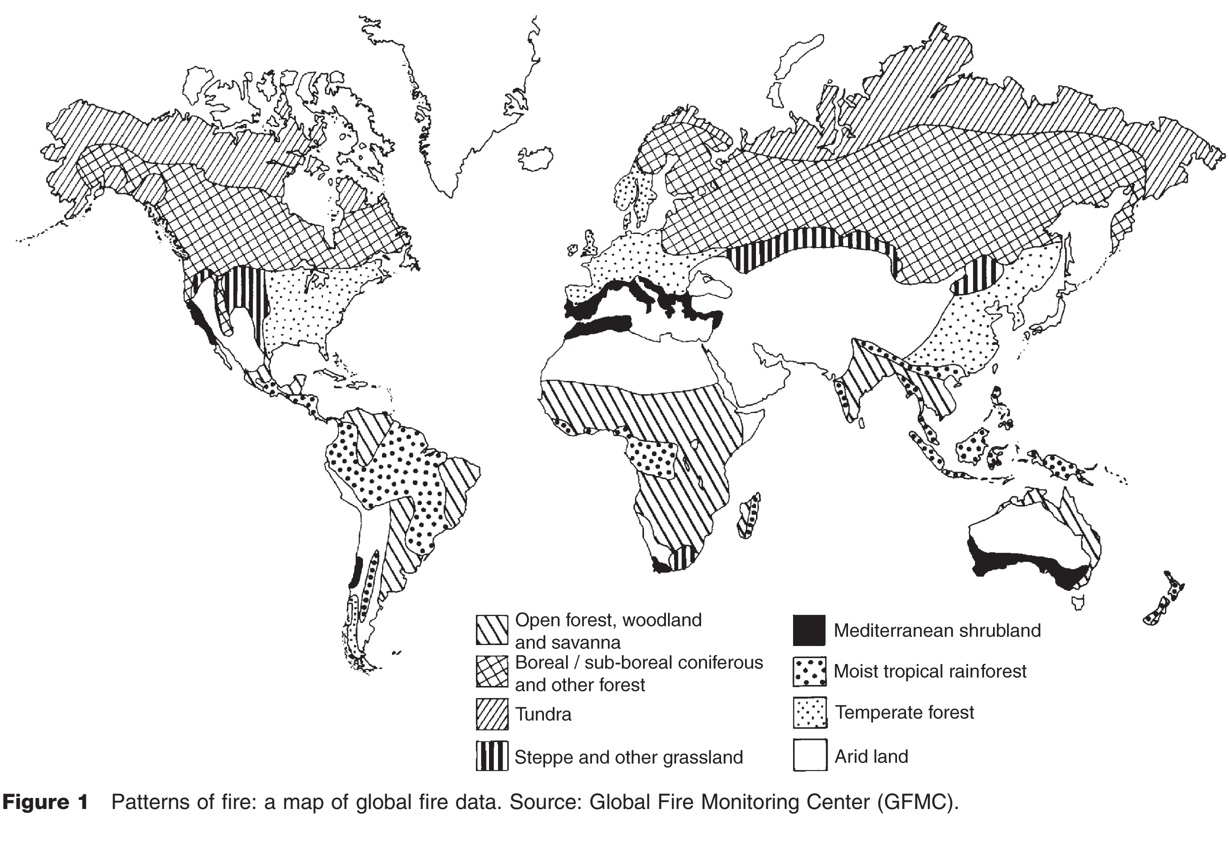


Figure 1 Patterns of fire: a map of global fire data. Source: Global Fire Monitoring Center (GFMC).

Fire Regimes

Fire regimes consist of three factors: fire intensity (severity), fire frequency (how often), and fire season (time of year). For example, the natural cycle of fire in southern Africa is 12 years, decreasing to 8 years towards equatorial Africa. The present almost annual widespread burning has already severely damaged many forest ecosystems in southern Africa, degrading them to bushland and gradually to open eroded seasonal grasslands.

Extensive fire research carried out for more than 45 years in Kruger National Park in South Africa and several other sites confirms the above assumption. The use of fire (silvicultural prescribed burning) needs to be more widely spaced out than the present 7-year cycle applied in the parks and other protected areas to maintain the natural composition of species.

Population Growth

Simultaneously, with the population growth in developing countries, other global changes in the shape of rapid industrialization also took place, resulting in severe industrial pollution and in the extended use of fossil fuels.

The combined effect of these trends resulted in a rapid increase in greenhouse gas emissions which in turn gradually started to change the traditional global weather patterns. This had a negative impact on human life and natural resources, affecting landscapes and livelihoods, causing haze pollution and deposition of unwanted pollutants, drought, insufficient food and widespread flooding.

In the early 1990s global changes reached proportions that led to the global meeting in Rio, Brazil. Changes in global fire dynamics and an increase in weather disturbances such as El Niño have now created a growing awareness that fires are a major threat to many forests and their biodiversity, and directly contribute to the climate change process.

Fire Prediction

Fire prediction used to be an activity carried out by the meteorological institution in each country; in a number of countries it is still the main source of fire information. However, in many countries the national weather service does not have the necessary facilities and field measuring points available for full coverage of the entire country, nor the communication equipment needed to relay information to the central unit. In these cases, fire predictions should be based on the existing database on local fire occurrence.

Silvicultural Factors Contributing to Changes in Fire Prediction

Tropical rainforests, in particular, which were once thought to be resistant to fire, are now experiencing large-scale fires due to unsustainable management practices. Contributing factors include:

- forest operations often prepare for a ready access into the forest in the form of immigration
- lack of management and protection of the forest after harvesting operations
- accumulation of forest debris after logging.

Temperate forests in the USA and eucalyptus forests in Australia, where controlled fires were deliberately suppressed for management and political reasons, are now experiencing devastating wildfires due to an unnatural accumulation of fuel exacerbated by extreme weather conditions. Large-scale fuel reduction programs are now underway in many regions to reduce the potential risk and severity of fires, especially in urban interface areas.

Human-Induced Fires

Globally, 95% of all fires originate from various human activities; these activities can be predicted and to some degree prevented well in advance. The difficulty lies in predicting and minimizing the impact of the remaining 5% of natural fires which are mostly caused by lightning. Predictions of lightning fires can also be made by special sensors measuring all lightning strikes; in recent fires in Australia more than 50 fires caused by lightning were burning simultaneously in Victoria.

Fire Danger Rating

Fire prediction is generally based on an approved national forest fire danger-rating system (FFDRS). The most widely applied system globally is the Canadian danger rating system which consists of two subsystems, fire weather index (FWI) and fire behavior prediction (FBP). Whilst weather application with current remote sensing facilities is quite accurate, FBP is still largely unknown in determining fire danger in many countries. Therefore the international fire community is presently carrying out extensive research in this area to develop reliable prediction systems. Another global dilemma soon crops up once fire prediction is accurately carried out; is the predicted fire a so-called ‘good’ fire that should be allowed to burn, or is it a ‘bad’ fire that should be extinguished? The Canadian FFDRS allows for ‘let burn’ decisions to be made by fire management due to low population densities in some geographic areas.

Fire Prevention

Since 95% of all global fires are caused by human activities it is clear that fire prevention strategies can play a key role in mitigating the global fire situation. There is a need to develop proactive fire management strategies aimed at preventing fires from happening, i.e., allowing fire to burn in useful or good fires, but preventing destructive or bad fires (wildfires) from starting and spreading.

Experience from a number of countries shows that fires cannot be prevented by tightening laws and regulations or by increasing supervision. Sustainable solutions require the ownership of local people in managing fires, including incentive schemes to assist the country in reducing wildfires.

Very little information and research exist about the reasons for forest and biomass fires; natural fires apart, it is difficult to prevent fires if the reasons why these wildfires occur are not known.

Efficient and effective fire prevention work requires networks to be established at global, regional, and national levels to exchange information on best practice raising awareness and training of multiple level and sectoral stakeholders.

Initial Steps in Fire Prevention

The work on forest fire prevention starts by finding out why wildfires burn; when the reasons are ascertained, then strategies for fire prevention can be prepared. Without knowing the reasons for burning, no effective awareness program can be developed, and it is impossible to direct the awareness program to the right target population (such as children, women, men, farmers, hunters, beekeepers, tourists, campers).

There are a variety of reasons why wildfires appear; more often than not, it is a question of ownership or proprietorship of the resource base – land or crop tenure rights can differ between formal laws and customary (traditional) laws. Success points to local management of forest and vegetation fires incorporating the transfer of 'fire ownership' (including land-use rights) from the government to local communities or villages. The term 'fire ownership' implies that, instead of being a top-down government law enforcement activity, fire management becomes a local activity in which fire is used daily as a management tool by the local population.

Integrated (Forest) Fire Management

Transfer of forest fire ownership needs to be coupled with an integrated forest fire management (IFFM) approach, in which a variety of stakeholders each have their agreed roles and responsibilities in managing fires.

The traditional role of agriculturists lighting fires and foresters extinguishing them no longer applies, yet this is still the approach in many countries.

IFFM requires stakeholders to have their agreed roles in fire prevention. At a national level there is a need to involve several ministries outside agriculture, forestry, and the environment, primarily the Ministry of Education and Ministry of Health. The entire population needs to be educated about the environmental functions of trees and forests, about their interdependence with rainfall, soil erosion, harvesting, and global climate. In addition, education and training are needed on the safe use of fire for a multitude of activities, primarily related to managing land and vegetation clearing.

Incentive Schemes

Incentive schemes in managing vegetation and forest are always coupled with the development of methods in how to quantify (in financial terms) the motivation and benefits for local people to participate in managing fires. In the savanna ecosystem, where 50% of all global fires occur, the importance of managing fires primarily centers on food security for local people rather than on the traditional concern to protect forest resources in the form of timber and wood products. These people are using hundreds of different NWFP for their daily survival, particularly the poorest households. The use of prescribed (controlled) fire to protect their resources is a sufficient incentive for the local population to manage their fires. In other parts of the world, people appreciate clean air, scenic beauty, or clean water as an incentive for managing fires, while others appreciate a safe environment surrounding their home, as in the USA lately.

Preparedness

Fire preparedness includes a variety of activities with the aim of improving the capability of reacting in case of fire. Fire preparedness requires the development of reactive fire management strategies.

However, fire preparedness may have a totally different connotation depending on the sociocultural and economic situation at the site of the fire. The preparedness also depends on whether the local people are using fire as a management tool in their daily lives or whether the fires in the area are caused by lightning, as two examples below illustrate.

In the USA

Fire preparedness at a district level may mean that budgets have been approved, funds allocated, staff trained, equipment tested, fuel reductions carried out, firefighters are on standby, the daily fire danger rating is monitored, and the general public have been informed about the fire weather. Satellite and aircraft are being used to monitor and detect any fires at the National Emergency or Alarm Centers. In addition cross-border collaboration agreements have been prepared and signed with a number of countries, such as Canada, Australia, and New Zealand; of annual operating plans/guidelines with these countries have been revised and signed.

In Namibia

The same preparedness at district level means that local communities have been applying prescribed burning or overgrazing using of cattle in strategic areas. Fuel breaks have been constructed in other areas, e.g., around local schools; the traditional chief or leader has been informed about the intention to burn a grass sward around the riverbank at road crossings. Locally, all farmers know the fire weather; additional training means that they understand the implications of fire weather and the skill of using fire in a controlled way, considering the local fire behavior and depending on the type of burn envisaged. Fire detection is generally carried out by local farmers gathering various NWFPs in the forest or herders moving their herds through the silvopastural areas. IFFM approaches mean that the local Council of Chiefs (Khuta) has been informed about the plans to burn some parts of the communal pasture areas at road crossings, thus expanding the activities (from silvicultural forest fire management) to silvopastural fire management. Traditional leaders in neighboring Botswana have also been informed about forthcoming planned burns.

Fire Suppression

Fire suppression or firefighting is the procedure or activity which mitigates the results of a fire that has already started.

Fire consists of three combined components (oxygen, heat, and fuel): removing any one of these components will kill a fire.

In forest fuel the principal inflammable component is carbon. The reaction is expressed as: carbon plus oxygen gives carbon dioxide plus energy ($C + O_2 = CO_2 +$ heat energy).

Suppression (combating fire) can be subdivided into tactics and techniques.

Tactics

Once remote sensing or aerial detection data and images/pictures have been analyzed it is time to start developing the tactical approaches to combat the fire.

Tactics describes how to use human resources, and equipment in the right place at the right time; techniques refers to the technical application in a given fire situation (handtools, pumps, water, foam, aircraft, etc.).

The tactics for extinguishing the fire depend on the resources at hand; it is difficult to remove or reduce oxygen, but it may partly be done. Air contains 21% oxygen; if this proportion is reduced to 15%, it will extinguish the fire. This is most commonly done in the case of light fuels whereby burned gases from the fire are fanned back towards the fire using a fire swatter, thus reducing the oxygen mix; or it may be done by putting sand or soil on top of fire. These methods both remove oxygen and remove heat (applying cold soil onto the source of the heat).

Heat is removed by applying a coolant, usually water, on to the fire; once the heat drops below 220–250°C, the fire will be extinguished.

Fuel can be removed in advance by applying prescribed burning or by other means, or during the fire by manual or mechanical means or by 'back-burning,' i.e., removing the fuel as well as oxygen in the face of the advancing fire.

Tactics will select the combination of activities that together will extinguish the fire. In industrialized countries, fire suppression methologies are well developed, including the use of aircraft, the use of chemical fire retardants mixed with water, and heat-spotting cameras. All these technologies require a high level of sophistication, heavy investment in equipment, and targeting the removal of heat.

In many tropical countries, especially developing countries, the peak fire season usually coincides with a water shortage. Therefore fire management is directly coupled with fuel management, using fire to remove fuel as well as extinguishing fire by lighting another fire. This involves concentrating on removing the fuel as well on a small-scale removal of oxygen, which again is only possible in light fuels.

Incident Command System

In the case of a fire accident or natural cause of fire, a reactive fire management strategy is needed to suppress these fires. Fire suppression is the straightforward action of killing the fire as fast and efficiently as possible.

Therefore it also resembles a military command system; the most efficient system developed for forest fire control is the so-called incident command system

(ICS) which may also be applied to all other kinds of national emergencies whether involving just a few or thousands of people.

Techniques

Firefighting aims to stop the running edge of the fire either by constructing a fire break (a line where all burnable material has been removed) or by applying water or a foam mixture to reduce the surface tension of water droplets for easier penetration into the soil or biomass layer (the same principle as used in dish-washing detergent).

The attack towards the fire may be direct or, if this tactic is not possible, the fire may be attacked indirectly from the flanks of the fire to narrow the moving fire edge. The fire may also be extinguished using another fire either to consume the fuel or the oxygen in front of the advancing fire; this technique is also called backfiring or backburning.

Mopping up

Mopping up is the last step in the process of extinguishing the whole fire. It may also imply that the fire in most of the area surrounding the burning spot is contained in such a way that the fire can no longer escape.

The size of the area to be mopped up depends on the fuel as well as on the location of any smouldering fires in relation to the perimeter of the area.

The failure or success of the entire fire suppression operation may depend on the quality of the mopping-up operation; in addition this may require lengthy patrolling of the burned area, even weeks or months after the initial fire was burning.

Once the fire is 'killed' and the danger is over, one may begin to plan the silvicultural rehabilitation of the burned area.

See also: **Ecology**: Human Influences on Tropical Forest Wildlife. **Environment**: Impacts of Elevated CO_2 and Climate Change. **Landscape and Planning**: Perceptions of Nature by Indigenous Communities.

Further Reading

FAO (2001) *Forest Resources Assessment (FRA-2000)*. Main report. Forestry paper 140. Rome, Italy: FAO. Available online at: http://www.fao.org/forestry/foris/webview/forestry2/index.jsp?siteld = 101&langld = 1.

FAO (2002) *Report on Legal Frameworks for Forest Fire Management: International Agreements and National Legislation*. Rome, Italy: FAO.

FAO (2002) *Guidelines on Fire Management in Temperate and Boreal Forests*. FFM/1. Rome, Italy: FAO.

Heikkilä T, Grönquist R and Jurvélius M (1993) *Handbook on Forest Fire Control*; *A Guide for Trainers*. FTP/21. Helsinki, Finland: Painotalo Miktor.

IFFN (2001) *International Forest Fire News* (ECE/FAO) no. 24 April 2001. Available online at: http://www.fire.uni-freiburg.de/iffn/iffn.htm).

IPCC (2001) *Inter-Governmental Panel on Climate Change, Summary for Policy-makers*. http://www.ipcc.ch/pub/wg25Mfinal.pdf

ITTC (International Tropical Timber Council) (2002) *Report* 33, vol. 24, no. 11. *Committee on Reforestation and Forest Management; Policy Issues: Forest Fires; Community-Based Approaches; A Tool for Sustainable Forest Management* (SFM) *to Solve Socio-cultural Causes of Fires*.

Max-Planck-Institut für Chemie, Abteilung Biogeochemie (1994) *Feuern in der Umwelt; Ursachen und kologishe Auswirkungen von Vegetationsbränden, Konsquenzen für Atmosphäre und Klima*. Freiburg, Germany: Max-Planck-Institut.

NRE (Department of Natural Resources and Environment, Australia) (2000) *Fire and Victoria's Parks and Forests, Using Fire to Manage our Parks and Forests, Effects of Fire on Victorian Bushland Environments; Information Package*. Victoria, Australia: NRE.

Trollope W (1998) *Effect and Use of Fire in the Savanna Areas of Southern Africa*. Alice, South Africa: University of Fort Hare.

USDA (United States Department of Agriculture) (1999) *Proceedings of the Symposium on Fire Economics, Planning, and Policy: Bottom Lines*. General technical report, PSW-GTR-173. San Diego, CA: USDA.

Virtanen K (2000) *An investigation of Attitudes to Forest Fires*. Namibia: Katima Mulilo.

HYDROLOGY

Contents

Hydrological Cycle

L A Bruijnzeel, Vrije Universiteit, Amsterdam, The Netherlands

Introduction

The notion that a good forest cover positively influences climatic and soil conditions, and therefore the amount of water flowing from forested areas, is deeply ingrained in the minds of foresters and the general public alike. Whilst the perceived positive hydrological effects of forests have come under scrutiny in recent decades, the contention that, of all the influences of a forest, that upon the supply of water in streams and upon the regularity of their flow is most important to human economy, remains as valid as ever. With populations rising explosively in some parts of the world, and per capita demands of water increasing in others, optimization of water resources (both streamflow and groundwater reserves) is becoming increasingly important. Also, rising demands for timber products require the establishment of large areas of fast-growing plantation forests, often on land that is currently not forested. Coupled with the continued indiscriminate clearing of the world's natural forests, which in many areas serve as the traditional suppliers of high-quality water, the associated degradation of soil and water quality due to erosion, and the possibility of less dependable precipitation inputs due to climate change, a sound understanding of the hydrological functioning of forests is arguably more important than ever before. In short, water and forests are two natural resources that are inextricably linked. The study of these linkages is called forest hydrology, including any changes in either that are brought about by natural or man-induced forest disturbance.

This article aims to review the current state of knowledge with respect to the chief hydrological processes taking place in forests and how these affect amounts and timing of streamflow. In addition, the effect of forest on amounts of precipitation (a continued bone of contention) is explored. In doing so, the principal focus will be on the more humid parts of the world (both temperate and tropical).

The Forest Hydrological Cycle

The principal features of the forest hydrological cycle are illustrated in **Figure 1**. Rain (P) is the main precipitation input to most forests, supplemented by snow at higher altitudes and latitudes, and by 'occult'

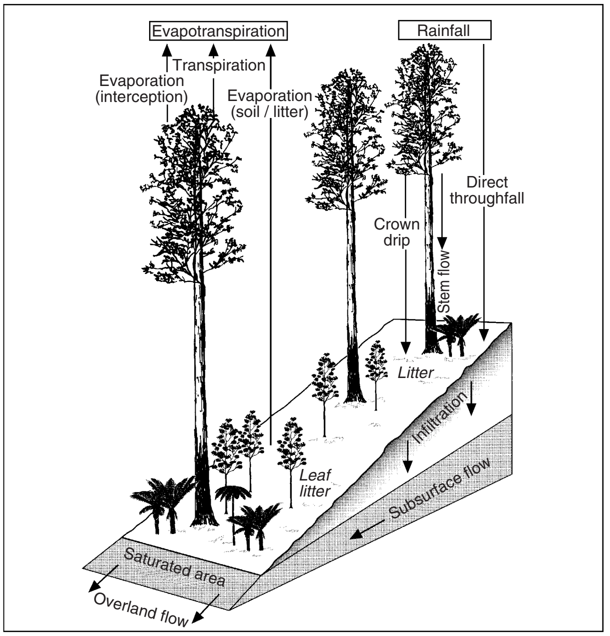


Figure 1 Key hydrological processes on a forested hillslope. Reproduced with permission from Vertessy R *et al.* (1998) *Predicting Water Yield from Mountain Ash Forest Catchments*, CRCCH Industry Report no. 98/4. Canberra: Cooperative Research Center for Catchment Hydrology.

precipitation (fog) in coastal or montane fog belts. A small part of the precipitation reaches the forest floor directly without touching the canopy: the so-called 'free' or 'direct' throughfall. Another (usually small) part travels along the branches and trunks as stemflow *(Sf)*. A substantial portion of the precipitation intercepted by the canopy is evaporated back to the atmosphere during and shortly after the storm (called interception loss, *Ei*), whereas the remainder reaches the soil surface as crown drip once the storage capacity of the canopy has been filled. Because direct throughfall and crown drip cannot be determined separately in the field, the two are usually taken together and referred to as throughfall (*Tf*). The sum of throughfall and stemflow is commonly called net precipitation and is usually substantially smaller than amounts of incident precipitation unless there are significant (unmeasured) contributions by occult precipitation. Thus:

$$Ei = P - (Tf + Sf) \quad (1)$$

If the intensity of net precipitation reaching the forest floor exceeds the infiltration capacity of the soil, the unabsorbed excess runs off as Hortonian or infiltration-excess overland flow (*HOF*). Due to the generally very high absorption capacity of the organic-rich topsoil in most forests, this type of flow is rarely observed in undisturbed forest unless there is an unusually dense clayey substrate or an excessive concentration of stemflow. Not all of the water infiltrating into the soil emerges as streamflow. A large part is taken up by the roots of the vegetation and returned to the atmosphere via the process of transpiration (*Et*). The term evapotranspiration (*ET*) is used to denote the sum of transpiration (evaporation from a dry canopy), interception loss (evaporation from a wet canopy) and evaporation from the litter and soil surface (*Es*). The latter term is often small, especially in dense forests where little radiation penetrates to the forest floor, humidity is high and the air virtually stagnant. Thus:

$$ET = Ei + Et + Es \quad (2)$$

where the respective terms are expressed in millimeters of water per unit of time (hour, day, month, or year).

If unobstructed by impermeable layers, the water not taken up by the vegetation will percolate vertically to the groundwater table and then move laterally to the nearest stream as groundwater (**Figure 1**). Alternatively, percolating water is deflected upon meeting a layer of impermeable subsoil or rock. It is then called 'throughflow.' Such water drains slowly and steadily, thus accounting for the 'delayed flow' or 'baseflow' of streams. In seasonal climates, baseflow reaches a minimum in the dry season and this is usually referred to as dry-season flow or simply 'low flow.' During rainfall, infiltrated water may take one of several routes to the stream channel, depending on soil hydraulic conductivity, slope morphology and soil wetness (**Figure 2**). So-called saturation overland flow (*SOF*) is caused by rain falling onto an already saturated soil. This situation typically occurs in hillside hollows or on

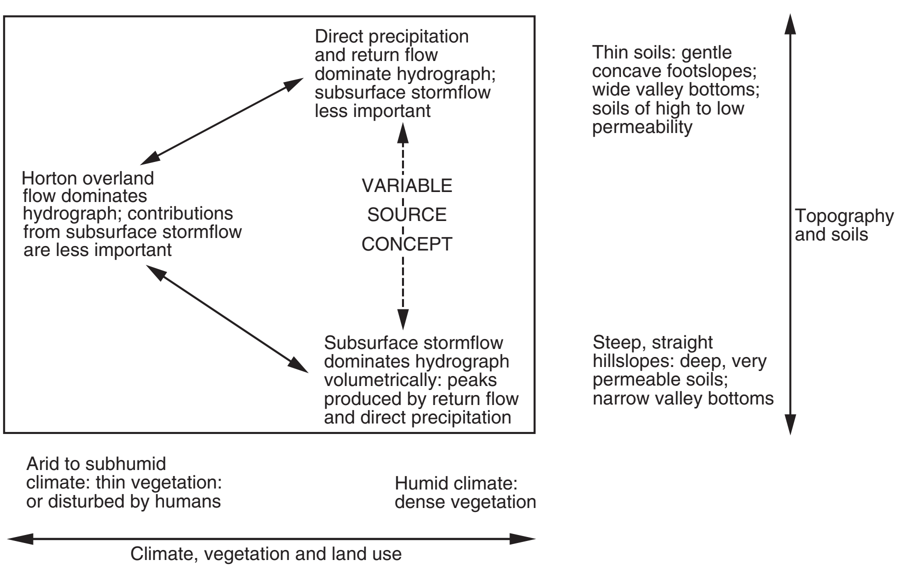


Figure 2 Schematic representation of the occurrence of various streamflow generating processes in relation to their major controls. Note: direct precipitation and return flow are equivalent to saturation overland flow, *SOF*. Reproduced with permission from Dunne T (1978) Field studies of hillslope flow processes. In: Kirkby MJ (ed.) *Hillslope Hydrology*, pp. 227–293. Chichester, UK: © John Wiley and Sons Ltd.

concave footslopes near the stream where the throughflow tends to converge and so maintains near-saturated conditions (**Figure 1**). Occasionally, widespread hillside *SOF* (i.e., outside concavities and depressions) has been observed during and after intense rainfall in the tropics in places where an impeding layer is found close to the surface. Rapid throughflow during storms (subsurface stormflow, *SSF*) usually consists of a mixture of 'old' (i.e., already present in the soil before the start of the rain) and 'new' water traveling through macropores and pipes. As a result of contributions by *SOF*, *SSF*, and in extreme cases *HOF*, streamflow usually increases rapidly during rainfall. This increase above baseflow levels is called 'stormflow' or 'quickflow' whereas the highest discharge is referred to as 'peak flow' (**Figure 3**). Peak discharges may be reached during the rainfall event itself or as late as a few days afterwards, depending on catchment characteristics, soil wetness, and the duration, intensity, and quantity of the rainfall. The total volume of water produced as streamflow from a catchment area over a given period of time (usually a month, season, or year) is called 'water yield.'

The interlocked character of the chief components of the hydrological cycle is summarized by the catchment or site water budget equation:

$$P = Ei + Et + Es + Q + \Delta S + \Delta G \qquad (3)$$

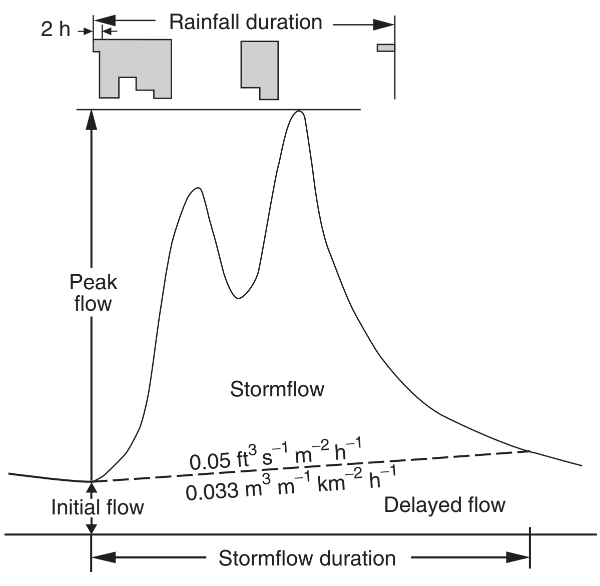


Figure 3 Storm rainfall, stormflow, peak flow, and other variables derived from measured streamflow and rainfall. The dashed line separating stormflow from delayed flow is arbitrary but often used in forest hydrology. Reproduced with permission from Hewlett JD and Doss R (1984) Forests, floods, and erosion: a watershed experiment in the SE Piedmont. *Forest Science* 30: 424–434.

where Q is amount of streamflow or drainage to deeper layers, ΔS change in soil water storage, and ΔG change in groundwater storage, with the remaining terms as defined previously. All values are expressed in mm water per unit of time (hour, day, week, month or year). Note that ΔS and ΔG may assume positive (gain) or negative (loss) values. In view of the seasonal cycle of soil water and groundwater storages in many areas, the values of ΔS and ΔG tend to approach zero on an annual basis. The annual water balance thus often simplifies to:

$$P = ET + Q \qquad (4)$$

Forests and Rainfall

There is a deeply ingrained notion that forests increase precipitation. Indeed, the higher amounts of rainfall that are usually measured in forested uplands or forest clearings compared to adjacent lowlands or agricultural areas would seem conducive to this idea. However, all early reviewers of the subject concluded that enhanced rainfall in forested areas could be attributed either to topographic effects (cloud formation in the uplands being greater simply because of the forced atmospheric cooling of rising air), or to differences in rain gauge exposure to wind (the gauges being more sheltered in forest clearings and usually more exposed in cleared terrain).

Two basic approaches are usually followed to study the effects of land cover on rainfall: (1) trend analysis of long-term rainfall records in combination with simultaneous information on (changes in) land use; and (2) computer simulation of regional (or global) climates under imposed land cover conditions (usually forest versus pasture). Circumstantial evidence for (at least temporarily) decreased rainfall abounds in the literature but such reports have rarely taken into account the large-scale cyclic fluctuations in rainfall that are known to be governed primarily by changes in ocean currents and solar activity. Investigators applying rigorous statistical tests to detect changes in rainfall have usually found trends to be either absent or nonsignificant, or at best only weakly significant. However, although large-scale deforestation has thus never been shown to lead to actual reductions in annual rainfall totals, there is increasing evidence of rainfall being reduced at the onset and end of the rainy season in monsoonal areas. Likewise, changes in the timing of cloud formation during the day and reductions in cloud cover after large-scale forest removal have been detected using satellite images, both under temperate and tropical conditions.

According to atmospheric modeling studies of these phenomena, such changes in cloud formation and rainfall may, at least partly, be caused by the large-scale replacement of forest by agriculture. Forests are aerodynamically rough, which means that they slow down the movement of air. As the air masses behind continue to flow in, the air above the forest is pushed up to greater heights. Also, tall and dark forests absorb more solar radiation than do short grassland or crops and they are therefore capable of returning more moisture to the atmosphere through evaporation. Provided the forested area is large enough (>1000–$10\,000\,km^2$), these two processes lead to enhanced atmospheric humidity and cloud formation over forested terrain.

Since it is impossible to compare differences in rainfall at a site under conditions with and without forest at the same time, computer simulations of the changes in climate associated with land cover change are on the increase. Many simulations have assessed the climatic consequences of the large-scale conversion of the Amazonian rainforest block to pasture. One of the more sophisticated of these simulations predicted an average increase in temperature of 2.3°C over Amazonia and a reduction in annual rainfall of 5–7% (110–150 mm $year^{-1}$), depending on the parameterization of the model. In reality, the actual change in rainfall may be expected to be smaller because the secondary vegetation that often replaces the original forest is much more forestlike than the more extreme grassland scenario used in the simulations. Elsewhere, oceanic influences on climate and rainfall may be more pronounced than in Amazonia (e.g., in Southeast Asia) and this will tend to further moderate the effect of land cover change.

Forests and 'Occult' Precipitation

Where fog impacts a forested area, particularly where the fog persists in the form of a montane cloud belt or coastal fog, additional moisture is intercepted by exposed plant surfaces (or any other obstacle) and precipitation may occur in the form of 'occult' or 'horizontal' precipitation, which is not recorded by rain gauges placed on adjacent open ground (hence the term 'occult'). An extreme example is found along the arid coast of northern Chile where the frequent occurrence of fog drifting in from the ocean has given rise to the development of a patchy forest that, in the near-complete absence of rainfall, thrives almost exclusively on fog water. Similarly, the famous redwood forests of California derive a considerable portion of their moisture (25–50%) from fog blown in from the ocean. At favorably exposed, windy locations the extra inputs stripped from the fog by trees (conifers especially) may reach hundreds of mm per year. Likewise, on wet tropical mountains, so-called 'cloud forests' are found. Net precipitation totals in such forests are often close to, or exceed incident rainfall. Because forest water use (evaporation) under wet, foggy conditions is reduced as well, headwater catchments with cloud forests are veritable water producers. There is circumstantial evidence that the clearing of these fog-ridden forests leads to diminished streamflow totals, particularly during the dry season when inputs by ordinary rainfall are usually low but those by fog at a maximum. Also, ridge-top cloud forests are under siege of global warming which tends to lift the average height of the cloud base.

Quantification of amounts of fog stripped by a forest is notoriously difficult, particularly if the fog occurs together with (wind-driven) rain. The usual approach is to compare amounts of net precipitation (often *Tf* only) beneath the trees with rainfall measured in the open, or to subtract the latter from the catch obtained with some kind of fog gauge. Fog gauge designs are numerous and include wire 'harps,' wire mesh cylinders, polypropylene nets, and louvered metal gauges, but none of these can mimic the complexities of a live forest canopy. As such, they are best used for comparative purposes (site characterization) (**Figure 4**). The throughfall method essentially provides an estimate of net fog drip as it includes an unmeasured amount of water lost to evaporation from the wetted canopy. In addition, the results are site specific. However, progress with the unraveling of fog–forest interactions is being made through the use of physically based deposition models and the often contrasting stable-isotope signatures of rain and fog water.

Figure 4 Wire harp to estimate occurrence of fog and wind-driven rain in northern Costa Rica. Photograph courtesy of K.F.A. Frumau.

Forests and Evaporation

Rainfall Interception Loss

Arguably, no subject in forest hydrology has received as much attention as the measurement of interception loss (*Ei*, i.e., the first major component of forest evapotranspiration *ET*), or rather: of throughfall (*Tf*) and stemflow (*Sf*) (see Eqn [1]). The following broad generalizations can be made:

- *Ei* is a function of incident rainfall (*P*) and typically declines more or less hyperbolically when expressed as a percentage of *P*
- both *Ei* and the canopy storage capacity (*S*) are generally larger for coniferous forests than for deciduous forests (growing season)
- winter values of *Ei* and *S* for deciduous forests are roughly half to two-thirds of summer values
- *Sf* generally constitutes only a modest fraction of *P* (typically $<3\%$), with the exception of smooth-barked species such as beech or maple (5–12%) or young trees
- *Ei* and *S* increase with stand density
- snowfall interception storage by coniferous canopies exceeds that for rainfall.

Usually, the results of interception studies are expressed as a percentage of gross rainfall *P*. Comparisons between different studies, even for one and the same species and age class, are rendered difficult, however, because of the more-or-less unique character of each forest stand in terms of density, undergrowth, exposure to prevailing air streams, and rainfall regime. An additional problem is that the notoriously uneven distribution of *Tf* (both in space and time) requires rigorous sampling strategies that are not always achieved. Spatial variability of *Tf* tends to increase with forest density, i.e., it is greater in summer than in winter for deciduous stands and much larger in tropical rainforest than in temperate plantations (**Figure 5**). The vegetation in most natural forests is made up of a mosaic representing different stages of growth, ranging from young rapidly growing trees in gaps to old-growth emergent trees on the decline. Throughfall in coniferous plantations has been shown to decrease with stand age (i.e., *Ei* increases) but in natural forests *Ei* may peak after about 30 years, with a gradual decline as the forest matures. At the micro scale, *Tf* often increases away from the trunks to reach a maximum just within the perimeter of the crown. In view of the high spatial variability of *Tf*, the use of a large number of rain gauges that are placed randomly underneath the forest canopy is usually recommended for adequate measurement. The use of regularly relocated ('roving') gauges is generally considered to give the best results as this allows a more representative sampling of so-called 'drip points' (i.e., places where $Tf > P$, often because of funneling of water by a particular configuration of branches) (**Figure 5**).

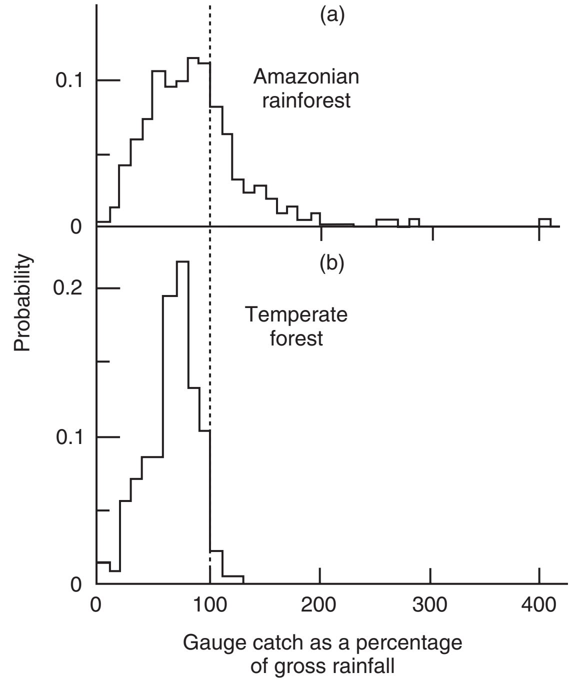


Figure 5 Probability distribution of throughfall gauge catch in a random grid expressed as a percentage of coincident gross rainfall for (a) Amazonian rainforest and (b) a pine forest in the UK. Reproduced with permission from Lloyd CR and Marques AdO (1988) Spatial variability of throughfall and stemflow measurements in Amazonian rainforest. *Agricultural and Forest Meteorology* 42: 63–73.

Figure 6 summarizes results for a number of British interception studies. Despite the large variation encountered within the deciduous forest group, *Ei* in deciduous stands is invariably lower than in coniferous forest for the same amount of *P*. A similar contrast has been noted for coniferous and (semi-) deciduous plantations such as teak and mahogany in the tropics. Although evergreen, the relatively light crowns and smooth stems of (young) eucalypt plantations intercept only modest quantities of rainfall (typically about 10–15%), both in the tropics and in their native Australia. Despite their much greater leaf surface area, lowland tropical rainforests intercept similarly modest amounts of rainfall. This reflects the typically short duration and high intensity of rainfall under such conditions as well as a relative abundance of drip points (**Figure 5**) and small amounts of stemflow (typically $<2\%$). There is reason to believe that interception assumes greater importance under 'maritime' tropical conditions

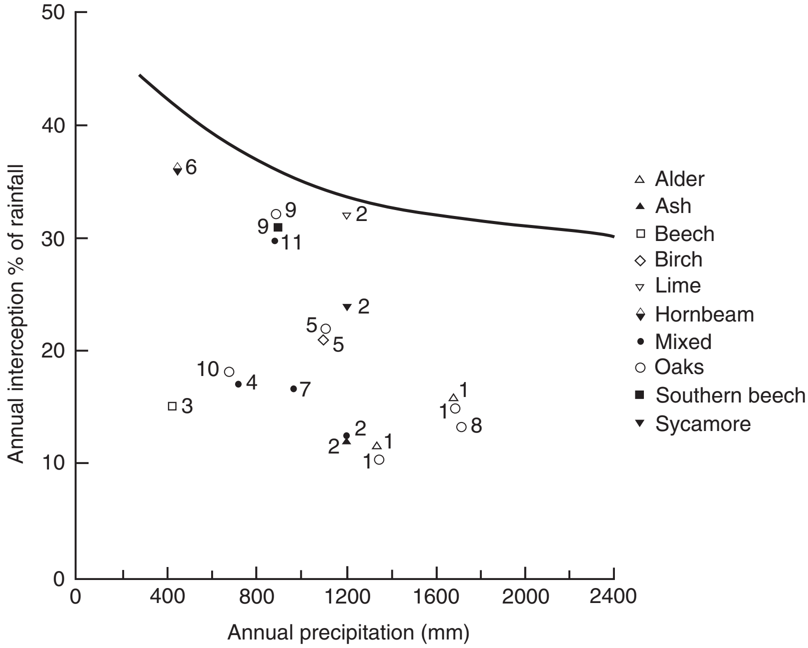


Figure 6 Annual interception loss (%) versus annual rainfall for European broadleaved trees. The solid line represents the annual interception percentage for coniferous forests in the UK. Reproduced with permission from Roberts JM (1999) Plants and water in forests and woodlands. In: Baird A and Wilby R (eds) *Eco-Hydrology: Plants and Water in Terrestrial and Aquatic Ecosystems*, pp. 181–236. London: Routledge.

($Ei > 25\%$), however, although reports to that effect may have been confounded by high spatial variability.

Interception by the Litter Layer

It has been argued that evaporation from the litter layer (*Es*) may constitute a significant component of overall interception loss and should therefore be determined separately. Litter evaporation has been shown to reach 2–5% of incident *P* in hardwood stands in the eastern USA (*c.* 50 mm year^{-1}), with the highest rates being observed in winter when the leafless condition of the forest permits increased ventilation and irradiation as well as maximum amounts of *Tf* to reach the forest floor. High values of *Es* occur mostly in stands with little to no understory vegetation and vice versa. Typical values of *Es* from the thick litter layers associated with temperate and tropical coniferous forests amount to *c.* 10% of *P* (100–150 mm) versus only 1–3% in dense lowland tropical rainforest with a poorly developed litter cover (50–70 mm).

Interception Modeling

Despite the numerous studies of rainfall interception conducted prior to the 1960s, little progress had been made with understanding the physics underlying the observed contrasts and inconsistencies in *Ei*, both between and within species and events. Explanations were usually worded in terms of differences in canopy storage capacity (in turn related to canopy density, deciduousness, etc.) or the intensity and duration of the rain. However, in the mid-1960s the previous largely empirical approach gave way to a more physically orientated process-based approach. This was followed by subsequent improvements in equipment for the measurement of above-canopy climatic conditions and, later, computational facilities. As a result, our understanding of the interception process has increased significantly.

In this more physical approach, evaporation from a vegetated surface is described quantitatively in terms of the amount of energy available for evaporation, other standard climatic parameters governing evaporation (such as temperature and humidity of the air, wind speeds), and various resistances against evaporation. Under dry canopy conditions the prime resistance to evaporation is that exerted at the leaf level (the so-called stomatal resistance), the cumulative value of which for the entire canopy is usually called surface or canopy resistance (r_c). The larger the canopy surface area, the smaller the value of this physiologically controlled r_c and, other variables remaining equal, the higher the resulting evaporation rate. However, when the vegetation surface is (fully) wetted by rain or fog, the canopy resistance effectively becomes zero and the evaporation process is dominated by the so-called aerodynamic resistance r_a. Whilst r_c signifies the resistance experienced by water molecules to transport from within the leaves to the surface of the leaves, r_a denotes the resistance to further upward transport into the overlying air. Unlike r_c, r_a is not controlled by the plants themselves. With increasing vegetation height, however, there is a corresponding increase in surface roughness. For a given wind speed, the associated enhanced atmospheric turbulence is reflected in a decrease in r_a. Also, r_a decreases with wind speed. Approximate values of r_a at a wind speed of $2.5\,\mathrm{m\,s^{-1}}$ measured at 10 m above the surface are 115, 50, and 10–15 $\mathrm{s\,m^{-1}}$ for short grass, field crops, and forest, respectively. Because values of the surface resistance to evaporation from a dry canopy (r_c) for grass and forest are much more similar than those of r_a (**Figure** 7), the net effect of the contrasts in aerodynamic resistance (much lower for forest) and in the degree of reflection of incoming radiation (much higher for grass) result in rather similar evaporation rates for grass and forest, as long as soil water is not limiting (**Figure** 7). This stands in great contrast to the finding that evaporation from a forest canopy under wet conditions (i.e., when the evaporative process is dominated by r_a) will proceed much faster than from a wet grassland (**Figure** 7).

Typically, rates of 0.2–0.5 $\mathrm{mm\,h^{-1}}$ are observed for evaporation rates from wet forest canopies, even in cloudy winter weather when the energy needed to sustain such rates must greatly exceed the available amount of radiant energy. However, temperatures of wet forest canopies have been shown to be slightly cooler than the air passing overhead. This, together with the low aerodynamic resistance of forest that is so conducive to rapid evaporation, allows the development of a downward flux of sensible heat capable of (locally) maintaining evaporation rates well in excess of available radiant energy. The degree to which the phenomenon influences annual interception totals obviously depends on the frequency of wetting of the canopy (i.e., rainfall regime) and thus on the overall setting of the forest. Thus, for a conifer plantation in the relatively dry eastern part of the UK (annual interception total 215 mm or *c*. 40% of total evapotranspiration *ET*), the effect is much less pronounced than for comparable forest in the more maritime setting of wet central Wales with its frequent passage of warm frontal rain (annual *Ei c*. 530 mm or *c*. 60% of total *ET*). Large-scale advection of relatively warm air from the nearby ocean is a likely source of energy for the enhanced evaporation at this and other near-coastal sites. Elsewhere, advection of warmer air flowing in from areas not wetted and cooled by rain may provide the extra energy. An alternative, and as yet insufficiently tested, explanation involves the release of heat that occurs when water that has been evaporated from the forest canopy condenses again. This would suggest a positive feedback of rainfall amount on the magnitude of *Ei* (and thereby condensation) as well as very rapid, local recycling of moisture.

Physically based models may help to elucidate the relative importance of different factors in the interception process which is difficult to assess from an actual interception record. The effect of varying rainfall intensities and wet canopy evaporation rates, canopy storage capacity and the distribution of the rain (continuous versus intermittent) on the magnitude of *Ei* using one such model (the so-called Rutter model) is illustrated in **Figure 8**. The limiting effect of low rainfall intensity at faster evaporation rates is clearly borne out by the simulations, as is the increase in *Ei* at rainfall higher intensities and for

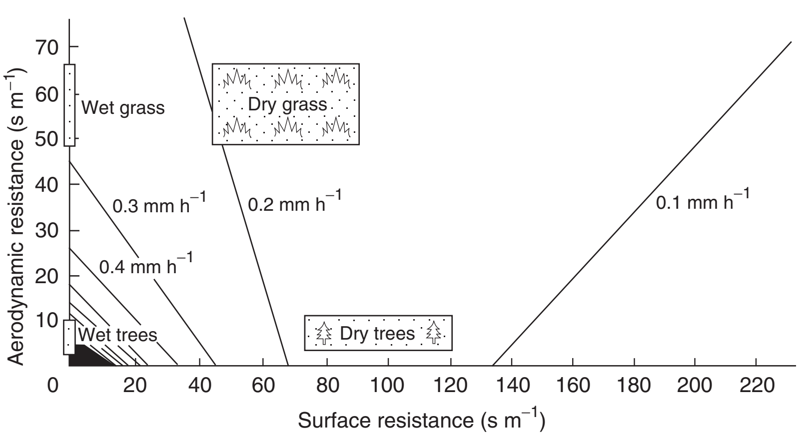


Figure 7 Evaporation rates calculated as a function of the aerodynamic (r_a) and surface (r_s) resistances to evaporation for cool summer daytime conditions. Reproduced with permission from Calder IR (1979) Do trees use more water than grass? *Water Services* 83: 11–14.

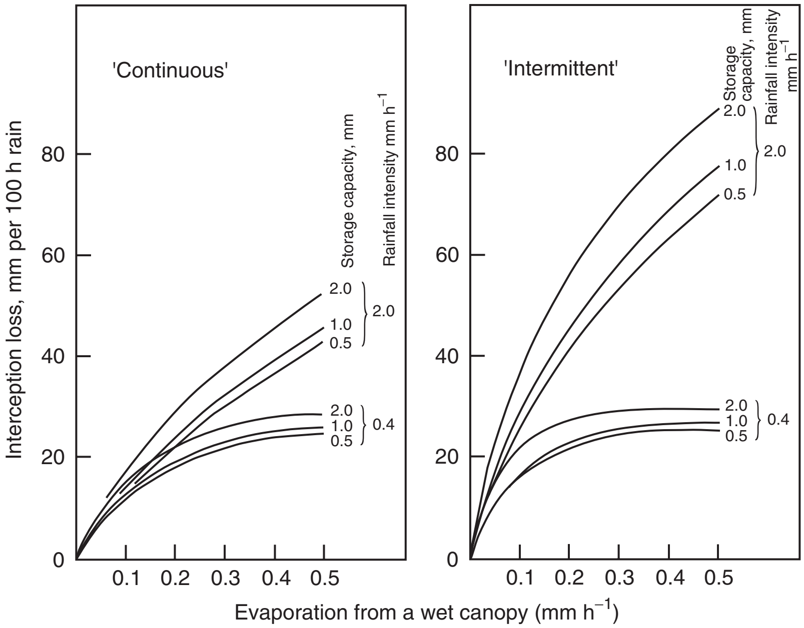


Figure 8 The interaction of wet canopy evaporation rate, rainfall intensity, rainfall distribution, and canopy storage capacity on interception loss from 100 h of rain. Reproduced with permission from Rutter AJ (1975) The hydrological cycle in vegetation. In: Monteith JL (ed.) *Vegetation and the Atmosphere*, vol. 1, pp. 111–154. London: Academic Press.

higher canopy storages, especially in the case of intermittent rain.

Transpiration

The second major component of forest evaporation is transpiration (*Et*, evaporation from a dry canopy). Like evaporation from a wet canopy, rates of *Et* are governed by the amount of available energy (mostly in the form of sunshine), air temperature and humidity (together determining the so-called evaporative demand of the atmosphere), and wind speed (affecting the rate with which evaporated moisture is carried away). However, unlike evaporation from a wet vegetation, which is largely controlled by the aerodynamic resistance of the vegetation (r_a) as we have seen earlier (**Figure 7**), *Et* is chiefly governed by the physiologically controlled canopy resistance r_c. In its turn, r_c is influenced by a range of environmental and plant variables, including light intensity, leaf area, leaf temperature, and leaf water potential (a measure of plant water stress), but also the humidity of the air and the amount of water present in the soil. The ease with which water molecules are evaporated from within the leaves to the surface of the leaves (as represented by the so-called canopy conductance g_s, i.e., the inverse of resistance r_s) increases with increasing light intensity and temperature (up to a maximum value). However, the conductance decreases as the air or the soil become drier; or, expressed in scientific terms, as atmospheric humidity deficit or soil water deficit increase (**Figure 9**). Although the actual interactions between g_s (or r_s) and the cited plant and weather variables are only partly understood and quantifiable, their combined effect under humid temperate or tropical conditions generally results in distinct daily patterns of g_s (or r_s) that change comparatively little with time as long as soil water stress does not occur.

The distinct response of leaf conductance to changes in atmospheric humidity deficit (**Figure 9c**) has been observed in vegetation types as diverse as northern conifers and tropical rainforests. Coastal species seem to be more sensitive in this respect than continental species, possibly because they are adapted to persistently high humidities. Although the precise underlying mechanism is still unclear, the strong feedback response between g_s and atmospheric humidity results in a significant dampening of instantaneous transpiration rates. Even though potential evaporative demands by the atmosphere may be much higher, daily forest transpiration totals typically remain below 4 mm in most humid climates (both temperate and tropical). There are notable exceptions, however, such as poplars or eucalypts grown in short-rotation coppice systems with unrestricted access to soil water. Although such trees are often called voracious consumers of water and have been used for centuries to help drain marshy areas, it is important to note that they do reduce their water uptake when soils dry out. The planting of eucalypts and poplars, particularly in subhumid areas, should

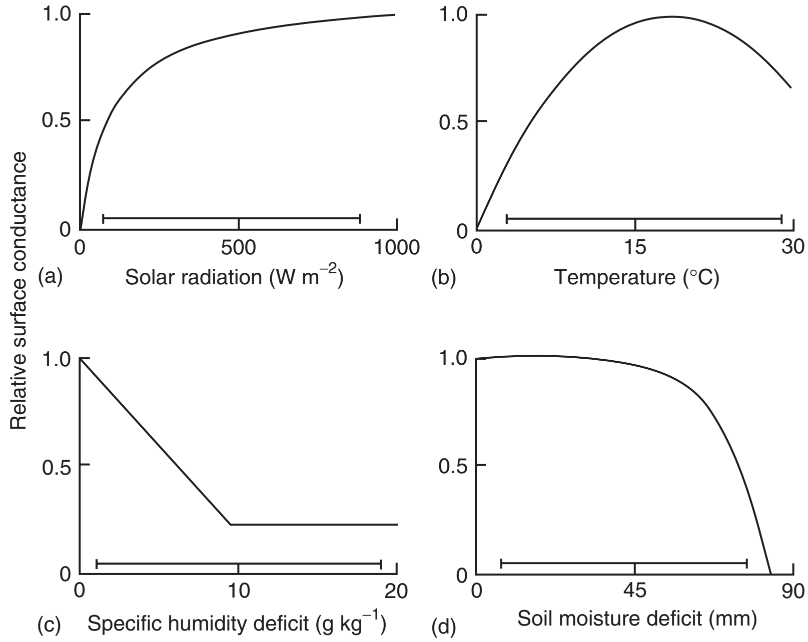


Figure 9 The general form of the dependence of the relative surface conductance on (a) solar radiation, (b) temperature, (c) specific humidity deficit, (d) soil moisture deficit. Reproduced with permission from Stewart JB (1988) Modelling surface conductance of pine forest. *Agricultural and Forest Meteorology* 43: 19–35.

therefore be based on judicious planning if over-exploitation of precious groundwater reserves is to be avoided.

Soil water stress has been shown to have a marked effect on *Et* in seasonally dry climates where the soil tends to dry out considerably. Often, however, the modest transpiration rates caused by the strong physiological sensitivity of the trees to drops in atmospheric humidity (**Figure 9c**) imply that a considerable portion of the soil water reserves (typically two-thirds to three-quarters) can be taken up before surface conductance is reduced further and transpiration starts to fall off (**Figure 9d**). As shown in **Figure 10** for a young eucalypt forest in south-eastern Australia, the soil water deficit at which transpiration becomes reduced tends to be reached earlier when rates of water uptake are high than during times of more modest uptake. As such, critical soil water deficits affecting *Et* will only be rarely attained in humid climates where uptake rates are modest, and may therefore be expected to play only a minor role in generating differences between species and sites.

In contrast to evaporation from a wet canopy (rainfall interception *Ei*) (**Figure 7**), annual totals of transpiration (evaporation from a dry canopy) show comparatively little variation between species and sites within a given climatic zone. For example, the average annual *Et* for coniferous and deciduous forests (excluding poplars) in Western Europe is not significantly different at 300 ± 35 and 335 ± 35 mm. This striking similarity in the water use of deciduous and evergreen species of varying age and habitats can be attributed to: (1) the strong feedback between atmospheric humidity and surface conductance (**Figure 9c**); (2) the relative insensitivity of *Et* to soil water availability (**Figure 10**); and (3) the compensatory effects of the presence or absence of understory vegetation. Indeed, overall transpiration for a dense forest with little to no undergrowth can be similar to that of open forests with much more vigorous understories. Large, deep-rooted trees have been shown to draw their water mostly from deeper layers or the groundwater table whereas small understory trees (whose roots are often unable to reach the groundwater) have to rely on soil water. Interestingly, during periods of drought stress, groundwater taken up by the deeper roots of the larger trees during the night is known to be released from shallow roots into the upper layers of the soil, where it is subsequently used by understory vegetation. This remarkable finding suggests that the water relations of over- and understory trees are more complex and perhaps less competitive than sometimes perceived. The process is known as 'hydraulic lift' and can be explained in terms of soil and plant water potential gradients.

In contrast to the relative abundance of transpiration estimates for humid temperate forests, information for tropical rainforests and plantations is scarce.

Estimates of average annual *Et* range between 900 and 1300 mm (average *c.* 1000 mm) for lowland rainforests versus 500–900 mm for montane rainforests not subject to appreciable amounts of fog. Transpiration in montane cloud forests may be as low as 250–300 mm year^{-1}. Most of these estimates are based on indirect (water budget based) methods, however, which must be considered relatively crude. Fortunately, the number of studies employing direct, micrometeorological techniques to measure evaporation from tropical forests is on the increase. The same holds for the use of physiological approaches measuring the rate of sapflow in individual trees. Whilst tower-based micrometeorological techniques tend to integrate results over larger areas, sapflow measurements need to be scaled up to the stand level. Considerable success has been reported with this approach in a variety of forests.

Total Evapotranspiration

Although it is beyond the scope of the present process-oriented chapter to discuss amounts of total evapotranspiration (*ET*) associated with different forest types and climatic zones, it can be concluded from the previous sections that changes in the interception component of evaporation (*Ei*) will be much more important than those of the transpiration component (*Et*). Taking Western Europe as an example, annual totals of *Et* have been shown to be quite similar for deciduous and coniferous forests over a wide range of soil and rainfall conditions. Conversely, absolute annual totals of *Ei* for these forests (**Figure 6**) range from about 120 mm (oak coppice under low rainfall conditions) to about 700 mm (spruce at a high rainfall location subject to advected heat from the ocean). Similar contrasts between variations in *Ei* and *Et* have been reported for the humid tropics where radiation loads, average temperatures, and rainfall are generally higher than in the temperate zone. As was the case for temperate conditions, the importance of intercepted rainfall to overall *ET* under maritime tropical conditions is tentatively confirmed.

Concluding Remarks

Considerable progress has been made since the mid-1960s in the conceptual understanding and mathematical description (modeling) of such key forest hydrological processes as evaporation from a wet canopy (interception), transpiration (evaporation from a dry canopy), infiltration and forest hillslope hydrological behavior (runoff generation), as well as forest–atmosphere interactions. The precise turbulent transfer mechanisms underlying the much enhanced rates of evaporation from wet forest canopies under maritime climatic conditions or the effects of large-scale deforestation under such conditions are not very well understood, however. Neither is too much known of the hydrological significance of fog interception by forests in montane cloud belts,

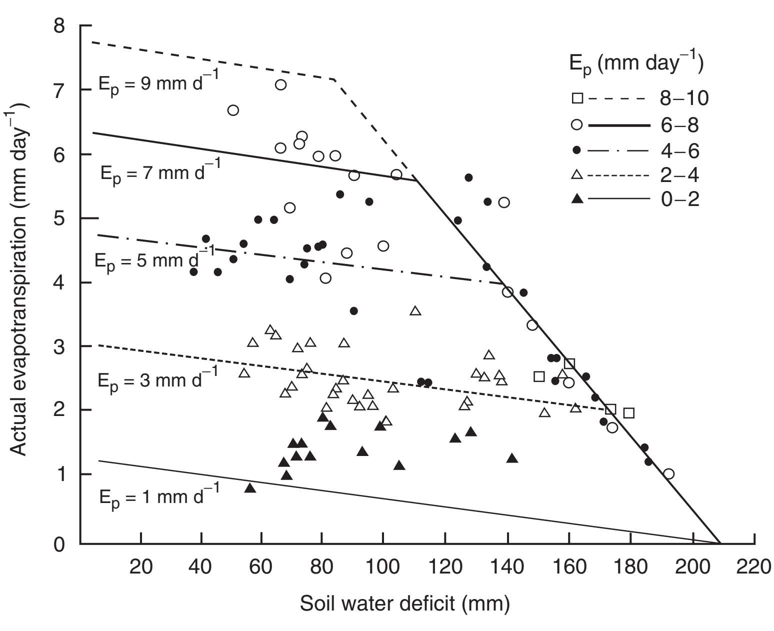


Figure 10 Actual evaporation rates for a young eucalypt plantation in southeastern Australia as a function of coincident potential evaporation rates and soil water deficits. Reproduced with permission from Dunin FX *et al.* (1985) A lysimeter characterization of evaporation by eucalypt forest and its representativeness for the local environment. In: Hutchinson BA and Hicks BB (eds) *The Forest–Atmosphere Interaction*, pp. 271–291. Dordrecht, The Netherlands: D. Reidel.

particularly in the tropics. Similarly, the data base for tropical forest water use is small. However, with the continued improvement of process-based hydrological models, equipment, data storing, and computational facilities, significant progress can be expected to be only a matter of time.

See also: **Hydrology**: Impacts of Forest Conversion on Streamflow; Impacts of Forest Management on Streamflow; Impacts of Forest Plantations on Streamflow; Snow and Avalanche Control. **Soil Development and Properties**: Water Storage and Movement. **Tree Physiology**: A Whole Tree Perspective; Forests, Tree Physiology and Climate; Root System Physiology. **Tropical Forests**: Tropical Montane Forests.

Further Reading

Brammer DD and McDonnell JJ (1996) An evolving perceptual model of hillslope flow at the Maimai catchment. In: Anderson MG and Brooks SM (eds) *Advances in Hillslope Processes*, vol. 1, pp. 35–60. Chichester, UK: John Wiley.

Bruijnzeel LA (2001a) Forest hydrology. In: Evans JC (ed.) *The Forests Handbook*, vol. 1, pp. 301–343. Oxford, UK: Blackwell Science.

Bruijnzeel LA (2001b) Hydrology of tropical montane cloud forests: a reassessment. *Land Use and Water Resources Research* 1: 1.1–1.18. http://www.venus.co.uk/luwrr.

Calder IR (1979) Do trees use more water than grass? *Water Services* 83: 11–14.

Calder IR (1990) *Evaporation in the Uplands*. Chichester, UK: John Wiley.

Calder IR (1998) Water use by forests, limits and controls. *Tree Physiology* 18: 625–631.

Chang MT (2003) *Forest Hydrology: An Introduction to Water and Forests*. New York: CRC Press.

Dawson TE (1996) Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree sizes and hydraulic lift. *Tree Physiology* 16: 263–272.

Dawson TE (1998) Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia* 117: 476–485.

Gash JHC, Nobre CA, Roberts JM, and Victoria RL (1996) *Amazonian Deforestation and Climate*. Chichester, UK: John Wiley.

Roberts JM (1983) Forest transpiration: a conservative hydrological process? *Journal of Hydrology* 66: 133–141.

Roberts JM (1999) Plants and water in forests and woodlands. In: Baird A and Wilby R (eds) *Eco-Hydrology: Plants and Water in Terrestrial and Aquatic Ecosystems*, pp. 181–236. London: Routledge.

Schellekens J, Bruijnzeel LA, Scatena FN, Bink NJ, and Holwerda F (2000) Evaporation from a tropical rainforest, Luquillo Experimental Forest, eastern Puerto Rico. *Water Resources Research* 36: 2183–2196.

Shuttleworth WJ and Calder IR (1979) Has the Priestley–Taylor equation any relevance to forest evaporation? *Journal of Applied Meteorology* 18: 639–646.

Wullschleger SD, Meinzer FC, and Vertessy RA (1998) A review of whole-plant water studies in trees. *Tree Physiology* 18: 499–512.

Impacts of Forest Conversion on Streamflow

L A Bruijnzeel, Vrije Universiteit, Amsterdam, The Netherlands
I R Calder, University of Newcastle upon Tyne, UK
R A Vertessy, CSIRO Land and Water, Canberra, Australia

Introduction

Trees and forests are valued for timber and forest products, for amenity, for biodiversity, and for the cultural and the spiritual well being we derive from their proximity. Forests and reforestation programs are also widely promoted with regard to their perceived hydrological benefits, although often these expected benefits are not realized. This article reviews the scientific knowledge and the public perceptions of important forest–hydrology links, focusing on the vexed questions of whether, when, and to what extent forests increase or decrease streamflow, reduce floods, and increase dry season flows. The effect of forest on rainfall, the impacts of various forestry activities (thinning, selection logging, clear-felling) on streamflow, and the soil and water impacts of reforesting degraded or agricultural areas are discussed elsewhere (*see* **Hydrology**: Hydrological Cycle; Impacts of Forest Management on Streamflow; Impacts of Forest Plantations on Streamflow). Similarly, effects of forest management and conversion to other land use on water quality, and ways to minimize any adverse impacts accompanying such conversions, are dealt with in other articles (*see* **Hydrology**: Impacts of Forest Management on Water Quality; Soil Erosion Control).

Forests and Water: Received Wisdom

Traditionally forests have been promoted as being ‘good news’ for the water environment. The conventional received wisdom, embodied often in government forest policy and promoted by international and national forestry interests and organizations is that, apart from reducing erosion and maintaining water quality, a good forest cover: (1) increases runoff, (2) reduces or even prevents 'flood,' and (3) boosts dry season flows. Yet when these statements are held against the light of scientific inquiry, the evidence is not always as favorable and sometimes even indicates the opposite.

Put simply, the most widely held view among the general public and, perhaps to a lesser extent, policy-makers and resource managers, is that forests act as 'sponges' absorbing excess rainfall and releasing the water slowly and evenly during lean periods. Because of this, forests are believed to be capable of preventing flooding, and increasing streamflow during the dry season. By analogy, their disappearance invariably brings about havoc (floods, droughts). Likewise, the effect of tree planting on degraded land is expected to result in (rapidly) improved streamflow regimes, i.e., elimination of peak flows and increased low flows. Such views are encountered especially in the tropical and subtropical parts of the world where the adverse hydrological effects of the land degradation that often (but not necessarily) follows forest clearance are felt the most. In the following, the claims with respect to the adverse effects of forest conversion ('deforestation') on streamflow are examined in some detail. The effects of the reverse, i.e., reforestation, are discussed elsewhere (*see* **Hydrology**: Impacts of Forest Plantations on Streamflow).

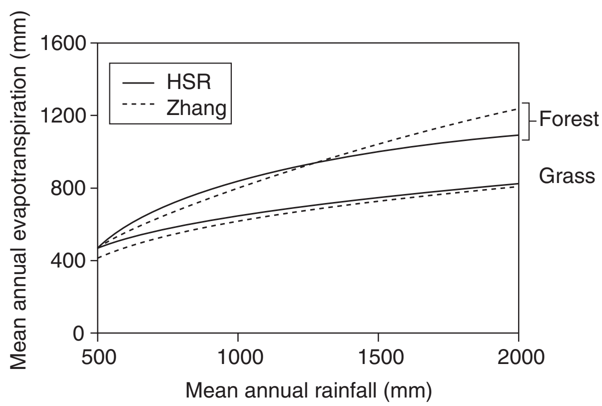


Figure 1 Relationship between land cover, mean annual rainfall and mean annual evapotranspiration, as predicted by the Holmes and Sinclair (1986) relationship (HSR) and the Zhang *et al.* (1999) model. Reproduced with permission from Vertessy RA, Zhang L, and Dawes WR (2003) Plantations, river flows and river salinity. *Australian Forestry* 66: 55–61.

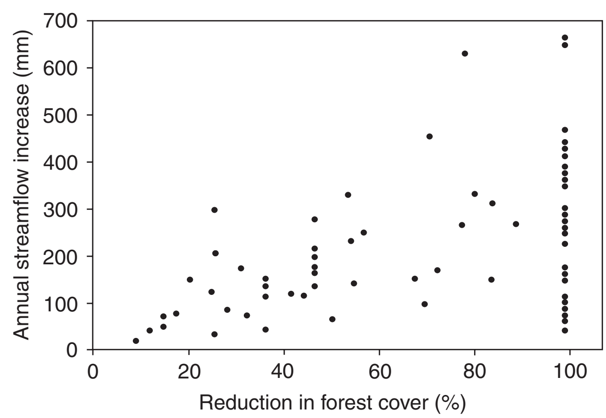


Figure 2 Relationship between reduction in forest cover and increase in catchment water yield. Reproduced with permission from Bosch JM and Hewlett JD (1982) A review of catchment experiments to determine the effects of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology* 55: 3–23.

Forest Conversion and Streamflow: The Scientific Consensus

Forests and Annual Water Yield

It is now recognized worldwide that evaporation from forested areas, with very few exceptions, will be greater than that from alternative land uses, such as pasture or annual cropping (**Figure 1**). Provided the soil is not disturbed too much upon forest conversion, the smaller water use of crops or grassland generally shows up as increases in groundwater recharge, in the volumes of water flowing annually from cleared catchments, and in increased seasonal (dry season) flows. Generally, the larger the proportion of forest removed, the larger these increases in water yield (**Figure 2**).

Whilst the increases in streamflow usually return to preclearing levels within 3–35 years where regrowth of the original vegetation occurs (depending mostly on the vigor with which regeneration takes place), the conversion of native forest to other types of vegetation cover may produce permanent changes in flow. For example, permanent increases in annual water yield are normally associated with the conversion of deciduous or evergreen native forest to agricultural cropping or pasture (cf. **Figure 1**). Depending on the nature of the conversion, degree of surface disturbance (affecting surface runoff), and rainfall, reported increases in flows range from 60–125 mm year^{-1} under humid warm temperate conditions to 140–410 mm year^{-1} in the equatorial tropics. These values are somewhat smaller than the maxima shown in **Figure 2** because the latter mostly refer to increases in flows shortly after forest clearance and before a new vegetation cover is established.

There are two principal reasons for the difference in evaporation between forests and shorter crops (cf. **Figure 1**). In wet climates with frequent rainfall, where the surfaces of vegetation tend to remain wet for long periods, rainfall interception by the canopies of forests is much higher than that by shorter crops. The intercepted water is evaporated back into the atmosphere and therefore does not reach the ground where it could have contributed to soil water reserves. Rates of evaporation from a wet forest canopy are so enhanced because the aerodynamically very rough surfaces of forests assist the turbulent transport of water vapor into the atmosphere much more than the smoother surfaces of grassland or low crops. This is analogous to the clothes-line effect: wet clothes pegged out on a line will dry much quicker than those laid out flat on the ground. Not only does the increased turbulent exchange between forests and the atmosphere increase the rate at which evaporated water molecules are moved up into the air; it also promotes the rate at which heat can be supplied by the passing air to the cooler vegetation surface underneath to support the evaporation process. This source of energy, known as advected heat, is of such significance that annual evaporation rates from forests in some wet climates can exceed those that could be sustained by direct radiation from the sun by a factor of 2. Large-scale advection typically occurs in near-coastal or mountainous regions (where the ocean or adjacent lowlands are the main source of relatively warm air, respectively). At a more local scale warmer air may be drawn in from areas that are not wetted and cooled by rain.

In drier climates or during prolonged rainless periods, forests are able to access and take up more soil water than short vegetation or agricultural crops because forests generally have much deeper root systems. This also contributes to higher evaporation rates overall. However, under conditions of ample soil water availability, the internal physiological resistance to evaporation is often slightly greater for trees than for short crops. As a result, the soil water uptake (transpiration) rates of forest may be *c*. 10% less than those of grassland and other short crops (as long as they are well watered) and this may to some extent compensate for the interception and increased rooting depth effects described above.

Although annual water yields from forested catchment areas can thus be expected to be (much) less than those for cleared areas (**Figures 1** and **2**), there are a few exceptions. The first of these concerns so-called montane cloud forests. These wet and mossy, fog-ridden forests are mainly found in the cloud belts of (mostly tropical) mountains and islands although fog-affected forests also occur along the western margins of the American continent. At favorably exposed locations cloud forests may receive hundreds of millimeters of extra water in the form of wind-blown fog and drizzle that impact on and drip from the canopy. In extreme cases annual amounts of fog drip may exceed incident rainfall totals, thereby more than compensating the losses associated with interception evaporation referred to earlier. Because soil water uptake rates are also low under these humid cloudy conditions, areas with cloud forests are generally considered excellent suppliers of water, especially during periods of low rainfall when fog incidence is often greatest. Concerns have been expressed that the indiscriminate clearing of cloud forests to make way for pasture or vegetable cropping will lead to reductions in streamflow because of the associated loss of the former forest's fog stripping capacity (**Figure 3**). Although evidence from the humid tropics for such declines in flows is circumstantial at best, it has been observed in the Pacific Northwest of the USA after the partial cutting of Douglas-fir forest subject to high fog incidence.

The second exception to the rule of increased streamflows after forest conversion relates to cases where old-growth forests with relatively low water use and vigor are replaced by young, actively growing secondary forest or exotic tree plantations. Examples include rapidly regenerating mountain ash (*Eucalyptus regnans*) forest after a wildfire in southeastern Australia, young secondary growth in Amazonia after the abandonment of agricultural fields or pasture, and (most probably) plantations of *Acacia mangium* replacing rainforest in Malaysia. Likewise, converting deciduous forest to coniferous forest will result in more-or-less seriously decreased streamflow totals, mostly because of the much higher interception evaporation associated with the evergreen conifers.

Figure 3 Converting tropical montane cloud forest to pasture may reduce catchment water yields through the loss of the forest's fog stripping capacity. Photograph courtesy of KFA Frumau.

Although the results of small catchment experiments provide a clear and consistent picture of increased water yield after replacing tall vegetation by a shorter one (and vice versa; cf. **Figures 1** and **2**), such effects are often more difficult to discern in (very) large river basins (>1000 km^2). Apart from continuous changes in the mosaic of different landcover types, each with their own influence on local runoff, there are the added complications of strong spatial and interannual variability in rainfall, and withdrawals of water for municipal, agricultural, and industrial purposes in densely populated areas. Nevertheless, a few studies have demonstrated a significant landcover change effect on the flows from (very) large basins. An increase in annual streamflow of about 110 mm has been reported for the Citarum River basin (4133 km^2) on the island of Java, Indonesia, between the 1920s and the 1980s despite unaltered rainfall totals. The increase was attributed to the replacement of irrigated rice fields (not forest) by settlements and industrial estates. Likewise, the conversion of *c.* 33 000 km^2 (19% of basin area) of so-called cerrado forest (scrub with scattered trees) to pasture in the subhumid Tocantins basin (175 360 km^2) of central Brazil was followed by an increase in streamflow of about 90 mm $year^{-1}$ (+24%).

At an intermediate scale (1100 km^2), increases in averaged annual flow totals occurred over a period of four decades in the Mahaweli catchment in Sri Lanka, despite a weak negative trend in rainfall over the same period. Although both trends were not statistically significant at the 95% significance level due to strong interannual variability in the data, the corresponding increase in annual runoff ratios (streamflow: rainfall) was highly significant (**Figure 4**). The increased hydrological response was ascribed to the gradual but widespread conversion of tea plantations (not forest) to annual cropping and home gardens on steep slopes without appropriate soil conservation measures (see also the section on forest and dry season flows below).

To summarize, despite the few exceptions outlined above, there is overwhelming evidence that streamflow totals from forested catchments are reduced compared with those under shorter vegetation. The effect of enhanced water yield after forest conversion has been demonstrated over a range of scales, including some very large river basins.

Forests and Floods

As long as the soil's water intake capacity is not degraded too much by surface compaction, the lower water use of grassland and crops compared to forest

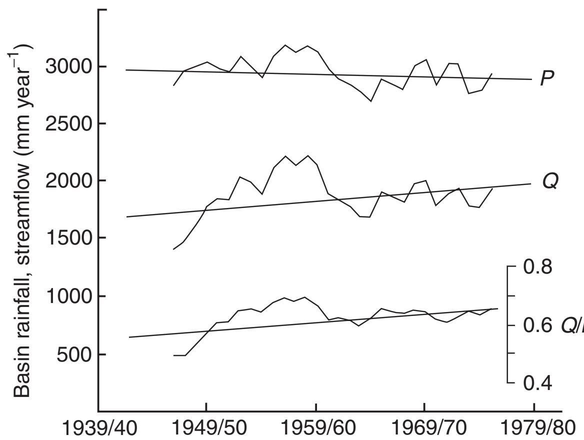


Figure 4 Five-year moving averages of annual rainfall *P*, streamflow *Q*, and runoff ratios *Q/P* for the upper Mahaweli Basin above Peradeniya, Sri Lanka. Reproduced with permission from Madduma Bandara CM (1997) Land-use changes and tropical stream hydrology: some observations from the upper Mahaweli Basin of Sri Lanka. In: Stoddard DR (ed.) *Process and Form in Geomorphology*, pp. 175–186. London: Routledge.

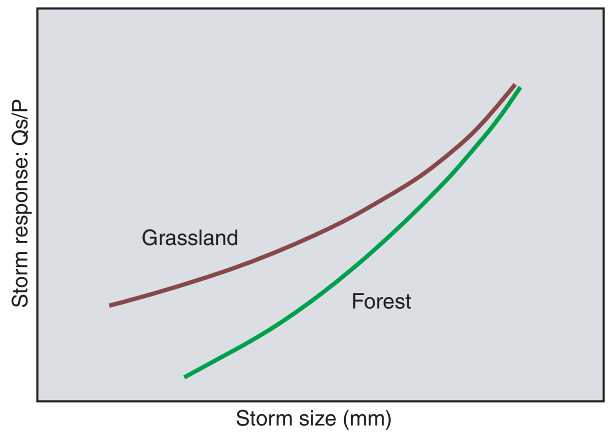


Figure 5 Conceptual relationship between the size of stormflow generating rainfall events (P) and the resultant stormflows and how these are affected by vegetation type. Reproduced with permission from Scott DF, Bruijnzeel LA, and Mackensen J (2004) The hydrological and soil impacts of forestation in the tropics. In: Bonell M and Bruijnzeel LA (eds) *Forests – Water – People in the Humid Tropics*. Cambridge, UK: Cambridge University Press.

(**Figure 1**) will manifest itself in the form of wetter soil conditions and thus increased streamflow (**Figure 2**). This overall increase in catchment wetness leads, in turn, to an expansion of storm runoff-producing areas. These are mostly wet, low-lying areas around watercourses and stream heads, but may also include footslopes and hillslope depressions. The consequence of this is that cleared catchments will respond more rapidly and more vigorously to rainfall; both stormflow volumes and peak discharges will be elevated (**Figure 5**).

Under conditions of minimum surface disturbance (e.g., when skyline logging techniques are used), relative increases in catchment stormflow response to rainfall are largest for small rainfall events (up to 300%), declining to less than 10% for large events. As such, the influence of vegetation cover or type is inversely related to the size of the rainfall event generating the stormflow (**Figure 5**). This can be explained as follows: for small storm events the combined storage capacity of vegetation canopies, ground-convering litter, surface microtopography and the soil mantle can be substantial relative to the size of the storm depth. Of these the soil mantle is potentially the largest water store, but its capacity to accommodate additional rain varies as a function of soil wetness. Where previous uptake by the vegetation has depleted soil water reserves, storage capacities will be relatively high but once the soil has become thoroughly wetted by frequent rains (typically at the height of the wet season), opportunities to absorb large additional amounts of rain will be very limited. Furthermore, as precipitation events increase in size, so does the relatively fixed maximum storage capacity of the soil become less influential (**Figure 5**). In other words, under conditions of extreme rainfall and soil wetness, the presence or absence of a good forest cover is no longer decisive. Catchment runoff response to rainfall is then governed primarily by the soil's physical capacity to store and transmit water.

Naturally, the effect of forest conversion on stormflow generation will be much more pronounced if soil disturbance is severe and the catchment's rainfall absorbing capacity becomes structurally impaired. Soils may be compacted by machinery during clearing operations and subsequently by grazing cattle, by exposure to intense rainfall (when no longer protected by vegetation or litter), and by the gradual loss of organic matter and the disappearance of burrowing soil animals during extended periods of agricultural cropping. As a result, total stormflow amounts from intensively grazed tropical grassland catchments are typically 25–45% higher than those associated with the forests they replaced. In the case of seriously degraded cropland (also in the tropics), however, the relative increase may easily be 300–400%. Often, catchment response to rainfall after forest conversion (but also in relation to forestry activities) is influenced most by the construction of roads and drainages, settlements and, in urbanized areas, industrial estates. On such densely compacted surfaces typically more than 70% of the rain is immediately turned into surface runoff. In addition, road construction is often accompanied by increased landsliding and erosion. The associated increases in stream sedimentation may, in extreme cases, cause the river bed to be raised to the extent that flood hazards are increased even further.

At larger scales, the overall effect of landcover change on catchment runoff response to rainfall will depend on the relative proportion of the various landcover types (including roads and settlements) and their hydrological behavior. Recent work in the Pacific Northwest of the USA trying to 'disentangle' the effects of logging and the presence of a road network on peak flow enhancement in the 150 km^2 Deschutes River basin suggests the separate effects of the two to be a rise of about 10% each. In contrast to the forest removal effect (cf. **Figure 5**), the road effect was shown to increase with the size of the flood peak (see also **Figure 6a**). Conversely, in northern Thailand relative runoff contributions from rural roads and trails to overall stormflow production in a largely deforested landscape were greatest for small storms but gradually 'drowned' by contributions from agricultural fields during larger storms.

It is generally found that the adverse local effects of forest removal on all but the largest stormflow response tend to be 'diluted' or even become undetectable at larger scales. This is because peak flows from one part of the basin will usually not coincide with those from other parts due to differences in the timing of the rainfall or in the hydrological response of different landcover types. Arguably the most publicized example of highland–lowland interactions in relation to downstream flooding is the Ganga–Brahmaputra–Meghna river system in northern India and Bangladesh. Disastrous floods in the area are almost always attributed to 'deforestation in the Himalayas' rather than to excess monsoon rainfall occurring at a time when most of the river basin has already been wetted up by previous rains. However, a detailed analysis of the hydrological and climatic records for the area over the past 40 years shows that neither the frequency nor the magnitude of flooding has increased over the last few decades. Indeed, flooding must be considered an unavoidable process given the geoclimatic setting of the Ganga–Brahmaputra river basin. Consequently there is no reason to believe that floods in the Indian lowlands have intensified as a result of human impact in the highlands although the degree of damage has increased because of greater floodplain occupancy.

Nevertheless, there is reason for concern, particularly with respect to tropical river basins. For example, most of the increase in streamflow observed after converting tea estates (not forest) to rainfed cropping on steep slopes in Sri Lanka (**Figure 4**) occurred during the rainy season whereas dry

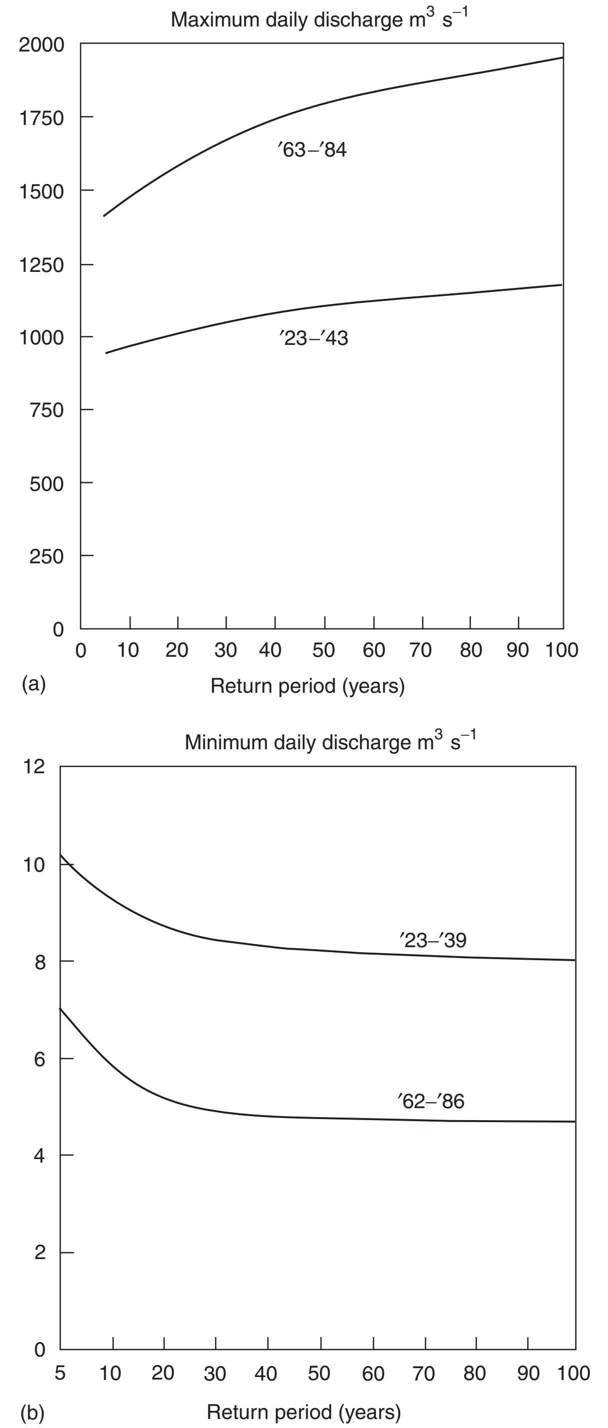


Figure 6 Changes in average maximum and minimum daily flows for the Citarum River basin, West Java, Indonesia between the periods 1923–1939/43 and 1962/63–1984/86. Reproduced with permission from Van der Weert R (1994) *Hydrological Conditions in Indonesia*. Jakarta: Delft Hydraulics.

season flows continued to decline, presumably as a result of steadily worsening surface infiltration conditions (**Figure 7**). Similarly, maximum flows in the densely populated Citarum River basin in

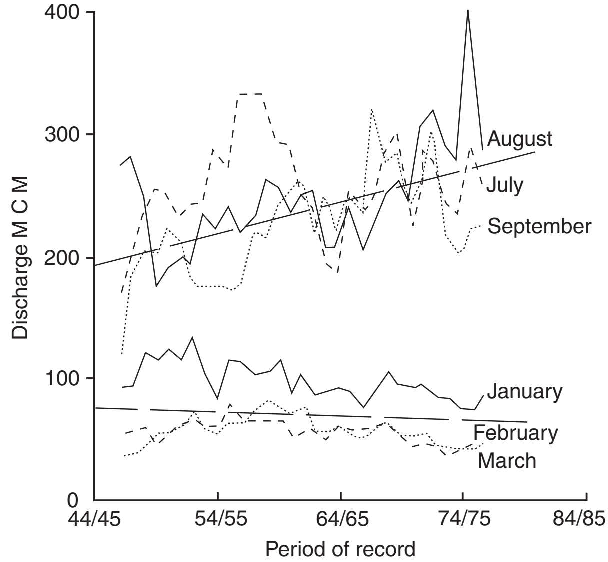


Figure 7 Seasonal trends in streamflow in the upper Mahaweli basin, Sri Lanka. Reproduced with permission from Madduma Bandara CM (1997) Land-use changes and tropical stream hydrology: some observations from the upper Mahaweli Basin of Sri Lanka. In: Stoddard DR (ed.) *Process and Form in Geomorphology*, pp. 175–186. London: Routledge.

Indonesia referred to earlier increased on average by about 50%, with even greater increases for the largest events (**Figure 6a**). This is believed to be caused by the conversion of irrigated cropland to settlements, industrial estates and roads. To make matters worse, dry season flows were also reduced (by about one-third; **Figure 6b**). Although event peak discharges in the much larger Tocantins basin in Brazil referred to earlier were not influenced by the conversion of 19% of its scrubland area to pasture, most of the 24% increase in annual water yield occurred during the wet season. In addition, the seasonal flood peak arrived about 1 month earlier than when the basin was fully forested. Neither urbanization nor altered rainfall patterns could be called on to explain this pattern. The most likely cause is, again, a gradual degradation of soil infiltration capacities, in this case due to the trampling effect of grazing cattle.

To summarize, the role of forest cover in flood mitigation or management is limited to small to medium-sized events. As the severity of the flood increases the impact of land use change appears to be reduced (**Figure 5**). Yet there is increasing evidence that in areas where gradual degradation of catchment infiltration opportunities beyond a critical threshold occurs, peak flows are enhanced considerably, even in (very) large river basins. Finally, there remains a need to better understand the complex relationships between land use change and stream sediment dynamics, including the build-up of river-beds and changes in channel form, and their effect on flood heights.

Forest and Dry Season Flows

In areas with seasonal rainfall, the distribution of streamflow throughout the year is often of greater importance than annual totals. Reports of greatly diminished flows during the dry season after forest conversion to cropping abound in the literature, particularly in the tropics. At first sight, this seems to contradict the evidence presented earlier that forest removal leads to higher water yields (**Figure 2**), even more so because most of the increases in flow after experimental clearing are generally observed during baseflow conditions. However, the controlled conditions imposed during the catchment experiments of **Figure 2** may differ from those encountered in some real-world situations. As we have seen, rainfall infiltration opportunities are often (much) reduced after forest conversion due to soil degradation, compaction or surface pavement. This is usually a gradual process and it is quite possible that many catchment experiments did not last long enough for sufficient degradation to happen. As illustrated by **Figures 4**, **6** and **7**, once infiltration becomes seriously impaired, increases in surface runoff during the rainy season may become so large that the recharging of groundwater reserves is reduced. When this critical stage is reached, diminished dry season flow is the sad result (**Figures 4** and **7**), despite the fact that the removal of the forest should have induced higher baseflows because of the diminished water use of the new vegetation (cf. **Figure 2**).

If, on the other hand, soil surface characteristics after clearing are maintained sufficiently to allow the continued infiltration of (most of) the rainfall, then the effect of reduced water use after forest removal will show up as increased dry season flow (**Figure 8**). This may be achieved through a well-planned and maintained road system plus the careful extraction of timber in the case of logging operations, or by the application of soil conservation measures (such as terracing, planting contour hedgerows, or grass strips) when clearing for agricultural purposes (**Figure 9**).

To summarize, the effect of forest removal on dry season flows will be positive where the infiltration capacity of the soil is maintained sufficiently to avoid excess surface runoff during rainfall. Where infiltration becomes seriously impaired, however, groundwater recharge may be reduced to the extent that dry season flows are decreased.

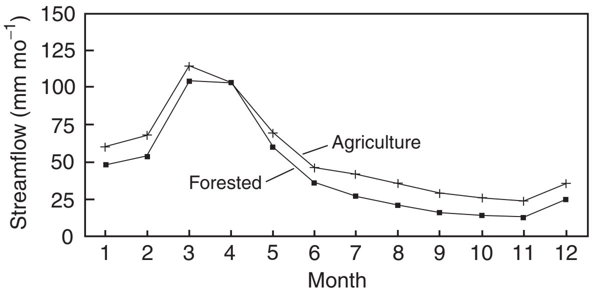


Figure 8 Changes in seasonal distribution of streamflow after replacing montane rainforest by subsistence cropping at Mbeya, Tanzania without significant surface degradation. Based on original data in Edwards (1979); after Bruijnzeel LA (2001) Forest hydrology. In: Evans J (ed.) *The Forests Handbook*, vol. 1, pp. 301–343. Oxford, UK: Blackwell Science.

Reconciling Public and Science Perceptions of Forest – Streamflow Linkages

The most common perceptions of the hydrological impacts of forest conversion ('deforestation') held by many forestry practitioners, policy-makers, and the general public (particularly in the tropics) on the one hand and (most) researchers on the other, are summarized in **Table 1**. Arguably, the contrast between the two is less great than claimed by some. A close inspection of the respective perceptions listed in **Table 1** reveals that in many cases these contrasting views relate to differences in degree or frequency of occurrence rather than representing true differences in kind.

Much of the confusion regarding the increase or decrease of streamflow following forest clearance can be traced to two aspects: (1) the need to distinguish between annual and seasonal water yields, and (2) the fact that most, if not all experimental catchment studies pertain to controlled land use changes, the hydrological impacts of which have been monitored over relatively short periods of time only (typically up to 3 years, occasionally longer). As to the first, in the absence of actual streamflow measurements it is difficult to tell whether the increases in rainy season stormflows and decreases in low flows witnessed by people living in gradually degrading catchments actually add up to increased total annual water yields or not (see **Figure 4**). However, there is little actual difference between the layman stating that 'deforestation' leads to diminished low flows due to the loss of the 'sponge effect' of the forest and the scientist having to agree, provided that surface infiltration characteristics have been degraded sufficiently over time for this to happen. Similarly, the public view that 'floods' invariably increase after

Figure 9 Adverse impacts on streamflow can be avoided largely by applying soil conservation measures following forest clearing. Photograph by LA Bruijnzeel.

forest clearance and that of the scientist acknowledging that stormflows do increase in all but the most extreme cases, and perhaps even then in the case of an extended road network, are not that different anymore either.

Therefore, it is arguably more productive to state that stormflows are increased after forest removal up to a certain threshold (beyond which the effect of landcover is overridden by those of extreme rainfall and limitations in soil water holding capacity), or that low flows will decrease once a certain level of surface degradation has been reached, than to merely dismiss the 'sponge theory' as folklore or an anachronism.

Furthermore, and as hinted at already, in the heated debate on the hydrological role of (especially tropical) forests it is generally overlooked that the circumstances associated with controlled (short-term) catchment experiments may differ from those of some real-world situations in the longer term. No experimental catchment study has lasted long enough, however, to document the long-term effects of increasingly degraded surface conditions on streamflow amounts and regime. As such, both views (diminished or increased dry season flows after clearance) must be considered correct, depending on the situation. Where infiltration is maintained sufficiently, as under controlled experimental conditions or rational land use, the reduced water use associated with forest rsemoval will show up as increased dry season flow (**Figures 8** and **9**). However, where infiltration and groundwater recharge become seriously impaired by surface

Table 1 Common perceptions about the streamflow impacts of 'deforestation'

Commonly held perceptions	*Scientific experience*	*Qualifications*
Forests act like sponges absorbing water during rainy season and releasing it evenly during the dry season. Cutting of forests dries up water supplies, particularly during the dry season, because the 'sponge effect' becomes lost.	Cutting of forests increases total water yield, particularly during low flow periods. Dry season flows reduced if soil water intake capacity seriously impaired (as in severely degraded or urbanized catchments). Clearing of cloud forests may lead to reduced dry season flows and possibly total yield.	Increased total and seasonal water yields under pasture or cropping only manifested as long as surface infiltration capacity is maintained. Fine-textured soils most vulnerable to degradation. Thus, whether the perceived 'sponge effect' remains or disappears depends entirely on postconversion land use practices.
Cutting of forests causes floods as the 'sponge effect' is then lost.	Cutting of forests affects stormflow volumes for small- to medium-sized events and at the local scale ($<10\,km^2$). Little or no impact on size of extreme events (floods) at any scale although adverse effect of extensive roading cannot be excluded. Wet season flows (but not events) from very large basins probably increase due to cumulative effect of reduced infiltration opportunities.	Postforest land use must afford good surface cover. Otherwise stormflows up to medium-sized events much increased (as in severely degraded catchments).

compaction and crusting, as is eventually the case in many real-world situations, diminished dry season flows inevitably follow despite the fact that the reduced evaporation should have produced higher baseflows. In the layman's terms, the 'sponge effect' is lost (**Figures 6** and 7).

A related aspect concerns the fact that long-term fluctuations in rainfall arising from natural climatic variability are not covered adequately by short-term experiments. Such fluctuations have both short- and longer-term impacts on catchment hydrology – notably the (more frequent) occurrence of peak flows during rainier periods or diminished dry season flows during drier periods – which may be attributed erroneously to changes in landcover rather than climatic variability. The massive floods in Central Europe in the summer of 2002 and the extreme drought during the next year are a prime example of the whimsical nature of many climates.

The lack of long-term catchment studies representing actual hydrological conditions experienced by countless people perhaps calls for more modesty on the part of scientists when communicating the results of (controlled) hydrological experiments to practitioners and the public at large. More importantly, it clearly illustrates the need for stepped up efforts to remedy this deficiency.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Roading and Transport Operations. **Hydrology**: Hydrological Cycle; Impacts of Forest Management on Streamflow; Impacts of Forest Management on Water Quality; Impacts of Forest Plantations on Streamflow; Soil Erosion Control. **Soil Development and Properties**: Water Storage and Movement. **Tree Physiology**: A Whole Tree Perspective.

Further Reading

Bonell M and Bruijnzeel LA (eds) (2004) *Forests, Water and People in the Humid Tropics*. Cambridge, UK: Cambridge University Press.

Bosch JM and Hewlett JD (1982) A review of catchment experiments to determine the effects of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology* 55: 3–23.

Bruijnzeel LA (2001) Forest hydrology. In: Evans J (ed.) *The Forests Handbook*, vol. 1, pp. 301–343. Oxford, UK: Blackwell Science.

Bruijnzeel LA (2004) Hydrological functions of tropical forests: not seeing the soil for the strees? *Agriculture, Ecosystems and Environment* (in press).

Bruijnzeel LA and Bremmer CN (1989) *Highland–Lowland Interactions in the Ganges–Brahmaputra River Basin: A Review of Published Literature*. ICIMOD Occasional Paper no. 11. Kathmandu: International Centre for Integrated Mountain Development.

Calder IR (1998) Water use by forests, limits and controls. *Tree Physiology* 18: 625–631.

Calder IR (1999) *The Blue Revolution: land use and integrated water resources management*. Earthscan Publications: London.

Froehlich W, Gil E, Kasza I, and Starkel L (1990) Thresholds in the transformation of slopes and river channels in the Darjeeling Himalayas, India. *Mountain Research and Development* 10: 301–312.

Giambelluca TW (2002) The hydrology of altered tropical forest. *Hydrological Processes* 16: 1665–1669.

Hewlett JD (1982) Forests and floods in the light of recent investigation. In: *Hydrological Processes of Forested Areas*, pp. 543–559. Ottawa: National Research Council of Canada.

Hofer T (1998) Do land use changes in the Himalayas affect downstream flooding? Traditional understanding and new evidences. *Memoir of the Geological Society of India* 19: 119–141.

La Marche JL and Lettenmaier DP (2001) Effects of forest roads on flood flows in the Deschutes River, Washington. *Earth Surface Processes and Landforms* 26: 115–134.

Madduma Bandara CM (1997) Land-use changes and tropical stream hydrology: some observations from the upper Mahaweli Basin of Sri Lanka. In: Stoddard DR (ed.) *Process and Form in Geomorphology*, pp. 175–186. London: Routledge.

Sandström K (1998) Can forests 'provide' water: widespread myth or scientific reality? *Ambio* 27: 132–138.

Vertessy RA (1999) The impacts of forestry on streamflows: a review. In: Croke J and Lane P (eds) *Forest Management for the Protection of Water Quality and Quantity, Proceedings of the 2nd Erosion in Forests Meeting*, Warburton, 4–6 May 1999, pp. 93–109. Canberra: Cooperative Research Centre for Catchment Hydrology.

Vertessy RA, Zhang L, and Dawes WR (2003) Plantations, river flows and river salinity. *Australian Forestry* 66: 55–61.

Impacts of Forest Management on Streamflow

L A Bruijnzeel, Vrije Universiteit, Amsterdam, The Netherlands
R A Vertessy, CSIRO Land and Water, Canberra, Australia

Introduction

The practical overall influence exerted by forests on hydrological processes is most clearly borne out by a comparison of streamflow amounts emanating from catchment areas with contrasting proportions or types of forest. Forestry activities (thinning, selection logging, clear-felling) and natural disturbances (extreme rainfall, hurricanes, fire) have the potential to more or less seriously alter forest water use and thus change the amount and timing of streamflow. Because climatic differences (notably rainfall) between sites or years, and unmeasured transfers of groundwater from one catchment to another, tend to obscure the effect on streamflow of the vegetation, the 'direct' comparison of streamflows from catchments with contrasting forest covers can be problematic. The same applies to a comparison of the flows from a single catchment before and after a change in cover. The classical approach to these problems has been the so-called 'paired catchment experiment' in which the streamflow from two (preferably adjacent) catchments of comparable geology, topography, exposition, and vegetation are expressed in terms of each other (using regression analysis) during a 'calibration phase.' Once a robust baseline calibration relationship has been established, one of the catchments is subjected to a land cover treatment (for example, strip-cutting or clear-felling) while the other catchment remains undisturbed as the control (**Figure 1**). Following the treatment of one catchment, streamflow from both catchments continues to be monitored. Any effects of the treatment are evaluated by comparing the actually measured streamflow totals from the experimental catchment with the flows that would have occurred if the catchment had remained unchanged. This is usually done by inserting streamflow totals determined for the control catchment into the calibration relationship (**Figure 1**). Although a more rigorous comparison between catchments is obtained in this way than in the case of 'direct' comparisons, the tacit underlying assumption of the paired catchment method is that any differences in groundwater leakage from the two catchments remain constant with time, regardless of the status of the vegetation cover. Also, to avoid unjustified extrapolation of the calibration line to accommodate extremes in streamflow during the treatment phase (e.g., because of drought or extreme rainfall), it is important that the calibration period includes both wet and dry years. This makes the paired catchment method a time-consuming (usually at least 5 years) and expensive affair. In addition, the method is essentially a 'black-box' requiring additional hydrological process research to reveal the relative importance of different causative factors to explain the observed changes in streamflow. All this, plus the limited resolution afforded by the paired catchment approach (usually more than 20% cover change is required for effects on streamflow to be detectable), have led to a general decline in the number of such studies in the last few decades and a gradually greater emphasis on computer simulations (modeling).

This article reviews the hydrological effects of (1) various forms of forest management (thinning, selective logging, removal of undergrowth or riparian vegetation, and clear-cutting) and (2) natural disturbances (mostly fire and storms), and subsequent regrowth. Effects on streamflow of converting forest to other forms of land use, and the establishment of forest plantations on former agricultural

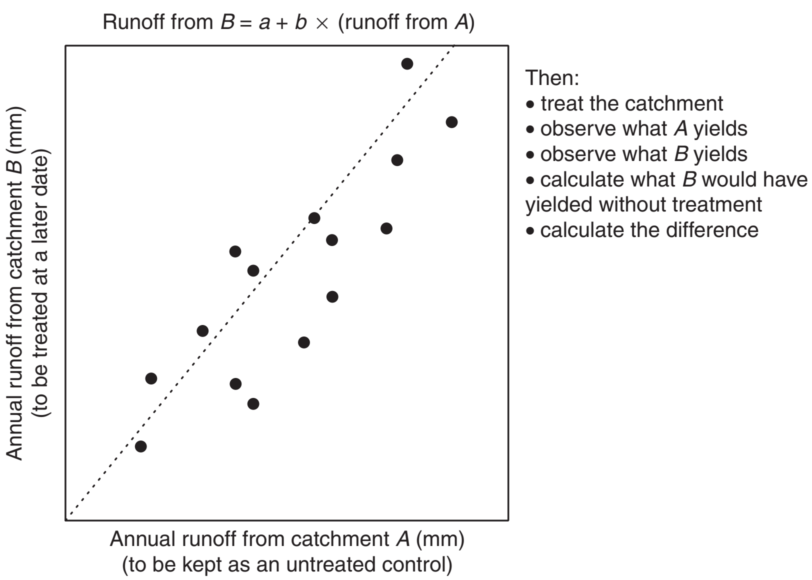


Figure 1 The paired catchment technique to evaluate the effect of landcover change on streamflow. Data shown represent flows as measured during the calibration period; the derived calibration relationship links the flows from the two catchments.

land or natural grassland are discussed in the respective companion chapters (see **Hydrology**: Impacts of Forest Conversion on Streamflow; Impacts of Forest Plantations on Streamflow).

Hydrological Effects of Thinning and Selective Logging

Effects on Net Precipitation

A forest canopy intercepts a large portion of the rain that falls on it. This process is called rainfall interception. Usually, the bulk of the intercepted water drips from the canopy as so-called throughfall, whereas a much smaller portion (usually a few percent) reaches the forest floor along branches and the tree trunks in the form of stemflow. The remainder of the intercepted water is evaporated again during and shortly after the storm and thus never reaches the ground. Therefore this term is often referred to as the interception loss. The sum of throughfall and stemflow is called net precipitation. It has long been recognized that amounts of net precipitation tend to be inversely related to the stocking of a forest. In other words, the denser the canopy, the smaller the amount of rainfall reaching the ground. Although this observation may seem trivial, amounts of intercepted water may be substantial, especially in the case of evergreen, coniferous forests (up to 45% of incoming rainfall). As a result, the amount of water available for infiltration into the soil and contributing to soil water reserves is closely related to amounts of interception. Therefore, it is of interest to examine the effect of management-related and naturally occurring changes in forest cover and structure on amounts of precipitation arriving at the forest floor.

In well-stocked coniferous forest (plantations), amounts of crown drip often show a steady decrease with forest age, reflecting the greater leaf surface area and surface roughness associated with older stands. Naturally, a larger leaf area is capable of intercepting and storing more rainfall whereas increased surface roughness enhances atmospheric turbulence and evaporation rates from the wet canopy, and thus total interception. Amounts of stemflow in these forests, on the other hand, decrease with stand age although the overall effect on net precipitation is small due to the relatively small amounts involved anyway. Together with an increased capacity of the litter layer to intercept and store rainfall in older coniferous stands the overall effect on net precipitation is that of a gradual reduction as these forests mature. For example, in stands of white pine (*Pinus strobus*) in the southeastern USA, net precipitation in 60-year-old stands was about 220 mm year^{-1} less than in 10-year-old forest. No such decline with age was found for (natural) deciduous forest in the same area. Apparently, *c*. 10-year-old deciduous forest has already acquired similar leaf biomass and roughess characteristics as the older forests. In evergreen mountain ash forest (*Eucalyptus regnans*) in Australia, on the other hand, an altogether different pattern has been observed. Here, rainfall interception increases rapidly to a value of about 25% of the rainfall during the first 30 years; then it declines slowly to about 15% at age 235 years, a difference of about 190 mm year^{-1} (**Figure 2**). Such changes reflect changes in the structure of the regenerating forest: in younger stands, the trees are closely spaced and there is little undergrowth. In old-growth forest, the trees are much more widely spaced but the understory is well developed.

Naturally, rainfall interception by deciduous forests during the dormant season is lower than during the growing season. However, the typically observed increase in net rainfall of 5–10% when the trees are leafless is by no means proportional to the reduction in leaf area which can be up to sixfold. Likewise, the decreases in rainfall interception that have been observed after forest thinning are typically three to four times smaller than the degree of canopy opening. For example, a 50% reduction in basal area of a Douglas-fir forest in France resulted in only a 13% drop in interception whereas a 13-fold reduction in basal area in a dense Sitka spruce (*Picea sitchensis*) plantation in Scotland (corresponding to a change in planting interval from 2×2 m to 8×8 m) was accompanied by a less than fourfold reduction in interception. Such findings can be explained by the fact that, although canopy cover is reduced by

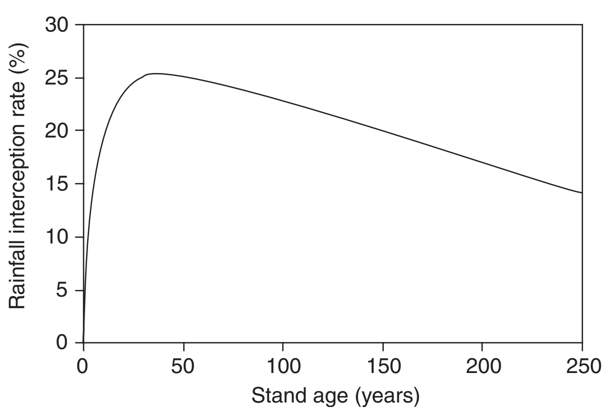


Figure 2 Relationship between mountain ash rainfall interception rate and stand age. Reproduced with permission from Haydon S *et al.* (1996) Variation in sapwood area and throughfall with forest age in mountain ash (*Eucalyptus regnans* F. Muell.). *Journal of Hydrology* 187: 351–366.

thinning or leaf fall, the aerodynamic roughness of the forest is also reduced. As a result, the turbulent exchange between the trees and the surrounding air decreases and rates of evaporation are reduced accordingly. In terms of soil water recharge the effect of forest thinning is even smaller when the felled trees are left to decompose on the site because the slash will intercept part of the gain in throughfall.

To summarize, to achieve significant increases in amounts of net precipitation entering the mineral soil, forest thinning would need to be substantial (up to 70% of basal area). In addition, for maximum effect the slash would need to be removed but this may have adverse implications for soil fertility (erosion and loss of organic matter and nutrients contained in the slash). In areas with snowfall, opening up of the forest will enhance both the rate and timing of snowmelt. Depending on the situation, this may be considered positive (higher water yields) or negative (aggravation of spring flooding).

Effects on Forest Water Use and Catchment Water Yield

Whilst the effect of thinning on interception and net precipitation is thus seen to be rather limited, effects on soil water (and ultimately streamflow) are likely to be smaller still. Opening up of a stand not only enhances the penetration of radiation to the understory vegetation and the forest floor (thereby enhancing evaporation), but also the remaining vegetation will start to compete for the extra moisture supplied by the initially increased throughfall. The magnitude and the duration of such effects will differ between locations, depending on the vigor of overstory and understory vegetation, climatic conditions (including slope exposure), and the configuration of the cutting, as shown by the examples below.

No changes were detected in the streamflow from a deciduous hardwood forest catchment of southeasterly exposure in the southeastern USA (Coweeta) after a selective logging operation had removed 27% of the basal area, whereas only a 4.3% rise in flows was observed after a 53% selective cut. Removing the entire understory (representing 22% of forest basal area) from a catchment of northwesterly exposure in the same area produced an equally modest change. Typically, the moisture gained by removing one component of the forest is rapidly taken up by others. In coastal Douglas-fir forest in western Canada soil water deficits developing during the summer have been shown to be very similar below dense, unthinned stands with little to no undergrowth, and thinned stands with a well-developed understory. After removal of the undergrowth, soil water uptake by the trees increased by 30–50% and the overall effect of the removal on soil water content was insignificant. In an experiment involving two 40-year-old Scots pine plantations of similar tree height but with a more than fivefold difference in stocking in the UK, tree water uptake (transpiration) in the widely spaced plantation was about two-thirds of that of the denser stand. However, relative transpiration rates per tree were more than three times higher in the thinned plot, and intermediate in magnitude between the relative increases in average water-conducting area (so-called sapwood) per tree (2.9 times) and leaf area per tree (4.2 times), compared to the unthinned stand. Therefore, although water use by the thinned forest had not reached prethinning levels yet, the large increases in leaf and sapwood areas of the remaining trees could be seen as representing a tendency towards complete re-equilibration following a set of physiological relationships aimed at maximum site utilization. Finally, in an extreme case from South Africa any positive effects on streamflow of three rounds of thinning (45%, 35%, and 50% after 3, 5, and 8 years) *Eucalyptus grandis* plantations were masked entirely by the continued reduction in flows resulting from the overall vigorous growth (and thus water uptake) of the trees. The message from these examples is a clear one: thinning has to be rather drastic before a marked effect on streamflows can be expected.

Selection logging in tropical rainforest does not produce measurable effects on streamflow for harvesting volumes up to $20\,m^3\,ha^{-1}$ but the much higher logging intensities practised in the rich forests of Southeast Asia have a marked effect. Typical increases in annual water yield under 'average' rainfall conditions (*c.* $2000\,mm\,year^{-1}$) and harvesting intensities (33–40% of the commercial stocking) amount to 100–150 mm but larger increases are possible where harvesting is more intense and disturbance of the soil more widespread. The effect usually disappears within a few years as logging gaps become recolonized (**Figure 3**) although compacted surfaces like tractor tracks, roads, and log landings continue to be sources of enhanced runoff for much longer (decades).

Apart from the degree of cutting, the configuration of the resulting gaps also has an influence. During the first dry season after the creation of differently sized gaps in tropical rainforest in Costa Rica, soil water reserves were depleted most rapidly under undisturbed forest, followed by 6-year-old regrowth, pioneers in an elongated narrow gap, and pioneer vegetation in the center of a large square gap (**Figure 3**). Only 1 year later, however, soil water depletion in the smaller gap already resembled that of the 7-year-old vegetation,

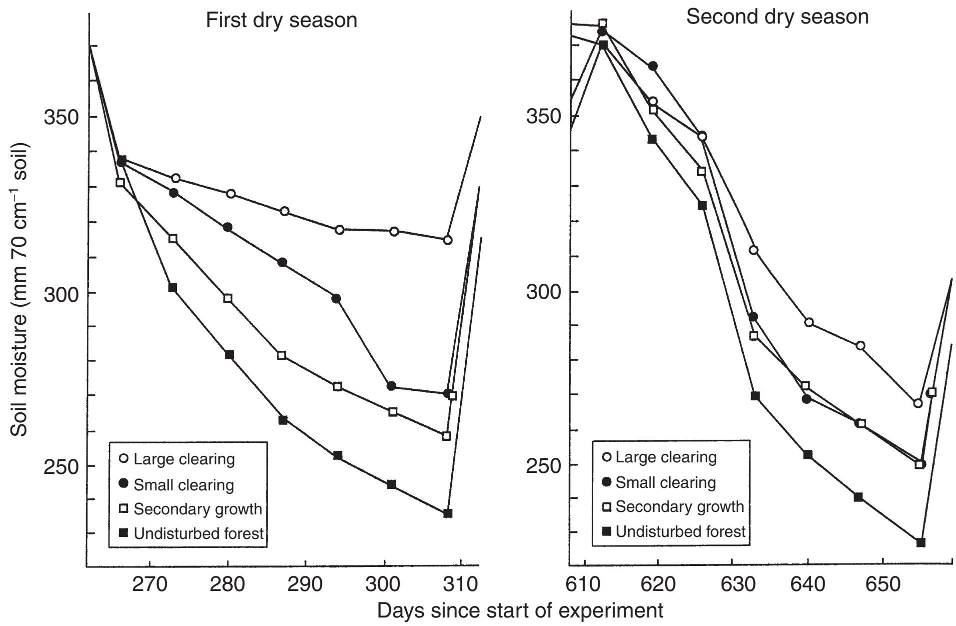


Figure 3 Soil moisture content in the top 70 cm of soil below undisturbed tropical rain forest, 6-year-old secondary growth, and in a narrow (10 × 50 m) and a large (50 × 50 m) clearing in lowland Costa Rica during two consecutive dry seasons. Reproduced with permission from Parker GG (1985) *The Effect of Disturbance on Water and Solute Budgets of Hillslope Tropical Rainforest in Northeastern Costa Rica*. PhD thesis, University of Georgia, Athens, GA.

whereas that for the larger gap had increased considerably as well. The higher water uptake by the vegetation in the smaller gap compared to that in the larger gap reflects the more rapid recolonization of smaller gaps as well as additional uptake by trees from the surrounding forest sending their roots into the gap (**Figure 3**).

The influence of the configuration of the cutting on the magnitude and duration of any increases in streamflow has been investigated in some detail. In the eastern USA the removal of 24% of the basal area from catchment LR 2 at Leading Ridge (Pennsylvania) caused a nearly twofold larger increase in flow than cutting 33% of the forest on catchment HB 4 at Hubbard Brook (New Hampshire) or catchment FEF 2 at Fernow Experimental Forest (West Virginia) (see **Figure 4**). The cutting at Leading Ridge consisted of a single block on the lowest portion of the catchment, whereas the cutting at Hubbard Brook took the form of a series of strips situated halfway up the catchment, and that at Fernow involved harvesting trees from all over the catchment. Therefore, increases in streamflow associated with strip cutting are smaller than for single blocks. This is in agreement with the finding of increased water uptake by surrounding trees upon opening up of the canopy (**Figure 3**) and the limited effect on rainfall interception by thinning described earlier.

No significant differences in streamflow increases were found between the cutting of the upper half of a catchment (such as at catchment 7 at Fernow; FEF 7 in **Figure 4**) or the lower half (catchment FEF 6 in **Figure 4**). Likewise, removal of the vegetation around

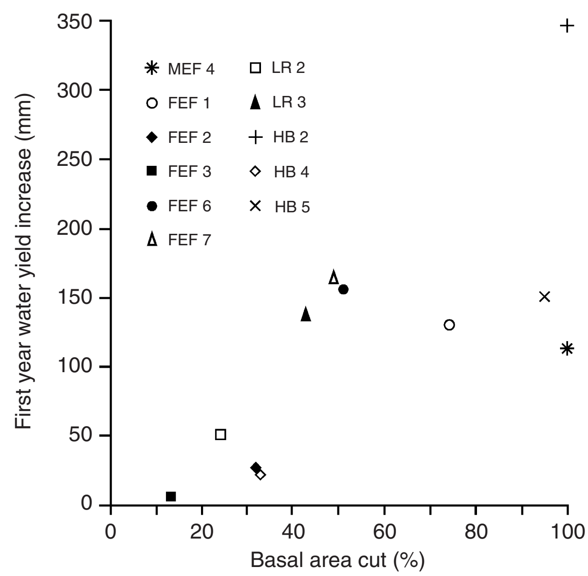


Figure 4 First-year increases in water yield in response to forest cutting in the northeastern USA. Reproduced with permission Hornbeck JW, Adams MB, Corbett ES, Verry ES, and Lynch JA (1993) Long-term impacts of forest treatments on water yield: a summary for northeastern USA *Journal of Hydrology* 150: 323–344. MEF, Marcell Experimental Forest, MN; FEF, Fernow, WV; LR, Leading Ridge, PA; HB, Hubbard Brook, NH.

watercourses in areas with a high rainfall surplus did not produce increases in water yield above those associated with the removal of an equal area of forest elsewhere in the catchment. However, where forest evaporation consumes a much larger proportion of the rainfall and where the terrain is more gently sloping than in the examples shown in **Figure 4**, the effect of cutting trees in the lower third to half of a catchment may well be rather more pronounced than that of cutting the upper third to half. Under such subhumid conditions, water uptake by trees having ready access to groundwater is usually higher than that of trees further up the slopes. High water tables are typically associated with the areas around streams (the riparian zone), footslopes and depressions in the landscape; these, in turn, are mostly found in the lower parts of catchments.

Effects of Forest Clear-Felling and Regrowth on Water Yield and Hydrological Response

Well over 100 (paired) catchment treatment experiments have been conducted (mostly in the temperate zones of the world) to ascertain the nature and extent of streamflow change resulting from forestry operations (mostly clear-felling). Analysis of the literature on catchment treatment experiments indicates that one can confidently generalize about the direction and approximate magnitude of streamflow changes following particular alterations in forest cover. Some of the more robust generalizations are discussed below.

Generalization No. 1: Forested Catchments Yield Less Total Streamflow than Cleared Catchments and the Difference Increases with Mean Annual Rainfall

Almost all catchment treatment experiments have shown that streamflow increases as forest cover decreases, and vice versa (**Figure 5**). The reason for this is that forests evaporate significantly more water than grasslands or crops. Although transpiration rates (soil water uptake by plants) under conditions of ample soil water do not differ much between forests and nonforest vegetation, rates of evaporation from vegetation wetted by rain (rainfall interception) are much higher from tall, aerodynamically rough surfaces like forests. In addition, the deeper roots of trees allow continued water uptake when more shallow-rooted plants have to give up during prolonged rainless periods. Because rainfall interception totals are higher in wetter years, the impact of forest clearance (i.e., after interception falls away) increases with mean annual rainfall (**Figure 6**).

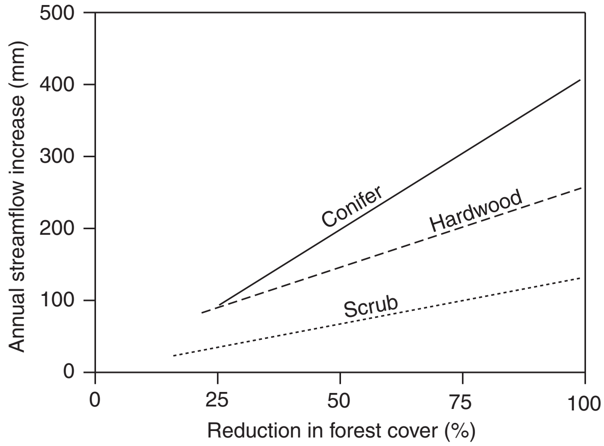


Figure 5 Relationships between reduction in forest cover and increase in annual catchment water yield. The general trend lines show the respective relationships for three types of woody vegetation. Reproduced with permission from Bosch JW and Hewlett JD (1982) A review of catchment experiments to determine the effects of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology* 55: 3–23.

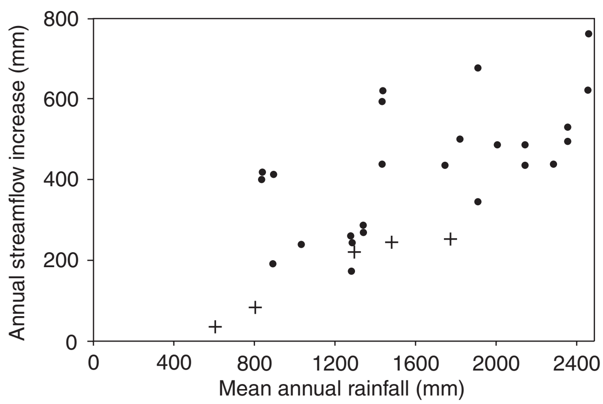


Figure 6 Effect of mean annual rainfall on increases in total water yield caused by total clearance of conifer and scrub vegetation (adapted from Bosch and Hewlett 1982). Crosses denote the expected gains in water yield from converting eucalypt forest to pasture in Victoria, Australia. Reproduced with permission on Holmes JW and Sinclair JA (1986) Water yield from some afforested catchments in Victoria. In: *Hydrology and Water Resources Symposium*, 25–27 November 1986, Brisbane, pp. 214–218. Melbourne, Australia: Institute of Engineers.

Apart from rainfall, the magnitude of the change in annual streamflow is also affected by forest type and slope aspect. Generally, the largest changes are observed in the case of clearing conifers, owing to their dense evergreen habit and high interception, followed by native (but not exotic) eucalypt forests, then deciduous hardwoods (leafless in winter or dry season) and finally woody scrub vegetation (found in low rainfall areas) (**Figure 5**). Mean annual streamflow can be expected to rise by between 10 and 80 mm (but usually between 25 and 50 mm) for each

10% of catchment area cleared of forest, depending on the forest type and rainfall as discussed above (**Figures 5** and **6**). The importance of catchment exposition is illustrated by the difference in first-year streamflow gain after cutting differently exposed deciduous hardwood forest catchments in the southeastern USA. Flows from northerly exposed catchments increased by about 130 mm $year^{-1}$ but increases from southerly exposed catchments (whose forests consumed much more water in response to the greater insolation of their slopes) were as high as 400 mm $year^{-1}$. Most studies indicate that the relationship between treated area and streamflow change is linear (**Figure 5**), although there is some evidence that in subhumid areas the magnitude of streamflow change is reduced if forest treatments take place away from streamside areas.

Generalization No. 2: Streamflow Increases Following Forest Cover Reduction Are Transient and Temporary when Same-Species Regeneration Occurs

In a forest which is cleared or killed by wildfire but permitted to regenerate with the same species, streamflow increases are both transient and temporary. Streamflow increases normally reach a peak within 2–5 years after clearance, then decline to pretreatment levels over a period of between 3 and 35 years (but usually within 10 years), depending on rainfall, soil factors, and forest regrowth rates. This pattern can be explained by the fact that a new vegetation first has to establish itself before water use is gradually increased again. Also, elevated streamflow levels tend to last much longer (15–35 years) when regeneration has to originate from seeds than when massive resprouting occurs (3–7 years).

Part of the increase in streamflow after cutting reflects an increase in catchment response to rainfall. Usually, such storm runoff is generated in wet spots in the landscape, mostly around streams and depressions. Runoff-producing areas are enlarged after forest removal because of the associated increase in water inputs to and reduced uptake from the soil. Once a new vegetation cover is established which starts to actively withdraw water from the soil the extent of the runoff-producing areas is reduced again. However, roads and other compacted areas continue to deliver storm runoff to the streams on a more permanent basis although their areal extent is usually small.

Generalization No. 3: Forest Age Affects Evapotranspiration Rate and Hence Streamflow

A small but significant set of catchment treatment experiments and hydrological process studies indicate that young forests have higher evapotranspiration rates than mature forests, resulting in notable streamflow differences between young and old-growth stands. One of the most comprehensive studies of forest age on streamflows concerns work undertaken in the mountain ash forests of southeast Australia. The ecology of these forests is distinctive, in that they only regenerate after severe wildfire which kills the trees and produces a heavy seedfall. These forests are thus usually even-aged and monospecific, and tend to live for several hundreds of years unless they are killed earlier by wildfire. Significantly, the eucalypts thin out naturally over time, resulting in major changes in forest structure and hydrologic function as stands age. It has been shown that regrowth mountain ash forests aged 25–30 years yield about half the mean annual streamflow of mature stands aged 200 years (i.e., 580 vs. 1195 mm $year^{-1}$ for 1950 mm mean annual rainfall). It has further been shown that it may take between 50 and 200 years before mean annual streamflow in a regenerating mountain ash catchment returns to levels observed in old-growth stands (**Figure 7**).

The effect of stand age on forest water use, and by implication streamflow, is not confined to mountain ash forests. Similar findings have been reported for mixed-species eucalypt forests in the northeast and southeast regions of New South Wales, Australia, in conifer plantations in South Africa, in deciduous hardwood forests in Japan and central France, as well as in coastal redwood forests in California and secondary forests in the Brazilian Amazon.

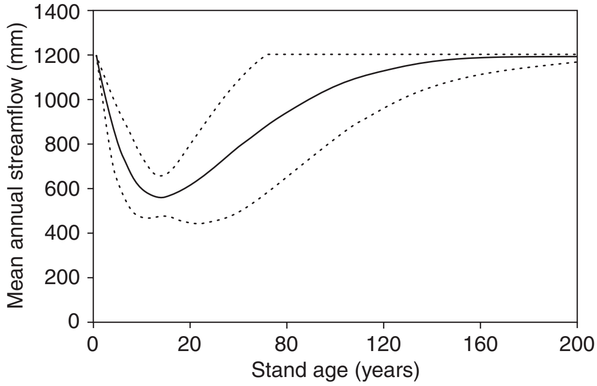


Figure 7 Relationship between forest age and mean annual runoff from mountain ash forest catchments, southeastern Australia. Dotted lines denote the 95% confidence limits on the relationship. Reproduced with permission from Vertessy RA, Watson FGR, and O'Sullivan SK (2001) Factors determining relations between stand age and catchment water yield in mountain ash forests. *Forest Ecology and Management* 143: 13–26.

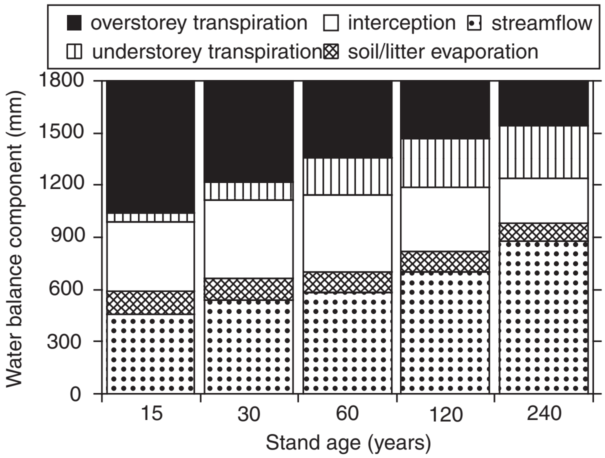


Figure 8 Water balance components for mountain ash forest stands of various ages in southeastern Australia, assuming an annual rainfall of 1800 mm. Reproduced with permission from Vertessy RA, Watson FGR, and O'Sullivan SK (2001) Factors determining relations between stand age and catchment water yield in mountain ash forests. *Forest Ecology and Management* 143: 13–26.

An explanation for the stand age–streamflow relationship in mountain ash forests has been provided by elucidating the leaf area and evapotranspiration dynamics of stands of various ages (**Figure 8**). As the forest matures, total leaf area declines and a greater proportion of the leaf area is allocated to the understory which experiences a gradually more humid and less ventilated microclimate. This results in lower overall water use and hence increased streamflow. Tree physiological measurements indicate that tree sapflow rates decrease with age, owing to increases in the resistance experienced by the flow as stems and branches lengthen and leaf ages increase. Such age-dependent effects on forest water use will tend to be maximized in long-lived, self-thinning, very tall forests.

Generalization No. 4: Forest Cover Affects the Magnitude of Streamflow Peaks for Small and Medium Events

As outlined earlier, the clearance of forests leads to an increase in catchment soil water status which tends to expand wet, runoff-producing areas. Therefore, cleared catchments respond more quickly and more vigorously to rainfall events. Most catchment treatment experiments show that the magnitude of discharge peaks is increased by forest clearance for small and medium-sized rainfall events, particularly when soils are disturbed by logging machinery and the establishment of road networks. However, it is generally accepted that modification of forest cover has little to negligible impact on flood peaks generated by extreme events, say those with recurrence intervals of 100 years and upwards. Under such extreme conditions, catchment runoff response is governed by the capacity of the soil to accommodate additional rainfall. If this capacity has been filled already by previous heavy rainfall, then the presence or absence of a forest cover is no longer decisive. Also, it is important to bear in mind that the local effects of forestry activities on stormflow tend to be diluted at larger scales by more modest flows from other areas receiving less rain or being less disturbed. Generally, the overriding factors in extreme flooding are the duration and intensity of the rain and the spatial extent of the rainfall field.

Nevertheless, there is reason for caution. Recent work in the Pacific Northwest region in the USA has demonstrated that forest clear-felling and the presence of an extensive road network each increased average stormflow volumes by *c.* 10%. Whilst the relative effect of the clear-felling diminished with the size of the stormflow generating event, the effect of the road network increased with event size.

Modeling the Hydrological Impacts of Forest Manipulation

As shown in the preceding sections, different forest manipulations affect the water flows through catchments differently. Traditionally, forest hydrologists have relied on costly and time-consuming paired catchment experiments to evaluate such effects. Whilst this approach enabled the construction of general curves from which changes in annual streamflow totals can be read as a function of annual rainfall (see **Figure 6**), or first-year increases in flow as a function of percentage basal area reduction and catchment aspect for particular areas at best, the results are often so variable as to render their applicability for more detailed water resources planning rather limited (**Figures 5** and **6**). Also, the black-box nature of the paired catchment technique is unable to evaluate the relative importance of the governing factors underlying the observed changes in flow, and this severely limits the possibilities for extrapolation of results to other areas or years.

Process-based hydrological models represent an alternative way of predicting how catchments might respond to different forms of management. Because many practical forest management questions have a spatial dimension to them, and because landscapes are usually made up of a complex mosaic of different land uses, such models should preferably be 'distributed,' that is: capable of taking into account spatial variations in topography, soils, vegetation, and climate. During the last 10–15 years, considerable progress has been made with the modeling of forest hydrological and ecological processes over a range of spatial and temporal scales. Within-catchment applications of such models relevant to forestry include the prediction of wet zones in the landscape (governing machine access) and the delineation of areas especially prone to surface erosion, gullying, or landsliding. Another example concerns the evaluation at the hillslope scale of the water balance and growth performance of different tree planting configurations (e.g., block planting vs. strip planting) under subhumid conditions. Whole-catchment applications include the simulation of changes in tree growth and water yield after clear-felling during forest regeneration or of a conversion of forest to pasture. To address forestry-related questions of catchment water management at larger scales (100–1000 km^2), simpler (but still spatially distributed) models have been developed and used to simulate (for instance) long-term changes in water yield due to forest fire and subsequent regeneration in a spatially distributed manner. Such models, if applied properly, can lead to more rational land and water management decision-making. However, whilst distributed models represent the only class of simulation models capable of capturing the complex feedback mechanisms that occur upon disturbing hydrological systems, they are also data-demanding. In addition, at larger scales there is the problem that good results require equally good data on the spatial distribution of rainfall. However, there is reason for optimism as various remote sensing technologies that are currently still in their infancy can be expected to become widely available within the next decade. This will greatly facilitate data acquisition and upscaling of hydrological results over larger areas.

The last decades have seen the waning of the 'empirical age' of catchment treatment experimentation and ever more rapid developments in our ability to model complex natural systems in a spatially explicit way. Although the arrival of process-based distributed hydrologic models and ongoing improvements in measurement equipment, remote sensing technology and computing power guarantee that there are exciting times ahead for forest hydrologists, continued field experimental efforts will remain important for model calibration and testing.

See also: **Harvesting**: Roading and Transport Operations. **Hydrology**: Hydrological Cycle; Impacts of Forest Conversion on Streamflow; Impacts of Forest Management on Water Quality; Impacts of Forest Plantations on Streamflow; Snow and Avalanche Control; Soil Erosion Control. **Operations**: Forest Operations Management. **Soil Development and Properties**: Water Storage and Movement. **Tree Physiology**: A Whole Tree Perspective.

Further Reading

Bonell M and Bruijnzeel LA (eds) (2004). *Forests, Water and People in the Humid Tropics*. Cambridge, UK: Cambridge University Press.

Bosch JM and Hewlett JD (1982) A review of catchment experiments to determine the effects of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology* 55: 3–23.

Bruijnzeel LA (2001) Forest hydrology. In: Evans J (ed.) *The Forests Handbook*, vol. 1, pp. 301–343. Oxford, UK: Blackwell Science.

Giambelluca TW (2002) The hydrology of altered tropical forest. *Hydrological Processes* 16: 1665–1669.

Hewlett JD (1982) Forests and floods in the light of recent investigation. In: *Hydrological Processes of Forested Areas*, pp. 543–559. Ottawa, Canada: National Research Council of Canada.

Hornbeck JW, Adams MB, Corbett ES, Verry ES, and Lynch JA (1993) Long-term impacts of forest treatments on water yield: a summary for northeastern USA. *Journal of Hydrology* 150: 323–344.

Jones JA and Grant GE (1996) Peak flow responses to clear-cutting and roads in small and large basins, western Cascades, Oregon. *Water Resources Research* 32: 959–974.

La Marche JL and Lettenmaier DP (2001) Effects of forest roads on flood flows in the Deschutes River, Washington. *Earth Surface Processes and Landforms* 26: 115–134.

Pearce AJ, Rowe LK, and O'Loughlin CL (1980) Effects of clearfelling and slashburning on water yields and storm hydrographs in evergreen mixed forests, western New Zealand. *International Association of Hydrological Sciences Publication* 130: 119–127.

Peel MC, Watson FGR, Vertessy RA, *et al*. (2000) *Predicting the Water Yield Impacts of Forest Disturbance in the Maroondah and Thomson Catchments using the Macaque Model*. Cooperative Research Centre for Catchment Hydrology Report no. 00/14. Victoria, Australia: Monash University.

Stednick JD (1996) Monitoring the effects of timber harvest on annual water yield. *Journal of Hydrology* 176: 79–95.

Stogsdill WR, Wittwer RF, Hennessey TC, and Dougherty PM (1992) Water use in thinned loblolly pine plantations. *Forest Ecology and Management* 50: 233–245.

Swank WT, Swift LW, and Douglas JE (1988) Streamflow changes associated with forest cutting, species conversions, and natural disturbances. In: Swank WT and Crossley DA (eds) *Forest Hydrology at Coweeta*, pp. 297–312. New York: Springer-Verlag.

Teklehaimanot Z, Jarvis PG, and Ledger DC (1991) Rainfall interception and boundary layer conductance in relation to tree spacing. *Journal of Hydrology* 123: 261–278.

Vertessy RA, Watson FGR, and O'Sullivan SK (2001) Factors determining relations between stand age and catchment water yield in mountain ash forests. *Forest Ecology and Management* 143: 13–26.

Watson FG, Vertessy RA, and Grayson RB (1999) Large-scale modelling of forest eco-hydrological processes and their long term effect on water yield. *Hydrological Processes* 13: 689–700.

Impacts of Forest Plantations on Streamflow

D F Scott, Okanagan University College, Kelowna, Canada
L A Bruijnzeel, Vrije Universiteit, Amsterdam, The Netherlands
R A Vertessy, CSIRO Land and Water, Canberra, Australia
I R Calder, University of Newcastle upon Tyne, UK

Characteristics of Plantation Forests

Tree plantations for the production of timber have been established for more than a century (tropical teak and mahogany plantations, for instance, date back to the mid-nineteenth century), but it is mainly in the last few decades that an exponential expansion of this form of land use has occurred. Taking one of the most popular tree types for plantations as an example, eucalypts have been planted on an estimated 17 million ha worldwide, of which more than 90% have been established since 1955 and roughly 50% during the last decade. The total plantation area around the globe is 187 million ha of which over 60% are in Asia, with Europe having the next largest share (17%). *Eucalyptus* and *Pinus* are the dominant genera within the broadleaved and coniferous plantations, respectively. Although forest plantations only occupy about 5% of the world's forest area, they are estimated, as of 2000, to supply 35% of all roundwood, a figure that is expected to rise to 44% by 2020 as natural forests continue to decline and demands keep rising.

Plantations are typically established at a regular spacing (1000–2000 stems ha^{-1}), and individual stands (compartments) have the same age and are composed of a single species or clone. Often plantations are particularly productive because the tree species being grown are exotic to the area and thus free of their native pests and diseases. Generally, a distinction is made between industrial plantations (aimed at producing wood for commercial purposes, including construction timber, panel products, furniture timber, and paper pulpwood) and nonindustrial plantations (aimed at fuelwood production, protection of catchment areas for soil and water conservation, provision of wind- or fog breaks, etc.).

Scope

There appears to be a significant disparity between public and scientific perceptions of the hydrological role of forests in general and of plantations in particular. Arguably, the contrasts in views are especially pronounced in tropical regions where calls for massive reforestation programs to restore reduced dry season flows or to suppress flooding and stream sedimentation are heard more frequently. Often, however, these expected hydrological benefits are not realized and in a number of cases forest plantations have even been observed to aggravate the situation. This article recapitulates the current understanding of how forest plantations affect the hydrological functioning of catchments. Other articles outline the principles of the forest hydrological cycle (*see* **Hydrology**: Hydrological Cycle) and indicate the hydrological effects of various forest management activities and forest conversion to other land uses (*see* **Hydrology**: Impacts of Forest Conversion on Streamflow; Impacts of Forest Management on Streamflow). Strictly speaking, the term 'reforestation' should be used to describe the planting of trees in areas that were once covered by natural forest whereas 'afforestation' applies to plantation establishment in areas that are too dry, or for other reasons, do not support natural forest vegetation. To avoid semantic problems, the term 'forestation' is used mostly in the following to denote either type of planting.

The Forest Plantation Water Budget

The hydrology of tree plantations is most easily discussed with the aid of a simple water budget equation, most simply expressed in equivalent units of water depth (mm per unit of time):

$$P = ET - Q + \Delta S$$

where P is total precipitation (mostly rainfall, sometimes also fog or snow), ET the sum of various evaporation components (often referred to as evapotranspiration), Q the surface runoff or streamflow, and ΔS the change in (subsurface) storage of water in the catchment (soil water and groundwater reserves).

Evapotranspiration ET dominates the water balance of all but the most humid forest plantations. Beyond an annual precipitation of *c.* 2000 mm and under conditions of lowered evaporative demand (e.g., montane or coastal fog belts) the balance between evaporation and streamflow tips toward streamflow. There are two main components to forest ET: transpiration (the water which is taken up from the soil by roots and passes through the trees to be transpired from the stomata of the leaves, E_t) and interception (the water that is caught in the canopy and evaporates directly back into the atmosphere without reaching the ground, E_i). Under closed canopy conditions, usually rather minor additional components of evaporation are evaporation from the soil surface (E_s), which in a forest includes interception by the litter layer, and evaporation from understory vegetation. The presence or absence of a forest cover has a profound influence on the magnitude of *ET*, and by implication, also on streamflow *Q*.

Rainfall Interception

Compared to short, simple vegetation canopies (grassland, agricultural crops), tree plantations increase evaporation losses by intercepting a larger portion of incident rainfall. Generally, annual interception totals associated with the dense canopies typical of evergreen coniferous plantations are higher than those of deciduous broadleaved forests. Interception is also particularly high (expressed as a fraction of total precipitation) where rainfalls are frequent but of low intensity, especially where the evaporation process is aided by the influx of relatively warm air striking a cooler vegetation surface, as is often observed in near-coastal areas. An example of this effect comes from the UK where conifer plantations have been established in upland heath and grasslands in Scotland and Wales. Here the nature of the precipitation, proximity to the ocean, and the change in canopy density may increase interception losses to as much as 35–40% of annual precipitation.

At the other end of the interception spectrum (E_i *c*. 6%) are the *Eucalyptus* plantations of the humid, subtropical eastern escarpment in South Africa. This is an area of high seasonal rainfall (1200–1500 mm), much of which falls in the form of infrequent storms of short duration but high intensity. Interception losses from pine plantations in the same area are somewhat higher (13%), reflecting their denser canopies compared to the more open canopies of the eucalypt stands. In the cooler southwestern part of South Africa, an area of winter rainfall of lower intensity, interception losses from pine plantations are higher again (18%) than in the pine plantations in the subtropical areas. In the case of both pine and eucalypt plantations, though, there is a net increase in interception over the grasslands and scrub vegetation they replace because of the higher leaf area, greater depth of canopy, and aerodynamic roughness associated with timber plantations.

Rainfall interception in tropical tree plantations ranges from relatively low values in eucalypt stands (*c*. 12%) (**Figure 1a**), to *c*. 20% for broadleaved hardwood species such as teak and mahogany (**Figure 1b**), and 20–25% for pines (**Figure 1c**) and other conifers (*Araucaria, Cupressus*), with the higher values usually found in upland situations where rainfall intensities are generally lower. Well-developed dense stands of the particularly fast-growing *Acacia mangium*, on the other hand, may intercept as much as 30–40% of incident rain. Typical interception values for the rainforests replaced by these plantations range from 10–20% in most lowland situations to 20–35% in montane areas.

Transpiration

Transpiration (soil water uptake) is the second large component in the evaporation budget of forest plantations. Usually, plantation water uptake rates are similar to those of natural forest occurring in the area of planting but under certain conditions water use of the (usually exotic) newcomers may be higher, particularly under subhumid conditions where the natural vegetation consists of more open woodland or scrub. Examples include the replacement of dry forest/scrub by fast-growing plantations of *Eucalyptus camaldulensis* and *E. tereticornis* in South India, and by *E. grandis* in southeastern Brazil and South Africa. Likewise, water uptake rates reported for (vigorously growing and densely stocked) stands of *Acacia mangium* in Malaysia and for various species planted in the lowland rainforest zone of Costa Rica are such that they must exceed the water use of the old-growth rain forests they are replacing, possibly by 100–250 mm year^{-1}. Even greater differences in transpiration can be expected where plantations are established in areas with (natural) grassland or degraded cropland. For example, whilst forest water uptake under humid tropical conditions typically exceeds that of pasture by about 200 mm year^{-1}, the difference may increase to as much as 500–700 mm year^{-1} under more seasonal conditions. Such differences reflect the contrasting rooting depths of trees and grassland as well as the tendency for natural grasslands to go dormant during extended dry periods while the (exotic) trees continue to take up water.

Total Evapotranspiration (ET)

It follows from the above increases in rainfall interception and transpiration that are typically associated with the establishment of tree plantations in areas of (natural) grasslands or (degraded) cropland that overall *ET* totals can be much increased after forestation. As shown in **Figure 2**, total *ET* values for actively growing plantations may approach 1500 mm year^{-1} and, occasionally, as much as 1700–1900 mm year^{-1}. Such very high values must be considered the exception rather than the rule, however, and probably reflect the advection of

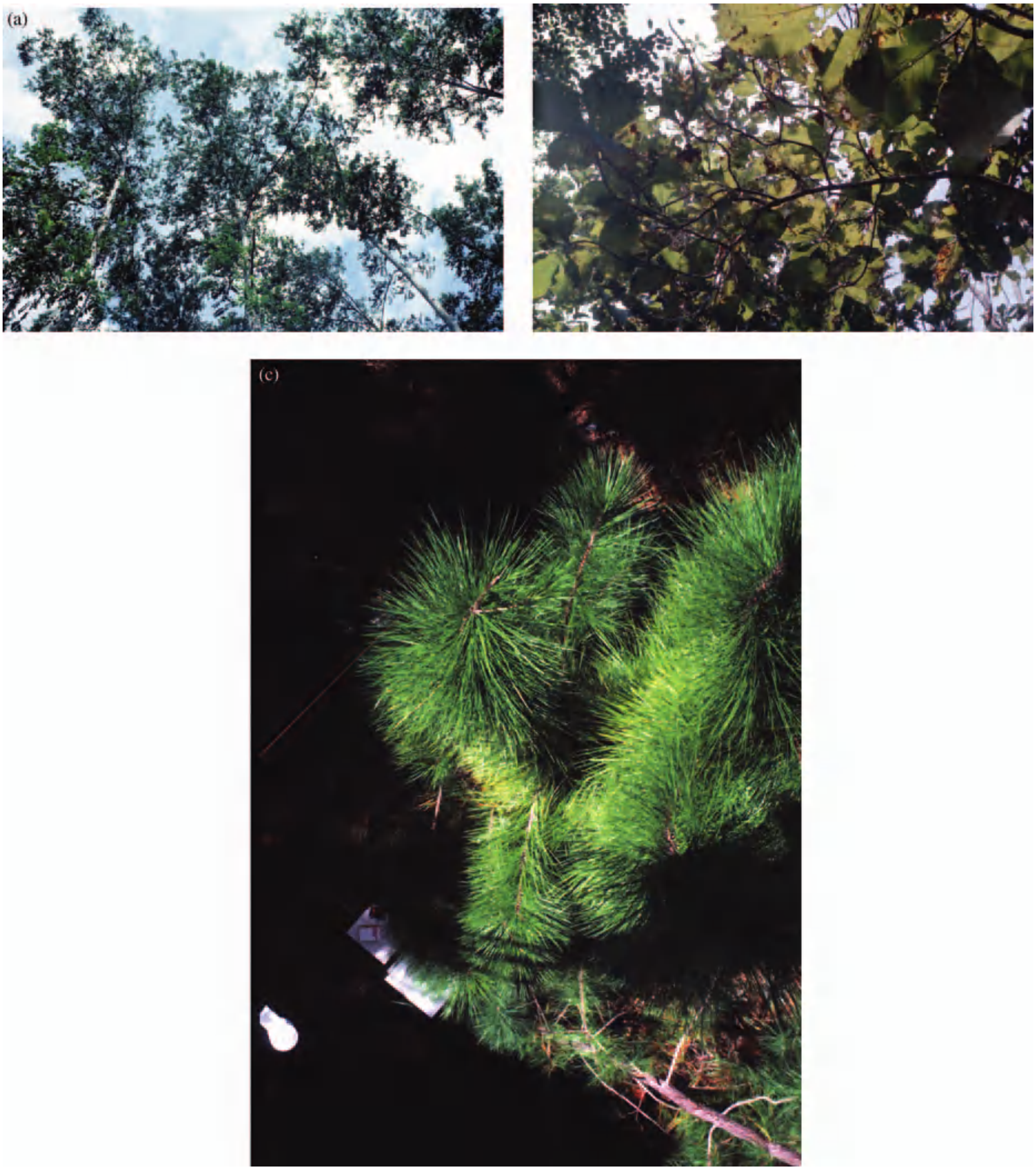


Figure 1 The contrasting canopies of (a) *Eucalyptus* spp., (b) teak (*Tectona grandis*), and (c) pines (*Pinus caribaea*) lead to differences in amounts of rainfall interception and in the drop size spectra (and thus eroding power) of water dripping from the canopy. Photographs by LA Bruijnzeel.

warm, dry air flowing in from adjacent grassland areas which tends to greatly enhance evaporation rates. Nevertheless, the fear is justified that the much increased water use of tree plantations compared to the grasslands and crops they replace will lead to substantial reductions in catchment water yields, particularly during the dry season, if entire catchments are planted.

Effects of Tree Plantations on Streamflow

Effects of Associated Land Management

In discussing the hydrological effects of establishing timber plantations, it is important to be clear about the site-specific conditions and management practices associated with the land-use change and their contribution to the effect of a change in land use.

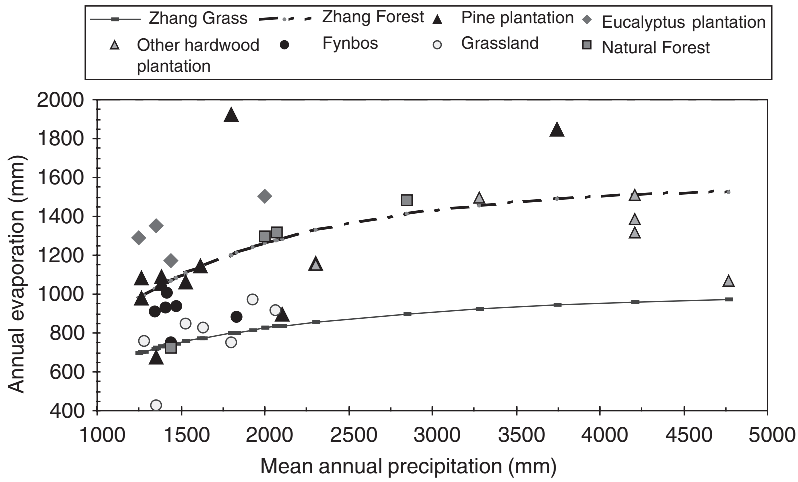


Figure 2 Total evaporation (*ET*) from forest plantations and other vegetation types as a function of precipitation. Data mostly from humid tropical (Bruijnzeel 1997) and South African plantations (courtesy of D Le Maitre, CSIR, South Africa, unpublished compilation). The curves define average forest and grassland water use in southeastern Australia (adapted from Zhang L, Dawes WR, and Walker GR (2001) Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research* 37: 701–708), and have been extrapolated for rainfall >2000 mm.

Such background information may be very important in assessing the overall hydrological effect of the plantations. The following examples illustrate the need to specify more than simply the change in vegetation cover itself.

Firstly, a forest or plantation would be expected, normally, to have a continuous groundcover of leaf or needle litter and some shade-tolerant shrubs. In parts of southern China and adjacent countries, however, all litter and understory plants may be collected for fuel, a practice that has a profound influence on the occurrence of surface runoff and erosion in the plantation (**Figure 3**). Elsewhere (as on the Indian subcontinent) forests and plantations are used to graze cattle, a practice that requires regular burning to stimulate the growth of fresh grass shoots. The combined effect of burning and trampling by livestock may promote massive surface erosion, sometimes to the extent of initiating gullies.

Contrary to popular belief, it is not the interception of rainfall by the main tree canopy that protects the soil underneath against the erosive impact of the rains. Rather it is the combined protection afforded by the understory vegetation and a well-developed litter layer that prevents the soil from being eroded. In fact, the erosive power of rain dripping from the canopies of tall trees is often greater than that in the open, because of the associated increases in drop sizes. The largest increases in drop diameters are observed for drip from large-leaved trees such as teak or *Gmelina*, whereas those falling from eucalypts or pines are more modest in size (**Figure 4**). Such findings underscore the importance of maintaining a good groundcover in plantations if runoff and erosion problems are to be avoided (cf. **Figure 3**).

A final example of the importance of management comes from the wet and peaty hill country of Scotland and the English borderlands, where surface drains are usually excavated prior to the planting of coniferous trees (mostly Sitka spruce, *Picea sitchensis*), to improve the success of tree crop establishment. However, the influence of the drainage ditches on streamflow has proved more important than the vegetation change from heath and moorland to tree plantation itself.

Forestation and Water Yield

The increased evaporation from timber plantations replacing shorter vegetation types (**Figure 2**), not unexpectedly, translates into decreases in annual streamflow totals after plantation establishment. Although there are no stringent (paired) catchment experiments in the humid tropics proper, there is overwhelming evidence to this effect from the subhumid tropics (notably India), the subtropics (mostly South Africa), and the temperate zone (including southeast Australia and New Zealand). Considerable differences have been observed between species but these are not necessarily the same in different areas. For example, in southeast Australia and New Zealand greater reductions in flow were observed after planting pines (*Pinus radiata*) on grassland than in the case of planting eucalypts (**Figure 5**). Conversely, in South Africa, other variables being equal, the effect of planting *Eucalyptus*

Figure 3 The practice of repeated removal of needle litter from coniferous forests in parts of mainland southeast Asia often leads to dramatic increases in surface runoff and erosion. Photographs by courtesy of C Cossalter.

grandis was more pronounced than that of *P. radiata* or *P. patula* (see **Figure 8** below). Such contrasts mainly reflect differences in growth performance between regions and to a lesser extent differences in rainfall interception dynamics.

Published experimental results often represent the maximum possible impacts on streamflow. In the real world, variations in site characteristics and plantation management may exert a moderating influence on the hydrological impacts of forestation. Moderating factors include the fraction of the catchment planted, planting position within the catchment (upstream or downstream parts, close to or away from the streams, blocks vs. strips, etc.), and variations in stand age and productivity between species. These factors are elaborated upon briefly below.

Catchments are rarely completely planted with trees because some land is usually reserved for other uses or it may be inaccessible or otherwise

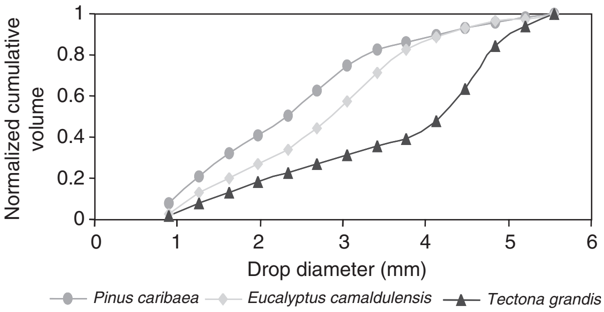


Figure 4 Characteristic drop size spectra for rain dripping from pine trees (*Pinus caribaea*), teak (*Tectona grandis*), and eucalypts (*Eucalyptus camaldulensis*) as measured in South India. Reproduced with permission from Hall RJ and Calder IR (1993) Drop size modification by forest canopies: measurements using a disdrometer. *Journal of Geophysical Research* 98: 18 465–18 470.

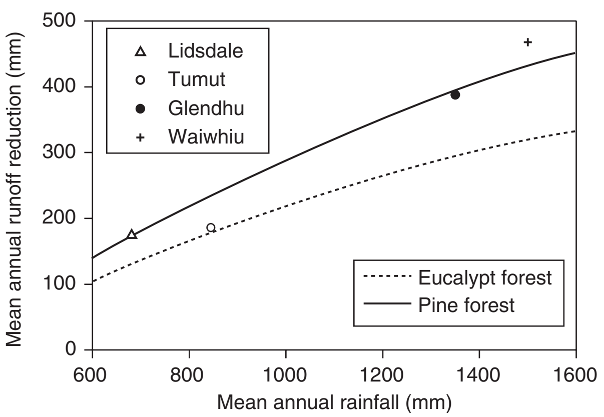


Figure 5 Potential reduction in mean annual streamflow estimated to result from forestation of grasslands with eucalypts and pines in southeast Australia. Shown (as symbols) are field data from four pine forestation experiments in Australia and New Zealand. Reproduced with permission from Vertessy RA, Zhang L, and Dawes WR (2003) Plantations, river flows and river salinity. *Australian Forestry* 66: 55–61.

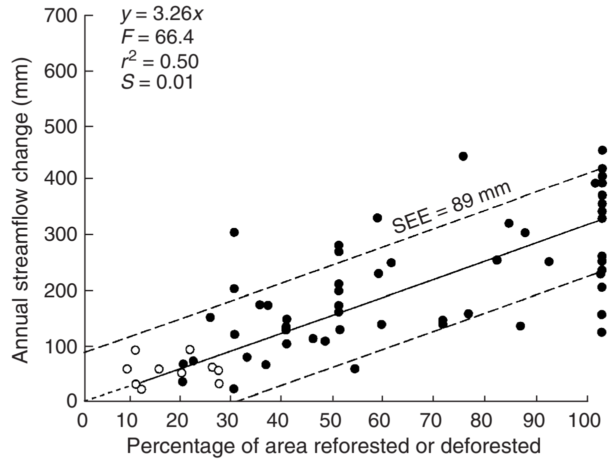


Figure 6 Changes in annual water yield vs. percentage forest cover change (solid circles denote experimental data of Bosch and Hewlett (1982); open circles those of Trimble *et al.* (1987). SEE, standard error of estimate. Reproduced with permission from Trimble SW, Weirich FH, and Hoag BL (1987) Reforestation and the reduction of water yield on the southern Piedmont since circa 1940. *Water Resources Research* 23: 425–437.

unsuitable. The classical forest hydrology literature suggests that the magnitude of the change in catchment water yield is linearly proportional to the percentage of catchment planted or cleared, with increases in flow after forest removal and reductions after forestation (**Figure 6**). Hence, in the case of plantations, one could assume that if only half of a grassland catchment would be forested then the estimated reduction in mean annual runoff would also be about half of the maximum reduction predicted by **Figure 5** for a given annual rainfall total (assuming that plantation position in the catchment does not influence the result).

Few experimental data are available on the influence of plantation position on catchment water balance changes. Under humid conditions in the eastern USA, the reverse operation (i.e., forest clear-cutting) did not show a significant difference in streamflow response after cutting the upper half of the catchment or the lower half. Also, elimination of the vegetation around streams in one experiment in the summer-rainfall zone of South Africa did not lead to greater increases in streamflow than when removing an equal area of forest away from the stream. However, several other experiments in South Africa showed that an area of plantation near streams had roughly double the effect of the same area of mid-slope planting.

Such contrasting results may be explained in terms of average soil water surplus or deficit, depth to the groundwater table and slope morphology. All these factors influence hillslope hydrological behavior. Where rainfall is plentiful, slopes steep and convex, and the groundwater table rather deep (say, more than 3 m), no major spatial effect is expected. This is because rainwater infiltrating into the soil percolates more or less vertically to the water table, then moves laterally as groundwater to the nearest stream without being taken up again by the roots of the trees. Conversely, where soil water is scarcer, slopes gentle and concave, and depth to the water table shallow, a more pronounced effect is possible because trees located closer to the stream will have more ready access to the groundwater table. As such, they are likely to consume more water than trees further away from the stream that have less direct access to groundwater to supplement diminished soil water reserves.

Furthermore, there is the intuitive notion that the further away one gets from a stream, the smaller the probability that water infiltrating into the soil will actually contribute to streamflow. These ideas have been tested in modeling experiments in the context of southeast Australia, the results of which lend support to the notion that plantation position could indeed affect catchment water yield under conditions of low rainfall (700 mm), gentle slopes, and high water-tables (**Figure** 7). Indeed, the predicted effect on streamflow of tree planting differed strongly depending whether forestation started at the top of the hillsides and progressively moved downslope or vice versa. The curves of **Figure** 7 also suggest that under the prevailing conditions planting of the lower 30% of the catchment would have a much greater impact than planting the uppermost 30%. Similarly, a related modeling study indicated that planting trees in strips about 40 m wide parallel to the contour with bands of pasture in between leads to greater tree water use and better growth than when the same number of trees are planted in a single block at mid-slope position.

More work is needed to ascertain optimal plantation positions to minimize the hydrologic impacts of forestation under contrasting climatic and topographic conditions. Process-based, spatially distributed hydrological models can be used to assess how different planting strategies would impact on catchment flow regimes. Whilst such models are difficult to set up and apply, the effort is surely worthwhile given the level of investment that goes into planning any significant forestation initiative.

Much can be learned on the effects of species, plantation age, and vigor from a particularly comprehensive series of long-term paired catchment studies of the hydrological effects of afforesting natural grasslands and scrublands in subtropical South Africa. Ten paired catchment experiments have studied the effects of afforestation with *Pinus radiata*, *P. patula*, and *Eucalyptus grandis* within catchments. The research sites are all in the high rainfall zone of South Africa (mean annual precipitation 1100–1600 mm). Experimental control was provided by catchments kept under native vegetation. Although generally steep, the catchments have deep, well-drained soils and show very low stormflow response to rainfall. The catchments are all in good hydrological condition (i.e., no significant surface erosion); thus, the experimental comparison is between the two vegetation covers, reflecting, ultimately, the differences in total evaporation.

The resulting streamflow reductions over time after planting follow a sigmoidal pattern comparable to a growth curve (**Figure** 8). There are clear

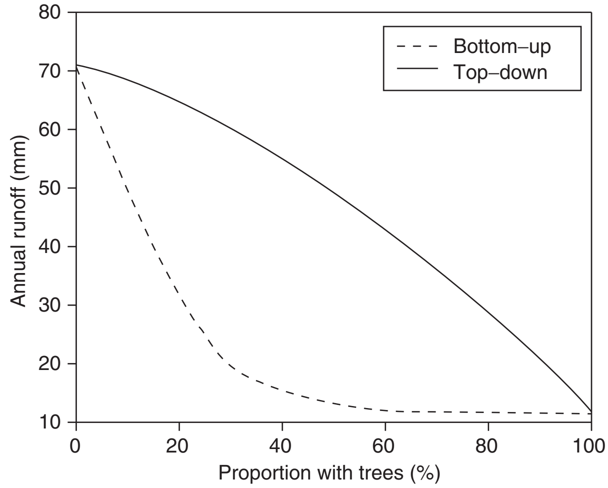


Figure 7 Results from a numerical modeling experiment showing two sets of predictions of annual streamflow after planting trees on a catchment under pasture in central New South Wales, Australia (mean annual rainfall 700 mm). The upper curve (solid line) shows changes in annual flow with forestation starting at the top of the catchment and progressing downslope. The lower curve (dashed line) shows the comparative response when forestation starts at the bottom of the catchment and progresses upslope. Reproduced with permission from Vertessy RA, Zhang L, and Dawes WR (2003) Plantations, river flows and river salinity. *Australian Forestry* 66: 55–61.

differences between the effects of eucalypts and pines, but there is also a large amount of variation from year to year within a single experiment and between different experiments, even in comparable catchments in one locality. The highest flow reductions occur once the tree crop is mature, and range, for a 10% level of planting, from 17.3 mm or 10% year^{-1} in a drier catchment to 67.1 mm or 6.6% year^{-1} in wetter catchments (**Figure** 8). As such, relative streamflow reductions (%), for a set age, are greater in drier catchments but absolute reductions (mm) are greater in wetter catchments. In other words, the reductions are positively related to water availability. The lower of these reductions in streamflow are similar to results obtained after planting *E. globulus* in high elevation grassland areas in the subhumid South of India (*c.* 20 mm per 10% forest year^{-1}) whereas the highest reductions in South Africa rather resemble the changes observed after planting *P. caribaea* on seasonal grasslands in Fiji (50–60 mm per 10% year^{-1}). Similar effects on streamflow have been recorded under the more temperate conditions of New Zealand (see also **Figure** 5), where conversion of pastures and tussock grassland to *P. radiata* plantations, over a range of climates, led to streamflow reductions of 20–45 mm year^{-1} per 10% of catchment planted, the amount again being dependent on water availability.

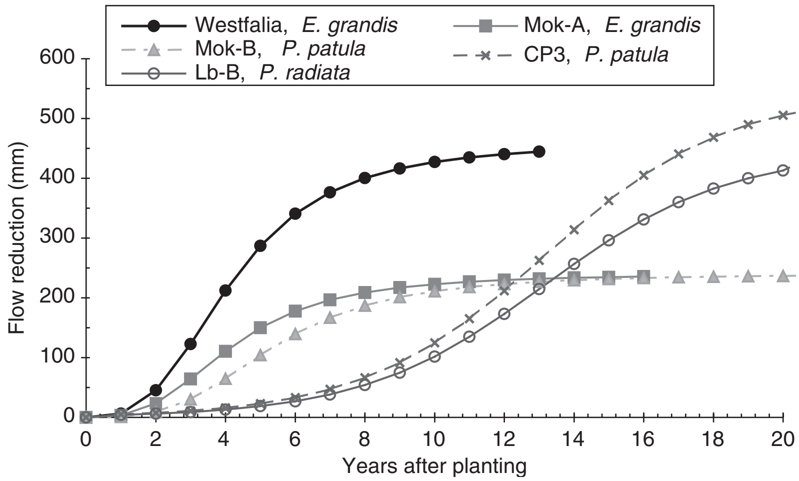


Figure 8 Reductions in streamflow as measured in five catchment afforestation experiments in South Africa. The curves are scaled for 100% planting of the catchment and smoothed to the mean annual runoff (MAR) prior to planting. Based on Scott DF and Smith RE (1997) Preliminary empirical models to predict reductions in total and low flows resulting from afforestation. *Water SA* 23: 135–140.

The timing of the first significant reductions in flow after planting varies quite widely depending on the rate at which catchments are dominated by the plantation crop. The pine plantations in the high altitude grasslands at Cathedral Peak in South Africa (CP in **Figure 8**) usually took several years to have a clear impact on streamflow. However, the same species of pine had an earlier effect on streamflow (within 3 years) under the drier conditions prevailing in the Mokobulaan B catchment in Mpumalanga Province (Mok-B in **Figure 8**). Other conditions remaining the same, eucalypts have a slightly earlier impact on streamflows than pines in South Africa, normally within 2–3 years.

A key factor influencing the degree of streamflow reduction after forestation is the vigor of the trees. Usually, there is a close link between the growth rate of a plantation and its overall water uptake. A new finding from the South African afforestation experiments is that the flow reductions are diminishing again during the postmaturation phase of the plantations, both in the case of pines (after about 30 years) and in at least one of the two eucalypt experiments (after 15 years). This undoubtedly mirrors the gradually decreased vigor of older trees as has also been observed in old-growth native eucalypt forest in southeast Australia and tropical rainforest in Amazonia. In industrial plantation forestry, short- and medium-length tree rotations will tend to keep the trees in their peak water use phase, but longer rotation crops, such as those aimed at producing good quality saw timber, are more likely to have a smaller effect on water yield later on in the rotation.

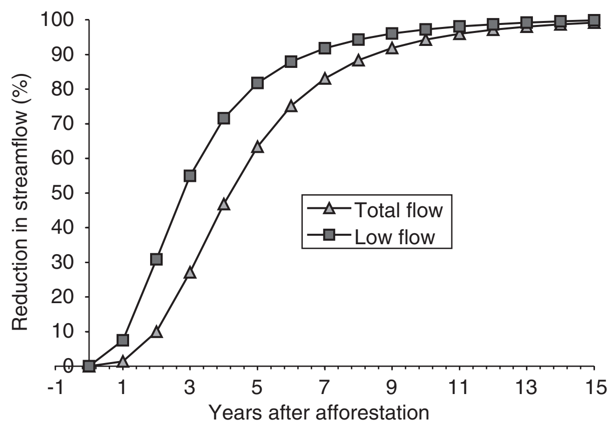


Figure 9 Pooled results from two eucalyptus afforestation experiments in South Africa, showing the pattern of flow reductions as a function of plantation age, and illustrating the greater and earlier effects on the low flow component (both catchments fully afforested). Reproduced with permission from Scott DF and Smith RE (1997) Preliminary empirical models to predict reductions in total and low flows resulting from afforestation. *Water SA* 23: 135–140.

Forestation and Low Flows

Declines in streamflow following the establishment of plantations are recorded in all components of the annual hydrograph (i.e., stormflows and baseflows). In South Africa, effects on total and low flows follow the same pattern, but low flows are decreased more than are total flows at the same age (**Figure 9**). Similar effects have been found in the temperate zone as well as in Fiji, India (even more so after coppicing and resprouting), and Malawi. The effect of forestation on low flows in subhumid areas has two supposed sources. First, exotic plantations, in contrast to the native grasses or scrub vegetation they replace, do not go dormant in the dry season. The second cause, though less easily quantified, is that of steadily reducing soil water reserves as the trees mature. Low flows are a reflection of the amounts of soil water and groundwater stored in the catchment and as these are steadily depleted by tree water uptake so low flow will diminish correspondingly. It is clear from the South African experiments that total water use by the tree crop can exceed annual rainfall in many years and that, once dry season flow has ceased altogether, the occurrence of rainstorms may not easily cause the streams to flow again.

Strongly reduced baseflows after forestation of (nondegraded) grassland or scrubland can thus be expected to be a generally occurring phenomenon. The magnitude of this effect is probably related to the capacity of the soils to store water and to the extent that this water can be accessed by the roots of the tree crop. Thus, where the new trees are able to occupy a much greater volume of soil through their deeper roots, reductions in baseflows following forestation can be expected to be proportionately larger than in situations where rooting volume is restricted.

Finally, it is important to bear in mind that the above examples concern situations where the soil is not degraded and rainfall infiltration generally proceeds unimpaired. Under such conditions, streamflow amounts will simply reflect the change in vegetation water use and low flows will be thus (much) reduced (see **Figures 2** and **6**). However, in areas with degraded, compacted soils where much of the rain may run off along the surface as overland flow (and therefore does not contribute to soil water reserves), the planting of trees can be expected to ultimately have a positive effect on infiltration. Theoretically, the extra water entering the soil through improved infiltration after forestation may moderate or, in extreme cases, even reverse the adverse effect of the larger water use of the trees on streamflow. In all cases, the net effect of tree planting on the baseflow from degraded areas will reflect a trade-off between these two effects. Where infiltration is already sufficient to accommodate most of the rainfall, any further improvements by forestation will not tip the balance. Rather, water yield will be reduced even further (**Figures 6** and **9**). However, where soils are deep but overland flow during rainfall is rampant and much is to be gained from improved infiltration (**Figure 10a**), it cannot be excluded that a net positive effect on low flows may occur. The

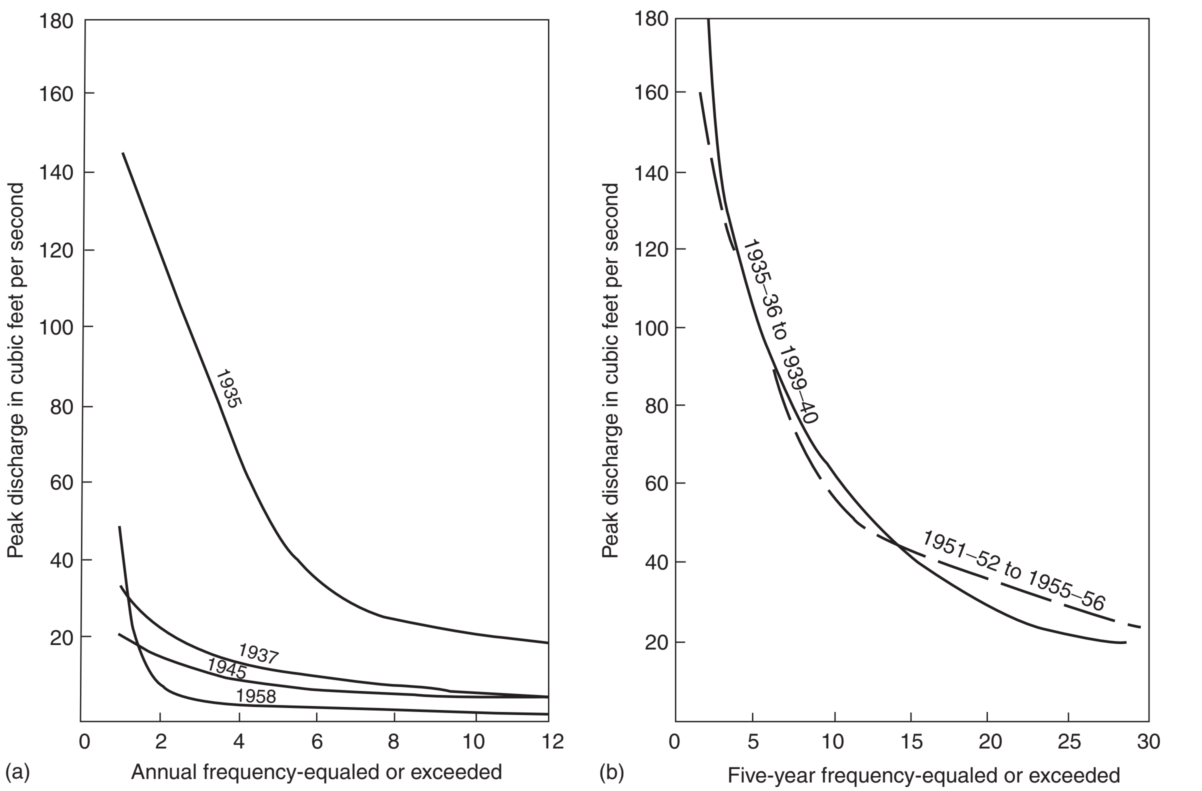


Figure 10 Frequency distributions for peak discharges during (a) summer and (b) winter in the While Hollow catchment, Tennessee, USA before (1935) and after (1937–1958) reforestation. Modified from Tennessee Valley Authority (1961) *Forest Cover Improvement Influences upon Hydrologic Characteristics of White Hollow Watershed, 1935–1958*. Report no. 0-5163A. Knoxville, TN: Tennessee Valley Authority.

experimental evidence for this contention is only indirect, however, and based on a comparison of observed reductions in stormflow response (having a positive effect on soil water reserves) (**Figure 10a**) vs. increases in vegetation water use (having a negative effect on soil water reserves) (**Figure 2**).

Forestation and Stormflows

Forest hydrological research has shown that the influence of vegetation cover or type on catchment runoff response to rainfall ('stormflows') is inversely related to the size of the rainfall event that generates the flows. This can be explained as follows: in small to medium storm events the combined water storage capacity of vegetation layers, litter, surface depressions, and the soil mantle will be considerable relative to the amount of rain delivered by the storm. As a result, the associated catchment response will be much reduced in the case of a good forest cover. The soil mantle is potentially the largest water store, but its capacity to accommodate additional rain varies as a function of soil wetness. Where previous uptake by the vegetation has depleted soil water reserves (as is often the case during summer), storage capacities, and thus stormflow reduction, will be relatively high (**Figure 10a**). However, once the soil has become thoroughly wetted by previous rains (typically during winter or the main rainy season), very little opportunity to store additional water will remain, regardless of vegetation type (**Figure 10b**). In addition, as rainfall events increase in size, so does the relatively fixed maximum storage capacity of the soil become less important in determining the size of the stormflows. In other words, the presence or absence of a well-developed forest cover has a significant effect in the case of small events but this typically makes very little difference (less than 10%) in the case of truly large events (floods) generated by extreme and prolonged rainfall (**Figure 10b**). Under such conditions, runoff response is governed almost entirely by the capacity of the soil to accommodate and transfer the rain.

However, where degradation of a catchment's soils has produced strong reductions in canopy and groundcover (including litter), and above all in infiltration capacity and soil depth through continued erosion (and thus overall soil water storage opportunity), reforestation could clearly lead to an improvement of most or all these factors over time. These ideas are conceptualized in **Figure 11**.

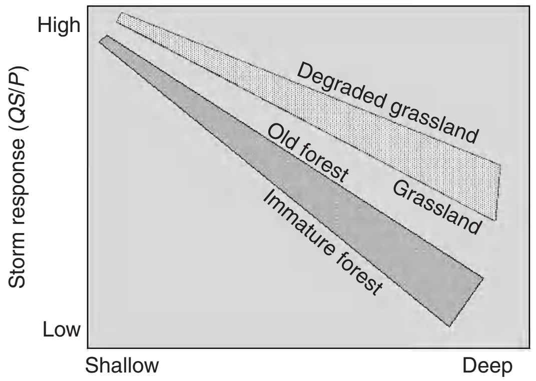


Figure 11 Postulated generalized relationship between catchment storage capacity and stormflow response to rainfall, as affected by vegetation cover. Reproduced with permission from Scott DF, Bruijnzeel LA, and Mackensen J (2004) The hydrological and soil impacts of forestation in the tropics. In: Bonell M and Bruijnzeel LA (eds) *Forests–Water–People in the Humid Tropics*. Cambridge, UK: Cambridge University Press.

Concluding Remarks

Catchment experiments all over the world have demonstrated convincingly that total amounts of streamflow emanating from catchments where forest plantations have replaced (natural) grassland or scrubland, or (degraded) cropland, are invariably much reduced. In addition, the reductions in baseflows during the dry season are relatively greater than during the wetter season. Small to medium-sized stormflows are also reduced significantly by forestation but the effect on occurrence and size of flood peaks associated with truly large rainfall events is very limited.

These observations differ strongly from the popular view held by many foresters, policy-makers, and the public at large that forestation will lead to (more or less rapidly) increased streamflows and the elimination of flooding. Although the establishment of forest plantations on degraded land will improve the soil's capacity to absorb rainfall, this is likely to take at least several decades. However, because water use by the trees is much increased within a few years compared to that of the former vegetation, the balance of probability is that low flows will also be reduced in this case. Establishing the precise hydrological effects of reforesting areas in various stages of soil degradation constitutes a prime research need.

See also: **Hydrology**: Hydrological Cycle; Impacts of Forest Conversion on Streamflow; Impacts of Forest Management on Streamflow; Impacts of Forest Management on Water Quality. **Plantation Silviculture**: Forest Plantations; Short Rotation Forestry for Biomass Production. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Soil Development and Properties**: Forests and Soil Development; Water Storage and Movement. **Tree Physiology**: A Whole Tree Perspective; Forests, Tree Physiology and Climate; Root System Physiology.

Further Reading

Bridges EM, Hannam ID, Oldeman LR, *et al.* (2001) *Response to Land Degradation*. Enfield, NH: Science Publishers Inc.

Bruijnzeel LA (1997) Hydrology of forest plantations in the tropics. In: Nambiar EKS and Brown AG (eds) *Management of Soil, Nutrients and Water in Tropical Plantation Forests*, pp. 125–167. Canberra, Australia: ACIAR/CSIRO/CIFOR.

Bruijnzeel LA (2004) Hydrological functions of tropical forests: not seeing the soil for the trees? *Agriculture, Ecosystems and Environment* (in press).

Calder IR (1999) *The Blue Revolution: Land Use and Integrated Water Resources Management*. London: Earthscan Publications.

Calder IR, Rosier PTW, Prasanna KT, and Parameswarappa S (1997) Eucalyptus water use greater than rainfall input: a possible explanation from southern India. *Hydrology and Earth System Science* 1: 249–256.

Dye PJ (1996) Climate, forest and streamflow relationships in South African afforested catchments. *Commonwealth Forestry Review* 75: 31–38.

Fahey B and Jackson RJ (1997) Hydrological impacts of converting native forests and grasslands to pine plantations, South Island, New Zealand. *Agricultural and Forest Meteorology* 84: 69–82.

Gilmour DA, Bonell M, and Cassells DS (1987) The effects of forestation on soil hydraulic properties in the Middle Hills of Nepal: a preliminary assessment. *Mountain Research and Development* 7: 239–249.

Hall RJ and Calder IR (1993) Drop size modification by forest canopies: measurements using a disdrometer. *Journal of Geophysical Research* 98: 18 465-–18 470.

Johnson R (1998) The forest cycle and low river flows: a review of UK and international studies. *Forest Ecology and Management* 109: 1–7.

McJannet DL, Silberstein RP, and Vertessy RA (2001) Predicting the water use and growth of plantations on hillslopes: the impact of planting design. In *Proceedings of MODSIM2001, International Congress on Modelling and Simulation*, December 2001, Canberra, vol. 1, pp. 455–460.

Scott DF (1999) Managing riparian zone vegetation to sustain streamflow: results of paired catchment experiments in South Africa. *Canadian Journal of Forest Research* 29: 1149–1157.

Scott DF and Smith RE (1997) Preliminary empirical models to predict reductions in total and low flows resulting from afforestation. *Water SA* 23: 135–140.

Scott DF, Bruijnzeel LA, and Mackensen J (2004) The hydrological and soil impacts of forestation in the tropics. In: Bonell M and Bruijnzeel LA (eds) *Forests–Water–People in the Humid Tropics*. Cambridge, UK: Cambridge University Press.

Sikka AK, Samra JS, Sharda VN, Samraj P, and Lakshmanan V (2003) Low flow and high flow responses to converting natural grassland into bluegum (*Eucalyptus globulus*) in Nilgiris watersheds of South India. *Journal of Hydrology* 270: 12–26.

Trimble SW, Weirich FH, and Hoag BL (1987) Reforestation and the reduction of water yield on the southern Piedmont since circa 1940. *Water Resources Research* 23: 425–437.

Vertessy RA, Zhang L, and Dawes WR (2003) Plantations, river flows and river salinity. *Australian Forestry* 66: 55–61.

Waterloo MJ, Bruijnzeel LA, Vugts HF, and Rawaqa TT (1999) Evaporation from *Pinus caribaea* plantations on former grassland soils under maritime tropical conditions. *Water Resources Research* 35: 2133–2144.

Zhang L, Dawes WR, and Walker GR (2001) Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research* 37: 701–708.

Zhou GY, Morris JD, Yan JH, Yu ZY, and Peng SL (2001) Hydrological impacts of reafforestation with eucalypts and indigenous species: a case study in southern china. *Forest Ecology and Management* 167: 209–222.

Impacts of Forest Management on Water Quality

S H Schoenholtz, Oregon State University, Corvallis, OR, USA

Introduction

In forested catchments the hydrologic cycle, involving precipitation, interception, evapotranspiration, overland flow, subsurface flow, groundwater flow, and stream flow (**Figure 1**) is closely linked to water quality in that water movement through the forest ecosystem also transports sediment, and dissolved nutrients, as well as fertilizers, and pesticides if they are present. Understanding relationships between forested ecosystems and quality of surface and subsurface water associated with these systems is a key component of sustainable forest management because changes in water quality may result from forest management practices. These changes can reflect either positive or negative outcomes of forest practices. For example, logging road construction and harvesting of timber with improper consideration for erosion control can cause increased sedimentation of stream water and a degradation of water quality. In contrast, conversion from agricultural crop production to forestland can improve water quality by decreasing erosion rates and creating long-term storage pools (e.g., forest floor, woody biomass) for carbon and nutrient retention. This article provides a synthesis of our current thinking regarding (1) the concept of water quality, (2) the role of forested watersheds in providing water of relatively high quality, and (3) commonly evaluated water quality parameters and potential effects of forest practices on these parameters. The primary focus is on the relationship between water quality characteristics of streams draining forested watersheds and forestry practices. Where information is available, effects of forestry practices on groundwater quality are also addressed.

Water Quality: The Concept

The concept of water quality is largely based on value judgments developed in relation to the beneficial or intended use of the water resource of interest. For example, water quality standards – comprising selected physical, chemical, and biological characteristics of water (**Table 1**) – developed for domestic use are likely to be different from water quality standards developed for other beneficial uses such as recreation, habitat for aquatic biota, or irrigation. As such, water quality standards are relative values that are dependent on the intended use of the water. The key to assessing whether or not change in a water quality parameter is a pollutant concern depends on its impact on beneficial uses.

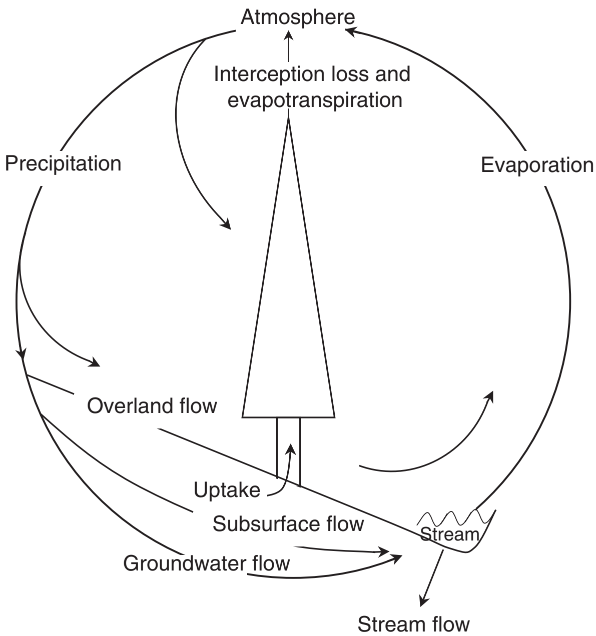


Figure 1 The hydrologic cycle for a forest. Adapted with permission from Brown GW (1988) *Forest and Water Quality*, Corvallis, OR: Oregon State University.

In cases where water quality is diminished because of anthropogenic influences, then pollution of the water resource has occurred. However, water quality can also be degraded by natural phenomena such as wildfire, volcanic eruptions, earthquakes, hurricanes, floods, and landslides. It is therefore important to consider anthropogenic influences on water quality in the context of the natural variation that is characteristic of water quality parameters. At times, changes in water quality resulting from natural causes can overwhelm effects of land use practices. Examples of this natural variation are provided by landslides, which often dramatically increase sediment loads in streams or by severe wildfires, which can also increase sediment loads as well as nutrient concentrations in stream water.

Importance of Forests for Water Quality

Water draining from undisturbed forested watersheds is generally of the highest quality, particularly with regard to beneficial uses including drinking water, aquatic habitat for native species, and contact recreation. A survey of the literature shows consistent patterns of relatively high water quality draining forested catchments in comparison to other land uses such as agriculture or urbanization (**Figure 2**). Recognition of the relative role of forests for providing water supplies of the highest quality has

Table 1 Commonly measured water quality parameters in forested watersheds

Parameter	*Influence on water quality*
pH	Influences chemical and biological reactions; toxic at extreme high or low values
Acidity	Capacity to neutralize base; affects chemical and biological reactions
Alkalinity	Capacity to neutralize acid; affects chemical and biological reactions
Conductivity	Estimate of total dissolved solids
Suspended sediment	Restricts sunlight and photosynthesis; smothers benthic communities; covers spawning gravels
Turbidity	Measure of water clarity; often surrogate measure for suspended sediment
Dissolved phosphorus	Essential nutrient; excess can cause eutrophication
Dissolved nitrogen	Essential nutrient; excess can cause eutrophication; forms can be toxic to stream biota and humans
Dissolved oxygen	Required for aerobic metabolic processes; affects chemical reactions
Temperature	Affects dissolved oxygen and metabolic processes
Biochemical oxygen demand	Measure of decomposable organic loading in water
Pathogenic bacteria and protozoa	Potential human health hazard
Pesticides	Forms can be toxic to stream biota

Figure 2 Undisturbed, forested watersheds generally produce outstanding water quality.

been one of the driving factors for establishment of forest reserves and for development of forest management practices designed to protect this high quality.

In some cases forest management activities such as road construction, harvesting, site preparation for regeneration of forest tree species, and fertilization of existing forests have been shown to alter water quality, primarily by causing changes in sediment loads, stream temperature, dissolved oxygen, and dissolved nutrients, particularly nitrogen. Fortunately, the wealth of literature addressing forest management impacts on water quality reports that, if impairment of water quality resulting from forestry practices is observed, it is relatively short-lived, diminishing rapidly as vegetation is re-established, and occurs at infrequent intervals because forest practices on a given site may only occur once or twice during a forest rotation (i.e., several years for intensively managed, fast-growing trees in the tropics to several centuries for unmanaged forests in areas of low productivity).

Effects of Forestry Practices on Water Quality

Suspended sediment, turbidity, stream water temperature, dissolved oxygen, and dissolved chemicals including nutrients and pesticides are the most studied characteristics of streamwater in relation to effects of forestry practices. Biological characteristics including pathogenic bacteria and protozoa in surface water have also received attention in forested watersheds because of their potential to impair human health and restrict water use. Other constituents that are commonly assessed for water quality characterization but have received less attention in relation to forestry practices to date include biochemical oxygen demand (an index of the oxygen-demanding properties of biodegradable material in water), pH, acidity, alkalinity, and conductivity (**Table 1**). The following subsections discuss (1) erosion and resultant sedimentation, (2) water temperature and dissolved oxygen, (3) dissolved nutrients in relation to nutrient cycling and fertilization, (4) application of pesticides, and (5) pathogenic microorganisms and their impacts on water quality in response to forestry practices.

Suspended Sediment

In general, forest lands produce very low sediment yield compared to other rural land uses (e.g., cropland). In many cases, much of the sediment observed in streams draining forested watersheds is the result of geologic weathering and erosion that are natural processes. Stream channels (including the stream banks) are also an important natural source of suspended sediment and are probably the dominant contributor of suspended sediment in undisturbed forested watersheds (unless in geologically unstable terrain prone to landsliding). For example, concentrations of suspended sediment measured during storm events may result from redistribution of sediment previously stored in the streambed or from the collapse of an unstable section of the stream bank. Nevertheless, excessive suspended sediment loads in streams are the major water quality concern for forest management because poorly planned forest management activities on hillslopes or in the vicinity of the stream channel that cause erosion can add to naturally derived levels of suspended sediment.

Increases in suspended sediment levels resulting from erosion and soil mass movement (i.e., landslides) can degrade drinking water quality, detract from recreational values, decrease stream depth, fill pools in the stream channel, increase stream width, and cause sedimentation of gravel beds which lowers their permeability and degrades their habitat quality for spawning fish (**Figure 3**). Furthermore, large accumulations of fine sediment can restrict sunlight and smother benthic communities thereby disrupting the aquatic food chain. Sediment also increases turbidity

Figure 3 Landslides and debris flows can cause downstream sedimentation.

Table 2 Factors commonly affecting rates of erosion in forested watersheds

Factor	*Characteristic*
Climate	Timing, intensity, duration, form of precipitation
Site	Forest floor composition, structure, depth
	Soil water content, infiltration capacity, texture, structure, depth
	Slope length and gradient
Vegetation	Composition, structure, age
	Rate of interception, evapotranspiration
Forestry practices	Road construction and maintenance
	Skid trail construction
	Mechanical site preparation
	Prescribed fire

and carries nutrients and anthropogenic chemicals (i.e., pesticides) that can degrade water quality.

Responses of suspended sediment concentrations are a function of the effects of climate, site characteristics, and forest practices on soil erosion (**Table 2**). More specifically, climate influences erosion rates through its effects on timing, quantity, intensity, and form of precipitation. Climate also affects erosion indirectly through its influence on soil properties and plant communities. The interaction between rainfall intensity and soil infiltration capacity plays a major role in controlling runoff. Soils with high infiltration capacities rarely have surface runoff and subsequent high rates of soil erosion unless rainfall intensity exceeds infiltration capacity. In most cases, forest soils have infiltration capacities in excess of common rainfall intensities, and therefore, surface runoff and erosion are often relatively insignificant in undisturbed forested catchments.

The interaction between rainfall and infiltration capacity is further modified by the composition and structure of the vegetation through its effect on transpiration, interception of precipitation, and resulting soil moisture. Vegetation also contributes organic matter through deposition of litter to the forest floor which provides a protective layer above the mineral soil surface. Plant roots help stabilize soil to further minimize soil erosion and soil mass movement. Additional factors affecting erosion rates and subsequent delivery of sediment to stream channels include slope length and steepness, and stream drainage density. Erosion rates are highest on long, steep slopes and delivery of sediment to stream channels is more probable (i.e., high sediment delivery ratio) where stream drainage density is high.

Even in forested watersheds that are not subjected directly to human disturbances, erosion rates are often highly variable both spatially and temporally. Natural events such as large storms, landslides, and fires can cause dramatic elevation of suspended sediment that exceeds water quality objectives. This natural variability is an important consideration in ascertaining the effects of forest management on suspended sediment.

Timber harvesting Accelerated erosion caused by forestry practices such as road construction, logging operations, and intensive site preparation can cause increased levels of suspended sediment as demonstrated by reports from timber producing regions worldwide. As such, excess sediment in streams is the most widespread water quality concern associated with forest management. Removal of vegetation and disturbance of soil, two activities that are inevitable at some level during forest harvesting, are driving factors that promote the erosion process. If mineral soil is exposed to rainfall through removal of the forest floor via machine disturbance or fire, then surface erosion can occur through detachment of unprotected soil particles and degradation of soil surface structure.

There is general agreement in the literature that forest road networks and skid trails developed to extract timber are the greatest threat to water quality because they are frequently a source of erosion and sedimentation. Compacted surfaces of logging roads and skid trails reduce infiltration and often carry surface runoff and suspended sediments during storms (**Figure 4**). The amount of sediment delivered to streams is often (1) proportional to the density of logging roads and skid trails within a watershed and (2) inversely proportional to the time since road and skid trail construction. Erosion rates are generally highest immediately after road construction and at times when roads are used during wet conditions. Water reduces frictional resistance and cohesion between soil particles making it much easier to

Figure 4 Improperly designed logging roads are often the source of increased levels of suspended sediment in streams.

dislodge soil particles via mechanical action of traffic on wet roads. These dislodged particles are immediately available for suspension and transport. Compaction and concentration of flow in tire ruts created in wet conditions can also concentrate flow and accelerate erosion on road surfaces. As roads age and vegetation becomes established, erosion rates decline. Therefore, minimizing the density of these disturbances through planned road and skid trail systems, followed by rapid revegetation of disturbed surfaces, which are not required for continued access, are likely to minimize stream sedimentation. Additional techniques commonly used to reduce road erosion and stream sedimentation include surfacing the road with gravel, decreasing the spacing of cross drainages, avoiding stream crossings, locating the road farther from streams to minimize direct drainage of roadside ditches into the stream, and limiting road gradients (*see* **Harvesting:** Roading and Transport Operations).

Soil mass movement such as landslides and debris flows can be triggered by improper road construction that disrupts drainage patterns and concentrates water flow under conditions of high rainfall in steeply sloped terrain. In cases where soil mass movement occurs, sediment delivery to streams far exceeds that from surface erosion and can cause extremely high levels of suspended sediment.

Increased sediment yields have also been noted as a result of ditching to provide drainage of peatlands and mineral soil wetlands. Drainage of these wetland soils is commonly utilized for commercial forest production and resulting changes in runoff as a result of drainage often increase sediment delivery to streams.

Soil disturbances and erosion caused by moving logs from the stump to a loading area vary with the type of skidding and yarding equipment. The most soil disturbance generally is caused by crawler tractors, followed by wheeled skidders. Cable logging systems are more expensive than ground-based systems but result in less soil disturbance because machinery is not traversing the site. Helicopter and balloon logging systems generally cause the least soil disturbance but are often prohibitively expensive for most operations. Logging systems designed to minimize compaction and disturbance of the forest floor generally result in minimum sediment delivery to streams.

Studies have shown that clear-cutting sites without the use of skid trails to transport trees to loading areas does not cause significant increases in sediment yield via surface erosion. In timber harvesting operations, contributions of felling, limbing, and bucking of trees do not contribute directly to sediment levels in streamflow because these activities do not often expose the mineral soil surface. However, clear-cutting often leads to greatly increased water yield and thus to the potential for enhanced streambed and bank erosion.

Increases in sedimentation from timber harvesting are commonly short-lived. Revegetation usually minimizes continued soil loss at rates first observed after the disturbance. Speed of revegetation is variable, depending on harvesting intensity, site preparation for re-establishment of trees, soil properties, and climate. In most studies, if elevated concentrations of suspended sediment are observed after logging activities, they return to preharvest levels within 1-5 years.

Fire Forest management practices sometimes utilize prescribed fire to control vegetation, reduce fuel loads, or to prepare sites for replanting after harvesting. Effects of fire on erosion and sediment yield are directly related to fire severity and degree to which the forest floor is consumed. Low-severity fires that do not completely remove the organic layer of

Figure 5 Surface erosion occurring after a severe forest fire.

the forest floor often do not cause significant increases in erosion and sedimentation. However, if fire severity is sufficient to remove the protective litter layer of the forest floor, thereby exposing mineral soil to raindrop impact, then increased erosion and sedimentation are likely (**Figure 5**). An additional concern that often causes accelerated erosion after fire is development of water-repellent hydrophobic layers in the soil surface that impede infiltration. Increases in suspended sediment after fires are most pronounced in steep watersheds with severe fires. Finally, fire lines that are established by bulldozers to control the spread of fire can be potential sources of sediment in streams. If fire lines are established under emergency circumstances, concerns for proper planning, avoidance of sensitive areas (i.e., very steep or excessively wet), and erosion control are not always paramount and accelerated erosion and sedimentation may result.

Temperature and Dissolved Oxygen

Water temperature is a key water quality parameter because of its direct effect on chemical and biological processes and properties in the stream. It is also a determinant of the amount of dissolved oxygen available for aquatic fauna (**Figure 6**). Solubility of oxygen decreases rapidly with rising temperature. Increases in water temperature generally accelerate biological activity and place greater demand on dissolved oxygen. Metabolism, reproduction, and other physiological processes of aquatic biota are controlled by heat-sensitive proteins and enzymes. A 10°C increase in temperature will roughly double the rate of many chemical reactions and the metabolic rate of cold-blooded organisms. Furthermore, the inverse relationship between water temperature and

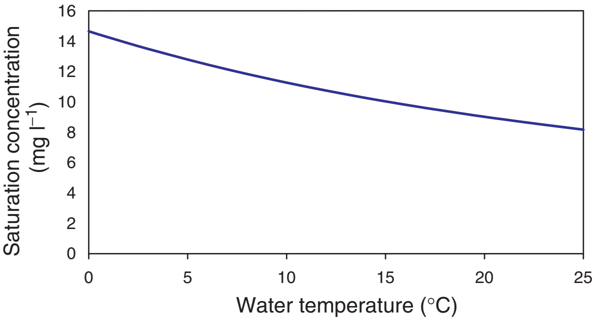


Figure 6 Solubility of oxygen as a function of temperature.

dissolved oxygen exacerbates the consequences of increased temperature. As such, temperature has a strong influence on composition of aquatic communities and maintaining stream temperature is a primary concern to many forest land managers.

Clearing of riparian vegetation is the primary forest management practice that can cause elevated stream temperature, particularly in small headwater catchments. This is the result of increased stream exposure to direct solar radiation. Temperature increases of as much as 15°C have been observed in forest streams when riparian vegetation has been removed. However, the magnitude of the response is tempered by stream discharge, streambed characteristics, channel morphology, stream surface area, and degree of hyporheic exchange and groundwater influx along the stream length. For example, streams with high degrees of hyporheic exchange and/or groundwater inflows may have less of a temperature increase when exposed to direct solar radiation.

Maintaining shade in riparian zones by retention of riparian buffers is a management practice that can be used to avoid most temperature increases in small streams. The key consideration in maintaining stream temperature is to maintain shade conditions that do not alter direct solar radiation from that of undisturbed conditions. However, as stream width increases, more of the water surface is exposed to direct sunlight and the influence of riparian canopy on stream temperature decreases.

Maintaining stream temperature at levels observed in undisturbed conditions is vital for aquatic organisms because of their dependence on dissolved oxygen. Use of streamside buffers to protect from temperature changes will also generally protect streamwater from corresponding changes in dissolved oxygen. However, dissolved oxygen is a function of its solubility in water (largely temperature driven) as well as the balance between oxygen consumption (e.g., respiration, decomposition) and oxygen replenishment (e.g., photosynthesis of aquatic plants, turbulent mixing of streamwater). Levels of dissolved oxygen are influenced by chemical oxidation of organic matter and decomposition of organic matter by aquatic microorganisms. Thus, addition of nutrients and logging debris to streams in response to logging practices has the potential to increase oxygen demand through increased decomposition. However, this demand generally decreases exponentially with time as decomposition proceeds; and if oxygen is readily available and the organic loading is not excessive, then oxidation proceeds without detrimental decreases in dissolved oxygen levels. Presence of streamside buffer zones generally prevents excess delivery of logging slash to stream channels, thereby helping to maintain dissolved oxygen levels similar to prelogging conditions.

Critical periods for water temperature and dissolved oxygen are during summer low-flow conditions when discharge is at a minimum and solar radiation is at or near a maximum, resulting in conditions of maximum stream temperature. Lethal levels of dissolved oxygen vary with aquatic species. For example, dissolved oxygen levels of $<1\text{–}2\,\mathrm{mg\,l^{-1}}$ are lethal for juvenile salmonid species and growth of these species is inhibited in the range of $5\text{–}8\,\mathrm{mg\,l^{-1}}$. In contrast, species occurring in warmwater streams are adapted to low levels of dissolved oxygen.

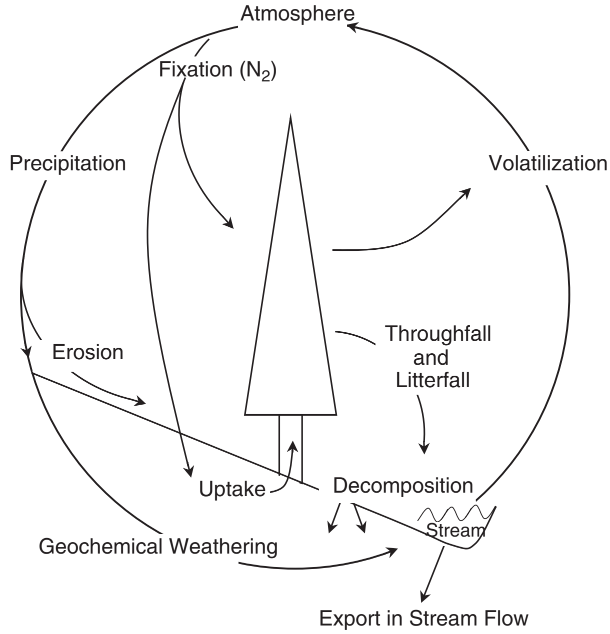


Figure 7 Nutrient cycling in a forest. Adapted with permission from Brown GW (1988) *Forest and Water Quality*, Corvallis, OR: Oregon State University.

Dissolved Nutrients

Nutrient concentrations in surface and groundwater draining undisturbed forest are generally very low because nutrients are used rapidly by ecosystem biota. Because of this limited nutrient availability, inputs of nutrients, particularly nitrogen (N) and phosphorus (P), in excess of background levels often lead to increased primary production, altered aquatic food webs, and potential eutrophication. Dissolved nutrient concentrations are a function of nutrient cycling processes that include (1) inputs from weathering of geologic parent materials (primary source of P, calcium (Ca), magnesium (Mg), sodium (Na), and potassium (K)) or directly from the atmosphere (primary source of N), (2) storage in the soil, (3) plant uptake from soil and storage in biomass, (4) release of organically bound nutrients via decomposition, and (5) outputs of nutrients via streamflow or leaching to groundwater (**Figure 7**). Precipitation and leaf fall are two additional important sources of dissolved nutrients to streams in forested ecosystems.

The two primary dissolved nutrients of concern to forest managers are phosphate-P (PO_4^{3-}, HPO_4^{2-}, $H_2PO_4^-$) and nitrate-N (NO_3^-) because they often limit productivity of aquatic plants and both can be elevated by forest practices such as harvesting, fertilization, and prescribed fire. Changes in stream P are uncommon after logging, but can increase after fertilization or high-severity fires. Both N and P are commonly applied as fertilizer in intensively managed forests and thus have the potential to alter nutrient cycling processes and affect water quality.

Dissolved N also exists as nitrite (NO_2^{2-}), ammonia (NH_3), ammonium (NH_4^+), and organic N. Dissolved P also occurs as complexes with metal ions and as sorbed phosphate on colloidal organic and inorganic particulate material. High concentrations of dissolved nitrate are a concern because of potential risks to human health if the water is used for drinking. The US Environment Protection Act and Canadian drinking water standard is $10\,\mathrm{mg\,l^{-1}}$ NO_3-N, whereas the World Health Organization and the European Union use a standard of $11.3\,\mathrm{mg\,l^{-1}}$ NO_3-N. Dissolved ammonia can be toxic to aquatic organisms, with concentrations as low as $0.03\,\mathrm{mg\,l^{-1}}$ NH_3-N being potentially toxic as acute concentration and toxicity associated with chronic concentrations of $0.002\,\mathrm{mg\,l^{-1}}$ NH_3-N. Nontoxic ammonium forms from ammonia at pH levels commonly observed in forested streams and is the predominant form observed. Phosphate is not toxic. The range of suggested water quality standards for P is 0.025–$0.1\,\mathrm{mg\,l^{-1}}$ as total P.

Worldwide, pristine rivers have average concentrations of ammonia-N and nitrate-N of $0.015\,\mathrm{mg\,l^{-1}}$ and $0.1\,\mathrm{mg\,l^{-1}}$, respectively. The concentration of nitrate-N averages approximately

0.23 $mg\,l^{-1}$ for large forested watersheds in the USA. Nitrate-N concentrations $>1.0\,mg\,l^{-1}$ generally indicate anthropogenic inputs. Because N is essential for plant growth, seasonal differences in plant uptake can cause variations in the concentration of N in soil and surface waters. In addition, rate of removal of N from forest streams is generally high. As water flows downstream, N compounds may be removed by biotic uptake, movement into sediments, or conversion to gas. Finally, the literature on synoptic patterns of streamwater chemistry suggests that influences of vegetation type, vegetation age, geologic substrate, stream order, basin size and morphology, and climate are controlling factors of dissolved nutrient levels. As a result, water chemistry can be highly variable within and among streams. For example, conifer forests tend to have more dissolved N in the organic form and hardwood forests tend to have more dissolved N in the inorganic form. Some regions, such as the red alder (*Alnus rubra*)/Douglas-fir (*Pseudotsuga menziesii*) forests of the Oregon Coast Range in the USA have high levels of nitrate naturally from N fixation provided by the alder stands that dominate the riparian zones. This interaction among controlling factors of streamwater chemistry illustrates a fundamental challenge in detecting significant responses to anthropogenic influences.

Timber harvesting Despite the confounding factors described above, studies throughout the world show that following intensive timber harvesting on well-drained soils, there is frequently an increased loss of nutrients from the logged area. Increased nutrient export from intensively logged watersheds is often partly caused by increases in water yield that usually accompany removal of vegetation. When trees are harvested from a site, a sequence of alterations in nutrient cycling occurs that can lead to loss of nutrients from the terrestrial ecosystem. Removal of vegetation results in less nutrient uptake, increased soil temperature, and increased soil water content. Accelerated release of nutrients occurs as decomposition of logging slash is stimulated by warmer, wetter soil conditions that generally favor decomposition. Enhanced decomposition increases mineralization of organic matter and nitrification, resulting in release of cations and nitrate that are available for leaching loss to streams and groundwater in the absence of adequate nutrient uptake and soil retention.

Nitrate-N concentrations in streams have received the most study and have shown increases in response to harvesting in some cases. However, extent of nutrient loss from sites disturbed by timber harvesting is highly inconsistent because of variable climate, geology, soils, plant community composition, and revegetation dynamics. Losses are generally lowest in deep soils with high clay contents which have a high capacity to fix leaching nutrients on exchange sites within the soil profile. The most susceptible sites to nutrient loss occur on shallow soils with low exchange capacity in systems where relatively high levels of nutrients are supplied to the site via precipitation and/or weathering. For example, in areas that are subject to N saturation from deposition of N compounds in air pollution, forest harvesting, or fertilization can produce significantly elevated concentrations of nitrate-N in streams and groundwater. Nutrient mobility from disturbed forests generally follows the order $N > K > Ca = Mg > P$. Thus forest practices such as timber harvesting generally produce larger responses in N concentrations in streamwater and groundwater than other nutrients. In contrast, P is delivered to streams primarily adsorbed to fine-textured sediments via erosion.

Fertilization Fertilization of managed forests is a common practice in the northwestern and southeastern USA, Canada, Japan, Australia, New Zealand, and regions of Europe and South America. Young commercial forest stands (~15–40 years) are commonly fertilized with N at $\sim 200\,kg\,N\,ha^{-1}$ as urea, ammonium nitrate, diammonium phosphate, or ammonium sulfate. Various forms of phosphate fertilizers are applied less commonly and at lower rates. In most cases, increases in dissolved phosphates after fertilization have not been observed in streamwater or groundwater.

The potential for negative effects of fertilization on streamwater quality has long been recognized and has resulted in considerable research and review in the literature. Studies have reported that applied fertilizer N can affect N concentration in streams, with losses to the stream ranging from 0% to as much as approximately 30% of applied N. Losses from the site of application depend on numerous factors, including amount and form of fertilizer, timing of application, weather during and immediately following application, stand composition and age, width of riparian buffers, amount of direct input to streams, N status of soils, quantity of organic matter in the soil, hydrologic processes (e.g., groundwater residence time, hyporheic exchange), and land use history (**Table 3**).

Fertilization of forests with urea-N often shows subsequent elevation in stream nitrate-N concentration, but not until nitrification of the urea-N has proceeded in the soil and several rainstorms have occurred to transport the resultant nitrate to the stream. As such, maximum nitrate-N concentrations

Table 3 Factors affecting nitrogen loss from forested watersheds via leaching or streamflow after nitrogen fertilization

Factor	*Characteristic*
Fertilizer	Form, amount, timing
	Amount of direct input to stream
Weather	Conditions during and immediately following application
Stand	Composition, age
	Width of riparian buffers
Soil	Nitrogen status
	Nitrification potential
	Quantity and properties of soil organic matter
	Soil depth, texture, cation exchange capacity
Hydrologic processes	Hyporheic exchange
	Groundwater residence time
Watershed geology	Landforms, soils
Land use history	Previous fertilizer applications

in streamwater are sometimes not observed until the winter after fertilization with urea. Most fertilization studies have shown peak concentrations of nitrate-N of $<2.0\,mg\,l^{-1}$. In cases where high nitrate-N has been observed (e.g., Fernow Experimental Forest in West Virginia, USA and in Sweden), N-saturated soils are present and excess atmospheric N deposition is well-documented. Most occurrences of elevated nitrate are short-lived, lasting for a few days to several weeks, because of uptake within the soil profile as well as N processing within the stream. Instream pathways for N processing include downstream transport and dilution, hyporheic retention and processing by microbial communities, uptake by benthic algae, and downstream transport and recycling via sloughed, particulate forms of algae.

Inadvertent application of fertilizer to unintended areas occurs to some extent during most aerial applications. Highest concentrations of streamwater N occur where fertilizer is applied directly to streams. Typically, pulses of dissolved urea, ammonia, or nitrate resulting from direct application quickly decline in concentration and are short-lived – usually lasting less than 1 month and often only a few days. Even under conditions of direct application, nitrate-N concentrations rarely exceed the standard of $10\,mg\,l^{-1}$ and ammonia toxicity is rarely observed because of rapid conversion to non-toxic ammonium.

Fire Numerous studies have reported increases in streamwater nutrient concentrations after wildfires and prescribed management fires, but these increases are usually limited in magnitude and duration. Nutrient loss to streams following prescribed fire is generally undetectable or very low. However, as fire severity increases, organic materials are oxidized creating oxides of metallic cations such as Ca, K, Mg, and Fe, which react with water and CO_2 to become soluble and more susceptible to leaching. This process increases potential for leaching loss of nutrients from the ash into and through the soil. Nutrients in the ash are also susceptible to loss by surface erosion. Overland flow from a rainfall event of high intensity following a severe fire can move large quantities of soluble ash compounds into streams, especially during the first year after the fire. This effect quickly diminishes as vegetation is re-established.

The potential for increased nitrate concentrations in streamflow is generally a function of accelerated mineralization of organic N, followed by nitrification in soils after burning. Where severe fires have removed vegetation, plant uptake of N is diminished and available nitrate resulting from the fire is susceptible to loss via leaching or erosion. This effect is also usually short-lived, and generally declines as revegetation occurs.

Pesticides

Applications of pesticides to forest lands are just a fraction of those applied to agricultural lands and pesticide concentrations associated with forest management practices are generally many times less than those used on agricultural lands. However, there are circumstances where forestry applications can cause degradation of water quality and potential impacts on stream biota. Pesticides, including herbicides for vegetation control and insecticides for control of damaging insects, are often used for intensive forest management.

Herbicides are used to control competing vegetation during forest stand establishment. This practice eliminates on-site soil and organic matter displacement, prevents deterioration of soil physical properties (i.e., compaction), and minimizes erosion when compared with mechanical means of site preparation and vegetation control. In most cases, these chemicals are distributed aerially and therefore a portion of the aerial spray can fall directly on surface water and create immediate contamination. Amount of spray drift is influenced by the pesticide carrier, size of spray droplets, height of spray release, wind speed, temperature, and humidity. Concentration of pesticide chemicals in streams is often a function of whether the stream originates in or flows directly through spray areas.

Pesticide risk to aquatic systems depends on persistence characteristics of the pesticide, hydrologic processes (i.e., leaching, surface runoff), and properties of the site. Rainfall rates, soil infiltration capacity and hydraulic conductivity, soil texture, soil depth, amount and character of organic matter, and slope can all affect pesticide transport. Conditions that slow rate of surface runoff and leaching will minimize stream contamination because a longer residence time in the soil provides more opportunity for volatilization, plant uptake, adsorption to soil colloids and organic matter, and chemical or biological degradation. Most currently labeled pesticides degrade rapidly and are available for overland flow for a short period (hours or days). Furthermore, in most forest soils, infiltration capacity exceeds most common precipitation intensities and overland flow rarely occurs. As a result, pesticide delivery to streams via runoff in forested settings is uncommon and water contamination is generally precluded.

Pathogenic Organisms

A broad spectrum of disease organisms can be transported by water. Of particular interest are waterborne pathogenic bacteria (e.g., *Escherichia coli*) and protozoal parasites (e.g., *Giardia* spp. and *Cryptosporidium* spp.) which can cause gastrointestinal illnesses in humans. Water samples are often tested for fecal coliform as an accepted surrogate for potential presence of pathogens. In general, there is a direct relationship between increased human and animal use of forested watersheds and concentrations of bacteria which indicate fecal contamination of water resources. However, most forest management practices with the exception of livestock grazing do not affect the occurrence of these pathogens directly.

Converting Farmland to Forestland

In cases where marginal farmlands (supporting either crops or pastures) are being converted to forestlands through afforestation efforts or simply through abandonment of the farmland, there is growing evidence that water quality improvements are likely to occur after the land use is altered. However, impacts of this type of conversion on water quality have received limited evaluation because there is limited documentation of comparisons between farmland and forestland on the same site. Net impacts on water quality depend on prior land use and crop management, current forest management practices, soil type, local hydrology, and climate. In general, conversions to forestland have the potential to reduce erosion and subsequent sedimentation (**Figure 8**), as

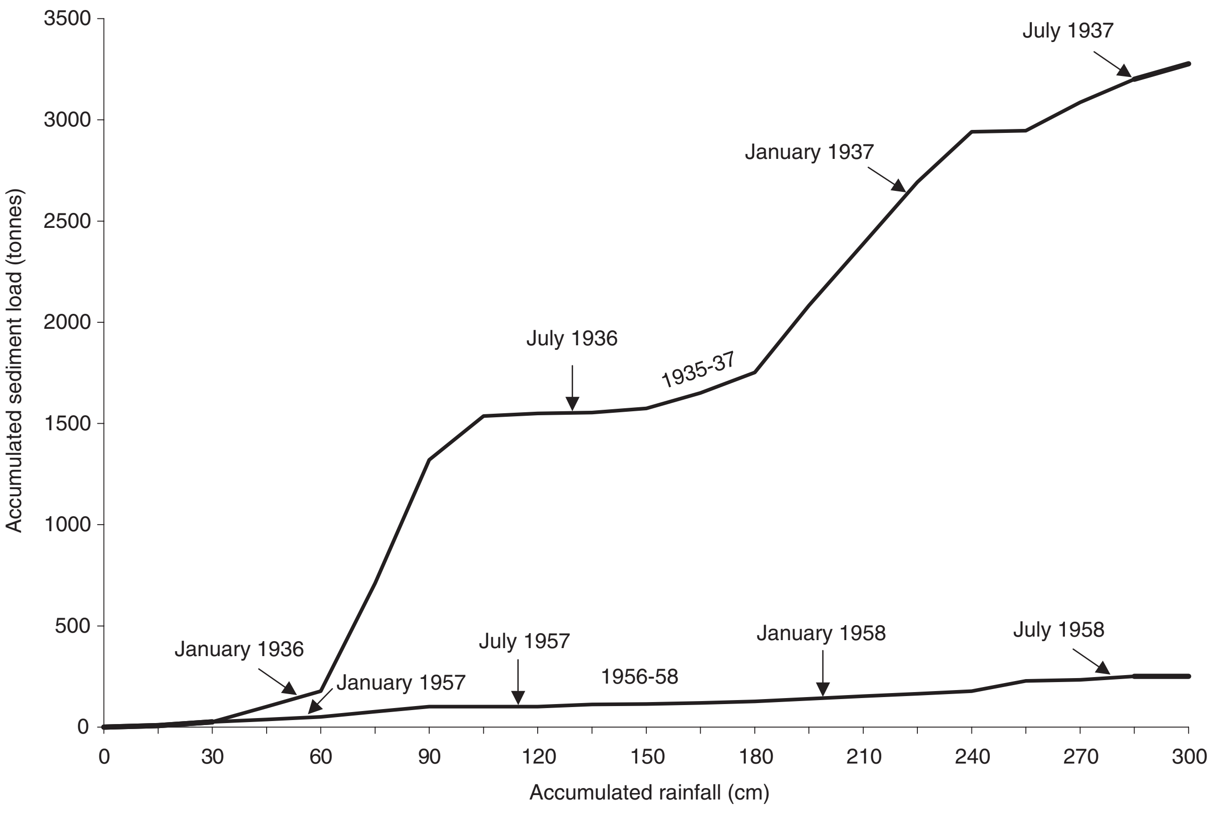


Figure 8 Cumulative sediment yields from White Hollow Watershed, Tennessee, USA, before and after reforestation. Adapted from Tennessee Valley Authority (1961) *Forest Cover Improvement Influences upon Hydrologic Characteristics of White Hollow Watershed, 1935–1958*. Report no. 0-5163A. Knoxville, TN: Tennessee Valley Authority.

well as reduce levels of dissolved nutrients and pesticides in surface runoff and groundwater. These improvements in water quality are a function of lower amounts of runoff and leaching as well as lower concentrations of potential pollutants that are expected to result from the conversion to forestland. For example, declines in quantities of runoff and leaching have been observed in response to increased interception and evapotranspiration occurring as forests become established. Increases in infiltration capacity also occur via increased litter cover, and resultant improvement in soil structure and porosity. Fertilizer and pesticide applications are eliminated or drastically reduced after conversion to forestland and thus, these potential sources of water quality degradation are eliminated or minimized. Establishment of new forests and sustainable management of existing forests are widely viewed as management practices that will improve or retain high quality water resources.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Roading and Transport Operations. **Hydrology**: Impacts of Forest Conversion on Streamflow; Impacts of Forest Management on Streamflow; Impacts of Forest Plantations on Streamflow; Soil Erosion Control. **Soil Development and Properties**: Nutrient Cycling; Water Storage and Movement.

Further Reading

American Public Health Association (1998) *Standard Methods for the Examination of Water and Wastewater*, 20th edn. Washington, DC: American Public Health Association.

Anderson C (2002) *Ecological Effects on Streams from Forest Fertilization: Literature Review and Conceptual Framework for Future Study in the Western Cascades*. US Geological Survey Water-Resources Investigations Report no. 01-4047. Washington, DC: US Government Printing Office.

Binkley D and Brown TC (1993) Forest practices as nonpoint sources of pollution in North America. *Water Resources Bulletin* 29: 729–740.

Binkley D, Burnham H, and Allen HL (1999) Water quality impacts of forest fertilization with nitrogen and phosphorus. *Forest Ecology and Management* 121: 191–213.

Brooks KN, Ffolliott PF, Gregersen HM, and DeBano LF (2003) *Hydrology and the Management of Watersheds*, 3rd edn. Ames, IA: Iowa State University Press.

Brown GW (1988) *Forestry and Water Quality*. Corvallis, OR: Oregon State University.

Bruijnzeel LA (1998) Soil chemical changes after tropical forest disturbance and conversion: the hydrological perspective. In: Schulte A and Ruhyat D (eds) *Soils of Tropical Forest Ecosystems: Characteristics, Ecology and Management*, pp. 45–61. Berlin, Germany: Springer-Verlag.

Dissmeyer GD (ed.) (2000) *Drinking Water from Forests and Grasslands: A Synthesis of the Scientific Literature*. Gen. Tech. Rep. no. SRS-039. Asheville, NC: US Department of Agriculture Forest Service, Southern Research Station.

Douglas I (1999) Hydrological investigations of forest disturbance and land cover impacts in South-East Asia: a review. *Philosophical Transactions of the Royal Society (London), Series B* 354: 1725–1738.

Grayson RB, Haydon SR, Jayasuriya MDA, and Finlayson BL (1993) Water quality in mountain ash forests: separating the impacts of roads from those of the logging operations. *Journal of Hydrology* 150: 459–480.

NCASI (2001) *Patterns and Processes of Variation in Nitrogen and Phosphorus Concentrations in Forested Streams*. Technical Bulletin no. 836. Research Triangle Park, NC: National Council for Air and Stream Improvement, Inc.

Vitousek PM, Aber JD, Howarth RW, *et al*. (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7(3): 737–750.

Soil Erosion Control

J Croke, University of New South Wales, Canberra, Australia

Introduction

Soil erosion control in managed forests is undertaken, and best achieved, for two main reasons. The first relates to soil protection for the sustainable productivity of the forest resource. The second relates to the protection of valuable water resources located in forested catchments. The potential impacts of increased soil erosion and the subsequent delivery of this material off-site, include a general reduction in water quality, adverse health effects on aquatic species, and an increase in the delivery of nutrients and sorbed chemicals to watercourses. This article discusses soil erosion control in managed forests from this twofold perspective. It uses a conceptual framework that emphasizes the link between on-site erosion and the subsequent delivery of this material off-site to the stream channel. The importance of adopting erosion control practices that encourage the reduction of surface runoff, and thereby off-site sediment delivery, is emphasized. The role and effectiveness of selected best management practices used in the control of soil loss and sediment delivery in forestry environments is also discussed within this framework.

General Principles of Soil Erosion

Soil erosion is the detachment and movement of soil by the physical agents of gravity, water, and wind.

The dominant agent of erosion in many forests is water, which describes the detachment of soil particles by raindrops and overland flow, and their transport and deposition as sediment. Water erosion is further categorized as rill, interrill, gully, and channel bank erosion. Rills, which may evolve to form gullies, are erosional features characterized by concentrated flow to a depth of <0.3 m (**Figure 1**). Interrill is the term used to describe the adjacent areas. As the hydraulic shear stress exerted by the flow in the rill is sufficient to overcome the binding forces between the particles, it is often seen as the primary detachment agent. The flow also acts to transport detached soil from both the rill and interrill areas. Detachment on interrill areas is primarily induced by raindrop impact, as flow depths are shallow and have limited erosive power.

The above forms of water erosion occur naturally in all environments, and can act singularly or in combination to determine the overall soil loss. Soil loss is defined as the amount of soil removed in a specified time period over an area of land that has experienced net soil loss (expressed in units of mass per unit area, $kg\,m^{-2}$). It is different to the other frequently used term, sediment yield. Sediment yield refers to a mass of sediment that leaves a boundary, such as the edge of a plot, bottom of a hillslope, or the outlet of a catchment (expressed in units of mass per unit area, $kg\,m^{-2}$ or $t\,ha^{-1}$, or total mass, kg). The sediment delivery ratio (SDR) describes the proportion of detached soil particles relative to the gross erosion of the basin that are delivered to a stream edge or catchment outlet. Mass wasting, although specifically not a form of erosion as it does not involve agents like wind or water, generates huge amounts of stream sediment and thus affects the SDR. Logging operations, especially clear-cutting, and the construction of cut-and-fill roads have been shown to affect the occurrence and frequency of shallow slips, which in some catchments dominate sediment delivery rates.

Key Factors in Soil Erosion Control

Much of the understanding of soil loss and the effect of various conservation practices is derived from research in agricultural areas. However, many of the factors remain the major determining influences of water erosion in other environments. One of the most commonly applied soil erosion models, the universal soil loss equation (USLE) incorporates the effect of factors such as soil erodibility (K), slope steepness (S) and length (L), rainfall erosivity (R), surface cover (C), and conservation support practice (P). These factors have been used in the USLE in the following factorial form;

$$A = RKLSCP \tag{1}$$

Only A, K, and R have dimensions. Rainfall erosivity (R) refers to the ability of rainfall to cause erosion. Soil erodibility (K) reflects a soil's ability to withstand the forces of detachment, a function of soil composition, and structure, and prevailing climatic factors, notably rainfall intensity and energetic loading.

Figure 1 Rills are regarded as the primary detachment agent in water erosion processes. Rill development can be exacerbated in forestry operations due to compaction and vehicular traffic on road and track surfaces. Photograph courtesy of estate of TC Whitmore.

Hillslope length (L) and slope (S) are expressed relatively to values from a standard 22.1 m and 9% hillslope used in the original experiments; cover (C) and conservation practice (P) vary between values of zero (full cover and conservation works in place) and 1 (no cover nor conservation).

Soil erosion strategies often aim to influence some of these factors, especially cover and conservation support, which are manipulated more effectively than topographic or climatic variables. Soil loss in many environments is managed, therefore, by controlling the rate of particle detachment through either maximizing surface cover or minimizing surface runoff. Surface cover management involves practices that aim to protect the soil from detachment by raindrops and water. Surface runoff reduction aims to minimize the accumulation of water into concentrated flows to reduce the detachment and transport of sediment in rills. Traditionally, on-site soil erosion has been managed through surface cover practices (e.g., mulching) and off-site soil erosion by reducing surface runoff (e.g., by terracing or bunding). However, large amounts of sediment cannot be moved off-site without sufficient discharges to transport this material. Surface cover management alone, for example, may reduce the erosional effects of raindrop impact but do little to reduce runoff accumulation, which may have a greater impact upon erosion processes both at a site and downstream in the catchment. This off-site delivery component of soil conservation is not well accommodated within empirical soil loss equations, which do not explicitly consider off-site sediment yield. Significant contributions from landslides and channel bank erosion are also not well considered in empirical approaches such as the USLE, although recognized to be major contributors to overall sediment supply in some cases. Research has highlighted the importance of sediment storage and redistribution which are often poorly represented in small plot scale studies of erosion. The deposition of sediment as runoff moves down the hillslope and in concavities has been recognized as an important, but largely unquantifiable component of the SDR. Spatial patterns of disturbance caused by logging, compaction, cover removal, and regeneration lead to complex patterns of erosion and deposition frequently leading to high rates of sediment redistribution within a compartment or hillslope but low overall rates of sediment yield. Our understanding of these processes and their contribution to catchment sediment yield is improved through larger scale plot studies incorporating sediment storage and redistribution terms together with the application of some sediment 'fingerprinting' techniques such as radionuclides that are used to trace the source and depositional history of sediment.

The following discussion of soil conservation practices in managed forests thus uses a conceptual framework that considers the need to conserve soil on-site both for the sustainable production of forests and for off-site water protection.

Soil Erosion and Forestry Operations

In pristine or undisturbed forests, soil loss due to the erosional effects of water, wind, and gravity is typically low due largely to the protective cover of abundant over- and understory vegetation, and, above all, a well-developed litter layer promoting infiltration of rainwater and the slowing down of any surface runoff that may develop. Soil loss is exacerbated by disturbances associated with tree removal. The opening or removal of forest canopies during harvesting or land clearing results in potentially large areas of bare soil being exposed to the erosional processes of raindrop splash, overland flow, and, under certain conditions wind (**Figure 2**). The extent of bare soil exposed to these processes understandably is greatly influenced by the nature of the logging operation, and varies significantly between selective logging and the more intensive clear-cutting operations. Some of the more commonly described, and somewhat universal impacts associated with logging include soil compaction, increased volumes of runoff, both surface and subsurface, and enhanced erosion. In some environments, the dominant hydrological regime will be dramatically altered due to compaction of the surface soil, in some cases changing subsurface dominated hydrological regimes to overland flow dominated regimes. Associated with these are corresponding

Figure 2 Canopy removal during harvesting exposes large areas of bare soil to the erosion processes of overland flow, raindrop splash, and wind. Photograph courtesy of LA Bruijnzeel.

reductions in soil permeability, soil fertility, and organic matter content.

Relative differences in the rate of soil loss are often the result of variations in the intensity of forest disturbances, quality of management and the prevailing climatic characteristics, notably rainfall erosivity. In both pristine and managed forests, rates of erosion and soil loss can be several orders of magnitude higher in areas characterized by high-intensity, short-duration rainfall events. Such intense rainfall events, typical of many lowland tropical environments, are characterized by large raindrop sizes that distribute high kinetic energy on impact, further exacerbating erosivity in areas of unprotected soil.

A recent advance in our understanding of water erosion processes in forestry environments has been recognition of the importance of the road and track network both in the generation and delivery of sediment (**Figure 3**). Forests roads and tracks are both a significant source of overland flow and sediment which if constructed and drained poorly often form a direct connection or pathway to the stream network. This coupling of the on-site erosion process with the subsequent delivery of the material off-site is a necessary advance in both the conceptualization and implementation of soil conservation practices in forests. Soil conservation practices should explicitly consider both the reduction of erosion on-site and the delivery of this material off-site through specific delivery pathways. Recognition of the importance of runoff-generating mechanisms in this process is paramount to the successful design of effective on- and off-site erosion control strategies.

Figure 3 Overland flow develops rapidly on compacted road surfaces that have infiltration rates in some environments as low as 1 mm h^{-1}. Photograph courtesy of A Malmer.

Runoff Production and Erosion Control

The first priority in designing effective erosion control strategies in managed forests is to develop an understanding of the dominant runoff production mechanisms and their potential alteration due to the harvesting regime. For example, infiltration-excess or Hortonian overland flow (HOF) is rare in undisturbed forests typically due to the generally very high infiltration capacity of the soil in most cases. In disturbed forest environments, overland flow generation, and especially HOF, is common because compaction from logging equipment and road building create areas of reduced hydraulic conductivity. Increased areas of compacted soil and altered groundcover due to timber harvesting and roading have been shown to alter hillslope hydrological processes, and overall catchment stream flows, to varying degrees.

Road surfaces may occupy less than 1% of the catchment area but contribute a disproportionate amount of water and sediment during low to moderate rainfall events. Infiltration rates as low as 1 mm h^{-1} have been reported on road surfaces which means that they respond very quickly to rainfall events and generate overland flow faster and in greater volume than other landscape surfaces. During long duration and higher intensity rainfall events, runoff contribution from other surfaces will be more dominant, simply because of their greater areal extent.

General harvesting areas (GHA) or logged hillslopes represent the largest land surface by area within a commercially logged forest. Although partially disturbed during selection harvesting operations, the retention of a high degree of forest vegetation contributes to reduced surface runoff accumulation and consequently limited sediment transport. Under such conditions, runoff generation on GHA is usually restricted to some Hortonian overland flow development, predominantly from bare or the more disturbed parts of the hillslope. Thus, widespread sheet flow is not common on the GHA and this is reflected in the relatively small volume of overland flow generated even under extreme rainfall events. Channelized flow in rills is also rarely reported within the GHA, limiting the ability of runoff to transport large amounts of sediment. A clear priority is to reduce the potential for run-on of overland flow onto these areas from the more disturbed and compacted areas. For example, runoff from tracks and roads which is discharged onto the GHA may increase the shear stress of the flow above some critical level and cause erosion of the surface soil layer. This will lead to rill and potentially gully development in these areas. In addition, increased runoff from compacted sources can contribute to the development of saturation-excess overland flow (SOF) on footslopes, in riparian zones, and other areas of near-surface flow convergence. The effective management of high runoff producing areas is paramount to the success of traditional on-site erosion control strategies. The hazard of managing high runoff production areas increases as the area of forest removed is increased, as is the case between a total clear cut operation compared with selectively logged slopes.

On-Site Soil Erosion Control

On-site control of soil erosion is designed to minimize the detachment and subsequent removal of soil from a range of disturbed land surfaces in a managed forest. There is a hierarchy of sediment sources in these environments ranging from the highly disturbed and compacted areas such as roads and tracks, logged hillslopes to the undisturbed streamside riparian areas (**Figure 4**). The greatest source of sediment in a managed forest is the road and track network, especially those used frequently by vehicles during logging operations. Logging tracks used by machinery during logging only and then often abandoned and regenerated tend to generate less sediment than primary roads. Sediment yields from logging roads show increases from twofold to 50-fold over background levels in undisturbed forests. As such, priority will be given here to discussing soil conservation strategies that may effectively reduce the generation and delivery of this material.

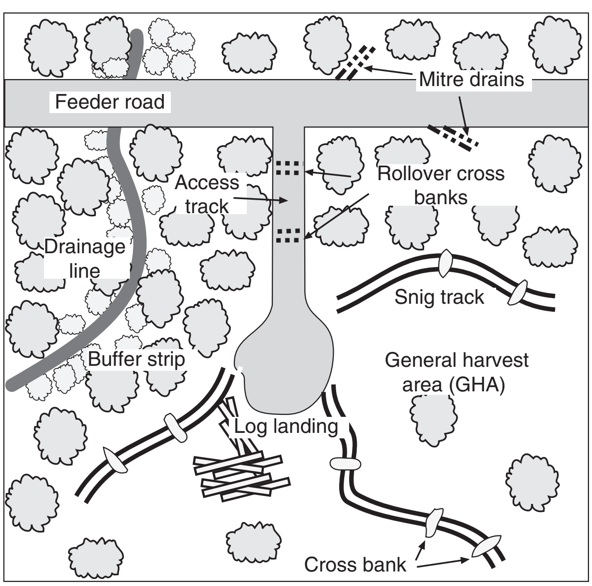


Figure 4 Range of sediment and runoff sources within a typical managed forest. Priority should be given to high runoff and sediment production areas such as roads and tracks.

Numerous strategies, including revegetation, graveling, regulation of use or traffic volume, and regular maintenance have been found to be successful in limiting sediment generation from forest roads and tracks. For example, the discontinued use of tracks and logging roads between cutting cycles is seen as a significant factor in limiting sediment availability for transport. The intensity of traffic usage is also seen as a key factor in the persistence of these areas as a sediment source (**Figure 5**). Sediment yields have been shown to decrease rapidly after road use is discontinued and logged areas regenerate (**Figure 6**). Road yields measured 5 years after logging produced less than five times the background values. Thus controlling vehicle access during wet weather conditions and limiting recreational use of roads in close proximity to streams should be considered integral to any erosion control strategies in the forest. The remobilization of previously deposited sediment during extreme events may pose a major problem in heavily disturbed areas, especially around hollow log culverts which tend to decompose over time.

The spacing of road drainage features is a key design variable for the effective management of overland flow on roads and tracks. Redistributing runoff at water bars or water diversion structures

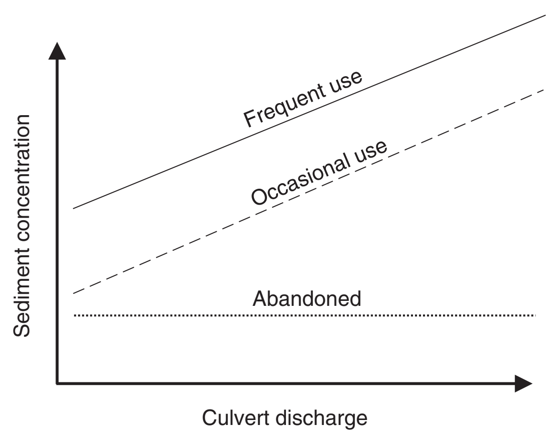


Figure 5 Generalized relationship between sediment concentration in road runoff and road usage. Well-used roads may have up to four loaded logging truck passes per day with lower-frequency traffic usage on the remaining use.

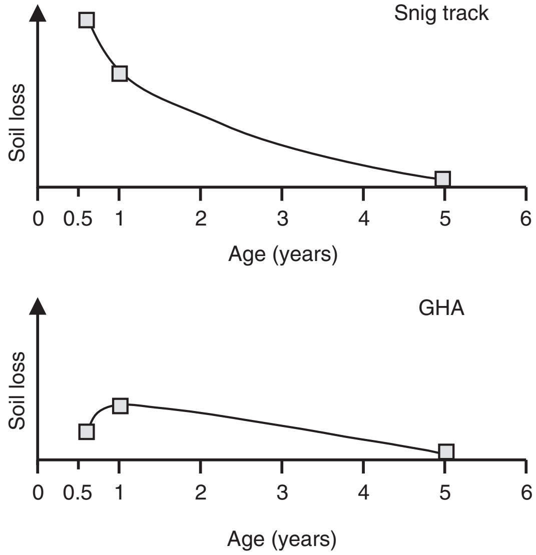


Figure 6 Generalized relationship between soil loss and time since disturbance typical of a humid temperate environment. Studies confirm the notable reduction in soil loss within a period of less than 5 years since harvesting. Erosion control strategies are essential in this period immediately post-logging when soil is exposed and natural regeneration has not occurred.

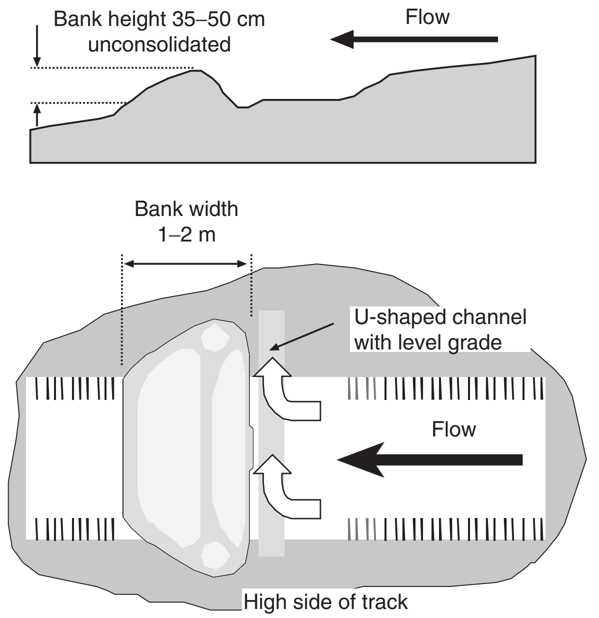


Figure 7 Construction of cross-banks or water bars at regular intervals along forest tracks is an effective control of overland flow development and sediment transport. These features do not need to be great tall mounds and are designed primarily to divert track runoff onto an adjacent hillslope so that roughness and cover can be effectively used to promote infiltration and sediment deposition.

along tracks immediately after logging is a successful method in reducing the contribution of water and sediment to streams, particularly during small to medium-size rainfall events (**Figure 7**). Design principles to guide the spacing of water bars and road drains have been developed based on maximum contributing track lengths and track slope (**Table 1**). Although not highlighted in the example provided in **Table 1**, rainfall intensity, frequency, and duration are important additional variables in determining the appropriate spacing of road drainage features for any given climatic area, but especially in tropical environments. The objective of these drainage features is to minimize the contribution of runoff and promote infiltration into the rough surface of the adjacent GHA. The high infiltration properties and roughness of these hillslope areas should be used as a natural erosion control strategy. The velocity and sediment transport capacity of runoff from tracks and roads passing through these areas will be reduced, promoting deposition and limiting sediment delivery to streams. Poor construction of these features can lead to the destruction of banks and water bars, especially under extreme rainfall events, resulting in catastrophic consequences for sediment supply and delivery.

Another important design variable is the position of the drainage outfall point in the landscape. For example, a culvert discharging into a stream head or first-order stream (gully) will greatly increase the impact of road runoff and sediment on the stream (**Figure 8**). In contrast, if a culvert directs road runoff onto a large divergent slope, surface erosion will be minimized, thereby reducing sediment delivery to the stream. In some instances, however, prevention of concentrated runoff on hillslopes at culvert outlets will also require implementation of protective measures such as masonry, grassed waterways, stone drops, etc. to provide resistance to scour at the culvert outlet.

Surface cover management provides an effective measure for the reduction of erosion and soil loss. Numerous studies confirm that surface cover of between 30–50% is effective at significantly reducing soil erosion processes at a site (**Figure 9**). There is also the potential to use effective time management in the harvesting process or provide artificial cover (e.g., straw bales, grass seeding) to protect more disturbed or bare areas until natural regeneration occurs. Natural or artificial regeneration procedures such as ripping or plowing up and fertilizing log landings have been used successfully to enhance the return of roughness and surface cover in these bare areas.

Off-Site Soil Erosion Control

Controlling the generation and delivery of sediment and attached nutrients is an important process in

Table 1 Example of road drain spacing guidelines, giving distance (m) between drainage structures varies with road travelway slope and the gradient of the hillslope at the discharge point. This table is developed for a forested catchment in Australia and can not be applied in other environments

Road travelway gradient (degrees)	*Drain discharge hillslope gradient (degrees)*							
	2.5	5.0	7.5	10	15	20	25	45
0	—	110	95	90	85	80	75	75
1	155	110	95	90	85	80	75	75
2	155	110	95	90	85	80	75	75
3	150	110	95	90	85	80	75	75
4	125	110	95	90	85	80	75	75
5	100	100	95	90	85	80	75	75
6	90	90	90	90	85	80	75	75
7	80	80	80	80	80	80	75	75
8	70	70	70	70	70	70	70	70
9	65	65	65	65	65	65	65	65
10	60	60	60	60	60	60	60	60
11	55	55	55	55	55	55	55	55
12	50	50	50	50	50	50	50	50
13	45	45	45	45	45	45	45	45
14	40	40	40	40	40	40	40	40
15	40	40	40	40	40	40	40	40

Figure 8 Erosion of the hillslope at road drainage outlets is a significant contributor to off-site sediment delivery in forested catchments. Large volumes of overland flow from road surfaces are discharged at single outlet points, often causing increased shear stress and the development of rills or gully erosion. These features form efficient transport pathways to streams enhancing the risk of off-site impacts to water quality.

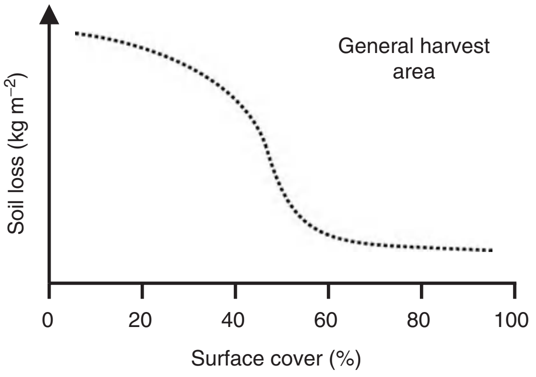


Figure 9 Generalized relationship between soil loss and surface cover. Most studies confirm that surface cover of >50% is sufficient to reduce surface erosion.

minimizing off-site impacts of forestry operations. The most effective measures of reducing sediment delivery for off-site protection in forestry environments include:

1. Reducing the volume of overland flow.
2. Minimizing direct connectivity of sediment sources with the stream network.
3. Promoting vegetative filtering.

Volume of Overland Flow

Reduction of the volume of overland flow can be achieved by reducing the contributing area of disturbed surfaces draining to a particular point in the landscape. This is effectively managed through conservation planning and practices that limit the size of harvesting coupes or include some strategy for alternate-coupe or patch harvesting. Likewise, adequately planned and constructed road and track drainage plays a key role in minimizing the volume of overland flow generated from compacted surfaces.

Minimizing Connection of Sediment Sources with Streams

The term connectivity is now commonly applied to describe the level of interaction between disturbed areas such as roads and tracks and the stream. There are a variety of degrees of connectivity that express whether a sediment source is fully or partially connected to the stream. For example, a road network is fully connected to a stream at a stream crossing or when there is a continuous gully that extends the full length from the source to the streams (**Figure 10**).

Opportunities to reduce overland flow through vegetated hillslope areas and streamside buffer strips are plentiful in forested catchments, as long as gully erosion does not occur. Runoff from roads and tracks can disperse in vegetated areas where flow is not concentrated and shear stresses remain low. The risk of gully development is increased as a result of poor road and track drainage and this should be avoided where possible. Once initiated, gully erosion is difficult to halt and these features then effectively bypass the potential filtering effect of vegetation in reducing runoff and sediment fluxes.

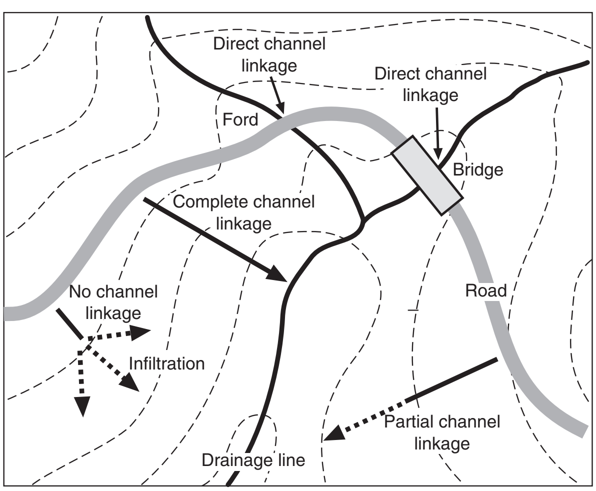


Figure 10 There is a range of degrees of 'connection' between sediment sources such as roads and receiving waters. Sources may be fully connected to a stream, as occurs at stream crossings or where a gully has formed at a road drainage outlet. Partial or nonconnected pathways also exist. Direct connection between a sediment source and stream should be avoided by appropriate planning of road location and drainage.

Connection between sediment sources and the stream can also be minimized by appropriate road and track planning. Minimizing the number of stream crossings by the location of roads along ridge-tops is preferable to the distribution of roads along valley bottoms where the distance to streams is short. The procedure of uphill yarding or snigging is also a key measure in minimizing connection between compacted surfaces, sediment sources, and the stream. This encourages the location of roads and tracks away from the streams and results in a downslope divergence of the associated skidder track pattern.

Vegetation Filtering

Riparian or streamside vegetated zones are recognized worldwide as having a key role in moderating the impact of land use on stream water quantity and quality (**Figure 11**). Riparian zones have several functions and the emphasis placed on each of these functions depends on a wide range of environmental and organizational issues. This riparian zone or buffer strip has a range of functions including maintaining the stability of the stream channel, providing riparian habitat and a long-term recruitment of woody debris, regulating light and water temperature in the stream, and acting as a vegetative filter for runoff between the areas of disturbance and the stream network. This final function may be considered as the last line of filtering as sediment generated on roads, tracks, and other compacted areas frequently pass through the general harvest areas prior to entering the buffer strip.

In terms of their sediment trapping ability, riparian zones have several characteristics that encourage deposition. Riparian zones are normally characterized by a very rough soil surface, often with an intact litter layer. Hence, the soil is porous, with many macropores; and the rooting zone is frequently deep. Sediment deposition occurs as a result of a decrease in flow velocity and volumes as the flow moves into areas of relatively high infiltration and dense vegetation. The very porous nature of the undisturbed riparian zone soil assists in this process, although the presence of a wet zone from a water table may inhibit total sediment deposition. Nevertheless, the surface roughness of the riparian zone continues to aid in trapping sediments even if saturated.

Overall, the literature confirms that vegetated areas perform well in relation to sediment deposition. Consensus on their ability to trap the very fine-grained silt and clay material under certain

Figure 11 Location of riparian or buffer strips along streams in a logged catchment. Vegetative filtering as runoff passes through these areas, often demarcated a set width from a major watercourse is an effective control strategy for reducing sediment delivery to streams.

hydrological conditions is less conclusive. The ability of the buffer strip to reduce the volume of overland flow by infiltration processes is sensitive to the prevailing hydraulic properties of the area and to the moisture-holding properties of the soil. Streamside buffer strips may also act as runoff sources themselves due to rising groundwater levels in wet areas immediately adjacent to the stream. The trapping of very fine-grained material is likely to be highly dependent upon runoff infiltration mechanisms within the buffer strip.

Soil Erosion Strategies for Off-Site Protection

Several best management practices (BMPs) are used in forestry operations to mitigate the potential impacts of logging on stream ecology and water quality. Some of the more universally applied practices include the use of riparian buffer strips, patch harvesting, siting and design of roads and road crossings to minimize sediment inputs, and restrictions to logging activities in relation to slope and soil type. There is little doubt that the effective implementation and construction of these practices can significantly reduce sediment delivery to streams in managed forests. While the positive effect of catchment-scale BMPs has been widely observed, the relative contribution of specific on-site practices is rarely reported. However, there are two erosion control strategies that are imperative to reducing off-site delivery of sediment in forested catchments. These are:

1. The standard implementation of an undisturbed vegetated area adjacent to the stream network.
2. The proper planning of the road network to avoid source-to-stream connectivity.

Riparian or buffer strips in forests Forest management practices in many countries are now obliged to leave an undisturbed vegetated buffer strip immediately adjacent to the majority of streams and drainage lines (**Figure 11**). The placement and width of buffer strips in catchments is a contentious issue due to potential economic loss of harvestable timber from streamside reserves. There are two possible approaches for locating buffer strips to mitigate the inflow of sediment and associated pollutants from the upslope areas; one is based on determining appropriate sediment transport distances through the buffer strip; and the other is predicated on protecting wet areas in the landscape as these are more liable to overland flow generation through saturation excess from rising water tables during rainstorms. In the case of the former, a 30 m buffer is typically regarded as effective in trapping most of the sediment from cleared areas, although absolute width is dependent upon specific site. In general, significant impacts of logging are more likely to occur where buffer widths are less than 30 m. However, the application of a universal buffer width remains a contentious issue as large parts of the forest resource can be locked away. For example, in many upland situations with high rainfall, drainage density is so high that the blanket application of 30 m buffer zones severely limits the area available for commercial logging.

Road planning and position Given the recognized importance of the road network in both the generation and delivery of runoff and sediment, emphasis should be given to these areas during the planning stages of forest harvesting. The connectivity concept as outlined above (**Figure 10**) provides a useful conceptual framework for forest managers to incorporate with other factors such as economical and topographic constraints. Maximizing the distance between the road and track network can be readily accommodated at the planning stage through the location of roads away from streams and by yarding the logs uphill (**Figure 12**).

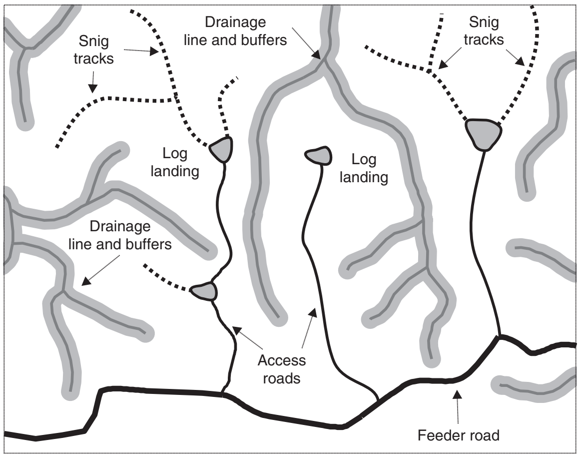


Figure 12 Road network in a logged catchment. The distribution of road networks throughout the catchment is best achieved during the planning phases where roads can be located along ridge-tops or at maximum distances from the stream. Uphill skidding and yarding is to be strongly encouraged as it results in a network of tracks that are divergent and away from the main stream network.

In many countries, forest managers are dealing with the legacy of an old road and track network that was constructed relatively close to the stream network. Rehabilitation of these surfaces or their removal from the catchment though expensive rehabilitation programs has been adopted in some countries. Ideally, many of the best strategies to minimize the potential for off-site impacts should be considered at the forest planning stages and optimum decisions made regarding the location and rehabilitation of these surfaces during the post-logging phase.

Summary

The understanding required to implement effective soil conservation strategies to manage surface erosion now exists. In many countries, harvesting and vegetation clearance is taking place at an alarming rate and the conservation and protection of many forest environments, and the associated water resources, are in jeopardy. Traditionally erosion control strategies have focused only on minimizing the detachment of soil particles through approaches such as surface cover management and runoff minimization. This review has examined both the generation and delivery of sediment in forests with a view to protecting the sustainable use of forests for future generations and the water resources located in these catchments. Effective erosion control strategies must be approached with this twofold objective in mind. Priority should be given to high runoff and sediment producing areas such as roads and tracks in both the planning and protection phases of forest harvesting. The combined beneficial effects of BMPs such as maintaining riparian buffer zones, the proper planning and construction of roads, and patch harvesting are now widely reported. The principles and processes for managing sediment delivery in forestry environments are basically understood. The effective implementation of these practices is thus often limited by economics or political pressure. Continuing development of practical and economical forest code prescriptions should be an ongoing focus of erosion research in forestry environments.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Forest Operations under Mountainous Conditions; Roading and Transport Operations. **Hydrology**: Impacts of Forest Conversion on Streamflow; Impacts of Forest Management on Streamflow; Impacts of Forest Management on Water Quality; Impacts of Forest Plantations on Streamflow. **Soil Development and Properties**: Water Storage and Movement.

Further Reading

Adams PW and Andrus C (1990) Planning secondary roads to reduce erosion and sedimentation in humid tropical steeplands. *International Association of Hydrological Sciences Publication* 192: 318–327.

Bonell M and Bruijnzeel LA (eds) (2004) *Forests, Water and People in the Humid Tropics*. Cambridge, UK: Cambridge University Press.

Bren LJ (2000) A case study in the use of threshold measures of hydrologic loading in the design of stream buffer strips. *Forest Ecology and Management* 132: 243–257.

Croke J and Mockler S (2001) Gully initiation and road-to-stream linkage in a forested catchment, southeastern Australia. *Earth Surface Processes and Landforms* 26: 205–217.

Douglas I (1999) Hydrological investigations of forest disturbance and land cover impacts in South-East Asia: A review. *Philosophical Transactions of the Royal Society (London), Series B* 354: 1725–1738.

FAO (1989) *FAO Watershed Management Field Manual*: *Road Design and Construction*. FAO Conservation Guide no. 13/5. Rome, Italy: Food and Agriculture Organization.

Grayson RB, Haydon SR, Jayasuriya MDA, and Finlayson BL (1993) Water quality in mountain ash forests: separating the impacts of roads from those of the logging operations. *Journal of Hydrology* 150: 459–480.

Hairsine P, Croke J, Mathews H, Fogarty P, and Mockler S (2002) Modelling overland flow plumes from track surfaces. *Hydrological Processes* 16: 2311–2327.

Lal R (ed.) (1994) *Soil Erosion Research Methods*, 2nd edn. Ankeny, IA: Soil and Water Conservation Society.

La Marche J and Lettenmaier DP (2001) Effects of forest roads on flood flows in the Deschutes River Basin, Washington. *Earth Surface Processes and Landforms* 26: 115–134.

Luce C and Black T (1999) Sediment production from forest roads in western Oregon. *Water Resources Research* 35: 2561–2570.

O'Loughlin CL (1984) Effectiveness of introduced forest vegetation for protection against landslides and erosion in New Zealand's steeplands. In: O'Loughlin CL and Pearce AJ (eds) *Effects of Forest Land Use on Erosion and Slope Stability*, pp. 275–280. Vienna, Austria: IUFRO.

Wallbrink P and Croke J (2002) A combined rainfall simulator and tracer approach to assess the role of Best Management Practices in minimizing sediment redistribution and loss in forests after harvesting. *Forest Ecology and Management* 170: 217–232.

Wemple BC, Swanson FJ, and Jones JA (2001) Forest roads and geomorphic process interactions, Cascade Range, Oregon. *Earth Surface Processes and Landforms* 26: 191–204.

Wiersum KF (1985) Effects of various vegetation layers in an *Acacia auriculiformis* forest plantation on surface erosion in Java, Indonesia. In: El-Swaify SA, Moldenhauer WC, and Lo A (eds) *Soil Erosion and Conservation*, pp. 79–89. Ankeny, IA: Soil Conservation Society of America.

Snow and Avalanche Control

M Schneebeli and P Bebi, WSL Swiss Federal Institute for Snow and Avalanche Research, Davos, Switzerland

Introduction

Snow has a strong effect on the hydrology of forests. In contrast to rain, much more snow is intercepted by the branches and temporarily stored on the forest floor. Snow also modifies the radiation balance of trees. Snow–forest processes are much more complex and important due to the increased three-dimensionality of trees than in open land (**Figure 1**). Management practices can strongly influence the snow storage capacity of forest, and therefore significantly contribute to runoff and runoff timing. This is especially important where water from mountains is used for irrigation and water supply (e.g., the Sierra Nevada in California, southern slopes of the Himalayas). Another locally very important effect in mountain regions concerns the prevention of snow avalanches. The preventive effect of forests on the formation of snow avalanches was recognized in different Alpine regions in Europe as early as the Middle Ages. By then, the intensified logging and clearing of mountain forests for timber and the creation of pastures had caused the formation of new starting zones and avalanche paths and required the relocation of farms and primitive measures for the protection of buildings. In addition, mountain forests were protected and declared untouchable by decree of local authorities. The physical processes underlying the formation of snow avalanches and the most effective ways of reducing their occurrence and intensity were investigated more intensively in the latter part of the twentieth century, mostly in the European Alps and the Rocky Mountains. The effect of forests on avalanche formation is limited; forests are unable to stop avalanches as soon as their size exceeds a few hundred square meters. In fact, avalanches carrying trees in their debris often cause larger damage than 'clean' snow avalanches. In this article an overview is presented of forest–snow relationships, which are important for the understanding of the hydrology of forests in regions where snowfall occurs, and snow avalanche formation in forested areas. In addition, the implications for forest management with respect to snow hydrology and avalanche protection are discussed briefly.

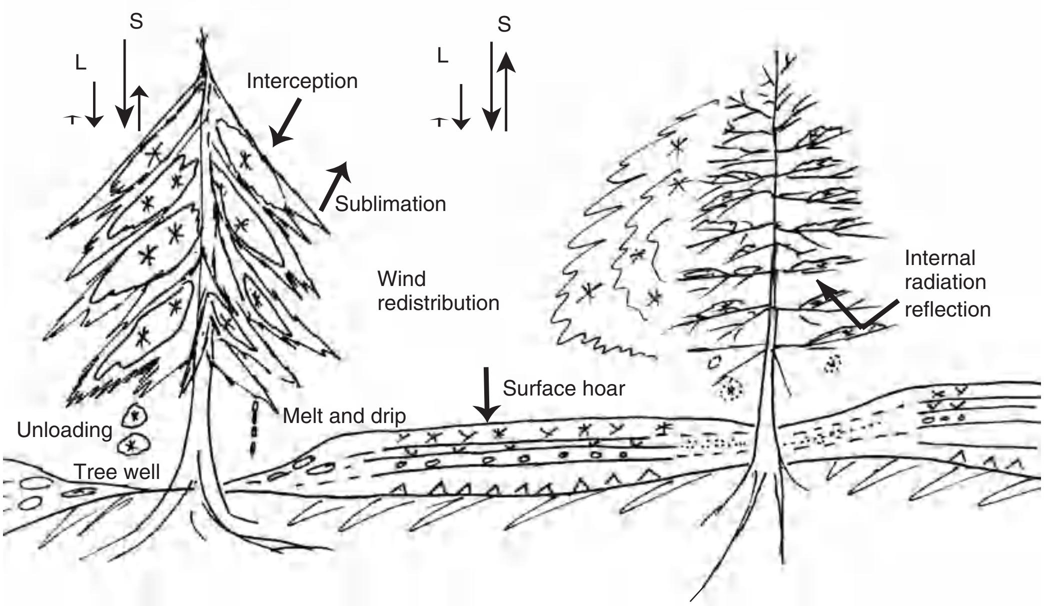


Figure 1 Processes in a snowy forest. The snow precipitation is unevenly deposited. Part of the snow is retained by interception on the trees, and later unloaded by mechanical shaking, melting and dripping as water, redistributed by wind, or sublimated back into the atmosphere. The intensity of these processes depends on weather and tree species. Incoming and outgoing shortwave solar radiation (S) and longwave radiation (L) depend on tree species, amount of interception, and topography. This modifies the condition for snowmelt and snow metamorphism.

Forest–snowpack Interactions

Snow changes the climate of a forest in winter and early spring through its high albedo and energy storage capacity (**Figure 2**).

Snow as the solid phase of water is stored at the surface of the forest floor, and because of the high energy necessary to melt it, its release as liquid water is delayed. These properties can be used to influence regional hydrology by specific forest management schemes. Snow deposition occurs in a forest at different heights and intensity, leading to a snowpack that varies spatially in terms of depth and water equivalent. Snow depth normally decreases with decreasing distance to the stem. Snow depth and water equivalent are usually higher beneath deciduous trees compared to coniferous species. In dry winter climates up to one-third of the intercepted snow is sublimated, thus reducing the amount of water available for melting in spring. Clearings with a diameter of up to seven times the height of the surrounding trees can increase the water equivalent of the snowpack, with maximum values around two to fives times tree height (**Figure 3**). However, the effect of wind erosion and redistribution of snow in alpine terrain can completely invert this behavior, such that the water equivalent of snow deposited in a spruce forest is 120% compared to that in shrub tundra.

The main effect of trees and forests on avalanche formation is through the modification of the snow's mechanical properties. Relevant processes include the interception of falling snow by the trees, the modification of the radiation and, therefore, temperature regimes beneath and around the trees,

Figure 2 Snow-covered branches of a spruce (*Picea* sp.). Solar radiation reflected by the highly reflective snow surface is absorbed by the dark underside of the branches, causing higher temperatures and melting or increased sublimation from the bottom.

and the reduction of near-surface wind speeds. External topographic factors are slope aspect and steepness. Direct support of the snowpack by tree stems is relevant in the case of dense forests and especially snow gliding. Continuous snow layers of low internal mechanical strength often show preferential fracture planes that favor so-called slab avalanche formation. The formation of such unstable layers is reduced in forests through the processes and factors mentioned earlier, i.e., snow interception (reducing the amount of snow reaching the ground) and the moderation of the radiation regime (reductions in both incoming shortwave radiation and outgoing longwave radiation), but also by increased unloading of intercepted snow from the trees by wind.

Snow Interception

Interception of falling snow by the branches of the trees is usually followed by partial unloading in the form of irregular lumps of snow caused by warming and wind. This tends to result in a highly irregular snowpack around the trees. The direct effects of this are typically visible within a distance of about 1.5 times the crown projection (see **Figure 4**). Such tree-induced disturbances of snowpack layering are most pronounced below evergreen trees; the effect is less visible in the case of deciduous trees which tend to intercept less snow due to their much reduced trapping capacity in winter. The overall stability of the snowpack as determined by mechanical tests is similar, however, between snowpacks in evergreen coniferous and deciduous forest.

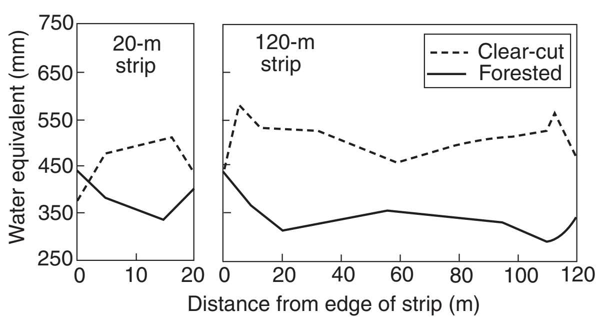


Figure 3 Transects of snow water equivalent monitored in alternate forested and clear-cut strips in the Fraser Experimental Forest, Colorado, USA. Reproduced with permission from Alexander RR, Troendle CA, and Kaufmann MR (1985) *The Fraser Experimental Forest, Colorado: Research Program and Published Research 1937–1985*. General Technical Report no. RM-118. Fort Collins, CO: US Department of Agriculture Forest Service. http://www.fs.fed.us/rm/fraser/pdf_blue_book.pdf.

Radiation

The energy balance within a forest is very different from that in the open. Both amounts and duration of solar radiation are much reduced beneath a tree cover whereas outgoing longwave radiation (mostly at night) is reduced as well (see **Figure 1**). Snow has a strong effect on the reflection of incoming radiation, as it is almost perfectly reflecting in the visible part of the spectrum and represents a near-perfect black body in the thermal infrared part of the spectrum. The associated fluctuations in surface temperatures cause the rapid formation of surface hoar frost in open fields. Surface hoar frost is a major cause of slab avalanche formation because this type of snow crystal is very brittle and can fracture after later burial by new snow. Surface hoar (and therefore slab avalanche formation) is much less probable in forest where fluctuations in snowpack surface temperatures are much more moderate because of the shielding effect of the canopy.

Wind

Wind is a major factor in the formation of avalanches in open areas through snow redistribution. Even the presence of rather open forest already causes a significant reduction in wind speed such that only minor relocation of snow occurs. This results in a more homogeneous distribution of the snow, and prevents extreme accumulation in gullies and depressions, as tends to occur in open areas.

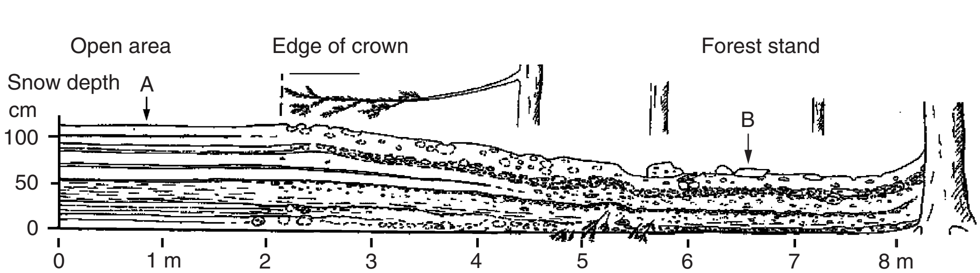


Figure 4 Snow profile in the forest. Reproduced with permission from Imbeck H (1987) *Schneeprofile im Wald*, Winterbericht Eidgenössisches Institut für Schnee- und Lawinenforschung 1985/86, no. 50.

Forests and Avalanche Control

Avalanche formation is also intimately linked to terrain features, notably slope exposure, steepness, and surface roughness. Trees and the associated modifications of the various physical processes described above form an additional modifying element compared to open, non-wooded slopes.

Terrain: Slope Angle, Aspect, and Roughness

A necessary condition for snow avalanche formation is a slope gradient exceeding 20°. In the Swiss Alps, avalanche formation on forested slopes has only been observed on slopes exceeding 30°. This value is probably valid worldwide, as the underlying mechanical processes will be similar. Slope aspect is especially relevant for the type of avalanche that occurs. Wet-snow avalanches occur mostly on sun-exposed slopes, while dry slab avalanches have only been observed on shaded sites. The frequency of avalanche releases is also higher on convex slopes (which tend to become steeper as one goes downslope) than on concave slopes where gradients generally decrease going downslope.

The roughness of the terrain underneath the snowpack is decisive for the occurrence of snow gliding and subsequent wet-snow avalanches. Grassy, abandoned meadows are especially prone to snow gliding. Fallen logs, remnant stumps of logged or snapped trees, root plates of upturned trees, and large rocks can all prevent the formation of small avalanches, but not extreme ones. Such surface features also promote regrowth by preventing subsequent mechanical damage by new avalanches to the young trees, and by providing favorable microsites for tree seedling establishment.

Effect of Forest Structural Properties

The density of a forest cover (both in terms of the number of trees per hectare and percentage canopy cover) and the size and distribution of forest gaps are often regarded as the chief forest structural parameters influencing the triggering of avalanches in forested areas. Although quantitative data on the minimum size for this 'gap effect' to happen are scarce, a first estimation of the quantitative relationships between stand structural and topographical variables may be derived from pioneering work conducted in the Swiss Alps. **Figure 5** shows the relationship between gap width and crown cover density for different categories of slope steepness based on a multivariate analysis of 112 avalanches triggered in coniferous forests in Switzerland. As gap width increases, the neighboring forest has to be increasingly dense so as to decrease the risk of avalanche formation. For a crown cover density of 60%, which is typical for subalpine forests in the Swiss Alps, a minimum gap width of approximately 20 m is expected to be sufficient to enable the triggering of avalanches on a 35° forested slope. When crown cover density decreases below 35%, the minimum gap width decreases to 10 m (see **Figure 5**).

Other important variables for avalanche control include gap length and the distance between the starting point of an avalanche in an open area and the nearest downslope forest edge. In contrast to gap width and crown cover density, which control the microclimatic influence of the forest (cf. **Figure 1**), these distances also affect the speed and, therefore, the destructive force of an avalanche. Generally avalanches with acceleration distances of more than 150 m cannot be stopped by forests, and the trees will be destroyed (**Figure 6**). For shorter acceleration distances, the efficiency of the forest's resistance to

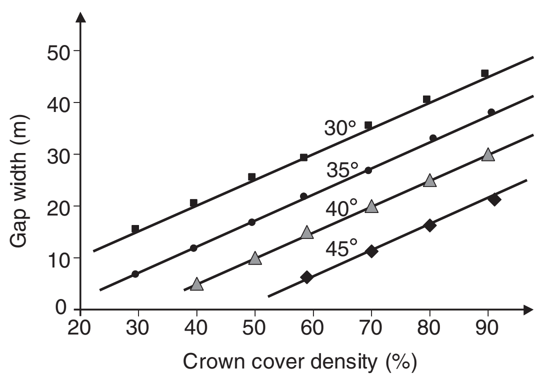


Figure 5 Relationship between critical gap widths and crown cover densities for the triggering of avalanches for different categories of slope steepness. The correlations are based on a multiple linear regression model of 112 avalanches in subalpine coniferous forests of Switzerland. R. Pfister, Swiss Federal Institute for Snow and Avalanche Research, unpublished data.

Figure 6 The devastating effect on a forest caused by an avalanche starting high above the tree line. Photograph by Swiss Federal Institute for Snow and Avalanche Research.

disturbance and the resulting degree of damage are mainly a function of slope angle, avalanche size and capacity, and the distribution and size of the trees.

Stand structural requirements for the triggering of avalanches in forests differ between evergreen forest types (mostly conifers) and broadleaved forests (mostly deciduous). The minimum gap widths required for avalanche formation are smaller in deciduous broadleaved forests. For example, in beech (*Fagus*)-dominated forests in the European Alps, a gap width of 5–10 m may already reduce the forest's snow interception capability below a critical threshold (see **Figure** 7). However, in contrast to the general perception, deciduous coniferous trees, such as larch (*Larix* spp.), are almost equally effective when it comes to preventing avalanche formation as are evergreen coniferous trees (spruce, fir), as long as stand densities are comparable. Deciduous trees are less effective in reducing avalanching than evergreen trees when the temperature during snowfall is lower. Under such conditions the snowflakes do not stick to twigs without needles.

Open-structured forests, which are more susceptible to the triggering of avalanches, are often more frequent at higher elevations and near the timberline. This is particularly valid in the case of coniferous forest in the northern hemisphere, where scattered, single trees and small clusters of trees tend to dominate in the subalpine timberline zone. Elsewhere, dense broadleaved forests (such as the *Nothofagus* forests in New Zealand) may continue all the way up to the timberline whereas under dry montane conditions open forests may form well below the temperature-controlled timberline (e.g., *Pinus ponderosa* forest in the Rocky Mountains).

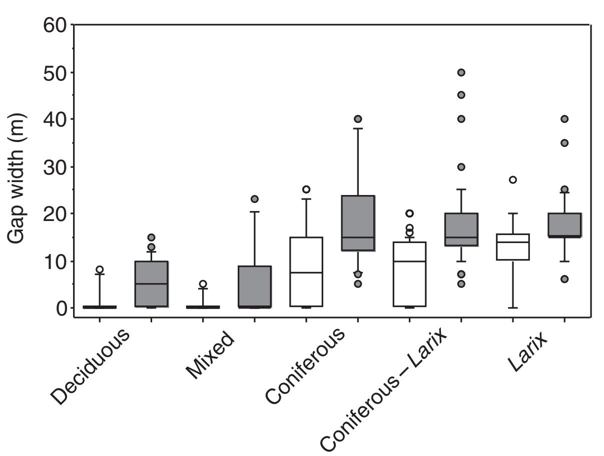


Figure 7 Interactions between gap width, forest type, and occurrence of avalanches starting within the forest. Solid bars indicate range of gap width in observed starting points. Open bars: range of gap width in control plots without avalanche release. Reproduced with permission from Schneebeli M and Meyer-Grass M (1992) Avalanche starting zones below the timberline: structure of forest. In *Proceedings of the International Snow Science Workshop*, 4–8 October 1992, Breckenridge, CO, pp. 176–181.

Stand properties related to avalanche control are permanently changing and may be altered dramatically after natural disturbances (extreme wind, landslides, avalanches, forest fires) or human intervention (mostly logging). The relevance of such disturbances in altering the forest's potential for avalanche control is dependent on: (1) the size and intensity of the disturbance, and therefore the degree of destruction, (2) the ability of remnant trees to maintain sufficient surface roughness, and (3) the time required for the establishment of a new effective forest cover.

Management Implications

In mountainous regions, the protection of human settlements against avalanches is often considered to be the most important forest function. When discussing management implications we therefore have to differentiate between cases where the forest fulfills such a protective function (German: *Schutzwald*), and where management should aim mainly at increasing forest water retention or timber production.

In a *Schutzwald*, the following measures may be applied to improve or support the protective role of forests with respect to the reduction and prevention of snow avalanches:

- silvicultural measures relating to the intensity and method of timber harvesting, and reforestation of open or deforested spaces
- structural measures including all kinds of engineering works like wooden avalanche defense structures (**Figure** 8)
- hazard mapping (as a base for land-use planning) on the basis of slope steepness, aspect, surface roughness, and tree cover
- organizational measures (early warning systems, forecasting of heavy snowfall or sudden increases in temperature, temporary road closure).

The practical importance of these measures is strongly related to population and infrastructural densities. Silvicultural and technical measures to improve avalanche control have a long tradition in steep, densely populated areas such as the European Alps, but such measures become less important in sparsely populated areas or where much damage may be avoided by the proper planning of settlements, roads, and other infrastructural works. In avalanche protection forests on very steep slopes, silvicultural measures generally aim to avoid the (persistent)

Figure 8 Avalanche starting zone in a gap within the forest protected with wooden defense structures in the Taminatal, Switzerland. The design life of such temporary wooden constructions is at least 50 years and allows time for young trees to become well established.

occurrence of large gaps and open forest. However, because natural regeneration in mountain forests often requires openings with sufficient light availability, optimal silvicultural measures for avalanche protection are often difficult to establish and time-consuming to execute. Where natural tree regeneration is too slow to guarantee a protective effect or is impeded by unfavorable microsite conditions, silvicultural treatment may have to be complemented by temporary or permanent technical support structures. Furthermore, as labor and material costs continue to rise, silvicultural and technical measures in remote mountain forests are gradually becoming less cost-effective. It is therefore inevitable to restrict such measures to the most critical areas and combine them with organizational measures wherever possible to achieve maximum effect against minimum expense. Logs lying about and upturned root plates often enhance the protective effect of a forest by increasing the overall roughness of the terrain and by providing favorable microsites for subsequent tree regeneration. Management strategies, both in disturbed and intact avalanche protection forests, should therefore rely more on naturally occurring forest dynamics and stimulate the inclusion of areas without silvicultural intervention in the planning process.

Storage of snow and therefore increased water retention of a forest can be optimized by limiting the size of any clear-cuts to about five times the tree height or by favoring a forest structure with variable heights. While these requirements are always fulfilled in the variously aged stands that are considered optimal for *Schutzwald*, this kind of management is rarely introduced where timber production is considered more important.

See also: **Ecology**: Natural Disturbance in Forest Environments. **Harvesting**: Forest Operations under Mountainous Conditions. **Hydrology**: Impacts of Forest Management on Streamflow. **Site-Specific Silviculture**: Silviculture in Mountain Forests. **Temperate and Mediterranean Forests**: Northern Coniferous Forests; Southern Coniferous Forests.

Further Reading

Alexander RR, Troendle CA, and Kaufmann MR (1985) *The Fraser Experimental Forest, Colorado: Research Program and Published Research 1937–1985*. General Technical Report no. RM-118. Fort Collins, CO: US Department of Agriculture Forest Service. http://www.fs.fed.us/rm/fraser/pdf_blue_book.pdf.

Arno SF and Hammerly RP (1984) *Timberline: Mountain and Arctic Forest Frontiers*. Seattle, WA: The Mountaineers.

Bebi P, Kienast F, and Schönenberger W (2001) Assessing structures in mountain forests as a basis for investigating the forests' dynamics and protective function. *Forest Ecology and Management* 145: 3–14.

Brang P, Schönenberger W, Ott E, and Gardner B (2000) Forests as protection from natural hazards. In: Evans J (ed.) *The Forests Handbook*, vol. 2, pp. 53–81. Oxford, UK: Blackwell Science.

Pomeroy JW and Gray DM (1995) *Snowcover: Accumulation, Relocation and Management*. National Hydrology Research Institute Science Report no. 7. Saskatoon, Canada: Environment Canada.

Schneebeli M and Meyer-Grass M (1992) Avalanche starting zones below the timberline: structure of forest. In *Proceedings of the International Snow Science Workshop*, 4–8 October 1992, Breckenridge, CO, pp. 176–181.

Schweizer J, Jamieson JB, and Schneebeli M (2003) Snow avalance formation. *Reviews of Geophysics* 41(4).

Weir P (2002) *Snow Avalanche Management in Forested Terrain*. Land Management Handbook no. 55. Victoria, Canada: Ministry of Forests. http://www.for.gov.bc.ca/hfd/pubs/Docs/Lmh/Lmh55.htm.

Whitaker A, Alila Y, Beckers J, and Toews D (2002) Evaluating peak flow sensitivity to clear-cutting in different elevation bands of a snowmelt-dominated mountainous catchment. *Water Resources Research* 38: 1172. doi: 10.1029/2001 WR000514.

I

Insect Pests *see* **Entomology**: Bark Beetles; Defoliators; Foliage Feeders in Temperate and Boreal Forests; Population Dynamics of Forest Insects; Sapsuckers. **Health and Protection**: Integrated Pest Management Practices; Integrated Pest Management Principles. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Integrated Pest Management *see* **Entomology**: Population Dynamics of Forest Insects. **Health and Protection**: Integrated Pest Management Practices; Integrated Pest Management Principles.

INVENTORY

Contents

Forest Inventory and Monitoring

M Köhl, Dresden University of Technology, Tharandt, Germany

Introduction

Decision-making processes require sound and reliable information. This assertion is well borne out in forest science, indeed in the practice of forestry, where decision-making must rest on many sources of information, all of which ultimately recognize the need to manage forestry resources wisely over long periods of time. Forest inventory and monitoring is an essential means of obtaining this information and is a basic component of the cycle of procuring information, decision-making, and control of operations.

Forest inventories offer a bundle of instruments, which provide decision-makers with a wide range of sound and reliable information concerning the forestry sector. Forest inventories utilize expertise from different fields such as sampling theory, surveying, information technology, remote sensing, geographical information systems, mensuration, or modeling.

In the following article a general introduction to inventory and monitoring forests will be given. This overview covers inventory concepts, attributes assessed, data sources, categories, and work phases of forest inventories.

Inventory Concepts

Sampling Designs

Due to cost and time constraints a full tally of forests must be ruled out and is generally replaced by sampling techniques. The use of statistical sampling techniques can be traced back to a period in the early nineteenth century that also witnessed the formation of statistical societies in Europe and North America. About 150 years ago the Danish forest service conducted a nationwide census of forests, which can be seen as the first national forest survey. About 1850, Brandis introduced strip surveys in Burma at 5% intensity for inventory and management. Linear strip samples were used in Sweden as early as in the 1840s. In the 1920s Swedish forests were assessed at a national level by measuring strips from the coast to the Norwegian border across the country and deriving estimates for the entire nation.

In the eighteenth and the beginning of the nineteenth century methods were developed that were based on the visual assessment of forest stands. In the nineteenth century a shift from fuel-wood to high-quality timber production forced a change in monitoring methods. Visual assessments were replaced by measurements and censuses of the quantity of standing timber. The German forest commissioner Schmidt wrote in 1891:

> *Unfortunately is this assessment method (i.e. the census) especially in dense stands time consuming and expensive, and one replaces it often and with pleasure by the plot assessment method. It is a known fact that hereby a conclusion is made from a part of the stand to the entire stand.*

Schmidt notes that the (rectangular) plots should be placed in those parts of the stand which represent the entire stand. According to Schmidt it is difficult to decide which plot design is suitable in heterogeneous stands to represent the entire stand, and that one can solve this 'embarrassing situation' by selecting several plots in different parts of the stand. He concludes that 'one comes the closer to the truth the more plots are selected.' In spite of a knowledge of statistical theory, Schmidt utilizes two major principles of sample survey: representativeness and replication.

As the tools of statisticians to collect, analyze, and draw inferences from data continued to expand in the twentieth century, forest research moved along to set statistical principles in the framework of forest resource assessments and to use those tools to understand better both the ecology of forests on local, regional, and global scales, as well as the environmental impact of forest management at these scales. In the 1930s sampling of forests started in North America. A lack of forest maps and limited knowledge about extensive forest resources gave rise to inventory techniques that were very different from those used in Europe at that time. Survey sampling in a sound statistical manner was first reported by Hasel in 1942.

A driving factor in developing sample-based inventory systems was the need to provide for cost-efficient methods for forest resource assessments. The general principle of sampling is to select a subset of elements (i.e., a sample) from a population, to measure this subset intensively, and to draw inferences from the sample to the entire population (**Figure 1**). Statistical theory is applied for the selection process by assigning each population element a (known) selection probability. The selection probability is then utilized for the inference process.

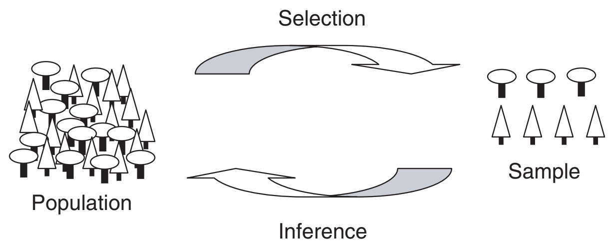


Figure 1 The concept of statistical sampling.

An outstanding number of sampling designs for natural resource assessments has been presented in the literature. They can be divided into two main groups: (1) sampling designs without utilization of auxiliary information, and (2) sampling designs utilizing auxiliary information. In sampling designs without auxiliary information, only observations on the attributes of interest that are obtained from population elements selected by the sample are used for inference. As, apart from the sample, other information about the population is often available or can easily be obtained, e.g., from aerial photography or satellite imagery, designs have been developed in which such information is used in estimation procedures. As a rule, sampling designs with auxiliary information are more efficient than those without. The major types of sampling designs with and without auxiliary information are presented in **Figure 2**.

Sampling Units

Before selecting a sample the population must be divided into parts that are called sampling units. The sampling units applied in forest resource assessments are single trees only in exceptional cases. In order to reduce assessment efforts and costs, groups or clusters of trees are selected. The clusters can be formed by selecting at each sample location a fixed number of trees (so-called nearest-neighbor or *n*-tree methods), or all trees that are located within an area of fixed shape and size, i.e., circular, squared, or rectangular plots (**Figure 3**). These alternatives assign a constant sampling probability to each tree. Typical plot areas are between 100 and 700 m^2. As stand density is related to tree size, large-area plots can result in

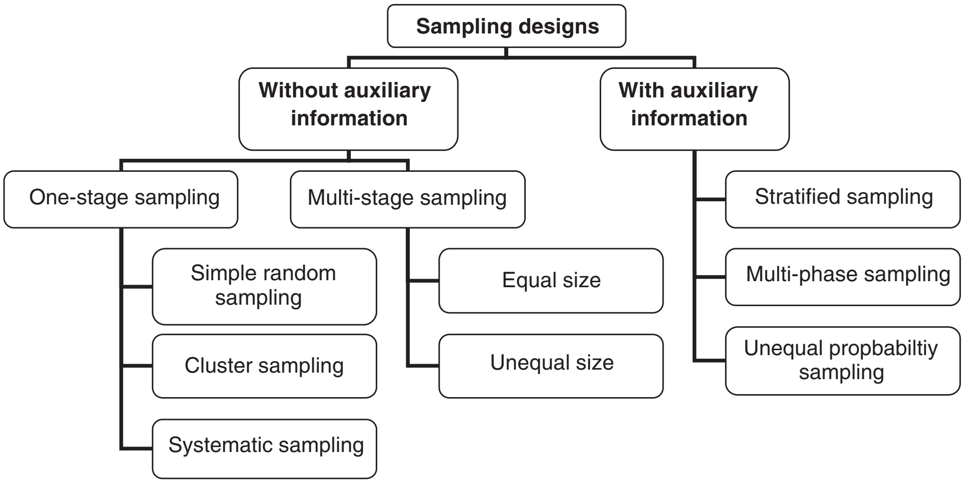


Figure 2 Sampling designs.

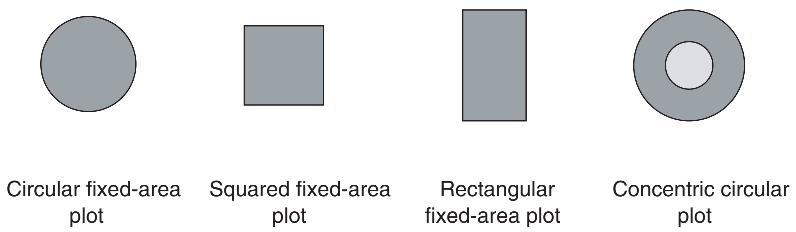


Figure 3 Fixed-area plots.

situations where a large number of trees (e.g., >100 trees) with small dimensions are located on a sample plot. To reduce the number of selected small trees and to increase cost-efficiency, concentric plots can be applied; these are a cascade of plots with different areas. On the smallest plot all trees are selected while for the larger plots only trees with larger thresholds of minimum diameter at breast height (dbh) are considered. For example, the Swiss national forest inventory utilizes two concentric sample plots with sizes of 200 m^2 and 500 m^2. On the smaller plot all trees are selected while on the larger plot only those trees with a dbh above 35 cm are selected.

Where the sampling probability of a tree is proportional to some tree attribute, the selection incorporates unequal probability sampling, e.g., probability proportional to size (PPS) or probability proportional to prediction (PPP). The most widely used unequal probability sampling approach in forest inventories is point sampling (also known as plotless sampling, angle count sampling, or Bitterlich sampling), where trees are selected with a probability proportional to their dbh (**Figure 4**). The selection procedure is realized by viewing all trees visible from a randomly chosen sample point within a forest by a constant angle. Those trees appearing larger than the constant angle are selected as sample trees. As a tree with a large dbh can be further apart from the sample point to be included in the sample (i.e., appears larger than the constant angle) than a tree with a smaller dbh, the procedure assigns a sampling probability proportional to the size of the dbh.

The selection of the optimal sampling design for a specific assessment program is an iterative process that is driven by the required information needs, the available resources, cost-efficiency, and the desired reliability of the information to be provided.

Monitoring Change by Sampling at Successive Occasions

The idea of describing the development of stands through permanent observations and thereby controlling the sustainability of forest management was born in the nineteenth century. In the 1930s, sampling methods, known as continuous forest inventory (CFI), were developed which were based on repeated measurements of a set of sample plots. With the CFI method, all sample plots, which are measured at the initial occasion, are measured again in successive inventories. Changes can be quantified by calculating the difference of estimates on two successive occasions.

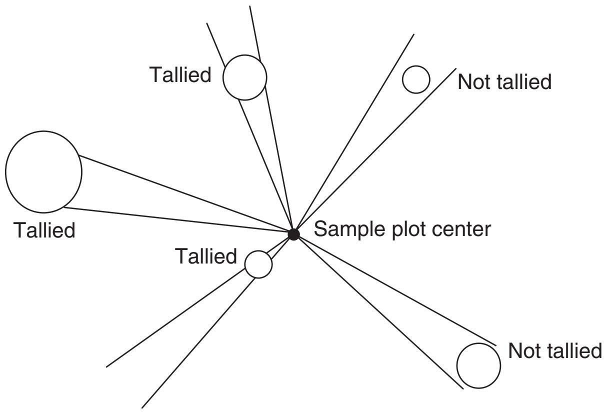


Figure 4 The principle of point sampling.

Remeasured plots are called permanent plots and are established at the first occasion by registering the plot location as well as the position of the trees inside the plots. Permanent plots can be realized by fixed-area plots, point samples (Bitterlich plots), or nearest-neighbor methods. As the location of each sample tree is known, it is straightforward to describe the individual tree history and thus the growth components formed by survivor trees, in-growth, mortality, and cuts.

The application of the CFI method over long periods of time may lead to problems caused by its rigid system of permanent plots. An initial set of plots may lack representativity when plots are lost, e.g., by disturbances or land use changes, or cannot be relocated in the course of time. When inventory objectives are changing over time, it may become necessary to establish additional plots at new locations. However, the statistical estimation procedures used with CFI are straightforward and can be understood intuitively.

A sampling method for field surveys that was introduced into forest inventory in the 1960s is sampling with partial replacement (SPR). With this method, part of the sample plots that are measured at one occasion are replaced by new sample plots at the next occasion (**Figure 5**). For two occasions three types of sample plots are obtained:

1. Sample plots, which are measured at time 1 as well as at time 2 (permanent sample plots, matched plots).
2. Sample plots, which are only measured at time 1 (unmatched plots).
3. Sample plots, which are only measured at time 2 (new plots).

SPR is a flexible design with several advantages. It is possible to replace lost plots and to allocate new plots according to changes of inventory objectives.

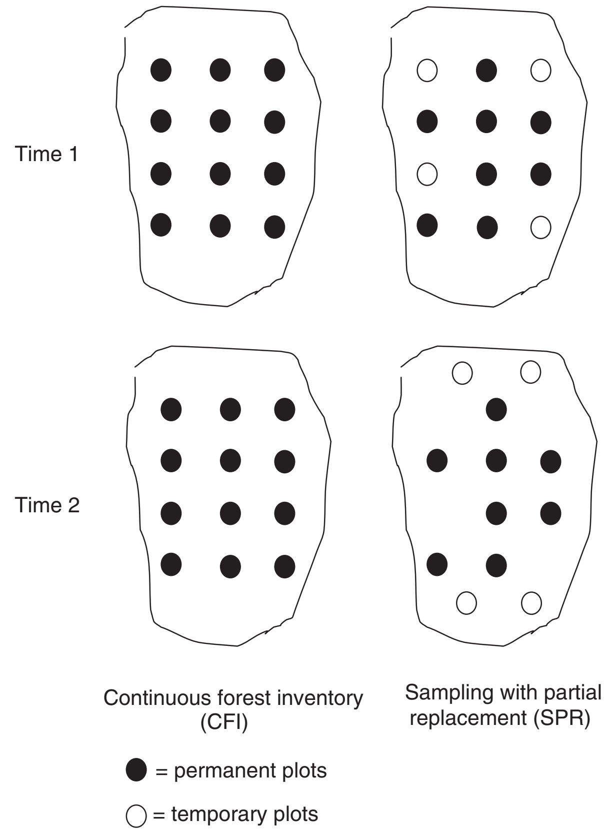


Figure 5 Sampling at successive occasions.

The number of unmatched and new plots does not necessarily have to be the same. By adjusting the proportion of new and matched sample plots it is possible to optimize cost-efficiency according to the focus on current state or changes. If only current state is to be considered, temporary sample plots often prove to be more cost-effective than permanent plots, since the expenditures for marking the sample plot centers and the registration of sample tree coordinates do not exist. However, permanent plots result in precise change estimates. A major disadvantage of SPR is that the estimation procedures become unwieldy and deterrent after more than two occasions.

Besides CFI and SPR, other approaches have been described to assess changes. Those approaches include independent assessment at each occasion, updating observations by modeling, or a combination of a low number of permanent plots and extrapolation of past observations by modeling.

A Typology of the Attributes Assessed

The sampling concepts described above determine the procedure by which the sample is selected from the populations. Once a sample has been selected, attributes are assessed at the individual sampling units. Attributes assessed in forest inventories can be related to individual trees or to areas such as the site or the stand. Only a limited number of attributes can be directly measured, such as tree height, diameters at different stem heights, crown length, bark thickness, bole length, basal area, or thickness of the humus layer. From a statistical perspective those attributes are observed on interval or absolute scales and allow for the computation of a variety of statistical parameters (e.g., mean, variance, standard deviation, coefficient of variation, median, or coefficient of correlation). A large set of attributes is assessed according to definitions, e.g., tree species, crown shape, defects, diseases, tree layer, soil type, development stage, or management activities. As those attributes are nominal or ordinal-scaled, they only allow for a limited number of statistical parameters (e.g., median, mode, range, or proportion). Attributes directly assessed can be used as input variables for models and form the base for a large set of derived attributes. Among those are, for example, stem volume, above-ground tree biomass, assortments, timber value, species mixture proportions, and site class.

Data Sources

The major data sources utilized by forest inventories are *in-situ* assessments. Attributes that cannot be assessed by field visits, such as ownership, past management activities, or investments in infrastructure, render data assessment by questionnaire necessary. Despite the fact that the location where data are assessed may be georeferenced, it is not possible to derive spatially explicit data (i.e., maps) from those data. The visualization of results in mapped format is restricted to the spatial resolution of the units of reference.

Since the beginning of the 1920s the use of aerial photography for forest resource assessments has been studied. The development of operational remote sensing techniques in the 1970s added a new data source to traditional information gathering. Remote sensing imagery provides wall-to-wall maps of land cover and forest types for entire inventory areas and allows for spatial analyses. However, the number of attributes that can be derived from remote sensing data is limited. The combination of remotely sensed and *in-situ* data by statistical approaches offers the potential to utilize both the depth of the thematic information of *in situ* assessments and the spatially explicit information of remote sensing data.

Beside field data, questionnaires, and remote sensing data, other data sources are utilized for forest inventory purposes. Among those auxiliary data are statistics, e.g., on population, timber markets, or economy, and thematic maps displaying topography, geomorphology, administrative boundaries, transport systems, climate, or location of settlements and industries. The availability of geographic information systems and their capability to handle spatially explicit data layers offer powerful tools for spatial analyses and spatial modeling.

Information Needs

Long-term sustainability motivated forest scientists to seek methods to monitor and predict the long-term development of forests. The principles of sustainable forest management were developed in times when public demands concerning forests concentrated on the production of timber. Thus traditional inventory and monitoring methods mainly focused on the balance of timber growth and timber utilization. During the past decades sustainability became a prominent concern in the entire environmental context. In the context of sustainable development forests are no longer seen solely as a timber resource, making sustainable forest management, according to the Intergovernmental Panel on Climate Change, ‘a system of practices for stewardship and use of forest land aimed at fulfilling relevant ecological (including biological diversity), economic and social functions of the forest in a sustainable manner.’

In order to meet today’s information needs the methodological background of forest inventories has been significantly widened in the past decades and allows information to be provided on the multiple wood and nonwood goods and services of forests. Forests are not solely treated as management systems but as a holistic concept subject to multiple ecological, economic, and social relationships. Sustainable forest management requires the observation of forests in successive points in time. Forest inventories thus provide tools to assess current information as well as information on changes. A set of successive forest inventories is often called a forest-monitoring system.

Decision-making in the forestry sector is realized at different levels and thus requires information for different spatial scales. Forest management planning has a high demand of spatially explicit, local information, while decisions at a political level render information aggregated to the regional or national scale necessary. National information can be cumulated on a multinational, continental, or global level and form the information base for multinational programs and initiatives. The vertical aggregation from task-specific to integrative and

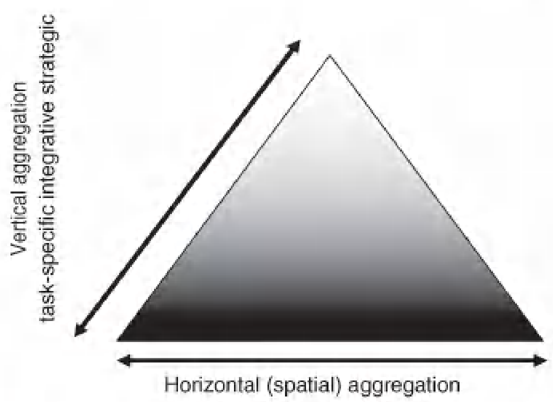


Figure 6 Horizontal and vertical aggregation of information.

strategic planning goes hand in hand with spatial (horizontal) aggregation, resulting in an increasing area of units of reference for which information is provided (**Figure 6**).

In the context of sustainable forest management, forest resource assessments may provide information on the current state and changes over time on the following thematic aspects:

- forest resources, including forest area and growing stock
- carbon balance
- health and vitality of forest ecosystems
- productive functions, including growth and harvested timber
- biological diversity
- protective functions
- socioeconomic functions and conditions.

For specific questions such as scenic beauty, forest ecology, or potential forest habitats, it can be necessary to study forests in a landscape context, rendering spatially explicit information of the location of forested land necessary.

Categories of Forest Inventories

According to the inventory objectives and the size of the area to be surveyed, different categories of forest inventories can be defined. Forest inventories are for the most part realized as multipurpose resource inventories and aim at an ample picture of the multiple functions provided by forests.

Global forest inventories are conducted to determine forest resources at a global level and were compiled by the Food and Agriculture Organization several times since 1946. Global forest resource assessments utilize existing national data to a maximum extent. As national assessments are aiming at specific national or regional information needs, they do follow individually designed inventory concepts and systems of nomenclature. Much discussion and readjustment of the results of national forest inventories is necessary before they can be compiled to give a global picture. Advances in remote sensing techniques allow satellite imagery to be applied to determine the distribution of forest vegetation throughout the world.

National forest inventories are already being conducted in many countries, especially in temperate and boreal regions. In Scandinavia national forest inventories have been running since the 1920s. Timber volume is usually employed as a key parameter, though information on the distribution of forested areas, the condition of the forest, and productivity also has to be collected. The non-wood functions of the forest are receiving increasing attention. Ideally, national inventories are planned as permanent surveys with periodic updates. Information obtained through national inventories is mainly applied in questions of national forest policy and international commitments and initiatives.

Land-use inventories extend the concept of forest resource assessments to other types of land use. Aerial photographs and satellite data are of especial importance here. In the scope of UN Framework Convention on Climate Change (FCCC) land use, land use change and forestry (LULUCF), land use inventories are a major tool in quantifying carbon sinks and sources.

The term 'regional forest inventory' is applied to a variety of inventories. Regional forest inventories register only a subset of the national forested area or an area which is assembled by two or more countries. The size of the area covered by regional forest inventories usually comprises between 50 000 and some hundreds of thousands of hectares. Similarly to national inventories, they are intended to provide a general picture of the situation regarding forestry. In a global framework the term 'regional forest inventories' is used to describe inventory areas that cover entire continents, parts of continents, or forest vegetation zones. Similar to global forest inventories, data available at the national level are utilized to a maximum extent.

Stand level inventories are the most intensive type of forest inventory and aim at detailed information for forest-planning purposes on individual stands and on intensively managed but restricted areas. Usually the data are computed on a stand-by-stand basis for each species. Information on increment, detailed forest maps, and data on the quality of the various sites are just as necessary as details on topography, ownership, and accessibility. As an integrated part of sustainable forest management, stand level inventories are normally realized as permanent inventories.

Reconnaissance inventories provide a rough insight of forest characteristics of a limited area. As well as the location and extent of forested areas, they register accessibility, species composition, tree dimensions, the distribution of various forest types, and initial data on timber quality and forest ecology. As reconnaissance inventories are conducted at minimum cost, the employment of remote sensing data is promoted while field surveys are restricted to the minimum. They frequently serve for the preparation of an intensive forest inventory by providing basic information on the degree of variation of forest attributes.

Exploitation surveys, logging plan surveys, and wood procurement studies are conducted to provide a basis for the planning of timber-harvesting operations. The main focus is on determining the current state of standing crop, classified according to species, dimensions, and assortments. Information on accessibility can be included in nonopened-up areas. Information on increment, sustainability, or ecological conditions is not in the focus of such inventories.

Forest health monitoring became prominent in European countries in the 1980s when forest decline was a public concern. In Europe and North America such surveys are conducted regularly in order to track the course of development of different types of damage. Among the attributes assessed are crown transparency, needle and leaf discoloration, regeneration, and mortality.

The typology of forest inventories described above does not represent a rigid classification scheme. Special surveys may be conducted to satisfy individual information needs. For instance, the assessment of current state and changes of woody biomass can be a major concern for carbon budgeting. The various types of forest inventories may overlap and increasing demands for information on nonwood goods and services and biological diversity may lead to new inventory types.

The Work Phases of Forest Inventories

The planning of forest inventories is a complex task that brings together experts with different technical backgrounds. The time span between the expression of the need for a forest resource assessment and the availability of inventory results may easily cover a decade. In order to plan and organize a forest inventory the proven rules of system analysis and project management are to be followed. Carrying out a forest inventory can be divided into four main work phases:

1. Definition of the inventory objectives and the information desired.
2. Development of the sampling design, the sampling methods, and the concept for data analysis.
3. Data assessment (field surveys, remote sensing data analyses, and collection of information in other data sources).
4. Data analyses and publication of the results.

See also: **Inventory**: Large-scale Forest Inventory and Scenario Modeling; Modeling. **Mensuration**: Forest Measurements; Growth and Yield.

Further Reading

Bachmann P, Köhl M, and Päivinnen R (eds) (1998) *Assessment of Biodiversity for Improved Forest Planning*. Dordrecht: Kluwer Academic.

Cochran WG (1977) *Sampling Techniques*. New York: Wiley.

Corona P, Köhl M, and Marchetti M (eds) (2003) *Advances in Assessments for Sustainable Forest Management and Biodiversity Monitoring*. Dordrecht: Kluwer Academic.

De Vries PG (1986) *Sampling Theory for Forest Inventory*. Heidelberg: Springer Verlag.

Hasel AA (1942) Estimation of volume in timber stands by strip samplings. *Annals of Mathematical Statistics* 13: 253–267.

IPCC (2000) *Land Use, Land Use Change and Forestry*. Special report. Cambridge: Cambridge University Press.

Köhl M (1993) Forest inventory. In: Pancel L (ed.) *Tropical Forestry Handbook*, pp. 243–332. Heidelberg: Springer Verlag.

Päivinen R, Lund HG, Poso S, and Zawila-Niedzwiecki T (eds) (1994). *IUFRO International Guidelines for Forest Monitoring*. IUFRO World Series Report 5. Vienna, Austria: IUFRO.

Särndal C-E, Swensson B, and Wretman J (1992) *Model Assisted Survey Sampling*. New York: Springer.

Schmidt K (1891) Das Kreisflächen-Aufnahmeverfahren des Herrn Oberforstrath Zetsche. *Allgemeine Forst- und Jagdzeitung* 11. Jg.: 73–76.

Schreuder HT, Gregoire TG, and Wood GB (1993) *Sampling Methods for Multiresource Forest Inventory*. New York: John Wiley.

Scott CT and Köhl M (1993) *A Method for Comparing Sampling Design Alternatives for Extensive Inventories*. Band 68, Heft 1, Birmensdorf, Germany: Mitteilungen der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft.

Thompson SK (1992) *Sampling*. New York: Wiley.

von Gadow K, Nagel J, and Saborowski J (eds) (2002) *Continuous Cover Forestry – Assessment, Analysis, Scenarios*. Dordrecht: Kluwer Academic.

Large-scale Forest Inventory and Scenario Modeling

T Nuutinen, Finnish Forest Research Institute, Joensuu Research Center, Joensuu, Finland

Scenarios as Tools for Planning for the Future

Forestry is facing trends such as population growth, uncertainties such as climate change or market fluctuations, as well as major drivers of change such as new governmental policies or international agreements, new markets for forest products, or new harvesting technologies. There is increasing need to manage forests effectively to meet multiple requirements (including preservation of biodiversity) and changing conditions, and to show it to the customers and the surrounding society. Scenarios are tools for planning for changes and uncertain future. It is possible to derive expert scenarios without computerized models. In forestry, scenarios are usually based on the complex analysis of ecosystems and human behavior at the national, regional, and global level. In the analysis, large-scale forest inventory data and computerized scenario modeling are needed to explore resources and their alternative futures.

Scenario Approaches

Scenarios integrate information on what might happen based on drivers, the probabilities of future events, and the interests of different actors. There are four different scenario approaches: (1) vision; (2) projection; (3) pathway; and (4) alternative scenarios. The vision scenarios are based on subjective hopes. Projections are based on past trends and they predict how people expect the future to be. The pathway scenarios compare the present and desired future to assist in the design of strategies on how a certain future is achieved. The alternative scenarios map the possible futures based on anticipated changes.

Forestry Scenario Models and Forest Sector Models

Forestry scenario models are sometimes defined as computerized models used to make long-term projections of forest resources over a large geographical region (from a couple of hundred hectares to global level). They may be referred to as timber inventory projection models, timber supply models, timber assessment models, or long-term strategic planning tools.

Forestry scenario models cover natural processes of forests as well as management activities. There are different ways to classify forestry scenario models. A common classification is based on the forest growth prediction method (yield tables, stand models, or individual-tree models). Another classification distinguishes timber assessment and timber supply prediction models. Timber assessment models illustrate the effects of different harvest levels on the forest. Timber supply models predict supply, taking into account the forest structure and growth as well as the expected harvest.

Forestry scenario models are closely related to forest sector models. Forest sector models cover both forestry and the forest industry and they can be classified according to how they deal with spatial markets. There are two region nonspatial models, multiregion nonspatial price equilibrium models, spatial equilibrium models, trade flow and market share models, and transportation models.

Forestry Scenario Systems

Forestry scenario analysis is usually based on quantitative models covering natural processes (trees, other species, soil, etc.), products and services, human activities and their economy, and their interactions. For the analysis these models are integrated into software systems where appropriate data and models are integrated to mimic the real world and interaction of its components and processes.

The common components for most forestry scenario systems are: large-scale (national) forest inventory data as input, a simulation model for projections, and a method for the actual scenario generation corresponding to the defined assumptions. Depending on the method used in the generation of scenario, the models can be divided into optimization or iterative simulation models.

Examples of Forestry Scenario Models

Typically, a large-scale forestry scenario model has been designed for particular conditions and forestry-related problems. In northern Europe, national-level forest scenario models are available, for example, for Finland, Norway, and Sweden. In other parts of Europe, the models have been mainly designed for specific tasks and regions. In the USA, strategic planning software has been used for decades in the land management of public forests. New Zealand has utilized integrated simulation and optimization in the management of plantation forests.

In Finland, the MELA model of the Finnish Forest Research Institute is used for forestry modeling and analysis. MELA was designed in the 1970s for the regional and national analysis of timber production based on national forest inventory (NFI) sample plot data. MELA has two components: (1) a forest stand simulator based on individual-tree distance-independent models to generate automatically a number of feasible (sound and acceptable) management schedules for the stands over time; and (2) optimization software. In MELA, JLP software is used as the solver. In principle, JLP is a general linear programming (LP) package for solving Model I-type forest management planning and conventional LP problems. However, JLP is characterized by its outstanding capacity and speed in solving large-scale multilevel LP problems. This is due to the capability to utilize the specific problem structure where several management schedules are simulated for each stand. The structure of JLP makes it possible to solve both a production program for the whole forestry unit and the management of hundreds of thousands of stands simultaneously based on user-supplied goals. In MELA, hundreds of variables are available as optional decision criteria, combining the state of the forests, physical production, and economy. A typical analysis is based on the maximization of net present value. Three rounds of national analysis based on the NFI sample plot data have been carried out for the preparation of national forest programs since the 1980s.

In Norway, a similar approach to the Finnish MELA, based on integrated simulation and optimization, was adopted. The GAYA-JLP is a forest scenario model based on simulation of treatments for stands and linear programming (JLP) for solving management at forest level. The growth models are standwise. In addition to GAYA-JLP, the Avvirk simulation model is used for national and regional timber production analysis based on NFI sample plot data.

In Sweden, the Hugin simulation model has been used for long-term forecasts of timber yield and possible cut based on NFI sample plot data since the 1980s. Hugin is a deterministic simulation model with some built-in stochastic components. The growth models are based on individual trees.

In Germany, several models exist. For example, the FORCABSIM model is used to study the effects of management practices on the value of forest land and timber stock, as well as the stocks and fluxes of carbon. The FORSKA gap model uses forest inventory plot data to study the impact of projected climate change and alternative forest management strategies. In the Netherlands, the HOPSY model, based on singular stationary Markov processes, is used for wood forecasting.

In the strategic planning of US public forests, SPECTRUM was developed to replace FORPLAN, which has been used for Forest Service land management planning since the 1980s. FORPLAN was originally built for integrated resource planning of national forests. SPECTRUM was designed to incorporate new analytical capabilities to address ecosystem management issues. Both FORPLAN and SPECTRUM are general modeling tools applicable in different conditions.

In Minnesota, the DTRAN model has been used to analyze state-wide timber supply. DTRAN deals with interactions concerning timber supply within a region, taking into account the specific product requirements at specific market locations. In general, DTRAN is an optimization model that minimizes cost while meeting forest-wide production targets over the planning horizon. The advanced feature of DTRAN compared with other forestry scenario models is its ability to take into account transport costs.

In New Zealand, the IFS/FOLPI model has been used in forestry modeling. IFS is an interactive forest simulator used by the New Zealand Forest Service. FOLPI is a system based on LP. The system automatically translates the planning problem into an LP formulation, solves the problem using a standard LP package, and interprets the solution. The basic data for both IFS and FOLPI consist of tables of initial areas by crop type and age class.

In addition to national models, there are models covering larger regions. At the European level two approaches are used: the European Timber Trend Studies (ETTS) regularly carried out by the United Nations Economic Commission for Europe (ECE)/Food and Agriculture Organization are compiled from national estimates and the EFISCEN – developed from the former International Institute for Applied Systems Analysis (IIASA) timber assessment model – is a harmonized model based on NFI data. ETTS includes scenarios for the outlook for supply and demand of roundwood and forest products in Europe. In ETTS V the demand and supply forecasts are the results of econometric models, and the roundwood supply is based on the aggregates of national scenarios considered most likely by national experts.

The predecessor of EFISCEN, the original IIASA model, was developed in the late 1980s. The IIASA model is an area matrix model into which the management regimes are given exogenously. The EFISCEN matrix model uses NFI results, including area, volume, and net annual increment by age classes for more than 2500 forest types. The

EFISCEN has been used, for example, to study the impact of climate change on long-term growth and development of European forests.

Examples of Forest Sector Models

The most famous forest sector models are the Timber Assessment Market Model (TAMM), the Price Endogenous Linear Programming System (PELPS), the Global Trade Model (GTM), and the Timber Supply Model (TSM). Both TAMM and PELPS are mainly used at national level. GTM and TSM are designed for global analysis.

TAMM is a spatial model of the US solid wood and timber inventory. TAMM provides annual volumes and prices in the solid wood products and saw timber stumpage markets and estimates of total timber harvest and inventory by geographic region for periods up to 50 years. TAMM has been used to examine issues ranging from log export policies to the impact of carbon sequestration through tree planting.

PELPS was originally developed for the North American pulp and paper industry but PELPS III can be used for any sector to predict consumption, production, and capacity by technology, and trade within or among several regions or countries.

GTM is a partial market-equilibrium economic model originally developed at IIASA to predict future world trends in forest product consumption and production, timber supply, and global trade. The model finds, at any time period, the market equilibrium solution for all regions and all forest products such that demand and supply are equal for each forest product in each region. National versions of GTM have been used, for example, in Finland (SF-GTM).

The Center for International Trade in Forest Products (CINTRAFOR) has extensively revised the original GTM into CGTM. CGTM has been used to assess the economic impacts of climate change on the global forest sector, impacts of US carbon mitigation strategies on US and global carbon accounts, impacts of timber supply shortage on land-use allocation, and impacts of supply constraints and trade policies on global tropical forests. In addition, the model has been utilized in studies on the development of tropical hardwood markets, effective trade policies on tropical deforestation, and on market distortions and their impacts on the forest sector in Latin America.

TAMM and GTM are static simulation models. A static simulation model utilizes econometrically estimated functions of supply and demand to determine the single period equilibrium price and harvest level. Both models simulate the supply as price changes and growing stock adjusts through growth and harvest of timber. The solutions in many periods are linked together to project market behavior over time. Supply and demand relationships derived from historic data may or may not hold up during the projections.

TSM is an optimal control model that uses dynamic optimization to determine (solve endogenously) the path of price, harvest, and management that maximizes the net present value of consumers' plus producers' surplus over all time periods in the future. In TSM timber supply is a function of price and the amount of harvestable age classes. In forest sector models, the control theory may be more suitable than static simulation for long-term analysis because it provides the theory for predicting harvest behavior in the future when econometric relationships may not be valid.

TSM has been used, for example, to analyze the economic impact of climate change on global timber markets. In addition, TSM has been used to forecast the likely response of industrial wood producers to increased or decreased demand for fiber over the long term, and to analyze the effects of further set-aside or the adoption of more costly forest management or harvesting systems on timber supply.

In the USA, two different model sets have been used to analyze US private timber resources: the TAMM/NAPAP/ATLAS/AREACHANGE (TNAA) system and the Forest and Agriculture Sector Optimization Model (FASOM). The TNAA system consists of four linked models: TAMM, The North American Pulp and Paper (NAPAP) model, the Aggregate Timber Land Assessment System (ATLAS), and the AREACHANGE model. The AREACHANGE model projects the shifting of timberland between forest and nonforest uses and among forest cover types. NAPAP is a static, price-endogenous, spatial equilibrium model – like TAMM. NAPAP projects consumption, production, prices, and trade in pulp, paper, paperboard, and fiber markets. TAMM deals with solid wood and provides an interface with the timber resource model ATLAS. The TNAA system has been used for more than 20 years, especially in US Resource Planning Act (RPA) timber assessments and updates. The RPA assessment is the evaluation of the supply and demand situation for timber in the USA mandated by Congress and carried out by the US Department of Agriculture (USDA) Forest Service. The purpose of RPA is to analyze the timber resource situation to understand the implications for future cost and availability of timber products. The basic set of models has also been used in regional studies, for example in the south.

FASOM is a spatial, intertemporal optimization model which links the US forest and agriculture sector. FASOM was originally developed to examine forest and agricultural carbon sequestration policies. The Office of Economy and Environment in the Environmental Protection Agency (EPA) initiated the development of a dynamic model of the joined forest and agriculture sectors to be able to model the competition for the land. In FASOM the management investments and land use options are endogenous. The model employs a joint objective function, maximizing the present value of producers' and consumers' surpluses in the markets of the two sectors, subject to restrictions on the disposition of the land base that is suitable for use in either sector.

Forestry Scenario Analysis

A typical forestry scenario analysis includes several steps. First, the scenario assumptions are outlined. Second, the appropriate data and model or models are selected and preprocessed to be compatible with each other and the assumptions, if necessary.

Scenarios are usually based on the existing forest inventory data. Sometimes problems arise due to incompatibility of the inventory (designed perhaps to serve other purposes) and the selected model. It is possible to select the model according to the data available (bottom–up) or synchronize data with the selected model (top–down) using other models. The complex chain of models may cause additional errors to the scenarios. Therefore a careful validation of the model integration should be included in the selection process.

The choice of model type should depend on the problem in question. In the analysis, any number of input assumptions and structural relationships are manipulated. Most models are different in the model theory, model scope, and exogenous assumptions applied and therefore their ability for analysis varies. The utilization of forest sector models in the analysis of timber supply is often limited because the simple and aggregated forestry submodel does not allow modeling options for forest management regimes. Forestry scenario models usually provide more detailed analysis of forest management. However, forestry scenario models fail to solve the optimal management of forests under market economy because they cannot model the balance between supply and demand through prices. A popular solution is to use iteratively a forest sector and timber assessment model. By linking different models it is also possible to cover a larger range of social, environmental, and economic measures from the local to the global level. The outputs from one model are used as (exogenous) input assumptions in the other model.

Third, the assumptions are transformed into scenario parameters relevant for the data and model or models selected. Fourth, actual scenario runs are carried out and the results interpreted. Sometimes it is necessary to iterate between steps 1 and 4 several times – either for the actual study or for sensitivity analysis.

Future Challenges of Large-Scale Forest Inventory and Scenario Modeling

Forestry scenario modeling is needed, for example, to solve ecologically, economically, and socially sustainable use of forest resources for national forest programs. In economic and environmental policy analysis, scenarios may be conditional predictions on what will be the carbon sequestration of forests if the amount of harvested wood is decreased or increased, or studies on how forestry should adapt to and mitigate the effects of climate change.

Due to globalization it is important to incorporate a global scope and trade into the analysis to understand how, for example, plantation establishment or aging in the emerging region, environmental pressure to reduce harvesting in certain regions, and technological change affect global, national, or regional timber markets. In these trade-off studies, the model should be able to describe simultaneously the quality differences and resulting price differences among wood producers and between wood and nonwood, the price adjustment when matching demand and supply, as well as how wood producers change their investment, management, and harvest decisions in response to changes in relative prices. The models should cover all the relevant phenomena. For example, when solving forest management endogenously, models for nontimber products and services, damages, biomass, carbon, and different ecological/landscape considerations may be needed.

In scenario analysis, the magnitude of relative differences between different scenarios is important. Sometimes the uncertainty due to the models used is greater than the difference between scenarios. Because errors and uncertainty are rarely incorporated into the models, the interpretation of results is often difficult.

In the future, research and development should pay more attention to the optimal choice and integration of data and models, as well as modeling stochastic phenomena and errors explicitly.

See also: **Inventory**: Forest Inventory and Monitoring; Modeling. **Mensuration**: Forest Measurements; Yield Tables, Forecasting, Modeling and Simulation.

Further Reading

Alig R, Adams D, Mills J, Haynes R, Ince P, and Moulton R (2001) Alternative projections of the impacts of private investment on southern forests: a comparison of two large-scale forest sector models of the United States. *Silva Fennica* 35(3): 265–276.

Cardellichio P, Youn C, Adams D, Joo R, and Chmelik J (1989) *A Preliminary Analysis of Timber and Timber Products Production, Consumption, Trade and Prices in the Pacific Rim until 2000*. CINTRAFOR Working Paper, no. 22. Seattle. Washington, DC: University of Washington, College of Forest Resources.

Hobbelstad K (2002) Avvirk-2000. In: Heikkinen J, Korhonen KT, Siitonen M, Strandström M, and Tomppo E (eds) *Nordic Trends in Forest Inventory, Management Planning and Modelling*, pp. 133–137. Proceedings of SNS meeting in Solvalla, Finland, April 17–19, 2001, Research Paper 860. Helsinki, Finland: Finnish Forest Research Institute.

Hoen HF, Eid T, and Okseter P (2001) Timber production possibilities and capital yields from the Norwegian forest area. *Silva Fennica* 35(3): 249–264.

Kallio M, Dykstra D, and Binkley C (eds) (1987) *The Global Forest Sector: An Analytical Perspective*. Chichester: John Wiley & Sons.

Lindner M, Lasch P, and Erhard M (2000) Alternative forest management strategies under climatic change – prospects for gap model applications in risk analyses. *Silva Fennica* 34(2): 101–111.

Nabuurs G-J and Päivinen R (1996) *Large-scale Forestry Scenario Models – A Compilation and Review*. European Forest Institute Working Paper no. 10. Joensuu, Finland: European Forest Institute.

Nabuurs G-J, Schelhaas M-J, and Pussinen A (2000) Validation of the European Forest Information Scenario Model (EFISCEN) and a projection of Finnish forests. *Silva Fennica* 34(2): 167–179.

Nuutinen T and Kellomäki S (2001) A comparison of three modeling approaches for large-scale forest scenario analysis in Finland. *Silva Fennica* 35(3): 299–308.

Päivinen R, Roihuvuo L, and Siitonen M (1996) *Large-Scale Forestry Scenario Models: Experiences and Requirements*. European Forest Institute Proceedings no. 5. Joensuu, Finland: European Forest Institute.

Rohner M and Böswald K (2001) Forestry development scenarios: timber production, carbon dynamics in tree biomass and forest values in Germany. *Silva Fennica* 35(3): 277–297.

Ronnila M (1997) An equilibrium analysis of the Finnish pulp and paper industry. *Scandinavian Forest Economics* 36: 315–324.

Sedjo R and Lyon K (1990) *The Long-Term Adequacy of World Timber Supply*. Washington, DC: Resources for the Future.

Wollenberg E, Edmunds D, and Buck L (2000) *Anticipating Change: scenarios as a tool for adaptive forest management. A Guide*. Bogor, Indonesia: Center for International Forestry Research.

Zhang D, Buongiorno J, and Ince P (1993) *PELPS III. A Microcomputer Price Endogenous Linear Programming System for Economic Modelling*. USDA Forest Service Research Paper FPL-RP-526. Madison, WI: USDA Forest Service Forest Products Laboratory.

Multipurpose Resource Inventories

H G Lund, Forest Information Services, Gainesville, VA, USA

Introduction

Resource inventories are often functionally oriented and confined to areas where resource management opportunities are the highest (e.g., timber inventories were only conducted as commercial forest land). However, many lands are now managed for a variety of benefits, including water, forage, wildlife habitat, wood, recreation, wilderness, and minerals. International agreements and recent legislation often require that we take an integrated approach in our decision-making, resource planning, and inventories. In order to address increasing concerns about the environment and sustainable development and to reduce costs, we are finding we need more information than we normally collect in traditional timber inventories. Faced with new information requirements and decreasing budgets, many resource inventories in the future will have to change from the traditional functional inventories we conduct now. They will have to meet more needs with less funding. Future inventories will need to concentrate on measuring basic resource attributes in a manner that will permit multiple use interpretations. The inventories must be comparable across forests, states, and regions. They must also promote a continuity of information and direction between major decision levels. Lastly, future inventories must link to the past, provide a basis for monitoring plan implementation, and provide information on changes and trends.

Multipurpose resource inventories (MRIs) help meet our needs. MRIs are data collection efforts designed to meet two or more needs. Integrated, coordinated, and multiple resource inventories are forms of multipurpose inventories. Such inventories help meet the new information requirements. Fundamental to the successful development and implementation of MRIs are information needs assessments, cooperation and coordination, standardization, objectivity, and control.

Background

In one regard MRIs are new, yet in another they have been around since humans evolved. The data-gathering techniques were reconnaissance-type, multipurpose inventories conducted by the scouts of the tribes and reported verbally. The primary use of these exploratory inventories was to determine if the lands should be settled. When the capability of the lands to produce food and shelter became exhausted, humans simply moved on.

As land became scarce and human populations grew, settlement took place. With settlement came more specialized information needs and data collection techniques to fill them. Timber inventories, soil surveys, agricultural censuses, mineral surveys, and wildlife censuses, emerged. **Table 1** lists some of the specialized or focused inventories that were conducted by the US Department of Agriculture (USDA) Forest Service on its national forests in 1987.

Most inventories were conducted for specific functional uses and generally confined to areas where those functional management objectives were to be emphasized. Some inventories, even at the national level, were redundant and resulted in conflicting information. There was little attempt to tie inventories between resource functions, administrative units, and planning levels. In addition, many inventories were designed for very short-term problems. Little consideration was given to long-term integrated development now required in our planning processes.

There are common data requirements for several of the inventories listed in **Table 1**. For example, all of the timber, range, and wildlife surveys require information on vegetation. In addition, recent laws required that the USDA Forest Service look at its resources in an integrated manner – that is to say, understanding the management of one resource would affect the sustainability of another. The agency could realize cost savings and meet its legal obligations by developing multipurpose or multiple resource inventories where attributes are measured once but used by many (**Figure 1**).

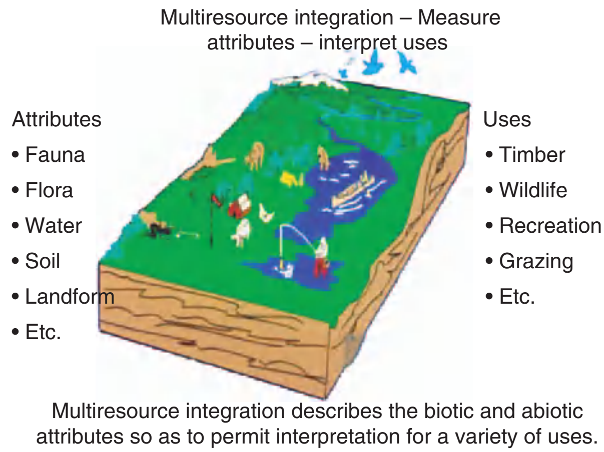


Figure 1 Measuring attributes and interpreting uses.

Table 1 Resource inventories conducted by the US Department of Agriculture Forest Service

Responsible staff	*Inventory subject*	*Major uses*
Forest research	State-wide forest survey	State survey reports, national and international assessments
Timber management	Forest-wide surveys	Forest planning
	Silvicultural examinations	Forest and project planning
	Timber cruises	Project planning
	Regeneration surveys	Project planning
Range management	Range analysis	National assessments, forest and project planning
	Noxious weed survey	National assessments, forest and project planning
Watershed and air management	Water-quality survey	National assessments, forest and project planning
	Air-quality survey	National assessments, forest and project planning
	Soil survey	National assessments, forest and project planning
Wildlife and fisheries management	Threatened and endangered species	National assessments, forest and project planning
	Wildlife and fish habitat survey	National assessments, forest and project planning
Recreation management	Cultural resource survey	National assessments, forest and project planning
	Recreation opportunity spectrum	National assessments, forest and project planning
	Visual management	National assessments, forest and project planning
Minerals and geology management	Common-variety minerals	National assessments, forest and project planning
Fire and aviation management	Fuels inventory	Forest and project planning
Forest pest management	Forest pest condition	Forest and project planning
Lands staff	Land status and utility corridors	National assessments, forest and project planning

Multipurpose Inventories

New concepts in resource management planning require periodic inventories that are free of political judgments and not conceived to support foregone conclusions about which lands will be used for what purpose.

Given today's funding, we cannot get the necessary information by each resource collecting data separately. We need to start collecting data so it can be used by other resource sectors. Multiresource inventory integration is a must.

If we are to avoid contradictory data and keep costs down, the same inventories we use at the local level should be used for national and global assessments. Multilevel inventory integration is needed as much as multiresource integration is needed.

As inventories are aggregated for national assessment, they must be compatible across states and provinces. This requires multilocation integration. Lastly, the success of our plans and programs needs to be monitored and evaluated. Temporal inventory integration has to be involved. Thus, multipurpose inventories may take on up to four forms of integration (**Figure 2**).

MRI Requirements

Successful multipurpose inventories depend upon the fundamentals of cooperation and coordination, standardization of terminology and techniques, objectivity in design, and control and responsibility. Without these, integration is not possible.

Cooperation and Coordination

The most important elements for successful inventory integration are cooperation and coordination – cooperation between data collectors and decision-makers so that inventories meet an organization's objectives and coordination among data collectors so that the required information is gathered most effectively. This may include cooperation between functional specialists, line officers, and research units.

Cooperation is needed to: (1) establish minimum requirements for meeting information needs irrespective of agency or organization; (2) establish inventory standards providing uniformity between data collectors; (3) provide minimum quality requirements against which inventories can be evaluated; (4) eliminate unnecessary duplication of data collection; and (5) increase utility of resulting information.

Coordination improves cost-effectiveness by eliminating redundant data collection and reporting and by incorporating alternative measuring and sampling techniques. Involving all interested parties clearly identifying intended uses, defining areas of responsibilities (particularly when inventories may be conducted by two or more individuals and agencies) and designing inventories that are multipurpose all improve efficiency.

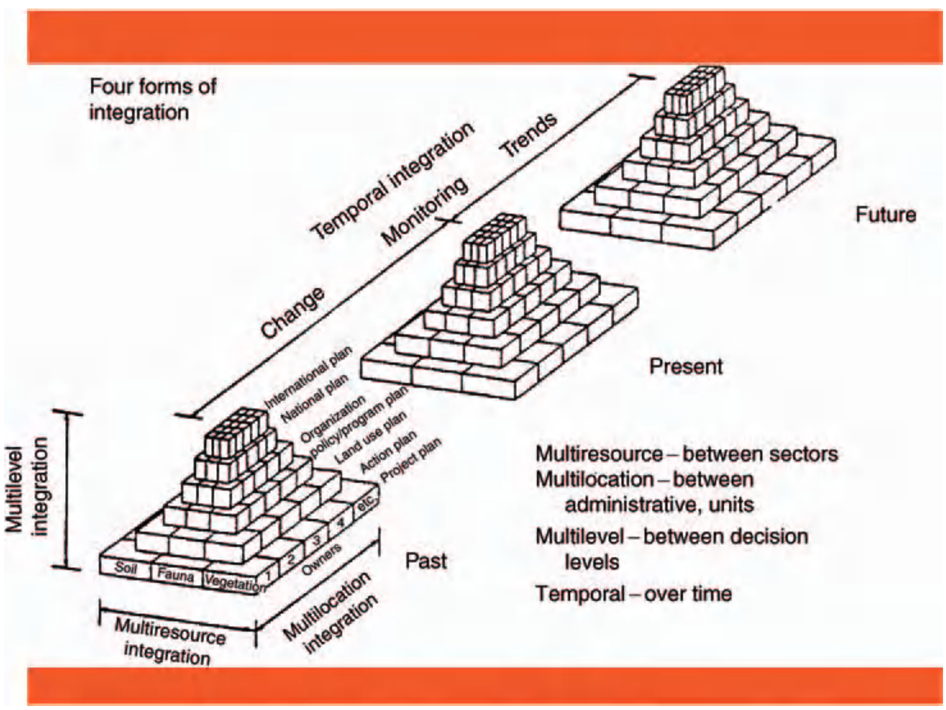


Figure 2 Four forms of integrated or multipurpose inventories: multiresource, multilocation, multilevel, and temporal.

Standardization

Standardization adds to the value of information, for information that becomes useful to more people and data can be compared and combined. Definitions, classifications, and measurement require standardization, but to encourage innovativeness, flexibility in how those standards are met should be allowed.

Objectivity

Objectivity in inventory designs is needed so that data from different sources can be scientifically compared and aggregated. Objectivity is maintained through the use of sound sampling strategies. The proper choice of sampling strategies involves minimizing bias, constructing a sample frame, and selecting a sampling technique.

- Implied in objectivity is that all locations or survey units be mutually exclusive (i.e., boundaries do not overlap) and data from all locations must be complete (i.e., all locations are accounted for).
- The inventory of each location must be based on complete enumeration or on a scientifically valid sample.
- Common definitions and standards must have been used or data collected in such a manner that they can be converted to common definitions and standards.
- The information produced from each inventory includes estimates of the mean (or total), the standard error of the mean (or total), and the probability level at which the standard error is calculated.

Control and Responsibility

Quality control provides the mechanisms for ensuring inventories are carried out according to specifications. Control includes assignments of responsibilities, choice of area bases, time frames, and data collection, compilation, and summary processes. Control should be established in an inventory plan and begun before the first field plot is established.

Responsibility Assignment of responsibility indicates who will do what, when, and how. Responsibility also includes assignment of authority to resolve any conflicts or questions that may arise in the course of the inventory. This authority should monitor the inventory work, make changes in inventory methodology, and ensure that users understand the processes and correctly apply the results.

Area control Decision-makers usually require area statistics as well as volume and production information. All those concerned with integrated inventories must utilize the same area control base from which to compute areas. Without an agreed-upon base, there would be no means of determining if areas are omitted or duplicated. The sum of the mapped and/or survey areas must equal the total area of interest.

Time frame In addition to utilizing a standard land base, inventories should also be within compatible time frames. If compatible time frames cannot be used, it is often necessary to update or 'grow' the inventory through simulation models, to make the data compatible. The models used, as well as the coefficients, may also become a form of control.

Data collection, compilation, and summary Measurements and observations should be made as objectively as possible. Detailed instructions should be provided for each step of the inventory from measurements to ensure uniformity. Checks should be made throughout the inventory to ensure procedures are being followed. The central authority should be available in case procedural questions arise. The more authority provided, the more compatible the multipurpose inventories become.

Advantages/Disadvantages of MRIs

The advantages of developing MRIs are that they:

- reduce overall costs of gathering data (US Forest Service table)
- provide more useable information for easier analysis of interactions
- get people talking and acting together
- eliminate confusion and duplication.

The disadvantages are that MRIs:

- are more costly than a single-purpose inventory as one is gathering more data
- require working with other people with different goals, agendas, and backgrounds
- require partnerships to share responsibilities, results, and credit
- require more time to determine information needs and to develop methods to collect the necessary data.

Information Needs Assessment (INA)

Decisions are often based in part on inventory summaries. To determine the kinds of summaries needed, we have to examine the kinds of decisions a large organization has to make. Then we need to look at the techniques and fundamentals available for designing inventories that can link these decisions together.

In planning for the management of its resources, a large federal agency can be involved at several decision levels, including international, national, agency, regional, forest, district, and compartment, and stand. Each level of decision has its own information needs, uses, and, requirements. Typical characteristics of various decision levels are given in **Table 1**.

You will note from **Table 1** that data collected at the local level are also needed at the national and international levels. **Table 2** shows the kinds of information needs at various levels of decisions.

The information required at a given decision level is usually more general and broadly based than the information required at lower levels. Users of the information also differ. Users of national-level information are usually more numerous and diverse than users of project-level information. At the same time, information needs change as an organization matures. When first created, an agency may have need for (and access to) only broad descriptive information about its resources. As management intensifies, more detailed information is needed and more information becomes available.

Integration between decision levels or multilevel integration is usually required to provide a continuous flow of information and management direction between the highest levels in the organization and the

Table 2 Typical decision level characteristics

Level	*Characteristics*
International	Goal: To develop international assistance programs or action plans to reverse the depletion of resources and degradation of the environment; foreign trade agreements to shift surplus to meet demands; or cooperative agreements to control pests and diseases or to address other catastrophic occurrences. Information sought includes the present state of the resources and the rate and pattern of change. An international group usually assembles data
National	Goal: To develop long-range federal policies and programs for public and private land-administrating organizations within a given country. National assessments often provide basic and relevant data on renewable resources held by all types of owners within a nation, appraising changes in supplies of resources and demands for them, the outlooks for the future, and possible alterations in these outlooks by changes in national program end policies. National assessments include descriptions of the present situation and estimated changes due to management, cultural influences, and natural or secondary factors. The data are usually assembled and compiled by a federal agency or an association dealing with a specific resource product. The primary users of the information are the executive branch, Congress, and regulatory agencies. Private industries also use long-range estimates of production and trends to develop their own strategies
Agency	Goal: To develop an overall strategy for the management of resources within the agency's jurisdiction; to define a policy; to express that policy as a set of regulations; and to carry out and execute the policy through the agency's program. The information required usually reflects current values and rates of change. Inventories conducted at this level may be considered as a prelude to the development of the resource. Inventories focus on the resource stock and the land's capability to produce on a sustained yield basis. The inventory units used in planning are usually based upon political or administrative boundaries. Broad management goals and objectives and financial plans for the organization are the eventual products
Region, forest, district	Goal: To develop long-term direction for each management or administrative unit (e.g., region, forest, district) within an organization. The resources and their condition and potential are described only in sufficient detail to direct the manager's attention to specific portions of the management unit for more intensive planning. Area, volume, and production estimates are usually tied to each unit. For timber planning, information sought includes areas by land class, soil-vegetation types, estimates of growing stock within the classes, and accessibility. The product is a management plan
Compartment and stand	Goal: To determine what, where, and when specific treatments are to take place. Decisions regarding timber sale locations and prescriptions for specific stands are examples. Inventories to assist the decision-maker often include maps of vegetation conditions by compartments and stands, description of vegetation and terrain within the units, and accessibility and relevant classification of the units with respect to the alternatives selected under the land use planning process. Data observed include vegetation factors, potential productivity, accessibility, and economic factors in order to determine specific management actions to take place within the treatment unit. The district usually conducts the inventories. The output is a functional action plan showing the treatment areas and indicating what is to be done when, where, and how. The plan is used for the day-to-day operations of the lowest-level field office

lowest levels. This ensures that the lowest units are carrying out the policies of the agency and that policies can consider the most recent data available. The differences in users, needs, and timing between decisions present special problems when trying to develop inventories to support multiple decisions.

Approaches for determining information needs There are two approaches generally used in determining information needs – a bottom–up and a top–down approach.

In the bottom–up approach, the information requirements are defined at the local level and accumulated upwards. The disadvantage is that the information identified may not include the information required at the top level of the organization.

With the top–down approach, information needs are defined at the highest echelons. At each subsequent decision level, more information is added to meet more local issues. A problem with this approach is that the people collecting the data at the project level feel burdened collecting information for which they do not feel a use.

If we assume that information needed at the top decision levels in an organization is needed at subsequently lower levels, the top–down approach is preferred.

To develop a workable information flow, decision-makers at all levels of the agency must be involved. Information needs and reporting formats must be identified at each planning level, starting at the highest or broadest level. This procedure establishes a minimum core of information and priorities required at all decision levels and ensures that the policies, regulations, and information needs of the organization are developed and fulfilled. The commitment to provide information from the lower levels will only be as strong as the field perceives the need for the information. Consequently, field units will be more cooperative in supplying information when they have been involved, and clearly understand why the information is needed and how it will be used to serve their needs.

Inventory design options There are two design options for meeting multipurpose information needs. The first option is to design a system in which the mapping and sampling is intense enough to meet the most demanding needs (i.e., at the compartment and stand decision levels). The second option is to conduct two or more inventories on the same piece of terrain but at times corresponding to different stages of development.

The first option has the advantage that one inventory would provide compatible information for all decision levels. However, because all lands may not be managed at the same intensity, this option can be costly if the production potential and management intensity of the lands are low.

Under the second option, a broad decision level is chosen as a base where the same detail of information is required across all lands. As with the first option, these inventories would be aggregated to provide more generalized information to the upper levels in the hierarchy and would provide defined survey areas for the lower echelons. Additional inventories for the more detailed planning levels would be conducted within those survey areas only when and where they are necessary, resulting in overall cost savings. Information from the broader inventory would be used to enhance, expand, and supplement the more intensive surveys.

Minimum data As a minimum and regardless of information source (imagery or ground observations) where possible measure, record and make available the following information:

- geographic coordinates of observation
- date of observation dominant
- vegetation type (life form as a minimum)
- height of dominant vegetation
- percent of canopy cover of dominant vegetation
- area classification surrounding point of observation to which observations apply.

This is the very minimum set of data that should be recorded for each plot or polygon in national vegetation inventory and mapping efforts. By using this information, one can resort the data to fit almost any international vegetation classification schemes, especially when used in a geographic information system with soils, climate, and topography data. In addition, these attributes can be used for developing classes, validation of classes, and for accuracy assessment.

Research Needs

Regardless of design used, data collection is still costly. The identification of indicators and development of models can reduce inventory costs.

Research on new products, uses, and cultivation of native vegetation is needed. As new products and uses are identified, new measuring and sampling techniques will need to be developed.

Production coefficients, linked to soil and climatic factors, need to be developed for existing and emerging uses. Without this information, we cannot develop resource management programs.

Statistical strategies for combining existing information also need to be strengthened. There is a wealth of data available, but how can we combine it, compare it, and disaggregate the information?

Finally, we need more research on integrated analyses to determine how changes in one resource will affect other sectors. For example, forest land is increasing in many parts of the developed world as agricultural lands are abandoned. Does this reduction of agricultural lands in the north increase deforestation in the developing world as lands are converted to agriculture?

Summary

Agencies such as the USDA Forest Service are taking an integrated approach to developing inventories. Inventories concentrate on measuring basic resource attributes in a manner that will permit multipurpose interpretations.

Cooperation and coordination, standardization, objectivity, and control and responsibility are fundamental in designing these inventories to ensure that the inventories can be summarized and used by decision-makers for a variety of purposes.

See also: **Biodiversity**: Biodiversity in Forests. **Inventory**: Forest Inventory and Monitoring. **Mensuration**: Forest Measurements. **Resource Assessment**: Forest Resources.

Further Reading

Conant F, Rogers P, Baumgardner M, *et al*. (eds) (1983) *Resource Inventory and Baseline Study Methods for Developing Countries*. AAAS Publication no. 83-3. Washington, DC: American Association for the Advancement of Science.

Eyre T and Kelly A (1999) *Multiresource Inventory and Forest Condition*. Project outline 1999–2000. FERA Technical Paper 99-16. Forest Ecosystem Research and Assessment, Queensland Department of Natural Resources, Australia.

Hassan HA, Mun CY, and Rahman N (eds) (1996) *Multiple Resource Inventory and Monitoring of Tropical Forests*. Proceedings of the AIFM International Conference, 21–24 November 1994. Kuala Lumpur, Malaysia: ASEAN Institute of Forest Management.

Holmgren P, Masakha EJ, and Sjöholm H (1994) Not all African land is being degraded: a recent survey of trees on farms in Kenya reveals rapidly increasing forest resources. *Ambio* 23(7): 390–395.

Lund HG (1998) *A Comparison Study of Multipurpose Resource Inventories (MRIs) Throughout the World*. Working paper no. 14. Joensuu, Finland: European Forest Institute.

Lund HG (ed.) (1998) *IUFRO Guidelines for Designing Multiple Resource Inventories*. IUFRO World Service, vol. 8. Vienna, Austria: International Union of Forestry Research Organizations.

Lund HG and Thomas CE (1995) *A Primer on Evaluation and Use of Natural Resource Information for Corporate Data Bases*. Gen. Tech. Report WO-62. Washington, DC: US Department of Agriculture, Forest Service.

Schmoldt DL, Peterson DL, and Silsbee DG (1995) Developing inventory/monitoring programs based upon multiple objectives. *Environmental Management* 18(5): 707–727. Available online at: http://www.srs.fs.fed.us:80/pubs/ja/9510.pdf.

Schreuder HT, Gregoire TG, and Wood GB (1993) *Sampling Methods for Multiresource Forest Inventory*. New York: John Wiley.

USDA Forest Service (1990) *Resource Inventory Handbook*. Zero code, chapter 10, chapter 20. FSH 1909.14. Washington, DC: US Department of Agriculture; Forest Service. Available online at: http://www.fs.fed.us/cgibin/Directives/get_dirs/fsh?1909.14!

Stand Inventories

O Eckmüllner, Institute for Forest Growth and Yield Research, Vienna, Austria

Introduction

Stand inventories are the classical way to build a management plan. The first step is the delineation of stands: useful for this are forest survey, aerial photography, or remote sensing technologies (*see* **Resource Assessment**: GIS and Remote Sensing). The second step is to collect information on each stand. This can be done by using inventory techniques (sampling techniques) or by using aerial photographs or remote sensing. In the future, a new approach could bring better results: airborne laser-scanning combined with high resolution satellite data, for example.

This article covers special stand inventory techniques based on considerations of precision and accuracy and tries to demonstrate the differences between stand inventories and forest inventories.

Historical Overview

The classical method to obtain data for a management plan is to use stand inventories. After the stands have been delineated, some information on each of them is collected. See **Table 1** for an actual example from the nineteenth century.

Table 1 An example from the nineteenth century of classical stand inventory, transformed, simplified, and translated from the method of Judeich

Stand number	*Area (ha)*	*Tree species*	*Age (years)*	*Volume ($m^3 ha^{-1}$)*		*Site class*	*Crown closure*
				Coniferous	*Deciduous*		
20a	3.03	8 spruce, 2 fir	79	400	–	3	0.8
20b	2.25	4 spruce, 3 fir, 3 beech	65	180	70	1	0.8
20c	5.06	10 spruce	5	–	–	1	–
20d	4.50	8 beech, 2 spruce	125	50	500	4	0.7

The stand borders were measured with a tape and a compass. The stand area was taken from maps using planimetric techniques. The stand age was derived from older information or by counting tree rings or whorls in younger stands. Tree species composition and crown closure were ocular estimations. The volume per hectare was estimated ocularly or measured by complete enumeration. Finally, the site class (relative yield class) was determined from yield tables using the age and the volume per hectare. These tables were only used to estimate the volume increment and the 'normal' volume (mean volume of a full stocked stand over a complete rotation).

In those days all information such as allowable cut and rotation length were derived from these data. Today stand inventories are more sophisticated, using a wide range of different estimation methods. Forest inventory covers the need for strategic information, and involves surveying the whole forest enterprise area with designed sampling and measuring techniques. Stand inventories are used to obtain area (stand) related data. This data collection is problem oriented and these data should form the database for decision support systems.

Stand Inventory Techniques

Ocular Estimation of Volume

This method is very crude, because the quality of obtained data is dependent only on the experience of the person doing the estimating. Precision (confidence interval at 5% level) has been reported from ±31% to ±38% and bias from 4% to 20%. This method is quick and cheap but neither the precision nor the accuracy are reliable.

Yield table estimation using dominant height, age, and ocular-estimated crown closure to determine the stocking degree An investigation of 1221 sample points showed a standard error of estimation of ±27% (calculating a regression between stocking degree and crown closure) but no bias. The results of this method will not be better than the results of ocular estimation alone.

Sampling techniques to measure the basal area In this case the basal area will be estimated using simple point sampling (counting only the trees) without control of borderline trees. The omission of these trees could introduce a bias (in one example we found a bias of 18% and a confidence interval at 5% level of ±16%). On the other hand the trade-off is that you need an appropriate yield table to estimate the volume – this is not true – only the form factor and the relation between dominant height and mean height will be used from the yield table.

Complete Enumeration Methods

Measuring all diameters This technique consists in measuring the diameter at breast height (dbh) of all trees in a stand and to record this in dbh classes (this can be also done by using special callipers with scales divided into 4-cm or 5-cm classes). As height measurement is time consuming, the height will only be measured on a subsample of trees (not smaller than 20 trees per stand).

Theoretically, this method should be error-free for the number of trees and the basal area. The error of the volume estimate will be inflated by height measurement error. During field camps students have applied this technique on 28 different stands with an area of ~1 hectare. A week later other students have measured the same stands. From these data the confidence interval at 5% level was calculated giving ±4% for the number of trees, ±5% for the basal area and ±11% for the volume. The confidence interval is strongly dependent on the sighting visibility condition in the stand: in pure stands without shrubs and regeneration the confidence interval is significantly smaller than in mixed stands with more layers, shrubs and regeneration. The minimum confidence interval found was ±2% and the maximum confidence interval found was ±9% for the number of trees.

Another reason for error could be the use of a minimum diameter – excluding the smallest dbh class from the above-mentioned data reduced the confidence interval to ±3% for the number of trees.

The higher confidence interval for the basal area can be explained by a diameter measurement error of

0.8–1.0 cm, which is approximately double the reported errors in the forest inventory. In complete enumeration the measurement instruction for dbh: ('on the hillside, 1.3 m above ground, direction downhill') cannot be carried out because it is too time consuming.

Complete enumeration with dbh measurement gives precise and accurate stand data and information on texture and structure. The stand area is not needed for the estimation, but this can be sometimes helpful. This technique is time consuming, with the investigation time being strongly correlated with the number of trees. This method can only be recommended for older stands of special interest.

Using ocular estimates of tree volume This method is an application of '3P' sampling techniques (sampling with probability proportional to prediction). The preliminary steps are:

1. Define either an average volume per tree in the stand (this is similar to the choice of the basal area factor (BAF) using point samples) or define a certain number of trees to be measured. In this case we need also an estimate of the stand total volume (ocular estimation or from an older management plan). The average volume per tree in the stand is obtained by dividing the stand total volume by the number of trees.
2. Create a list of equal distributed random numbers between zero and the average volume per tree in the stand.

Field operation For each tree of the stand the volume will be ocularly estimated. These values must be summed and compared with a random number from the list (every random number is to be used consecutively only one time for one comparison). If the estimated volume is greater than the random number then the volume of the tree must be measured. This can be done by measuring the dbh, the height, and occasionally also an upper diameter. These data should be recorded as well as the tree species and the estimated volume.

The stand volume is finally calculated by multiplying the sum of ocular estimations with the average ratios between measured tree volume and ocular estimated tree volume. The confidence interval of the stand volume is equal to the one calculated from the ratios. The principle of 3P sampling assumes that these ratios between measured and estimated volumes are constant over the range of trees sampled. In a similar way to the number of trees in complete enumeration the sum of ocular estimates is affected by a certain confidence interval from $\pm 2\%$ to $\pm 3\%$.

Complete enumeration using ocular volume estimation of each tree gives accurate results for the total stand volume and for the number of trees by counting the used random numbers; the precision depends on the quality of the ocular estimates and on the number of trees with measured volume. This technique gives only fair information on texture (derived from measured trees) and no information on structure. This technique is faster than complete enumeration but the time taken also depends on the number of the trees in the stand. Considerable experience and knowledge of the stands being sampled is needed.

Sampling Techniques

The following sampling techniques are applied in stand inventories:

- point sampling
- rectangular, quadratic, or circular plots
- *n* tree sampling (point-to-tree distance method)
- tree-to-tree distance method.

Common Problems of All Sampling Techniques Used in Stand Inventories

Correction of finiteness A stand has a defined area. To calculate the correct standard error from a sample a correction of finiteness is necessary. This finite population correction multiplier is generally the square root of 1 minus the quotient of investigation (sampling fraction). This quotient can be calculated as cruised area divided by the stand area (recommended for rectangular, quadratic, or circular plots, *n* tree sampling (point-to-tree distance method), tree-to-tree distance method); or as measured number of trees divided by total number of trees in the stand (recommended for rectangular, quadratic, or circular plots, *n* tree sampling (point-to-tree distance method); or as measured cross-sectional area divided by the stand basal area (recommended for point sampling).

The sample size formula for sampling without replacement from finite populations will differ from the formula for infinite populations

$$n = \left(\frac{t\mathrm{CV}}{A}\right)^2$$

for infinite population

$$n = \frac{1}{\left(\frac{A}{t\mathrm{CV}}\right)^2 + \frac{1}{N}}$$

for finite population where CV is the coefficient of variation in percent, A is the allowable error expressed as a percent of the mean, Student's-t (2-tailed) has $n-1$ degrees of freedom, N is the number of sampling units in the population (e.g., number of trees in the stand), and n is the number of required samples in the stand.

Edge effect bias or boundary overlap In stand inventories sample plots or points can lie near or at the stand boundary. These samples will not be wholly in the stand. This problem, commonly referred as edge-effect bias or boundary overlap, can introduce a bias. In forest inventory with temporary plots this boundary-overlap problem is often solved by moving the plot until the entire plot lies within a stand. This method is not suitable for forest inventory with permanent plots (new boundaries can arise) and for stand inventories because the trees near the edge can be different to the trees in the remainder of the stand, and the trees in the edge zone may be undersampled.

One method of dealing with the edge-effect bias problem is to apply the mirage technique in the field. Another possibility is a computational correction. When the plot center falls near a stand boundary the surveyor measures the distance from plot center to the boundary. If the computational correction is to be applied then this distance is tallied. Otherwise a correction-plot center is established by going this distance beyond the boundary. All trees in the overlap between the two plots are recorded twice. This simple method can be used for circular plots and for point samples (**Figure 1**).

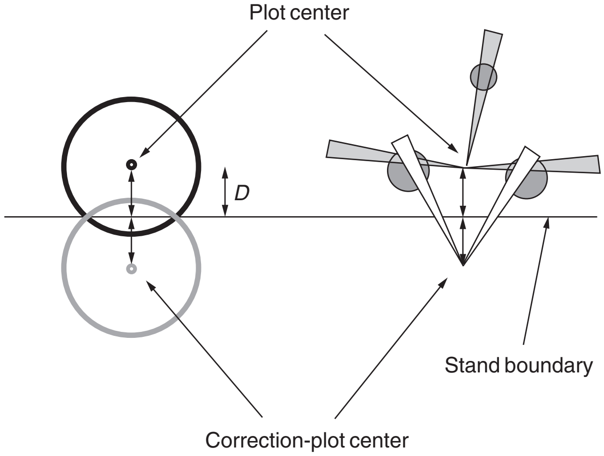


Figure 1 The mirage method for correction of boundary overlap bias when circular plots (right side) or point samples (left side) are used. Trees falling in the control plot are tallied twice.

Computational correction If we define $x = \frac{D}{R}$ with D the distance between the plot center and the stand boundary, and R the radius of the circular plot respectively

$$R = \frac{\text{dbh} \times 50}{\sqrt{\text{BAF}}}$$

in point samples where BAF is the basal area factor and dbh the diameter at breast height in meters. The correction factor can be calculated for the whole plot respectively for each single tree in point samples (but only for trees with R greater than D) with one of the following formulas (arccos gives results in radians, $\cos^{-1}$ gives results in degrees):

$$bf = \frac{1}{\left(1 - \frac{\arccos(x)}{\pi} + \frac{x}{\pi}\sqrt{1-x^2}\right)}$$

$$bf = \frac{1}{\left(1 - \frac{\cos^{-1}(x)}{180} + \frac{x}{\pi}\sqrt{1-x^2}\right)}$$

If a plot falls near to two edges then move the plot along the nearest boundary until the problem is reduced to a one edge effect (**Figure 2**). In very small stands or fractal stand boundaries a complete enumeration is recommended.

Sampling size versus plot size Small sample plots usually exhibit more variability; the coefficient of variation is greater than in large plots. In the literature often the formula suggested by Freese is cited:

$$\text{CV}_2 = \text{CV}_1\left(\frac{P_1}{P_2}\right)^{\frac{1}{4}}$$

where CV_2 is the estimated coefficient of variation for the new plot size, CV_1 is the known coefficient of variation for plots of previous size, P_1 is the previous plot size and P_2 is the new plot size.

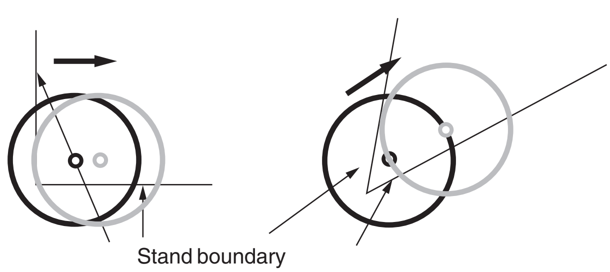


Figure 2 Multiple boundaries overlap: moving the plots along the nearest stand boundary to reduce the problem to a one-boundary overlap.

This formula is a very fair approximation in forest inventories and wrong in stand inventories. In a stand this relation depends on the stand structure. The theoretical correct formula for stands with spatially random distributed trees is:

$$\mathrm{CV}_2 = \mathrm{CV}_1 \left(\frac{P_1}{P_2}\right)^{\frac{1}{2}}$$

The simulation of artificial stands with structure ranging from a quadratic distribution (Clark and Evans index = 2), random distribution (Clark and Evans index = 1), and clumped distribution (Clark and Evans index = 0.5), with different densities (from 400 to 2500 trees per hectare in steps of 300 trees per hectare), and different plot sizes ranging from $12.5\,\mathrm{m}^2$ to $800\,\mathrm{m}^2$ (doubling space) gave the following results:

In uniform stands the calculated exponent is 0.8 with a range from 0.78 to 0.85; in the stands with a random distribution of the trees the exponent is 0.5 with a range from 0.48 to 0.52; and in the stands with a clumped tree distribution the exponent is 0.52 with a range from 0.50 to 0.54. In stands with a clumped tree distribution the effect of enlarging the plot size is slightly more efficient than increasing the sample size. In so-called 'Poisson' forests (random distribution of the trees) there is no difference in the efficiency. But changing the plot size in uniform stands (e.g., plantations) can be very efficient. In uniform populations the coefficient of variation is very small, therefore the influence of different plot sizes in forest inventory is very small, but in a given stand this effect is very high. In one reported study the exponent was calculated to be 0.43 using nine out of 10 stands. Only for one stand was the exponent 0.22 (close to 1/4). This stand was described as including gaps larger than the maximal plot size.

A 'loss of effectiveness' also occurs if spatial correlation exists in the stand , or if the stand can be stratified. In these cases the approximation of Freese is also wrong but can be useful.

Temporary versus permanent plots In stand inventories permanent plots are only useful for investigating special problems or for accurate growth information. Usually temporary plots are sufficient to obtain the required data and results. The major argument against permanent plots in stand inventories is the change in stand boundaries over time, and due to stand dynamics the change of variables of interest (e.g., in a regeneration period browsing is of interest, or several years later precommercial thinning could be important; the variables to investigate will not be the same).

Slope compensation This problem is common to all sampling techniques on steep terrain. Special care must be exercised. There are three possibilities to avoid bias:

1. Compensation by the surveyors. For distance measurement this could be provided by holding the tape more or less horizontal (the maximum remaining slope must be less than 6° or 10%). For point sampling using a stick gauge or a wedge prism, one of the surveyors measures the dbh with a calliper and moves this calliper into the horizontal. The limiting factors are the slope and the plot size. The maximum compensation difference is dependent on the height of the surveyors, somewhere between 2 and 3 meters (taking into account the 6° or 10% mentioned above).
2. Compensation by the measurement instrument used: slope compensation is automatically provided by the Spiegel (mirror) relascope in point sampling. Distance measuring instruments based on laser or ultrasonic technologies can often also measure the slope angle and calculate the horizontal distance.
3. Computational correction of the slope: this can be done either in the field or a posteriori in the analysis. For the latter, the slope angle must be measured and recorded in the field. For field correction a new radius (circular plots) must be calculated:

$$R_{\mathrm{new}} = \frac{R}{\sqrt{\cos(\alpha)}}$$

where R is the intended radius of the circular plot (valid only in flat terrain), and α is the slope angle. The plot will be established holding the tape parallel to the ground. Respectively the new BAF (basal area factor) in point sampling must be calculated as

$$\mathrm{BAF}_{\mathrm{new}} = \frac{\mathrm{BAF}}{\cos(\alpha)}$$

and as field correction this must be applied on the stick length with multiplying the length with $\frac{1}{\sqrt{\cos(\alpha)}}$. For computational compensation the plot size must be calculated as $R^2.\pi.\cos(\alpha)$ and the BAF must be corrected according to the above-mentioned formula. Note that if these computational compensations are used, the means and standard deviations must be weighted to obtain statistically sound results.

Special problems with some sampling techniques

***n* tree sampling (point-to-tree distance method)** This technique is known as *n* tree sampling. One of the advantages of this method consists in the fixed number of trees to be measured per plot, and therefore a more or less clearly defined amount of time taken on each plot. The efficiency of this method decreases when the number of measured trees increases. The surveyed area to find the tree number *n* follows a quadratic function.

Using this technique all means must be calculated by weighting with the area, and the standard deviation can only be approximated by the error propagation law (first term of the Taylor-algorithm – without correlation).

Tree-to-tree distance method In recent years, caused by an emphasis on continuous-cover forests, a very old technique suggested in the nineteenth century has unfortunately had a second revival (the first was in 1940–1960). This sampling method is known as tree-distance technique. The density (number of trees) is estimated from the distances to the nearest neighbor tree. Different proposals deal with the distance to the next, the second or the mean distance between the second and the third nearest neighbor tree. In all these cases a correction factor is reported (e.g., using the distance to the second nearest neighbor tree this correction factor is 0.78 to 0.85 according to different authors).

For the simplest possibility, distance to the next neighbor tree, the correction factor is as follows. Transforming the formula of Clark and Evans (describing the spatial distribution of the trees in a stand),

$$\mathrm{CE} = \frac{2.\bar{e}}{\sqrt{\frac{10000}{N}}}$$

where $\bar{e}$ is the average distance from a tree to its nearest neighbor tree, and N is the number of trees per hectare, will result in the following formula:

$$N = \frac{10000}{\bar{e}^2}\left(\frac{\mathrm{CE}}{2}\right)^2$$

The distance between neighbor trees is dependent on the spatial distribution of the trees in the stand (stand structure); therefore without information on the stand structure the number of trees per hectare (density) can never be derived from tree-to-tree distance information.

Looking Forward

In the future a new technology, airborne laser scanning, could bring a revolution in stand inventories. The first investigations and reports indicate a high performance in the development of digital elevation models but also of digital canopy elevation models. The precision of derived tree or stand height is higher than in terrestrial measurements. Stand and single-tree delineation approaches promise good results under certain (simple) conditions.

See also: **Experimental Methods and Analysis**: Biometric Research; Statistical Methods (Mathematics and Computers). **Landscape and Planning**: Spatial Information. **Mensuration**: Forest Measurements; Growth and Yield; Timber and Tree Measurements. **Resource Assessment**: GIS and Remote Sensing.

Further Reading

Avery TE and Burkhart HE (1994) *Forest Measurements*, 4th edn. New York: McGraw-Hill.

Beers TW (1966) *The Direct Correction for Boundary-Line Slopover in Horizontal Point Sampling*. Research Progress Report no. 224. In: West Lafayette, Purdue University.

Bitterlich W (1984) *The Relascope Idea*. Slough, UK: Commonwealth Agricultural Bureau.

Cochran WG (1977) *Sampling Techniques*, 3rd edn. New York: John Wiley.

De Vries PG (1986) *Sampling Theory for Forest Inventory*. New York: Springer-Verlag.

Freese F (1962) *Elementary Forest Sampling*. US Department of Agriculture Handbook no. 232. Washington, DC: Government Printing Office.

Grosenbaugh LR (1965) *Three-Pee Sampling Theory and Program THRP for Computer Generation of Selection Criteria*. US Department of Agriculture Forest Service Research Paper no. PSW-21. Washington, DC: Government Printing Office.

Husch B, Miller CI, and Beers TW (1972) *Forest Mensuration*, 2nd edn. New York: Ronald Press.

Kramer H and Akca A (1982) *Leitfaden für Dendrometrie und Bestandesinventur*. Frankfurt am Main, Germany: J.D. Sauerlaender's Verlag.

Lund HG and Thomas CE (1989) *A Primer on Stand and Forest Inventory Designs*. General Technical Report WO-54. Washington, DC: US Department of Agriculture; Forest Service. (http://www.fs.fed.us/rm/ftcol).

Lund HG, Landis E, and Atterbury T (1993) *Proceedings – Stand Inventory Technologies*, 1992 September 14–18, Portland, OR. Bethesda, MD: American Society of Photogrammetry and Remote Sensing.

Prodan M (1965) *Holzmesslehre*. Frankfurt am Main, Germany: J.D. Sauerlaender's Verlag.

Prodan M (1968) *Forest Biometrics*. New York: Pergamon Press.

Sagl W (1995) *Forsteinrichtung auf dem Prüfstand*. Vienna: Österreichischer Agrarverlag.

Modeling

T M Barrett and J S Fried, USDA Forest Service PNW Research Station, Forest Inventory and Analysis, Portland, OR, USA

Published by Elsevier Ltd., 2004

Description and Terminology

Modeling is used extensively in forest inventory applications. Models, which are described as deliberate 'abstractions of a system,' are used to calculate forest attributes that cannot be easily measured, to understand how forest ecosystems function, to extrapolate forest attributes over space, and to project how forests change over time.

Until the early twentieth century, models used in forest inventory consisted of hand-drawn graphs and tables. Over the course of the past century, models were increasingly expressed in mathematical terms and modelers used statistical methods in model development and evaluation. The rapid development of computers in the past few decades has facilitated increasing sophistication of modeling techniques and broadened the scope of model application.

Modeling terminology in forestry follows that of other fields where modeling is applied. Models can be deterministic, where a single outcome is predicted, or stochastic, where random elements are incorporated. Statistical models are created with a development data set, but evaluated with an independent validation data set. Modelers sometimes distinguish between validation, a formal test against the independent data set, and verification, or the internal consistency of the model. Models are often tested with sensitivity analysis, the evaluation of model performance when input parameters are varied. Models are adjusted to local conditions through the use of calibration. Model complexity is influenced by model scope, the area of interest, and model resolution, the amount of detail in the model.

Modelers in forestry have liberally borrowed ideas and terminology from other fields, with the result of occasionally inconsistent use of terminology. For example, scale in geography represents the ratio of map units to real-world units, with the unfortunate result that small-scale is used to refer to spatial models (maps) of large land areas. In other fields, such as ecology, it is common to use small-scale to refer to things that are small in scope or area. In forestry literature, examples of both uses of the term may be found, and the meaning must be inferred from the context.

Some modeling terminology in forestry has developed coincident with particular classes of models that are specific to the field. Growth and yield models are one such example. Growth and yield models, developed within the field of forestry, are sometimes contrasted with process models, developed within the field of ecology. Both may model tree or stand growth, but are characterized by some general differences. Growth and yield models tend to be empirically based, use statistical techniques to relate variables that may not have a direct causal relationship, and are intended to aid prediction. Process models tend to be conceptually based, often use a large number of variables that represent the ecological components of a system, and are intended to increase understanding. In practice, most models have a mix of these characteristics, and the classes are imperfectly distinguished.

Growth models are often combined with forest planning models to project how inventory will change over time. Such models can have very substantial impacts on forest policy, even though they have at times proved inaccurate (**Figure 1**). Inventory projections such as those shown in **Figure 1** have been used in debates about how much forestland should be maintained in reserves, to influence policies of taxation and trade, and to support various types of forest regulation. It is likely that projections of forest inventory will play a role in international debate about carbon storage and global climate change.

Models, in short, play a variety of roles in forest inventory, from the relatively simple function of replacing or augmenting field measurements, to sophisticated policy models with far-reaching implications. The following sections illustrate the great variety of methods and applications.

Modeling Tree and Forest Attributes

For Efficiency in Forest Inventory

In some cases, field measurements of a tree or forest attribute are replaced by modeled values to increase efficiency of the inventory. Individual tree height, the length from the base of the tree trunk to the tip of the apical meristem (tree top), is an example of this type of model use. Tree heights can be measured in the field with a variety of techniques, including height poles, clinometers, and laser instruments. Tree height measurements are important values for calculating timber volume, biomass, or forest structural characteristics. However, tree height measurements take more time than measurements of many other individual tree attributes, such as tree diameter or

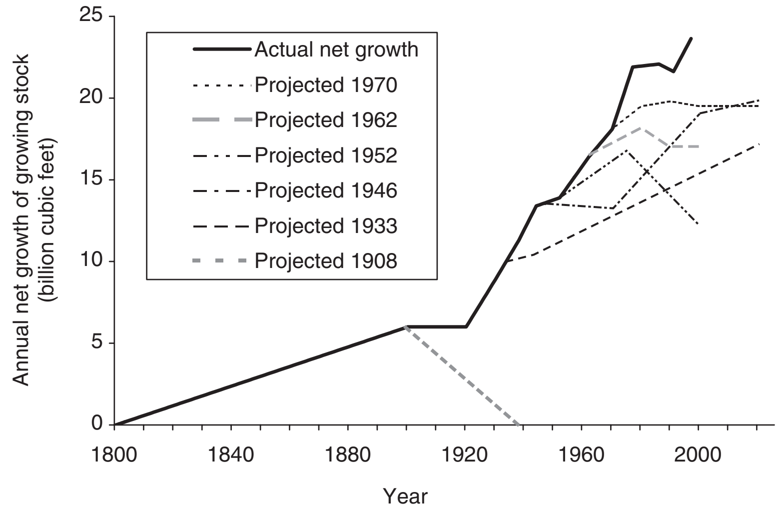


Figure 1 Annual net growth of timber in the USA, 1800–2000, and projections of future growth made in 1908, 1933, 1946, 1952, 1962, and 1970. Reproduced with permission from Clawson M (1979) Forests in the long sweep of American history. *Science* 204: 1168–1174, fig. 4. Copyright 1979 American Association for the Advancement of Science.

species. For this reason, some types of forest inventories measure heights for a subsample of trees and model heights for the rest.

Early height models for a geographic region used equations that expressed individual tree height as a simple polynomial function of tree trunk diameter; model forms have changed over time, but it is still common to use regression techniques to relate height to diameter (**Figure 2**). Although additional variables may be used, such as density or site quality attributes, the purpose of the model is prediction rather than an understanding of why different trees have different heights.

Site quality measurements are also sometimes based on models of tree heights. ‘Site’ is the local environment where a tree grows; ‘site quality’ refers to the potential productivity of this area. Site quality is most frequently measured with site indices, which are models of dominant tree height in relation to tree age. Other methods of measuring site quality include use of indicator plants, recent height growth, or physical attributes such as slope, aspect, and soil properties.

Crown cover is another inventory attribute that is commonly modeled. Crown cover is the percentage of the ground that is covered by the vertical projection of tree crowns or leaves. In recent decades, measurements of crown cover have been used in assessments of wildlife habitat and fire hazard. Similarly to height measurements, a variety of specialized methods have been developed to measure crown cover, including instruments such as densiometers or canopy cameras, and techniques such as interpretation of aerial photographs. A strong allometric relationship exists between tree crowns and tree trunk diameters; in the early days of aerial photography, this relationship was used to model tree diameters from crown widths, so that estimates of timber volume could be made. As interest in crown cover itself became important; the same allometric relationship was used to model crown widths from tree diameters. For continuous coverage of large land areas, crown cover information is often developed from models using a combination of remote sensing data and field inventories.

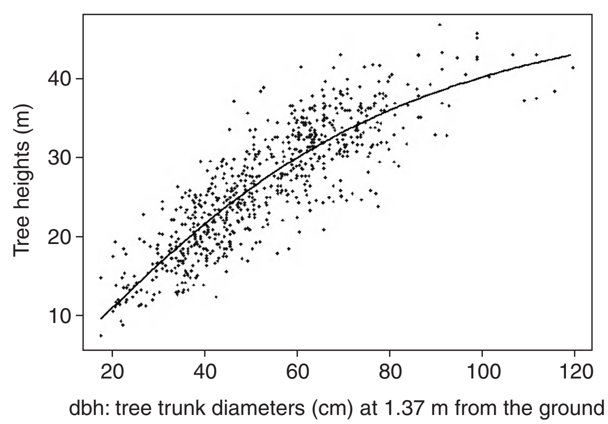


Figure 2 Nonlinear model (black line) of tree height as a function of diameter for *Pinus ponderosa*. Model is Richard’s form: height = 1.37 + 47.11 (1 − exp (− 0.021 diameter))^1.50. Data are from Forest Inventory Analysis program, west coast of USA.

When modeled values are used to replace inventory measurements, as may occur with tree heights or crown cover, both bias and imprecision can contribute to errors. Although modeled values may be less accurate than measured values, the decreased costs of data collection make the technique useful for some types of inventory where efficiency is particularly important. Knowledge of the accuracy of the models is critical to correct use. For example, the imprecision of the height model shown in **Figure 2** would make it unsuitable for many applications.

Computed Inventory Attributes

Even when an inventory contains an extended list of field-measured attributes (e.g., the US Forest Inventory and Analysis Program includes up to 50 tree attributes in its core measurement protocol), the attributes of greatest interest to inventory users almost always require modeling. Timber volume has long been the most commonly modeled tree attribute. Now, a recent focus centers on estimating biomass and carbon, not only for standing live trees but also for standing and down dead wood, such as snags and logs. At the plot level, all manner of management-relevant attributes are routinely estimated, such as biodiversity, wildlife habitat potential, fire hazard, and susceptibility to insect attack.

Whole-tree volume equations are widely available for most tree species utilized as timber and can be found in articles, published compendiums, and documentation of inventories. For the most common species, it is not uncommon to find several equations to choose from, for example, equations designed primarily for a particular region, for various merchantability and processing standards, in various units of measure, or for old versus second growth stands. Most such equations take field measured diameter at breast height (dbh), height, and sometimes site index as inputs, and produce estimates of either total bole volume or bole volume within locally prevailing merchantability limits (e.g., above a specified stump height up to a minimum top diameter). For species not commonly utilized, the selection of equations is often quite limited, and inventory compilers must choose between using equations developed for other species believed to be similar or resort to using basic geometric formulas, an approach that fails to account for variation of tree form or taper. Such formulas are also useful for estimating the volumes of down wood pieces (dead woody material on the ground, such as logs or branches), with the choice of formulae constrained by which diameters are measured (e.g., large end, small end, or at the point of transect intersection).

Some inventories involve field estimation of the numbers of logs in each tree, and, sometimes, the diameter at the breakpoints between logs (e.g., via reloskop). This opens the possibility for modeling volume for each log using volume formulas or tables designed around log size, or modeling tree volume based on dbh and the number of logs in the tree. This extra effort is sometimes justified when more precise merchantable wood volume estimates are needed.

Tree biomass is frequently estimated to assess biological productivity and ecological dynamics, to characterize fuel loadings for fire hazard assessment, and to serve as a basis for modeling carbon stores and dynamics. Bole biomass can be estimated as a scalar multiple of cubic volume, where scale factors reflect wood density and are estimated separately for each species or species group. Branch and leaf/needle biomass attributes are usually estimated via allometric relationships with dbh, and sometimes site index and/or height, which are developed via destructive sampling – harvesting, clipping, drying, and weighing of these plant parts from a representative sample of trees for each species of interest. Biomass of shrubs and herbs is also of great interest, and can be estimated from cover and height measurements taken in the field; however, there can be considerable variation among species, and cover-based biomass equations have been devised for very few shrub and herb species, making the use of equations from 'comparable' species a common fallback.

Amounts of elemental carbon can be derived as a scalar multiple of biomass, with different scale factors used for woody and herbaceous plant parts. Carbon and biomass amounts in down wood must be adjusted for the degree of decay/decomposition that has already occurred in the down-wood piece. Adjustment factors are generally specified when a down-wood decay class system is established for field classification of decay degree.

Wildlife habitat is another increasingly important forest attribute that can be modeled from forest inventory data. Habitat for individual species may be described by forest attributes such as average tree size or canopy cover. For example, a 2002 analysis of habitat for northern spotted owls (*Strix occidentalis*) in Washington, USA, found that averaged roosting habitat variables were tree dbh of 37 cm, canopy cover of 84%, 51 snags ha^{-1}, and 120 tonnes ha^{-1} of down wood. Such information can be paired with forest inventory data to build models estimating how much habitat might exist for this species. Such a model would be an example of calculating habitat attributes specific to an individual species.

Another common approach uses a standardized forest classification system that is then given species-specific rating values. For instance, one class in the California Wildlife Habitat Relationships system is tree species of red fir with average tree diameter greater than 61 cm and canopy cover $>60\%$; for feeding habitat, this class is rated as 'high' for the spotted owl, 'medium' for the big brown bat (*Eptesicus fuscus*) and 'low' for the mountain lion (*Puma concolor*). Additional habitat elements, such as presence of water or decaying logs, can contribute to these ratings of habitat suitability. Both species-specific and generalized classification systems are most often nonspatial, but an active area of research is spatially based models that factor in attributes such as patch size, proximity to water, distance between patches, and extent and type of edges.

The most common accuracy assessment method is to correlate model predictions with the presence or absence of wildlife species. Habitat alone is not enough to understand wildlife population distributions, because of impacts such as hunting, predation, intra- and interspecies competition, and migration. None the less, habitat classification is a useful method for understanding how impacts that change forest species, age, or structure may affect wildlife species.

The increasing frequency of large, wildland fires and broad agreement that, in many areas, fire exclusion has led to changes in forest structure that make today's forests more vulnerable to stand-replacement fire, has generated substantial interest in predicting fire and fuel attributes from inventory data. Such models can be ad hoc, for example, indices of stand density or standing biomass thought to be related to potential fire impacts. Others, which involve processing inventory data through formal simulation models, predict attributes related to fuel laddering and crown fire, such as torching and crowning indices, which depend on height to crown base and crown bulk density (itself a modeled attribute). When such models are coupled with stand-projection models, attributes like crown fire potential can be evaluated at many points in the trajectory of a stand, and under a variety of silvicultural management and fuel treatment regimes.

Other fire-modeling approaches utilize whatever field-measured inventory data attributes are available. They impute additional attributes by relating measured attributes to those in a database of reference plots, and ultimately predict levels of a multitude of surface fuel, surface fire behavior, crown fire potential, and fuel consumption attributes. Enthusiasm for all of these fire-modeling approaches is tempered by the scarce validation evidence associated with these models, and the substantial challenges to obtaining such evidence in adequate quantities.

Inventory data are also used to model surface fuel characteristics via classification (e.g., into stylized, surface fuel 'models') based on forest type. When a multipurpose inventory includes down-wood measurements (most commonly collected via line-intersect sampling transects), along with litter depth and mass and understory height and cover, surface fuel loadings by fuel size class can be directly estimated, potentially enhancing the specificity and accuracy of fire behavior and outcome predictions.

Spatial Modeling of Forest Inventory

Paper maps were the earliest form of spatial models used in forestry and they continue to enjoy wide use. Primitive, computer-based mapping systems were developed in the late 1960s, and these ultimately evolved into the modern geographic information systems (GIS) now used routinely in forest inventory applications.

Field measurements of forest inventory rely on sampling, or the selection of units from a larger population. The desirability of spatially continuous models as a basis for many applications has motivated the development of numerous techniques for extrapolating plot measurements to larger landscapes. Aerial photographs have long been used to map a forest through delineating stands (contiguous groups of trees that are similar in age, species, or structure). Forest attributes may be assigned directly by the air photo interpreter. For attributes that are difficult to estimate, an alternative is to delineate stand boundaries through photo interpretation, but assign attributes calculated from inventory plots or transects that were measured within the stand boundaries.

Since the 1970s, remote sensing imagery has been used to provide continuous spatial models of forest attributes (*see* **Resource Assessment**: GIS and Remote Sensing). Remote sensors do not directly measure the attributes of interest. With the most commonly used sensors, the digital data represent electromagnetic radiation intensity in different spectral bands or wavelengths. A number of standardized ratios of intensity in one band relative to another, and texture measures (typically based on variance in reflectance within a moving window) have also proved helpful. With the aid of additional sources of information such as geo-referenced plot information or stand maps, mathematical models are then used to relate this digital data to the forest attributes of interest. Although Thematic Mapper data collected by LANDSAT satellites have been most widely used, other remote sensing information such as AVHRR, SPOT, SLAR, and aerial infrared video have proved useful for specific applications. As part of the earth-observing system (EOS), a variety of new sensors began to be launched in 1999, and may prove useful for large-area ecological modeling of forests. There is also great interest in using the hyperspatial (~1 m resolution) and hyperspectral data recently available from space-based platforms to provide species-level and even tree-level representations of the forest, and many believe that light detection and ranging (LIDAR) imagery shows great promise for remote sensing of canopy structure and subcanopy vegetation layers.

The mathematical models used to create spatial models of forest attributes have evolved over time. Automated or semiautomated classification has been the standard method for mapping forests from satellite imagery for over two decades, including supervised and unsupervised approaches. Classification relies on statistical procedures, usually based on maximum likelihood estimation, to assign each pixel in the landscape to a forest-type class. Density and size classes are also sometimes assigned from image data. Classification accuracy is typically assessed via a confusion matrix – essentially a cross-tabulation of predicted and observed values, where the latter are derived from a set of ground control points that are either visited in the field or manually interpreted from aerial photographs. It is generally the case that the larger the number of classes (e.g., forest type by size by density) attempted in the classification, the lower the overall accuracy of the classification. Despite experimentation with various fuzzy classification approaches that assign partial credit for near-misses, overall accuracy rarely exceeds 85%.

Disillusionment with classification accuracy and the comparatively greater flexibility (e.g., in modeling derived attributes) that comes with continuous modeling of inventory attributes has led to the increasing popularity of imputation approaches to spatial interpolation of inventory plot data, including most similar neighbor (MSN), gradient nearest neighbor (GNN), and *k* nearest neighbor (*k*NN) variants. The first two impute all of a single inventory plot's attributes to all unsampled pixels in the landscape judged most similar on the basis of a similarity- or gradient-based weight matrix (**Figure 3**), and the third combines the *k* plots nearest in attribute space to an unsampled pixel to assign attributes to that pixel. Neural nets have also been used to merge inventory data and remote sensing data to provide spatial models of vegetation. Developers report that the technique can be used to develop maps of acceptable accuracy rapidly, but the models function as 'black boxes' that provide little insight into how a map was produced. The accuracy of any of these imputed maps can be assessed via cross-validation with samples not used in the development of an imputation model. As with other types of models, the appropriate use of spatial, GIS, and remote sensing models requires understanding the accuracy of the model for the specific application being tested.

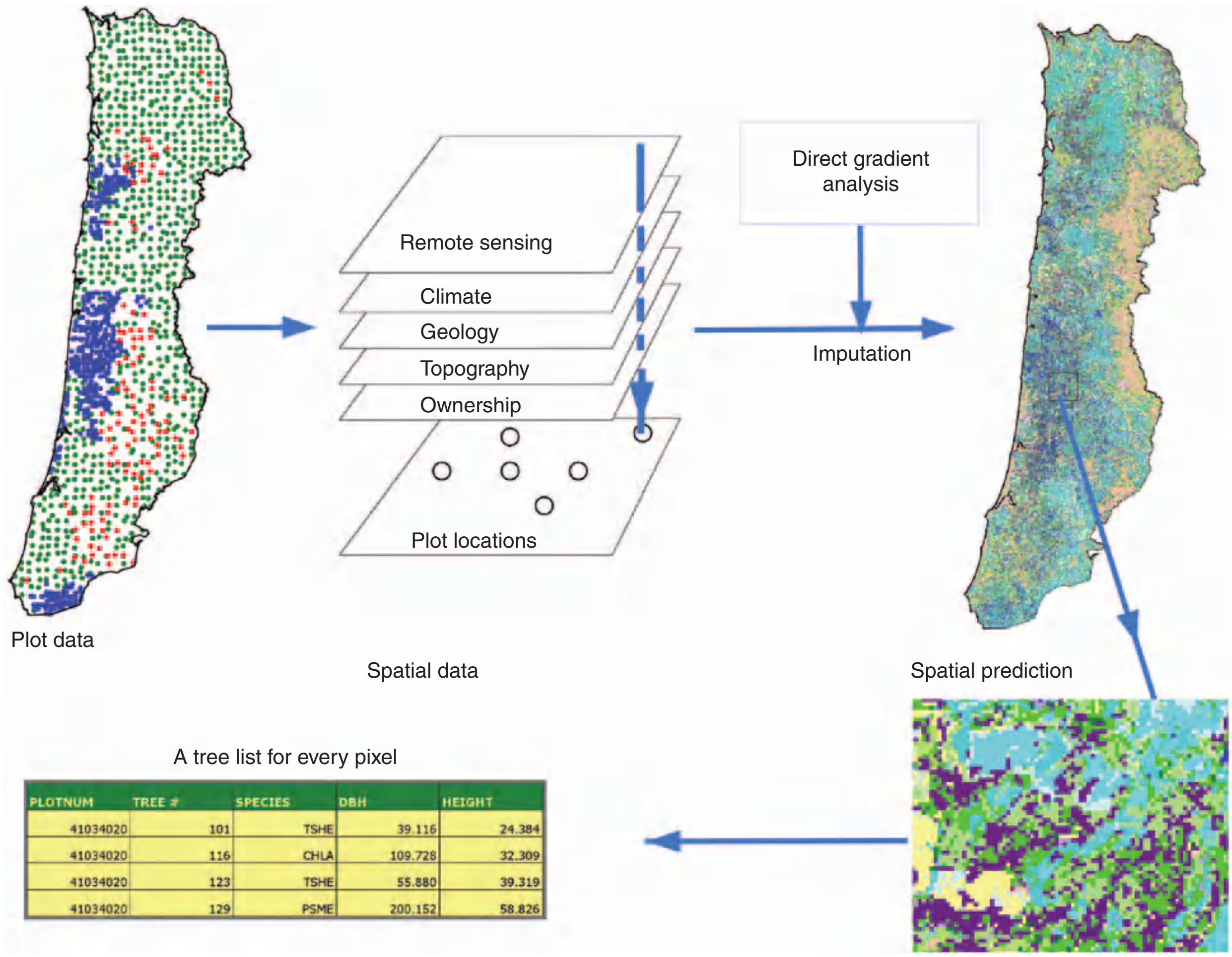
One application that combines spatial and temporal modeling is inventory updating. Continuous forest inventory (CFI) systems often measure a portion of plots each year. This approach results in having a portion of inventory data always current, but it also means that most data are from previous years. The national inventory of the USA uses such a system, and a variety of methods have been proposed to update inventory to the current year. Some methods involve imputation, or the substitution of information from similar trees or plots. Other methods use modeling procedures to update the plots, with or without the use of ancillary remote sensing data.

Temporal Modeling of Forest Inventory

Temporal modeling helps us understand how forests have changed in the past and predict how they will change in the future. Temporal modeling that accounts for management alternatives often serves as a basis for planning, and can help ensure the sustainability of forest resources.

Yield tables, which display timber volumes for forests of different ages, were one of the earliest and simplest temporal models. Simulation models that dynamically project forest attributes over time now serve as the basis for most temporal modeling (*see* **Mensuration**: Yield Tables, Forecasting, Modeling and Simulation). Growth models of various types are typically embedded within forest planning models, and use initial conditions and a set of assumptions to project forest characteristics over time. The planning model is used to vary the assumptions, establish a basis for choosing among management alternatives, and to synthesize and display forest-wide outputs. For example, a nonspatial individual tree growth model that predicts height and diameter growth for every tree may be used to project forest inventory for a set of silvicultural alternatives. The planning model might combine the output from the growth model with cost and revenue information, include an optimization algorithm to allow decision-makers to test different management strategies, and link to a GIS or visualization program to display what the forest would look like in the future.

Different purposes require approaches that vary in scope (spatial and temporal scale) and resolution. Planning models may cover very short time frames for small land areas, or they may cover long time frames and large land areas. Foresters divide



PLOTNUM	TREE #	SPECIES	DBH	HEIGHT
41034020	101	TSHE	39.116	24.384
41034020	116	CHLA	109.728	32.309
41034020	123	TSHE	55.880	39.319
41034020	129	PSME	200.152	58.826

Figure 3 Inventory plot data can be imputed via the method of gradient nearest neighbors using multivariate techniques like canonical correspondence analysis. This approach creates a full suite of internally consistent plot attributes for every pixel in a forested landscape based on the similarity of remote sensing and ancillary geographic information systems (GIS) layers at plot and unsampled locations.

planning models into hierarchical levels to reflect this range. Strategic models may be used to project forest inventory attributes over a 50–200-year time horizon, typically use time steps of 10 or 20 years, are used for forests of 20 000 to 200 000 ha, and generalize vegetation into fairly broad classes. Tactical models may be used to project forest inventory over a 10–100-year time frame, are used for forests of 1000–20 000 ha, may use smaller time steps, and may allow spatially explicit projections of vegetation over time. Operational models may be used to project forest attributes over short time horizons of 10–20 years, often use single-year time steps, are applied to forests of less than 1000 ha, recognize stands as unique entities, and are focused on short-term decisions such as what harvesting system to use, which roads to build, and which roads to close. As computing power has grown exponentially over the past two decades, these hierarchical distinctions have become blurred and it has become common to include greater detail and spatial resolution for large land areas and long time horizons.

Strategic, tactical, and operational planning models use a variety of mathematical techniques to aid in selecting silvicultural and management alternatives. Until the 1990s, linear and goal programming were the most common solution methods. Spatial restrictions between neighboring stands, whether imposed by regulation or necessitated by management goals, required different techniques. Integer programming and a number of heuristic methods, including simulated annealing, genetic algorithms, and tabu search, have been applied to spatially restricted planning problems.

Extremely large land areas are addressed with forest sector models, which are used to project forest inventory on a national or international scale. Forest sector models differ from planning models by relying

Figure 4 Visualization model of hemlock-fir inventory plot as measured in 2000 (left), and after 100 years using models of growth, mortality, and snag decay (right). Plot data are from Forest Inventory and Analysis program, growth model used is Forest Vegetation Simulator program, and visualization program is the Stand Visualization System.

on supply and demand functions rather than treating prices as fixed. Forest sector models also differ in that they are not explicitly linked to management decisions, although they may project future inventory levels for a variety of possible scenarios. Forest sector models provide useful insight into how forest inventory levels change in response to trade restrictions, technology development, or general demand trends.

Along with growth models, forest planning models, and forest sector models, many other kinds of models aid in projecting inventory attributes over time. Snag models may be used to understand how dead trees are recruited, decay, and fall down. Forest fire simulation models are used to predict how forest stands or landscapes would burn under different assumptions of weather, initial conditions, and suppression strategies. Ecological process models have been used to understand how net primary productivity and biomass would change under different climate and atmospheric carbon dioxide levels. Visualization models are used to generate graphic displays of how trees, stands, and landscapes would look in the future under alternative management scenarios. Models are frequently combined in any particular application (for example, see **Figure 4**). Relatively little research has been devoted to the effect on error and accuracy of predictions when models of different spatial and temporal scales are combined.

Modeling has become a regular component of day-to-day forest management. Improvements in validation may follow as the specific fields of application mature. The vast change in the past century, from simple hand-drawn graphical models of basic allometric relationship, to elaborate computer models intended to simulate global ecosystem processes, indicates that modeling in forestry will continue to be an active area of research.

See also: **Biodiversity**: Biodiversity in Forests. **Inventory**: Forest Inventory and Monitoring. **Landscape and Planning**: Forest Amenity Planning Approaches. **Mensuration**: Yield Tables, Forecasting, Modeling and Simulation. **Operations**: Forest Operations Management. **Plantation Silviculture**: Sustainability of Forest Plantations. **Resource Assessment**: GIS and Remote Sensing.

Further Reading

Avery TE and Burkhart HE (2002) *Forest Measurements*, 5th edn. New York: McGraw-Hill.

Davis LS, Johnson KN, Bettinger P, and Howard T (2001) *Forest Management*, 4th edn. New York: McGraw-Hill.

DeStefano S and Haight RG (eds) (2002) *Forest Wildlife–Habitat Relationships: Population and Community*

Responses to Forest Management. Bethesda, MD: Society of American Foresters.

Kohn KA and Franklin JF (eds) (1997) *Creating a Forestry for the 21st Century: The Science of Ecosystem Management*. Washington, DC: Island Press.

Ohmann JL and Gregory MJ (2002) Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. *Canadian Journal of Forest Research* 32(4): 725–741.

Moeur M and Stage AR (1995) Most similar neighbor: an improved sampling inference procedure of natural resource planning. *Forest Science* 41: 337–359.

Waring RH and Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scales*, 2nd edn. San Diego, CA: Academic Press.

L

LANDSCAPE AND PLANNING

Contents

Perceptions of Forest Landscapes

M J Meitner, University of British Columbia, Vancouver, BC, Canada

Context and Limitations

For many centuries people have been concerned with perceptions of the natural world. Philosophers have written about it, psychologists have studied it, and, more recently, foresters have become concerned with it. However, when we speak of 'perceptions of forest landscapes' in relationship to forest science, we are typically referring to a variety of assessments and their associated methodologies applied to the quantification of some visual aspect of forested lands rather than the larger context of what it means to perceive the world around us. Because of this, perceptions of forest landscapes can be seen as a restricted subset of a larger body of generalized perception research that will not be dealt with in much detail in this article. First, the discussion will be limited to forested landscapes and will not deal with perceptions of urban or built environments, for which there is a great deal of research. Additionally, this article will focus on topics related primarily to visual perception. This is an obvious simplification/reduction of the larger construct of perception but has certainly received far more attention over the years than all of the other senses combined. Lastly, of all of the measurable dimensions arising from these visual perceptions of forested landscapes, scenic beauty will receive more attention than a host of alternative dimensions (such as general preference, acceptability, visual impact) since it has historically been quite important to forest managers and the decisions that must be made regarding the balance of competing forest values.

Both the preponderance of research and this article concentrate on scenic beauty as a central issue of forest management. Going back at least as far as the ancient Greeks, aesthetics has been of fundamental concern to thinkers of the day. Most simply, aesthetics relates to appreciating, perceiving, or describing the beautiful. It then follows that forest aesthetics must relate to appreciating, perceiving, or describing what is beautiful about a given forest.

Object and Observer

We are often told that 'beauty is in the eye of the beholder' but, in the absence of an external world to behold, this would have little meaning. Conversely, consider this famous quote by William James (the father of American psychology):

> Imagine an absolutely material world, containing only physical and chemical facts, …without even an interested spectator: would there be any sense in saying of that world that one of its states is better than another.

(James, W (1891) The rural philosopher and the rural life. An address to the Yale Philosophical Club, published in the International Journal of Ethics April 1891)

Taken together these ideas lead to the supposition that beauty is transactional, where forest aesthetics is a perceptual state brought about by the interactions of the visible biophysical features of a forested landscape and the perceptual processes of an individual observer. Since the beauty of an object depends on the properties of that object as well as on an observer who can experience the beauty, any property in virtue of which an object is found to be beautiful or aesthetic is a relational property – it is a property of the object, but one which depends on something in addition to the object. In this case, the object must be related to a person who can experience the property in virtue of which the object is said to be beautiful. Simply stated, the experience of natural scenic beauty depends on properties of an individual and properties of an object where:

- properties of the observer include sense perception, thought, and feeling
- properties of the object are its perceived properties – sense data such as color and shape
- properties of both the observer and the object interact creating the foundation on which the experience of natural scenic beauty is laid.

Object

Let us then first turn our attention to the object. Traditionally aesthetics has been intimately tied to the study of art, but more specifically it is concerned with objects that give rise to aesthetic experiences. In the context of forest aesthetics this is rarely a constructed 'art' object. The more typical unit of analysis is often the view afforded by a certain location in the natural world. The term 'landscape' has also been used quite a bit in this field and for the most part it is synonymous with photographs or paintings of the visible portion of the topography and vegetation/landcover of a given place or region. This, however, is not without its controversy and, at times, 'landscape' will be used to denote regions akin to ecosystems or other logical subdivisions of an environment. In this case, the unit of analysis would be a bounded region of forest and the aesthetic qualities of that region would need to be assessed using multiple views sampled from within its borders. While this aggregation of views raises a number of problems of its own, the fundamental issue still revolves around how one might go about the business of evaluating a given view of a forest along an aesthetic dimension and so we must revert to the more restrictive definition of landscape as a view before we think about issues of aggregation. However, it is not the study of the views themselves but the perceptions of those views that form the basis for the study of natural scenic beauty in the broader context of forest aesthetics.

Observer

Perceptions require an observer and few people would argue with the statement that people (observers) are complex. We are driven by an often conflicting array of needs, wants, and desires to which each of us reacts/responds in a variety of ways. Our attitudes and motivations are influenced by our upbringing, our culture, our self-image, our need for recognition, etc. We possess the capacity for both rational and irrational thought, at times motivated by emotion, while other times we act in a cold and calculating manner. All of this variation in the human condition makes the study of environmental perception a challenging one. Current psychological research has shed some light on this complexity and indications are that perception follows a certain time course as percepts travel through various regions of the brain.

For example, imagine you are out walking and a grizzly bear (*Ursus arctos horribilis*) suddenly crosses your path. Initially, light from the bear strikes your retina. Shortly thereafter, your body reacts by activating your sympathetic nervous system (the so-called 'fight or flight' response). As you begin to move, you become aware that you are frightened as evaluations of the percept in conjunction with internal indicators of body state become available to the emotional centers of your brain. Now you are aware that you are scared and moving but have yet to fully appreciate why. You begin to access the higher centers of cognitive brain activity and are able to retrieve linguistic representations of the object in question (the bear). It would not be until that point that you would be able to formulate the utterance 'That's a scary-looking bear. I'm getting out of here.'

While it might be said that there is a somewhat innate aesthetic response given the affective (emotional) components of the aesthetic experience mentioned above, it cannot be expressed, nor even consciously experienced, without some form of cognitive apparatus and as a result cannot wholly be considered innate. This leads us to conclude that the fundamental aspects of an aesthetic response, which some have argued are evolutionarily driven, must be affected by our learned understanding of what it means to 'be' beautiful. More simply put, both 'nature' and 'nurture' are necessarily implicated in the assessment of forest aesthetics. One possible explanation for how our evolutionary history might be relevant in the assessment of forest aesthetics can be found in the savannah hypothesis. This postulation states that humans lived for nearly 2 million years on the savannahs of East Africa where certain features of the landscape offered greater chances for both individual and group survival. Therefore evolution should have predisposed us to prefer these landscape features that are beneficial to our survival. Experimentally there is some evidence to support this including a tendency for children to prefer savannah-like environments over all other biomes, our collective tendency to create gardens with savannah-like characteristics and cross-cultural studies that have shown amazing similarities in our landscape preferences.

Common definitions of environmental perception include cognitive, affective, interpretive, and evaluative components, all operating at the same time across several sensory modalities. However, these components of environmental perception have historically been approached from a great diversity of intellectual viewpoints. The expert approach to environmental perception has attempted to develop formal rules for the quantification of forest aesthetics while the psychophysical and cognitive paradigms have traditionally focused on studying perceptual processes to gain insights into how our evaluations of forest aesthetics are derived. In simple terms, the psychophysical and cognitive paradigms have mainly differed in subtleties of this debate with the former ascribing more weight to the mostly passive sensing of our external world and the later focusing more on how information is given meaning by our mental processes. Lastly the experiential model sees humans as integral parts of the world around them deriving their understanding of forest aesthetics by a set of transactional experiences. Certainly each of these perspectives has something unique to offer, but despite these differences the field of environmental perception remains focused on understanding how we move through time, from state to state, influenced by what came before and our visions of what is to come, attempting to make sense of our internal condition (thoughts and feelings) in light of our evaluations of the external world. It is in these evaluations of the external world that we are concerned in the study of forest aesthetics but we must always keep in mind that these seemingly overt valuations are responses to complex conditions of perception.

Assessment and Evaluation

Most perplexing to those who devote their careers to studying the aesthetic experience in a natural setting is the difficulty of arriving at adequate methods for assessing the relative merits of one forested landscape configuration versus another. This is related to the fact that the aesthetic experience is a complex one. This can be explained intuitively if you think about your own personal reactions to the world around you. For example, at any given time a researcher might ask you to verbally characterize or explain your current aesthetic experience. After being given some reasonably detailed explanation of what this means (similar to the one you have just read) you would then need to come up with a story of how you perceive, make sense of, and then report on your reactions to the world around you, even though you are now somewhat removed from that experience by a new one (namely the researcher asking you the question in the first place). You then need to remember your experience and relate it back to the question being asked of you. Surprisingly enough, people are actually quite good at tasks such as this and measures of reliability point to a degree of consistency in these evaluations not intuitively expected.

Common Methods

Common quantitative methods for measuring these subjective evaluations include forced choice (choose which one of these is more beautiful), Q-sort (placing relevant images in categories), rank order (highest to lowest on some dimension), or some form of scaled response (rate the images on a scale from 1 to 10 representing low to high scenic beauty). This is generally done using photographs (or more recently computer images) as surrogates for onsite experiences of forest aesthetics, though field assessments can also be conducted. A variety of qualitative methods have also been employed, such as open-ended survey type questions, naturalistic observation, and a multitude of ethnographic methods including the camera method (e.g., give out disposable cameras and have recipients take photographs of what they think are the most beautiful views in the area). When combined these methods allow forest aestheticians a great diversity of tools with which to approach a multitude of research questions.

Temporal Integration

In order for us to respond to a researcher's questions we must typically access our memory. This opens the door to possible misattribution of the cumulative effects of past experience (both cognitive and affective). For example, in the case of a slide presentation where we are rating images on a 10-point scale (relative to one another), we must remember the context of the slides that have come before and assign a rating based on our perceptions of where the current image falls on that scale. Even more problematic in this regard are survey methods, which may ask us to recall a walk down a forest trail or a recent camping trip, causing us to need to integrate information over longer periods of time. Recent research by Daniel Kahneman and others has uncovered some interesting effects that may begin to explain how accessing memory representation could affect our perceptions and ultimately our expressed assessment/evaluation of a given forest scene. This research can be summarized by briefly explaining the peak–end rule. This rule states that the affective value (preference rating) of a given moment is a simple average of the most extreme affect in a set (peak) and the affective state that is present near the end of an experience (end). While this research has focused mainly on our perceptions (and evaluations) of pain, it may likely extend to the visual assessment of forest aesthetic dimensions.

Experts versus the Public

Additionally, aesthetic experiences of forests are not limited to formal visual rules but are also colored by our scientific understanding of the underlying systems. In other words, visual beauty is but one component of a fully fleshed out aesthetic experience, which may also be affected by differing frames of perception based on dissimilar experiences in one's life. For example, a forester may find a particular ecosystem quite beautiful due to its rarity, while the average observer may be unaware of this and may judge the ecosystem on its visual characteristics alone. There is no a priori reason why the aesthetic value of a forest could not be intellectual in addition to being perceptual, or even intellectual rather than perceptual as some ecologists advocating a move to an 'ecological aesthetic' would suggest. However, this raises a number of normative issues and to date no method has been suggested to evaluate who among us is sufficiently qualified to determine what that new aesthetic might be. This premise of 'unique perceptions' has led to the formulation of the idea that 'experts' should be employed in the evaluation of forest aesthetics. To that end, the US Department of Agriculture Forest Service, having become the largest US employer of landscape architects in the early 1970s, tasked these 'forest aesthetics experts' with categorizing the scenic resources of the National Forests based on formal aesthetic features of the landscape (e.g., form, color, texture, etc.) (*see* **Landscape and Planning**: Visual Analysis of Forest Landscapes).

This expert-based method can be contrasted with a competing perception-based approach of forest aesthetics assessment where groups of ordinary citizens are enlisted to evaluate landscapes rather than individual expert assessors. Intuitively, the perception based approach is less susceptible to individual variation because evaluations of landscape aesthetics are based on numerous individual evaluations. This leads to greater confidence in our estimates but comes with some cost as well due to the increased burden of deriving multiple measures for every landscape assessed. For this reason the expert-based approach has historically been applied more to the practice of public land management while the perception-based approach has been employed predominately in landscape assessment and environmental perception research.

While both of these paradigms are alive and well in forest aesthetics research, the remainder of this article will deal exclusively with the perception-based approaches. The tradition of landscape architecture approaches is described in detail elsewhere (*see* **Landscape and Planning**: Visual Analysis of Forest Landscapes).

Results and Applications of Research

Much as artworks presuppose artists who produce them, and audiences who can be aware of them, forestry presupposes foresters who produce altered landscapes, in light of public opinion which serves to critique these management actions. Therefore, foresters must be conscious of the intent to do something, thereby creating a new object for evaluation, which ultimately becomes the public's primary means to understand and interpret the underlying properties of that landscape that the forester hopes to maximize. In the case of forestry, these underlying properties are typically multidimensional and are often in conflict; attempts to resolve conflicts involving aesthetics need to be grounded in the results from perceptual research.

Rules of Thumb

Over the years, a great deal of research has been done (particularly in the Western world) to aid foresters in understanding the linkages between manageable landscape characteristics and predictions of perceived scenic beauty. While this research area is still an active one, with many unanswered questions, a number of rules of thumb can now be derived from this body of knowledge. Overwhelmingly, people prefer natural to urban scenes. In addition, this principle has been extended to more natural scenes though indices of naturalness, such as 'evidence of humans,' common in current recreation management frameworks (*see* **Recreation**: Inventory, Monitoring and Management; User Needs and Preferences). Visible evidence of facility development and site modifications (denoting human use) are typically seen as negative contributors to scenic beauty.

Another of these rules of thumb can be derived from perceptual studies that have investigated the configural aspects of landscape. This line of research has been quite productive. People of diverse cultures, languages, or experiences, tend to prefer open areas with fairly low groundcover punctuated by clumps of trees and shrubs, as demonstrated for example in Western public parks and green spaces. This is not to say that there are not significant individual or group differences, but that they have typically been small in magnitude when compared to the degree of concurrence. A similar convergence is found in our clear preference for water in a forested landscape. This can be evidenced through direct means such as a lake or stream but can also be realized indirectly through indications of the presence of water such as abundant greenery and flowering plants.

More generally, mature trees are preferred to saplings; this is especially true in even-aged stands but there remains a great deal of variation in preferences when considering highly complex multi-aged stands. Dead and downed wood has also been shown to negatively impact preference where live plants are always preferred with a minimum of visible debris. However, caution should be used in interpreting this finding since downed wood that is sufficiently decomposed to support other plant life will appear as live plant material in a purely visual assessment. This is also related to the finding that the presence of low groundcover (grass and forbs) is often implicated in positive forest evaluations.

Research into the preference for the form of individual trees may also be of value in understanding this topic. Researchers have consistently found that deliquescent tree form is preferred to excurrent tree form. Furthermore, deliquescent trees that bifurcate closer to the ground, like the acacia tree, also seem to be preferred. These findings can be thought of in terms of preferred biomes, where some researchers have suggested that savanna-like environments are most preferred, followed by deciduous forests, coniferous forests, tropical rainforests, and deserts. These findings have also been shown to be mediated by experience, where the trends in preference are most clear for younger participants, whereas adults tend to elevate biomes with which they are more familiar when compared to the average. However, it should be noted that, while experience seems to have some effect on landscape preference, resulting differences are rather small in comparison to the larger similarities as evidenced by the bulk of empirical studies in this area.

The Promise of Visualization

Fundamentally aesthetics can be seen as related to quality of life or a more generalized sense of well-being so far as a life lived in the absence of beauty would certainly leave much to be desired. So far, we have seen how perceptual assessments of current forest conditions may offer advice to foresters in incorporating visual aesthetic components of the landscape into a multi dimensional management framework common in today's era. However, if we are to truly manage forest aesthetics, we must be able to project the likely aesthetic outcomes of our proposed management alternatives so that perceptual evaluations might be employed as input to the planning process rather than simply reacting to past management and attempting to uncover rules of thumb to guide future management. One exciting technology that offers promise in this regard is data-driven environmental visualization (*see* **Landscape and Planning**: The Role of Visualization in Forest Planning). Currently we are able to create near photorealistic images based solely on data descriptions of possible management alternatives. This may allow for the development of an entirely new method for incorporating public evaluations of forest aesthetics in the near future beyond its use in research.

Beauty necessitates and fundamentally relates to experience. This can be seen as the gold standard for the application of research findings in the area of perceptions, and as a result we must always strive to understand how this body of research relates to the larger issue of the human condition. The appropriate management of our forested environments obviously has a large part to play in that concern. Forest aesthetics has a long tradition of importance in this context and research into the interactions of human perception and forested landscapes will hopefully lead us to a better understanding of the fundamental principles related to its management. A great deal of advancement has been made in this area and technological advances offer new opportunities for exploration of these issues. The challenge now is to continue to develop research questions that adequately address the complexities of our experiences of forest aesthetics, while attempting to maintain a link from theory to practice.

See also: **Landscape and Planning**: Perceptions of Nature by Indigenous Communities; The Role of Visualization in Forest Planning; Visual Analysis of Forest Landscapes. **Recreation**: Inventory, Monitoring and Management; User Needs and Preferences,

Further Reading

Brown TC and Daniel TC (1986) Predicting scenic beauty of forest timber stands. *Forest Science* 32: 471–487.

Daniel TC (2001) Whither scenic beauty? Visual landscape quality assessment in the 21st century. *Landscape and Urban Planning* 54: 267–281.

Lothian A (1999) Landscape and the philosophy of aesthetics: is landscape quality inherent in the landscape or in the eye of the beholder? *Landscape and Urban Planning* 44: 177–198.

Palmer JF and Hoffman RE (2001) Rating reliability and representation validity in scenic landscape assessments. *Landscape and Urban Planning* 54: 149–161.

Parsons R and Daniel TC (2002) Good looking: in defense of scenic landscape aesthetics. *Landscape and Urban Planning* 60: 43–56.

Zube EH, Sell JL, and Taylor JG (1982) Landscape perception: research application and theory. *Landscape Planning* 9: 1–33.

Visual Analysis of Forest Landscapes

S R J Sheppard, University of British Columbia, Vancouver, BC, Canada

Introduction

This article examines the broad concepts and methods underpinning the management of visual resources in forestry, and describes some of the key scientific methods of addressing the often difficult issue of aesthetics and public perceptions of forested landscapes. It draws on accumulated research knowledge on public perception (*see* **Landscape and Planning**: Perceptions of Forest Landscapes) and provides general concepts and methods employed in more specific procedures for managing landscape values under visual resource management (VRM) (*see* **Landscape and Planning**: Visual Resource Management Approaches) and other multiple-value forestry programs. The topic of visual analysis focuses on the main human perceptual sense of vision, rather than appreciation of other aesthetic values such as sound and smell, which can also be very important in their own right though typically less critical than visual values in forestry.

What is the purpose of visual analysis? There are a number of reasons to conduct visual analysis or to be aware of its methods and underlying theories:

1. It can provide support for rational VRM and broader forest management decision-making, supplying credible scientific data on human perceptions, scenic quality, and visual design that can be used on an equal basis with ecological, economic, or other social data.
2. It provides systematic support for project planning and design where aesthetic values are important
3. It can be used to monitor visual qualities and VRM performance (at the regional to project level), as part of social sustainability assessments and forest certification efforts.
4. It can provide an indicator or predictor of public perceptions about some forest management issues, which can be useful as background for developing effective public involvement strategies.
5. It can provide visual documentary evidence for monitoring visible conditions over time (e.g., vegetation growth, human uses, etc.) that are important to various sustainability values or management issues other than aesthetics.

The history of visual analysis as applied today in forestry can be traced back most clearly to the practice of landscape architecture in Great Britain, where deliberate design of larger-scale somewhat naturalistic landscapes for aesthetics began in the eighteenth century. Certain principles of landscape design and analysis were first systematically applied to forestry by Sylvia Crowe, an English landscape architect working for the Forestry Commission in the 1960s. Since then there has been a tradition of landscape architects developing visual analysis and management approaches in forestry, incorporating both design principles and a growing body of research on aesthetic responses to forest landscapes. Researchers, most notably R.B. Litton Jr., and other landscape architects in the USA, developed the field of visual analysis in the 1960s and 1970s. The introduction of the National Environmental Protection Act (NEPA) in 1969, which recognized the need to protect the rights of Americans to aesthetic enjoyment, and the 'clear-cut crisis' in the US National Forests, led to the implementation of a major program of VRM in the US Forest Service, adapting Litton's work. This in turn has led to development of visual analysis procedures and VRM programs in other regions and jurisdictions, such as British Columbia in Canada. Other systems of landscape assessment and visual analysis have developed somewhat independently in various parts of the world, though mostly in the more developed and affluent nations.

Visual Landscape Description and Inventory

This section reviews some basic principles of visual perception and landscape characteristics, which govern how observers see landscapes. It represents the first stage of visual analysis, which permits quantifiable, objective analysis that does not require much interpretation or argument. It is based on a review of documented observation and research, as well as landscape design principles.

Fundamental Visual Characteristics of Landscapes

The process of vision exerts various influences on visual perception of landscapes. Key aspects of the physiology of vision include: visual acuity and contrast, which enables detection, and recognition of landscape elements; the field-of-view (horizontal and vertical extent); and the nature of eye movement, which automatically records visual information from certain points within the field-of-view. Vision is affected by variables of light transmission within the visible spectrum.

Litton in his seminal work *Forest Landscape Description and Inventories* was the first to develop comprehensive principles for analyzing and inventorying the visual characteristics of larger-scale natural landscapes. This work has been supplemented since by many others, such as the US Forest Service series on National Forest Landscape Management. Such methods are based on definitions of certain visual elements, which can be used to describe objectively the perceptual characteristics of landscapes (**Figure 1**). These elements include:

- color, including hue, value (lightness–darkness), and chroma (saturation or brilliance)
- texture
- scale (in absolute terms, relative to landscape scale, or relative to human scale)
- form (comprising three-dimensional (3D) forms and two-dimensional (2D) shape)
- line/edges
- position in the landscape
- movement in the landscape.

These elements can be used to describe the visual characteristics of the landscape and its principal components: landform, vegetation, water bodies, human land uses and structures, and atmosphere. The combination of these components and visual elements forms the landscape patterns and spatial (3D) structure that we see. The elements can be measured through approaches such as color charts or specifications, photographic image analysis, and pixel counts applied to representative images of the landscape.

Litton also described various perceptual relationships which affect how we see the landscape. These relationships include: diurnal/seasonal aspects of temporal variation (such as lighting direction, shade/shadow, weather); viewing distance and scale effects; observer position (superior, normal, or inferior with respect to the landscape being viewed); and observer motion (determining the effective field-of-view and viewing sequence).

In any natural landscape situation, various landscape compositional types can be identified, as follows:

1. Fundamental/large-scale compositions or spatial configurations.
   - panoramic: offering wide, unobstructed views over a large area
   - feature: views dominated by a major landscape feature such as a mountain peak or waterfall (**Figure 2**)
   - enclosed: views confined by enclosing elements such as forest edge or hills
   - focal: views focused in a particular direction by the alignment of topographic or other landscape components, e.g., a view down a narrow valley or road corridor.
2. Supportive/small scale compositions.
   - canopied: views within a forest stand, with overhead closure

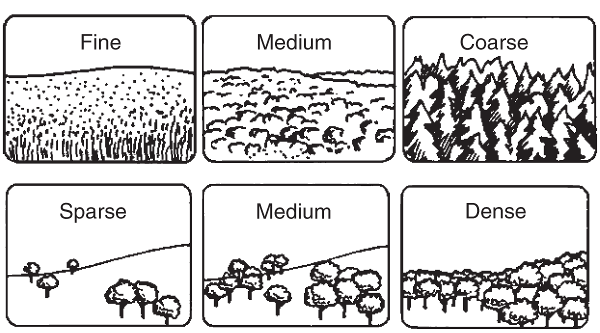


Figure 1 Example of a visual element texture that can be objectively described in the landscape. Graphic by Richard Alcina, reproduced with permission from Sheppard SRJ (1989) *Visual Simulation: A User's Guide for Architects, Engineers & Planners*. New York: Van Nostrand Reinhold).

Figure 2 Feature landscape with view dominated by a mountain peak.

- detailed: close-up views of small-scale landscape features, e.g., wild flowers.

Temporal landscape patterns can also affect landscape perceptions, sometimes dramatically. Ephemeral landscapes include views of short-lived or rapidly changing landscape features, such as fall color on trees or reflections in lakes. Change of landscapes over time are usually evaluated in terms of visual impact prediction for specific projects such as forest harvesting activities (see 'Visual Impact Assessment' below); here, there is a tendency to assess 'before and after' conditions, rather than the landscape dynamics of natural disturbance regimes, succession, or forest rotation cycles over time. The rise of landscape ecology has focused more attention on some visual descriptors of the results of natural disturbance events, in the form of a classification of landscape mosaics into patches, corridors, networks, matrix, etc. These can be quantified, but common landscape ecology metrics do not appear to be closely related to aesthetics.

Landscape Inventory Concepts

This section describes conventional approaches used to document and classify the existing ('baseline') landscape conditions.

Visual units Various organizational frameworks for mapping and classifying visual landscapes have been suggested, on a hierarchy of scales that can be related to physiographic regions, biogeoclimatic zones, forest types, the 'landscape' or watershed level, and stand level. However, these other landscape description systems cannot be expected to correspond closely with visual mapping, due to the integrative nature of the essentially visual experience: a visual landscape is defined by the totality of what is seen within the viewshed, not necessarily what it consists of in any one place.

Each of these landscape scales can be described in terms of geographic extent, boundaries/edges, landform, vegetation, water forms, and focal attractions/local features. This combination of landscape components defines what the US Forest Service calls the 'Characteristic landscape' and what in Europe is referred to as landscape character.

The visual unit level most closely approximates the scale of the forester's meaning of the word 'landscape,' although visual units can range from small valleys to very large basins. A visual unit represents a distinct area of recognizable unified character, often defined by spatial enclosure such as basins, valleys, watersheds, etc. Visual units have been mapped as the basic spatial units for visual assessment in many studies. Descriptors of visual characteristics of individual units, commonly used in many larger scale inventories, include:

- scale (extent)
- boundary definition
- spatial configuration/proportions
- landscape patterns
- unifying/detailed features
- other sense-of-place indicators that contribute to the unique character of each place.

Some visual landscape inventory systems also recognize landscape subdivisions at a subunit level, such as a particular hillside or other landform component (**Figure 3**).

Landscape visibility Beyond the broad organization of spatial and temporal landscape patterns,

Figure 3 Identification of landscape subunits (termed visual sensitivity units) using the British Columbia Ministry of Forests method. Image by Ken Fairhurst; courtesy of Greater Vancouver Regional District.

visual inventories often attempt to measure the visibility of specific areas, points, or objects in the landscape, as seen from certain viewing locations. This is often termed viewshed mapping or ‘seen area’ analysis. Clearly, visibility factors are critical in determining whether or not there can be a direct visual impact from forest operations or natural disturbances.

Visibility of landscapes depends upon the viewer location. Viewpoints are usually identified as certain use areas (e.g., recreational sites, residential areas, or other community gathering points) and travel routes. These can be specific points, often termed key observer points (KOPs), or linear travel sequences. Selection of appropriate viewpoints for analysis is often conducted with knowledge of relative observer concerns (see below). Observer position (elevation) makes a considerable difference in terms of what can be seen of a particular forest landscape.

Visibility is limited by topography, vegetative screening, man-made structures, atmospheric conditions, and, over long distances, by the curvature of the earth. Visibility can be described in terms of viewing distance, viewing angle (horizontal and vertical), and visual penetration (the extent to which observers can see through screens or filters of intervening objects, such as tree belts).

Techniques used to map visibility include linear map notation, cross-section analysis, manual mapping of visible areas from on-the-ground viewpoints, and computer viewshed analysis using 3D geographical information system (GIS) datasets. Whether these techniques take into account tree height in calculating and mapping visibility can make a difference in terms of accuracy in lowland landscapes or detailed, site-specific studies.

Visual Landscape Assessment

Visual landscape assessment goes beyond the relatively objective inventory of conditions, to evaluate and interpret forest landscapes for certain characteristics or qualities important to forest planning and management. These can involve prioritizing areas of the landscapes that are suitable for certain management regimes or actions, or identifying particular constraints, risks, or opportunities that are important to bear in mind in forest planning and design. Various methodologies for landscape assessment have been applied to large-scale landscapes. These are important as a possible framework for VRM decisions to predict aesthetic values and for modelling of future management outcomes.

In the interpretation process, there is the need to consider both the landscape characteristics described above (typically evaluated by trained experts), and the characteristics and concerns of observers. Both can be mapped and to some extent quantified. Both landscape and observer characteristics can be assessed by expert methods, public perception testing, or a mix of these methods.

In general, methods of visual analysis usually address one or more of the following major aspects of visual landscapes (although they may not be defined in these terms and often overlap within the assessment methodology):

- visual absorption capability
- viewer sensitivity
- visual quality
- landscape meanings.

Visual Absorption Capability

Visual absorption capability (VAC) is defined as a measure of the landscape’s ability to absorb alteration and maintain its visual character. It expresses the likelihood that a landscape change will be noticeable, and serves as a general predictor of visual impact (**Figure 4**). It describes how well a landscape

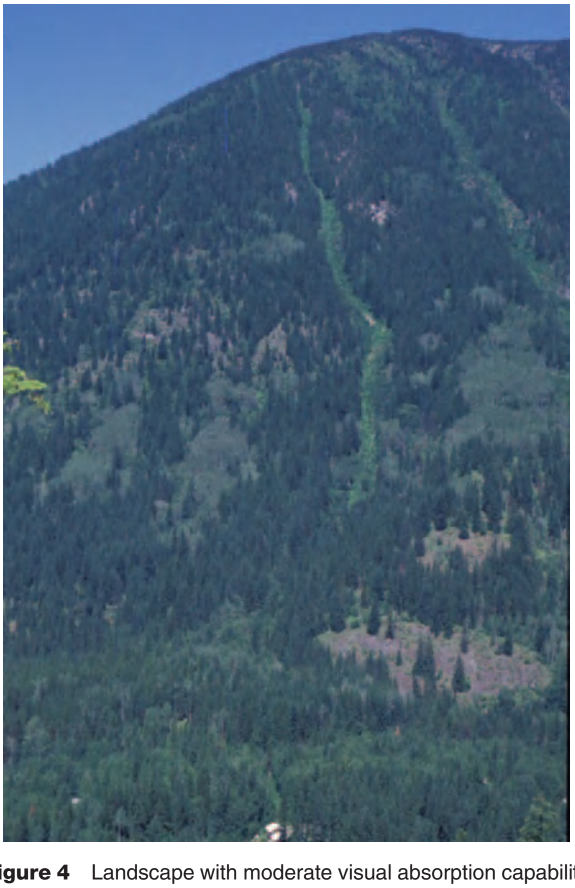


Figure 4 Landscape with moderate visual absorption capability due to strong vegetative patterns but steep terrain.

disturbance might fit in to the landscape. Typical indicators of VAC may include:

- slope (angle and screening)
- vegetation pattern (color, texture, orientation, uniformity)
- soil erosion potential
- soil color
- landform screening/surface variations
- vegetation screening
- aspect
- man-made features/urban clutter.

Typically, the steeper the slope and the more uniform the surface patterns, the harder it is to design a forest intervention that will be unnoticeable or acceptable to the public. VAC evaluation is usually conducted by visual resource experts, and is intended to help locate and/or design forestry activities to fit the landscape character.

Viewer Sensitivity

Classically, viewer sensitivity levels have been defined as a measure of people's concern for the scenic quality of the landscape. While this can be obtained directly from or verified by community representatives, in most cases viewer sensitivity is assessed based on a set of assumptions about what viewers are likely to care about. It embraces the concepts of landscape visibility (how the landscape is viewed) and viewer concern (how much viewers care about the visual characteristics of the landscape). The key indicators usually used include a few quantifiable and mappable factors:

- type of viewer: recreation users, sightseers/visitors, and residents are commonly considered to be the most concerned
- number of viewers (use volumes)
- visibility and viewing distance from key observer points: foreground and middleground views are most sensitive
- viewing duration and frequency
- other viewing conditions, e.g., roadside screening, direction of view, view angle, etc.
- land designation/policy indicators, e.g., parks, wilderness area, scenic area, scenic highway corridor, designated urban viewshed.

Mapping procedures for viewer sensitivity include composite viewshed mapping from viewing areas and division of visible areas into distance zones (foreground, middleground, and background).

In essence, this part of the assessment weights those areas that are seen most closely and most often by people with a high expected concern for aesthetics in that area. Landscapes that are more seldom seen, or seen mainly by workers, for example, are typically considered to be less sensitive to human disturbance (on visual grounds). While this tends to work in practice, this often-adopted policy has been criticized as representing an 'out of sight, out of mind' approach, and may also raise issues of social justice. It is generally understood that it is best to verify expert assumptions on viewer sensitivity with real perception data from a sample of the affected public.

Visual Quality

Visual quality has been defined in various ways by different researchers and practitioners, but it is often used in forest management as the overall dimension for aesthetics. It is sometimes referred to as scenic beauty, aesthetic value, or a measure of visual preference, factors that approach the landscape as a source of aesthetic enjoyment. It is sometimes directly addressed by forest policies and management practices, though often in a vague manner.

Classically, VRM approaches recognize that landscapes with the greatest visual variety or diversity have the greatest potential for high scenic value (**Figure 5**), using indicators such as slope, rock form, vegetation pattern, and water forms (*see* **Landscape and Planning**: Perceptions of Forest Landscapes). Research and practice have found that such features can create visual interest and draw people's attention. The landscape can therefore be mapped by experts in terms of its level of distinctiveness within a regional landscape character type. This usually assumes a typical observer in a first-encounter viewing situation. Some systems have developed methodologies that recognize a broader range of indicators of visual quality, such as vividness, variety, intactness (freedom from obvious human-made changes), and overall visual unity or harmony of the parts.

Figure 5 Landscape with high visual variety and distinctiveness.

Relatively few studies have attempted to assess the effects of natural disturbance on visual quality. Some scientists believe that cultural forces in Western nations have led to forest landscape preferences (and assessment approaches) that favor a static, visual mode of landscape experience, and an aversion to the death of trees and the 'messiness' which results from rapid landscape change.

In North America and some other countries, human influences on the forested landscape have until recently been viewed as positive features only where they represent limited, traditional (usually pastoral or historic) features of largely rural cultures. Most human interventions in landscape assessment approaches are treated as negative 'visual intrusions' by default. The largely expert-based US Forest Service Visual Management System in 1974, for example, equated departure from natural-appearing conditions with reduced visual quality, on the assumption that the public visiting the US National Forests held an expectation of a naturally appearing landscape character. Western research on human perception of timber harvesting does provide support for these assumptions: visual preferences generally decrease as the perceived degree of disruption (i.e., sudden change, perceived destruction, and 'messiness') increases, and people tend to prefer smaller-scale clear felling or plantations, for example, over larger changes. Expert evaluations of existing visual condition (EVC) attempt to map and quantify the apparent naturalness of or level of human disturbance in the landscape, as a contribution to overall visual quality at a given time.

In more obviously developed and culturally modified regions, there is no baseline of a natural landscape that can readily be used in visual analysis, and a richer set of issues and influences on aesthetic values needs to be considered. In some countries with long cultural histories of landscape manipulation, for example in Europe and China, formal views of aesthetic quality have arisen from art appreciation, landscape design, and other cultural or religious movements, which recognize human modifications or transformations of natural landscapes as closer to the ideal (**Figure 6**). These beliefs can lead both to an expert view of appropriate or higher-quality scenery, and popular appreciation of certain landscape characteristics. These values can be applied to forests by means of landscape assessments or appraisals by experts, which identify the important aspects of both natural features and landscape heritage to be protected.

Other approaches to assessing visual quality have relied exclusively or partly on soliciting people's opinions on different landscapes or landscape conditions. This can take various forms, from direct judgments about levels of scenic beauty to general questions on preference (like/dislike). Public perceptions can also be gathered on one or many of the factors described in the expert assessments, such as viewer sensitivity. Such methods can be used to verify the criteria and results of experts, though this practice is still rare. Methods have not generally been well documented, and range from very loose public participation exercises to rigorously controlled psychological experiments. One of the few methods of measuring and predicting public perceptions that has been formalized and documented is the Scenic Beauty Estimation method developed by Terry Daniel of University of Arizona, which associates people's stated scenic beauty judgments with physical features of forested landscapes, such as stand density or openness of views. A variety of methods are available to collect public perception information: workshops, stand-alone surveys with images to be rated (e.g., photo-questionnaires), public meetings where surveys are administered, user-selected field photography exercises, etc.; certain methods may not be equally suitable for all cultural contexts.

Figure 6 Wychwood Forest, Oxfordshire, UK: an example of a pastoral landscape with relic woodlands which hold substantial cultural meaning to local residents.

Landscape Meanings

While it is generally believed that visual quality of forested landscapes can be associated closely with human preference, it is also understood that many other factors beyond a concern with aesthetics or beauty are invoked by the look of the forest. These other meanings that the forest landscape may have for people may be confirmed, suggested, or exaggerated by certain visual characteristics. With indigenous cultural groups in North America and elsewhere, visual quality can be difficult to separate from other cultural, spiritual, and use values of the land and forests.

Assessment of public observer factors needs to take into account the particular sociocultural context, drawing on cultural traditions, use areas, documented public preferences in the area, past project experience, etc. There are many possible influences on human perceptions of landscape and their appreciation of it (*see* **Landscape and Planning**: Perceptions of Forest Landscapes). Both instinctive and cultural factors may exert an influence. Factors that may need to be taken into account in evaluating landscape meanings for forested areas include: familiarity and level of knowledge of observers with local conditions; the ability of the landscape to offer further information for viewers, e.g., through following a path or attaining a prospect over the surrounding landscape; and the relationship of the viewer to forestry activities (e.g., logger versus environmentalist). Theories such as information processing of landscape scenes and prospect-refuge theory underpin some of these kinds of analysis. Simply because a given forest landscape is not particularly scenic or unusual does not preclude strongly held local values for that landscape and how it appears to be managed. There is considerable literature documenting the values in the ordinary local landscape.

Methods of evaluating landscape meanings from observers include the range of public perception gathering techniques discussed above plus anthropological and sociological methods such as oral history documentation and cognitive mapping of community areas.

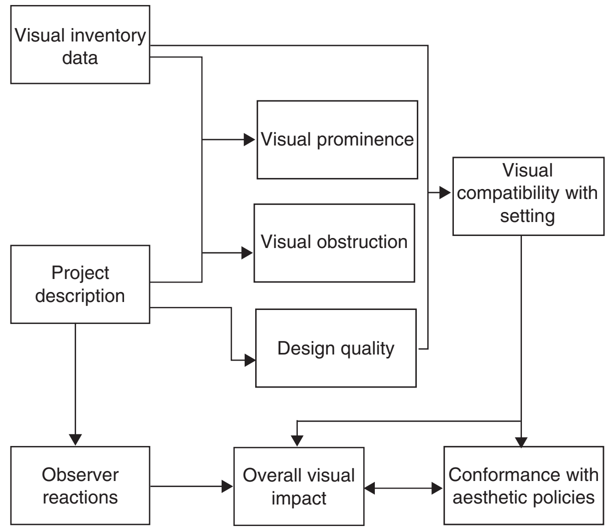


Figure 7 Example of criteria used in the process of visual impact assessment for proposed management activities. Reproduced with permission from Sheppard SRJ (1989) *Visual Simulation: A User's Guide for Architects, Engineers & Planners*. New York: Van Nostrand Reinhold.

Visual Impact Assessment

Visual impact assessment has the purpose of supporting project level decisions and design activities, for consideration alongside assessments of other ecological and social impacts. Expert impact assessments normally determine whether and to what extent the proposed activity would be visible (using techniques such as viewshed mapping), and then describing and evaluating the expected landscape changes (**Figure 7**). Often, visual simulations (or landscape visualizations) are used to assist the process by depicting the expected visual condition of the landscape (*see* **Landscape and Planning**: The Role of Visualization in Forest Planning). Many of the same issues addressed in the overall landscape assessment described in the preceding section also apply to the more particular assessment of project visual impacts.

Visual impact assessment is based on the same general principles and procedures as other resource impact assessments, derived from international and regional environmental impact assessment guidelines codified for example in the National Environmental Protection Act in the USA and World Bank policies. Typically, visual impact assessments contain a baseline assessment, description of visual aspects of the project, assessment of expected visual effects (magnitude and significance), review of compliance with visual quality objectives (VQOs) and policies, mitigations required or desired, and assessment of any residual visual impact. Visual impact can be considered positive or negative/adverse, with impacts described in terms of type, severity, significance or otherwise. Mitigation methods identify visual characteristics that can be modified through the redesign process to achieve a lower or more compatible level of visual impact.

A variety of criteria have been used for assessing the visual impact of forest management activities. Most commonly these address the prominence or visual dominance of the activity relative to the surrounding landscape (**Figures 8** and **9**), and comparison with the desired objectives established through a visual analysis (VRM) process. Thus, a proposed timber harvesting operation might be assessed in terms of the expected visual condition relative to the VQO established for the area. Less visibly contrasting management actions, such as dispersed partial cutting, are more likely to meet a given objective or maximum dominance level than a more contrasting technique such as clear-cutting (**Figure 10**). However, other criteria may be important, such as view blockage, design quality, or other indicators of visual compatibility with the local landscape. Some agencies have developed structured and comprehensive

Figure 8 Harvesting approaches using a geometric pattern of removal tend to be visually dominant. Photograph by P Picard, Collaborative for Advanced Landscape Planning (CALP).

methods of assessing visual impacts, such as rating visible landscape modifications in terms of strong to weak visual contrasts in form, line, color, and texture of the landscape. Some visual impact assessment systems also evaluate harvesting plans on criteria of design (e.g., 'Does it exhibit elements of good visual design?'), and scale (e.g., 'What portion of the visual landscape do existing alterations and proposed operations represent in perspective view?') These criteria can sometimes be quantified through image measurements or professional scoring. However, some research suggests the more numeric systems may suffer in terms of reliability between raters.

Again, public perception information can be used in assessing visual impacts of forestry. People can be asked to judge the visual impact level or acceptability directly, or they can be asked to indicate the criteria important to them for evaluating visual impact, which can avoid bias due to direct 'voting' for an alternative preferred for a variety of aesthetic and other reasons. Public perception data are useful for verifying effects on local or public values, but consistent data should not be expected for all individuals. The view of a cut block or plantation may be a symbol or trigger for many other emotional or cognitive responses, which originate in other sources of information beyond the landscape itself, e.g., cultural background, recent news events, etc. In recent years, a movement headed by Gobster has advocated the improved understanding of ecological processes as a basis for a more informed landscape preference: the 'ecological aesthetic.' The experience of community forests and pre-industrial-scale forestry traditions in many countries suggests that increased activity by local forest managers working inside the community, demonstrating care for the local landscape (sometimes termed 'visible stewardship'), may lead to higher community acceptance of timber harvesting than would reduced or concealed forest management activity. This suggests that visual impact assessments should consider the informational process by which landscape changes are planned, presented, and implemented.

Nonetheless, in Western countries, public reaction to change in the forest setting often demonstrates a negative association with large-scale or rapid landscape disturbance. It is possible to predict the severity of visual impact by examining the proposed project approach to particular practices likely to trigger public concerns, such as perceived waste of resources when slash and snags remain on site (**Figure 11**) or where there are ineffective and wind-prone buffer strips between the viewer and the activity.

Visual impact assessment needs to consider the time elapsed since the activity took place. In general, the longer the time from the disturbance, the lower the visual impact. Vegetation succession tends to reduce visual contrasts, and at some point people may no longer recognize the area as disturbed by humans. Active management areas, once regenerated, may have higher scenic value to people. Perception studies conducted in British Columbia, for example, found a significant threshold, termed Visually Effective Green-up, with tree heights of 3 to 8 meters in clear-cuts.

The foregoing discussion has been couched in terms of predicting visual impacts from future forestry activity. However, visual impact assessment is also necessary for monitoring and assessing visual conditions after the management activity (e.g., post-harvesting assessments) and on a regular basis as part of certification or adaptive management programs.

Conclusions and New Directions

Visual analysis has evolved over the last few decades into a suite of approaches that can be used to describe objectively and even quantify many aspects of the appearance of forest landscapes. The analysis and prediction of public responses to landscape conditions is much more complicated and uncertain, although in certain cultures (notably younger Western nations with a strong image of the natural landscape), research and forestry practice have revealed strong patterns of preference for certain levels and types of forest management practice. In these conditions, prescribed forms of visual analysis leading to VRM programs have proved fairly robust

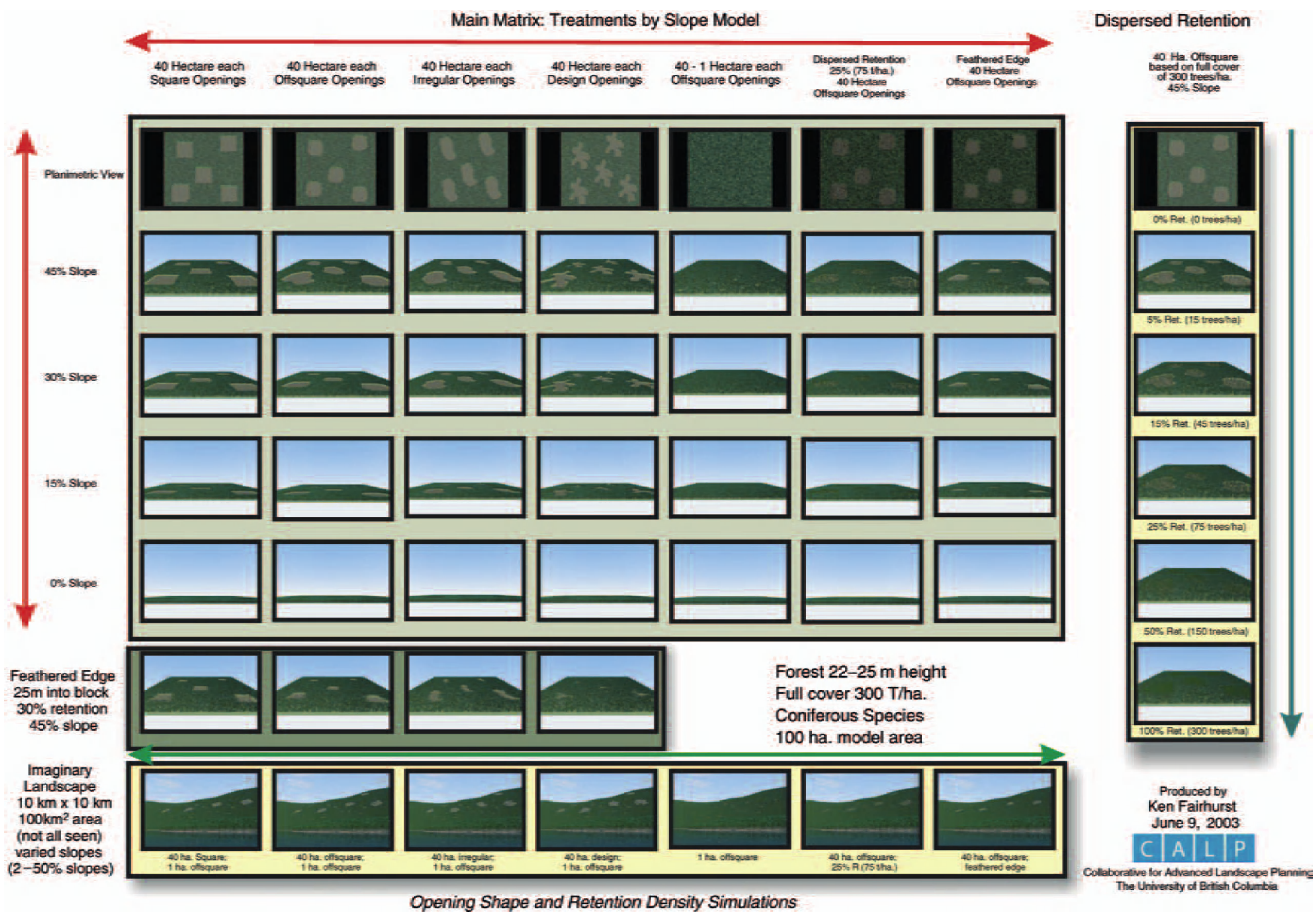


Figure 9 Controlled landscape visualizations of hypothetical forest harvesting treatments, showing differing levels of visual dominance with different design approaches. (Figure by Ken Fairhurst, CALP, reproduced with permission from British Columbia Ministry of Forests.)

Figure 10 Examples of partial cut (left) and a square clear-cut (right) as seen in winter. Photographs by Paul Picard, CALP.

Figure 11 Foreground view of landscape showing 'messy' waste material from a logging operation.

(*see* **Landscape and Planning:** Visual Resource Management Approaches). Here, visual analysis can provide a credible basis for policy objectives and design.

The applicability of such methods in other cultures has yet to be comprehensively established. There are as yet no accepted universal standards for aesthetic enjoyment of forest landscapes, and much more work needs to be done on the analysis of landscape meanings and sense of place, as part of defining social sustainability. In the meantime, there seems to be small risk in a careful, detailed attempt by experts to survey and describe landscape conditions, so long as the spiritual, cultural, and historic aspects of the landscape are given full weight, and expert evaluations are compared to and integrated with the knowledge and priorities of local people and other concerned users. The evolving role of other factors such as information, education, and economic necessity in determining public preferences must also be acknowledged. Expert-driven visual analysis should always begin with objective inventory and description before attempting more judgmental evaluations and interpretations, which should be grounded in the local landscape conditions and cultural context.

There do appear to be many places in the world where forestry is conducted without a sensitivity to visual concerns, and many would draw parallels between this experiential deficiency and the long-term unsustainability of the associated forest practices. The interactions between ecological values and aesthetic values require much more study. Time will tell whether emerging concepts in Western countries, such as an ecological aesthetic and visible stewardship, are able to transform how the public views forest management activities; it is interesting to speculate whether such movements will take Western nations back towards the more holistic views of landscape and human use observed in many indigenous cultures. Certainly, more research is needed on the effects of information of various kinds on people's preferences for forest landscapes.

We can expect increased use of visual monitoring methods to track data on both general forest conditions and aesthetic qualities: inexpensive systems of key observer points or 'landscape control points' need to be set up to provide long-term, systematic measurement and documentation of landscape change in perspective view through standard photography, to augment remote sensing data. Such systems, and visual analysis in general, should not be seen as relevant to just 'front-country' situations, in places most visible from current human-use areas: even remote landscapes are being increasingly used for recreation and tourism, and the internet provides the mechanism to broadcast imagery from anywhere in the world to a concerned public that is likely to judge forestry by its appearance.

See also: **Landscape and Planning**: Perceptions of Forest Landscapes; Perceptions of Nature by Indigenous Communities; The Role of Visualization in Forest Planning; Visual Resource Management Approaches. **Recreation**: Inventory, Monitoring and Management.

Further Reading

Appleton J (1996) *The Experience of Landscape*. Chichester, UK: John Wiley.

Bell S (1999) *Landscape: Pattern, Perception, and Process*. London: E & FN Spon.

Brown TC and Daniel TC (1986) Predicting scenic beauty of timber stands. *Forest Science* 32(2): 471–487.

Crowe S (1966) *Forestry in the Landscape*. Forestry Commission Booklet no. 18. London: HMSO.

Gobster PH (1995) Aldo Leopold's ecological esthetic: integrating esthetic and biodiversity values. *Journal of Forestry* 93(2): 6–10.

Institute of Environmental Assessment/The Landscape Institute (1995) *Guidelines for Landscape and Visual Impact Assessment*. London: E & FN Spon.

Litton RB Jr. (1968) *Forest Landscape Description and Inventories*. US Department of Agriculture Forest Service Research Paper no. PSW-49. Berkeley, CA: US Department of Agriculture, Pacific Southwest Forest and Range Experiment Station.

Lucas OWR (1991) *The Design of Forest Landscapes*. Oxford, UK: Oxford University Press.

Province of British Columbia, Ministry of Forests (1996) *Clearcutting and Visual Quality: A Public Perception Study*. Victoria, BC: Range, Recreation and Forest Practices Branch, Province of British Columbia, Ministry of Forests.

Province of British Columbia, Ministry of Forests (2001) *Visual Impact Assessment Guidebook*, 2nd edn. Victoria, BC: Forest Practices Branch, Province of British Columbia, Ministry of Forests.

Sheppard SRJ (1989) *Visual Simulation: A User's Guide for Architects, Engineers & Planners*. New York: Van Nostrand Reinhold.

Sheppard SRJ and Harshaw HW (eds) (2001) *Forest and Landscapes: Linking Ecology, Sustainability and Aesthetics*. Wallingford, UK: CAB International.

Smardon RC, Palmer JF, and Felleman JP (eds) (1986) *Foundations for Visual Project Analysis*. New York: John Wiley.

US Department of Agriculture Forest Service (1973) *National Forest Landscape Management*, vol. 1. *The Visual Management System*. Agriculture Handbook no. 434. Washington, DC: US Government Printing Office.

US Department of Agriculture Forest Service (1974) *National Landscape Management*, vol. 2. *The Visual Management System*. Agriculture Handbook no. 462. Washington, DC: US Government Printing Office.

Visual Resource Management Approaches

S Bell, Edinburgh College of Art, Edinburgh, UK

Background and History

The issue of visual resource management in forestry largely came to prominence after World War II, as the increasing network of highways and mass car ownership enabled large numbers of people to explore the countryside or natural landscapes of North America, Europe, and other developed countries. This period also coincided with greatly increased forestry activity such as afforestation programs in Britain, Ireland, and New Zealand and with increasing levels of timber harvest in the USA, Canada, and Scandinavia, especially on public lands. By the mid-1960s public concerns over the appearance of both newly planted forests and logging operations had increased, prompting agencies such as the British Forestry Commission and the US Forest Service to look for ways in which to safeguard the landscape. The models developed in Britain and the USA followed different routes, partly due to the scale of the forests and forest operations but also reflecting the type of forestry.

The US Model

In the USA logging took place (and still mainly takes place, at least in the National Forest System) in extensive natural forests, where the visual impact of sudden changes to the scenery, occurring over a large-scale landscape, can be very great. While the impact of an individual cutblock could have a negative visual effect, the cumulative impact over large areas was often considered to be greater still. This prompted the development of an approach to suit the scale of the landscape, the extent of the forest, and the need to try to control the rate of landscape change and its degree of impact, an approach that is generally referred to as 'visual resource management' or VRM. This approach aimed to manage the level of impact of logging on the natural scenery, especially as seen from key viewpoints, and this led to a highly developed visual management system intended to prioritize areas within large tracts for different levels of scenic protection (described below in more detail).

The UK Model

In Britain, the program of afforestation led to significant landscape change but each new planting project was relatively self-contained and there was some degree of flexibility over the layout of such forests. Owing to the fact that conserving an existing landscape was not an option, and considering the freedom to create new landscapes offered to the foresters of the time, a design-led model was developed following the appointment of a landscape architect, Sylvia Crowe, to be a consultant to the Forestry Commission, which aimed to use creative landscape design to produce new forest landscapes of good visual quality to fit into the landscape, especially as seen from significant public viewpoints. This is referred to as the 'proactive design approach.'

The Picturesque and the Natural

Although these approaches are generally quite different, they do have some similarities. Both models emphasized the value of the scenic, external mode of landscape experience. Viewers observe the scene from a distance and the aesthetic quality is associated with the notion of the picturesque, the landscape aesthetic model that emerged in the late eighteenth century and which for the first time celebrated the wild beauty and sublime qualities of untouched nature. Viewers expect to see 'natural' scenery and the presence of unnatural elements disturbs the quality (although in many countries, especially Britain, there is no actual natural scenery left). Design aspects were included in the American system, though not so highly developed and not so rigorously applied, while in Britain a degree of management based on relative sensitivity or landscape importance (based on visibility and numbers of likely observers) meant that some areas were designed more carefully than others.

Both Britain and the USA have hills and mountains that are highly visible from roads, settlements, hiking routes, and mountain summits, which partly explains the importance given to the scenic external mode of viewing and appreciation. Forest policy-makers and managers in other heavily forested countries with less dramatic topography, such as Sweden or Finland, where views of the landscape are confined more to forest interiors, did not feel a need to develop VRM programs to the same degree until much more recently. Nor did countries with forested mountains and high scenic qualities, such as Alpine countries, where the forests are managed by continuous cover or selection types of silviculture system. In these areas, although the landscape is highly visible and valued for its scenic, picturesque qualities, dramatic changes to the landscape tend not to take place because there is no clear-cutting, so that the perception of a never-changing natural landscape can be maintained.

The Former Soviet Union

In the countries of the Soviet bloc a much simpler approach was taken which remains in force in many of the former Soviet countries and in Russia itself. Here the forest was divided into three groups. Forests in Group One, accounting for some 25% of the forest area, include many forest reserves, protected for a variety of reasons, landscape and scenic value being one. In such reserves clear-cutting or any form of final felling is not permitted. Therefore, the landscape tends not to suffer dramatic changes, once more preserving the illusion of the never-changing character of the natural forest. Special landscape zones, where such landscape protection is applied, are frequently along roadsides, around cities and towns, and in other places where people can be expected to want the landscape to be protected. It was a highly centralized, regulation-based model, with no support from public preference studies or other evidence. Group Three forests are those where commercial exploitation is permitted (about 70% of the area) and Group Two forests represent an intermediate category. Such a system is effective at controlling the rate of landscape change in visually sensitive areas as long as the land is owned by the state and the central control is strong. Countries of the former Soviet Union, such as Latvia, which became independent and where much of the land was given back to its former owners, were forced to abandon such methods and look elsewhere (see below).

Following the development of the VRM systems in the USA and Britain, the other countries where these methods were adopted also tended to be where either large-scale clear-cut logging or significant afforestation took place in dramatic, highly visual landscapes and where the population expressed concern for the landscape (or where tourism in such areas was important). Thus, places like British Columbia in Canada, New Zealand, parts of Australia, and Ireland tended to be interested in developing similar systems. In the case of New Zealand, an early landscape design-based system was developed independently, whereas in most of the other cases it was adapted from either the USA or Britain, or included elements from both countries.

The Visual Management Approach

The US Forest Service developed a comprehensive system, starting in the 1960s and continuing through the 1970s. The first stage of development was to hire a researcher, R. Burton Litton Jr, to look at forest landscapes and to develop a visual resource inventory and evaluation program. Following this a basic description, analysis, and classification system was developed and implemented. The system was presented in a series of booklets, the first of which explained how to consider a landscape, how to describe and analyze its various characteristics and it introduced some basic design principles, such as line, form, color, and texture and considered the effect of scale, light, time, viewpoint, etc. on how landscapes are perceived in order to introduce some rigor and rationale into the subject (**Figure 1**).

The second booklet presented a method of landscape inventory and analysis so that a forest area could be divided into landscape units, emerging from an overlay analysis, each with its own combination of visual character, visibility, and level of sensitivity. This enabled planners to ascribe a series of visual quality objectives (VQOs) to each landscape unit. For example, in a highly sensitive landscape – one that was very visible to a lot of people, with a high visual quality (often meaning an undisturbed canopy of climax mature forest) and no visible logging – the foreground area might be given the VQO of 'preservation' where no logging was allowed, and the middle ground area, a little further from the viewer, given a VQO of 'partial retention,' where some logging was permitted as long as it did not disrupt the character of the area and any visible logging was subordinate to the rest of the landscape. The base level of VQO for the least sensitive areas was always 'maximum modification,' which meant that logging could proceed free of visual constraints (in some ways the implementation of the system was very similar to the Soviet model, though with some democratic input at the forest plan approval stage). Subsequent books in the series dealt with more detailed aspects such as the design and layout of logging, roads, utilities, and range issues to minimize visual impact.

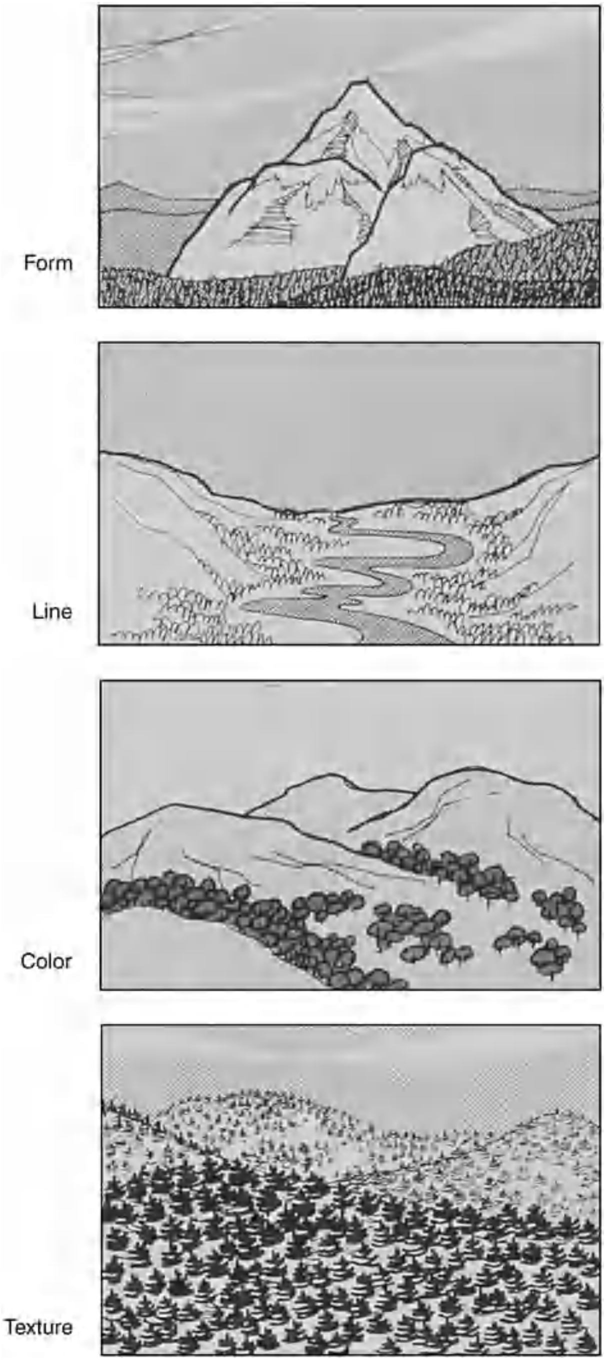


Figure 1 An example from the early US Forest Service visual landscape management system, presenting basic design principles for use in forestry. From US Department of Agriculture Forest Service.

Implementation

The implementation of this system was often prioritized for the visual portion of the landscape as seen from roads and key viewpoints (given that maximum modification was the baseline VQO supposed to be applied everywhere). Viewshed analysis identified what was and was not visible from a set number of viewpoints and the landscape was divided into units, analyzed, and given visual quality objectives. VQOs, set by experts, therefore represented the desired requirements for the visual resource, to be incorporated into the wider forest planning process which included many other resources, such as timber, water, wildlife, recreation, range, and so on. All these competing requirements had to be balanced and this led, in some circumstances, to the visual resource being overridden by other values.

As forest management came under increasing pressure from campaigners for biodiversity and the protection of endangered species (during the late

1980s and 1990s) ecological factors and ecosystem management began in many cases to supersede the significance of the visual and other resources. Logging in some forests of the Pacific Northwest was reduced in scale or ceased altogether for a time, so that changes to the visible landscape became less significant.

Scenery Management System

During the 1990s the system, then some 25 or more years old, was in need of an overhaul and the result was the Scenery Management System. This incorporated much of what was good about the original system but placed more emphasis on landscape character, which recognized the uniqueness of every area and the contribution made to it of cultural as well as natural features.

The current system starts with an Ecological Unit Description, sometimes called a mapping unit description, which represents the common starting point for both the Scenery Management System and for Ecosystem Planning. This was introduced in order to integrate scenery and ecosystem management to some degree and to overcome perceptions that the two aspects could be in conflict with one another. From the Ecological Unit Description an objective (i.e., factual) description of biological and physical elements is extracted, and combined with attributes for landscape character to produce a landscape character description. The idea is to be able to group the combination of scenic attributes that make each landscape distinct, identifiable and unique. This description provides the baseline or reference for the next stages, of defining scenic attractiveness classes and degrees of scenic integrity.

Scenic attractiveness classes are used to determine degrees of relative scenic value of different areas within a particular landscape character zone. There are three possible classes: A – Distinctive, B – Typical, and C – Indistinctive. The method of calculating relative scenic value is to describe the landscape elements that make up each character zone in terms of line, form, color, texture, and composition. Scenic integrity indicates the degree of visual disruption of landscape character. If a landscape has very low disruption it has a very high degree of scenic integrity and vice versa. There are six classes of scenic integrity, from Very High to Unacceptably Low.

The next stage examines the visibility of the landscape and takes into account two factors: (1) the relative importance to the public of various parts of the landscape and (2) the relative sensitivity of the scene based on its distance from observers. Relative importance to the public may come from a variety of sources, including special perception and preference studies. Constituent analysis (a technique for evaluating the views of different people) is used to gauge a level of public concern about aesthetic qualities, assessed as high, medium, or low. Distance zones of foreground, middle ground, or background are used to classify relative sensitivity.

The scenic attractiveness classes and landscape visibility data are combined to create Scenic Classes, ranging from 1 to 7, which indicate the relative importance or value of discrete landscape areas. These scenic classes are used during forest planning (**Figure 2**).

Landscape Value Maps

It is also possible to prepare a landscape value map using overlays in a geographic information system (GIS), in order to present the information spatially for use in various planning procedures. During the development of a plan for a forest area, the descriptive aspects of landscape character are used to develop landscape character options that are deemed to be realistic within the overall multi-objective forest plan. Once the forest plan has been adopted, the landscape character description becomes a management goal and the scenic integrity levels become scenic integrity objectives. These are very similar in nature to the previous visual quality objectives. The idea is that a given level of scenic integrity should not be reduced by forest activities, although it is also recognized that the degree of scenic integrity can change over time through natural landscape processes. In order to meet a specific integrity level and to carry out logging or road construction some design is needed. This is where the system is weakest: it provides very little guidance and few examples of how to achieve a satisfactory result.

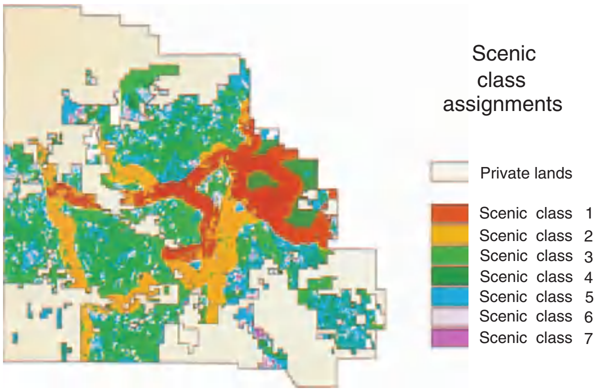


Figure 2 An example of a map showing Scenic Classes derived using the Scenic Management System. From US Department of Agriculture Forest Service.

There have been a number of spin-offs from the US Forest Service systems. The US Bureau of Land Management adopted the VRM system and also incorporated a systematic visual impact assessment process into it. This system was widely implemented during the 1980s and 1990s.

The British Columbia System

The VRM approach was also adopted by the Ministry of Forests of British Columbia, Canada. British Columbia is mountainous and densely forested, and also relies heavily on the timber industry for its economic well-being. In the early 1970s managers recognized that as more and more logging became visible on prominent mountainsides and from significant tourist routes, whether roads or shipping lanes, some kind of visual resource management was necessary. A landscape forester was charged, in 1979, with developing this based on the US Forest Service system, with many adaptations.

The system as originally developed and applied consisted of three steps. Step 1 is landscape inventory, where three elements are identified. The first is the identification of the extent of the landscape visible from established viewpoints such as roads, settlements, and recreation areas. The second element is the suite of landscape features present, both natural and human-made. The third element is landscape sensitivity, calculated from physical factors and viewer-related factors such as numbers of viewers, viewing distance, viewing duration, and perception.

Step 2 is landscape analysis, consisting of detailed mapping, the recommendation of VQOs, and the final establishment of VQOs by the forest manager, taking into account the other resource factors that have to be balanced against aesthetics. Step 3 is design and layout of roads and cutblocks, Step 4 is logging and silvicultural practices, and Step 5 is follow-up (**Figure 3**).

In 1997 a revised method was approved, moving to a more quantitative, numeric and prescriptive

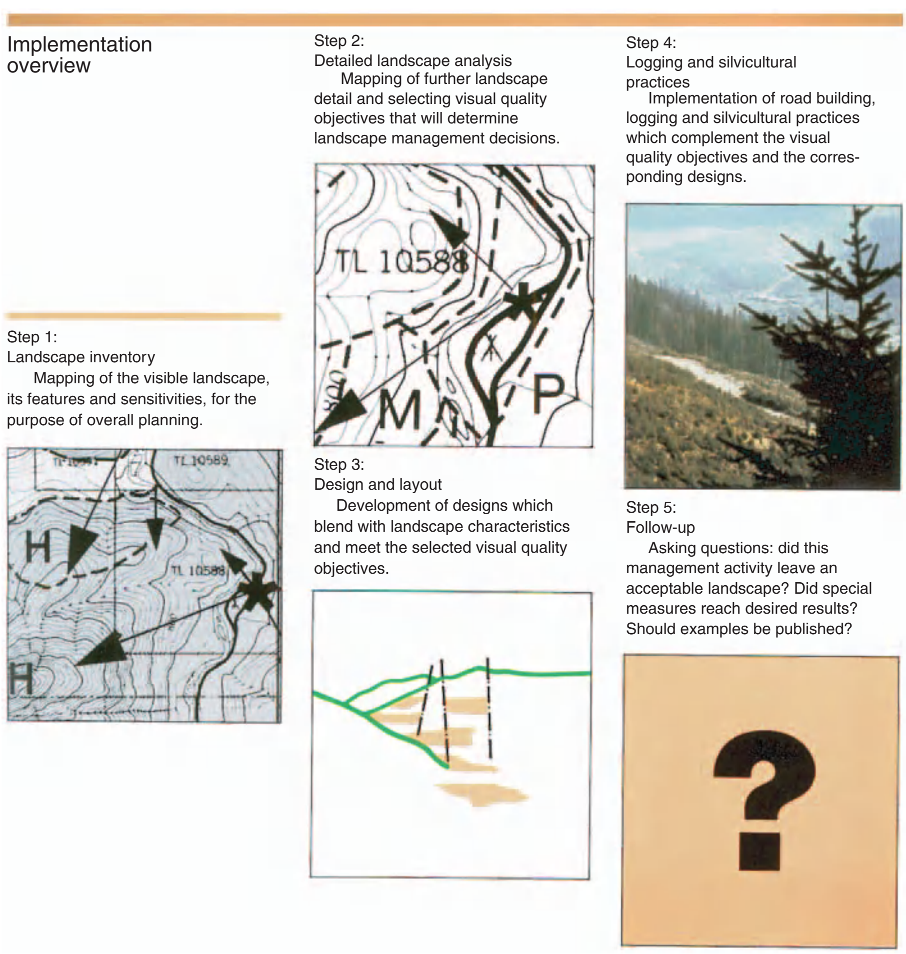


Figure 3 A section from the British Columbia Forest Landscape Handbook demonstrating the five steps of the original version. From British Columbia Ministry of Forests.

system of Visual Sensitivity Classes (similar to VQOs) within preidentified Visual Sensitivity Units.

The information is incorporated into the forest database on the GIS at each forest district and used to inform planners working for both the Ministry of Forests and forest licensee companies. By the early 1990s managers realized that the concept of visual management only achieved a limited level of landscape quality: it could direct how much harvest was possible in a given landscape unit but was not very successful at achieving good design. Thus a form of the proactive design approach was introduced to supplement the visual management system (see below).

Visual impact assessment is the logical development of the visual landscape management system in British Columbia. Where a timber harvest is being planned in a known scenic area with established VQOs, a visual impact assessment is required, in order to prove that the VQOs will be met. It is considered to be an integral part of Step 3 of the process described above. For this it is necessary to prepare a design for the proposed activity and to illustrate how it will look from established viewpoints using various simulation tools, and then to justify how it will meet the VQOs. This includes a qualitative assessment based on the adherence to design principles and also a quantitative assessment based on a concept of 'percent alteration,' where the proportion of the visual scene that will be altered by the proposal is calculated (in perspective, not plan). A table is used to assign allowable percentages in relation to different VQOs.

Australia

The US Forest Service system was also introduced into Australia. The states of Victoria and Tasmania adopted it and, especially in the case of Tasmania, developed their own variations. In Tasmania, the whole island has been divided into broad regional landscape character types. This was an integral part of the Visual Management System following US methodology, giving priority for visual management and generalized visual objectives to be achieved. It did not include design-based principles as in the UK but rather specified generic guidelines for various viewing situations and forestry related operations (**Figure 4**). The system is controlled by staff in the Forestry Practices Board, who regulate the environmental quality of logging proposals.

The most recent version of the Tasmanian Visual Management System incorporates a new tool for rating the importance of any area of the landscape and setting visual objectives to guide management, especially of the location and management of plantation forests. This is called the Rural Landscape Priority rating and has accompanying Plantation Landscape Objectives, which relate to three scales of the landscape and viewing. The new visual objectives are 'Integrated effect,' 'Codominant effect,' and 'Dominant effect,' based on the acceptable degree of influence of the plantation forest in the landscape.

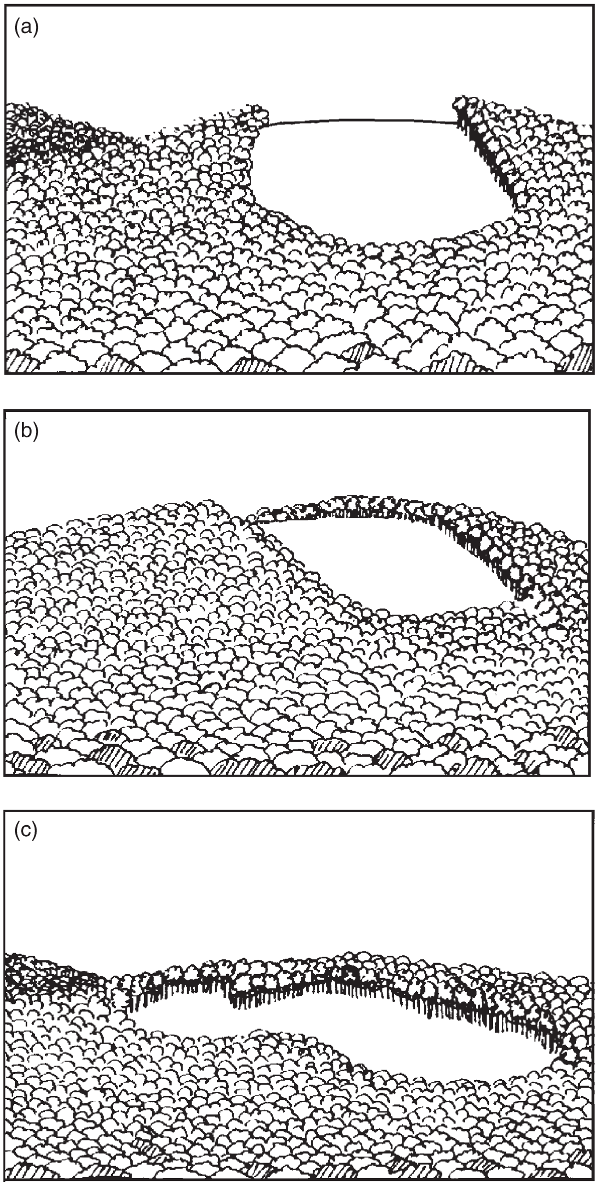


Figure 4 A sample of applied design from the Tasmanian handbook, demonstrating design in relation to a skyline. Skyline notches can have a strong visual impact even when seen in the distant background. (a) Skylines should not be cut directly across in the direction of the principal viewpoint, as the coupe edges will remain clearly visible for many years. (b) If skyline cutting is necessary, arrange the harvest at an angle to the main viewpoint. (c) The impact is lessened if the harvest is along, instead of across, the skyline. From Tasmanian Forestry Practices Board.

In the most sensitive landscapes the assumption is that the integrated effect would be appropriate using strongest adherence to positive design. However all three objectives require the application of principles taken from the proactive design approach (see below).

As an adjunct to the new visual objectives, local visual units are identified and corresponding landscape character attributes defined as a guide to forestry (**Figure 5**). The aim is generally to retain (and in some cases improve) the character diversity between different visual units by achieving specific designs for harvesting and establishment within each visual unit. This is being applied progressively to operations but could be most useful for strategic planning. Thus the management system evolved into a series of local design guidelines as well as incorporating the concept of visual quality objectives based on a viewing rating.

Computer Visualizations

The systems employed in the USA, Canada, or Australia also used early versions of computer visualization software to test the extent to which proposals for logging would meet the established VQOs (*see* **Landscape and Planning**: The Role of Visualization in Forest Planning). In this way a degree of quality control could be exerted in the design and approval process. More sophisticated visualization systems are now available to present much more realistic simulations, especially useful for public participation processes, public consultation, and visual impact assessment.

As well as the visual resource management methods described above for large-scale landscapes, some jurisdictions have developed guidance aimed at the smaller scale of individual logging operations. These concentrate on the leaving of screening belts along roadsides, reducing the impact of slash, ruts caused by harvesting machinery, and road construction. Attention to this kind of detail is important, especially when most views are from within the forest. US states such as New Hampshire and Minnesota have produced booklets describing such practices.

The Proactive Design Approach

In Britain, with its program of large-scale afforestation and, more recently, felling and replanting of its plantation forests, an approach has been developed based on designing forests to fit into the landscape. This originated in the 1960s, aimed mainly at new plantations of nonnative conifers that were being planted on bare, deforested hills and mountains. The original layouts were often highly regular, with

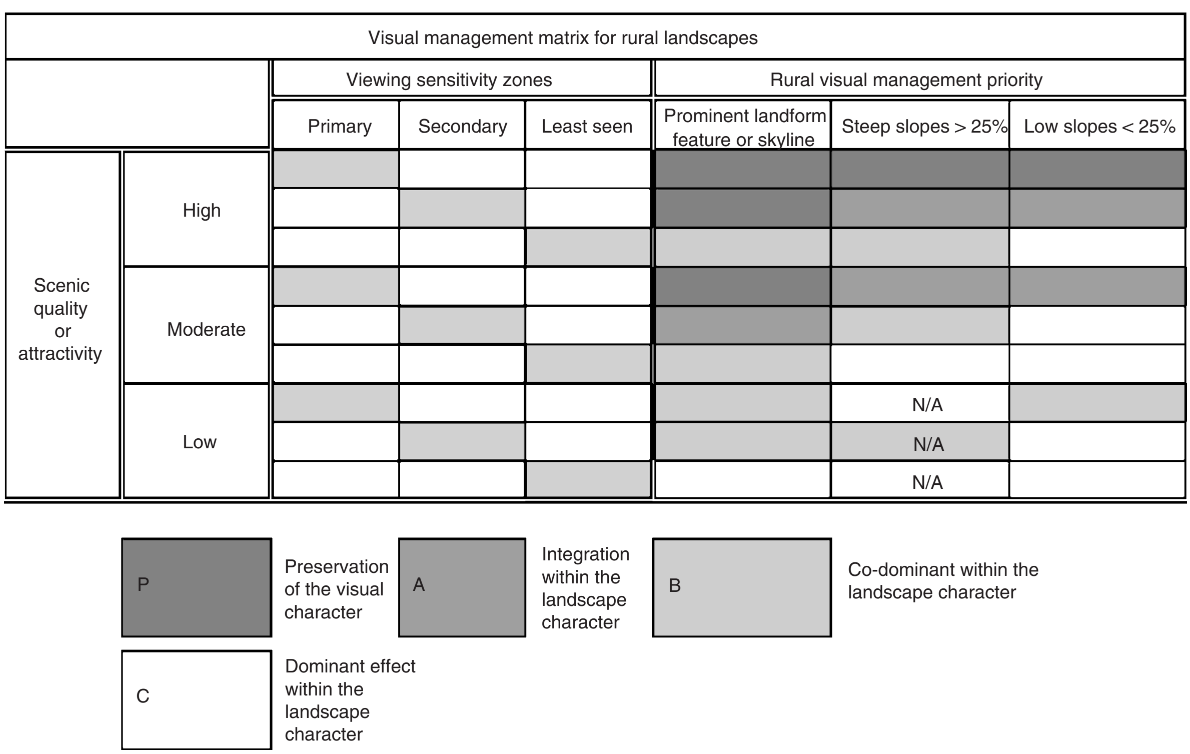


Figure 5 The new visual management matrix for rural landscapes, part of the Tasmanian system. From Tasmanian Forestry Practices Board.

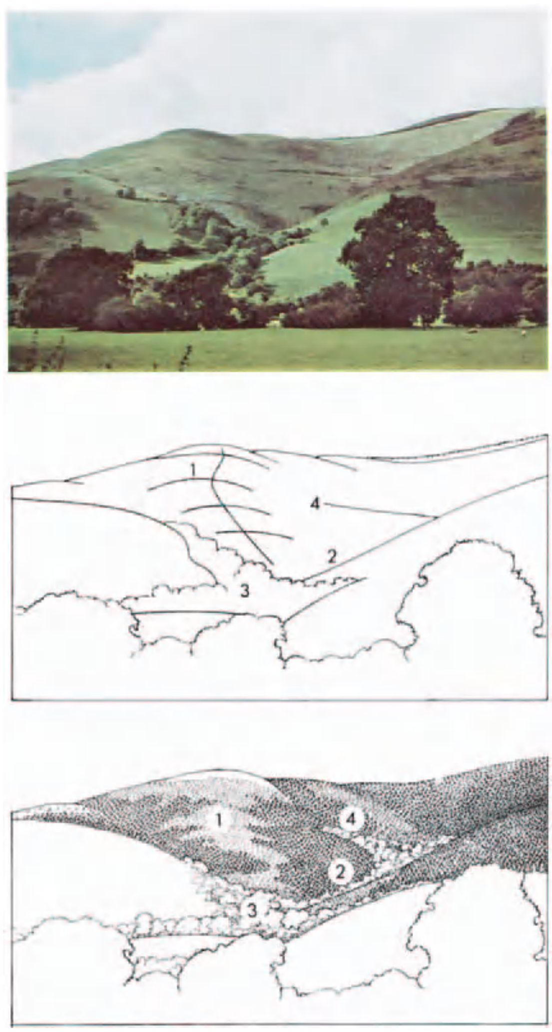
rectangular compartments, vertical fence lines and horizontal upper margins where the trees were planted up to a contour line.

To overcome the artificial appearance of these forests a number of design principles were adopted from landscape architectural practice, for example considering the shape of the forest, its scale and proportion, the degree of diversity of different species, the unity of the forest with its surroundings, how it related to landform, and so on. These principles were developed from the initial work of Sylvia Crowe (**Figure 6**) by Duncan Campbell, Oliver Lucas, Simon Bell, and later generations of landscape architects working for the Forestry Commission.

By the 1980s many of the early forests were ready for harvest and the rate of new planting declined, so the focus shifted to designing the patterns of felling, and the opportunity was taken to use the process of gradually harvesting these forests to completely redesign them, especially if they had not had much design input at planting. At this point a series of detailed guidelines on forest landscape design were published, aimed not only at the state forest sector but also at private forest owners. These guidelines describe what standards are expected and how to achieve them (**Figure 7**). They set out the way the design principles should be applied to aspects of the forest layout but as they need to be interpreted to fit each unique landscape area, they avoid being too prescriptive.

Forest Design Plans

This forest design approach was adopted in the early 1990s as the primary forest-level planning method to be used in Britain. Today, sophisticated 'forest design plans' are the main tool for planning and managing the forests, and they contain a significant element of



The great beauty of this landscape lies in the subtlety of the land-formation.

Analysis
The strongly modelled shoulder (1) flanks the amphitheatre-shaped valley (2). The drift of broadleaves (3) accentuates the composition whilst the forest road (4) cuts across it.

Solution
The modelling of the shoulder could be accentuated by larch (1). Broadleaves would accentuate the valleys (2), linking them to the existing trees (3). The encouragement of native growth at the sides of the forest road (4) curving down to join the valley broadleaves could permanently heal the road scar.

Figure 6 A sample from the first design book prepared by Sylvia Crowe for the British Forestry Commission. © Crown Copyright, reproduced with permission of the Forestry Commission.

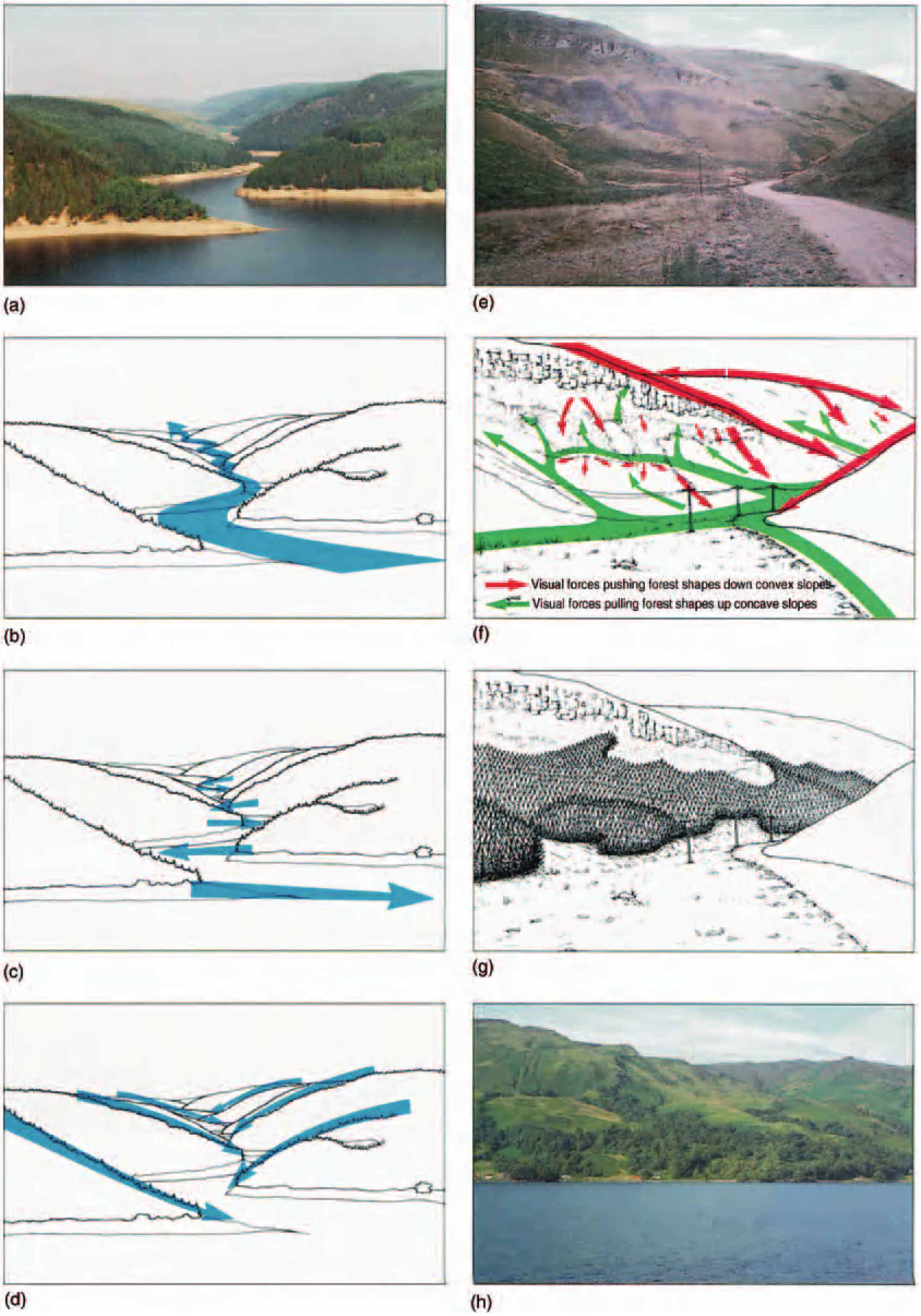


Figure 7 A sample from the Forest Landscape Design Guidelines. (a) Llyn Brianne, Dyfed. (b) The eye is drawn bouncing from one spur to another. (c) The spurs appear drawn together, each into the bay opposite. (d) The eye is drawn downwards on the spurs. (e) A landscape in Northumberland. (f) Analysis of visual forces. The strongest arrows illustrate the largest and most pronounced forms, the smallest the more subtle shapes. (g) The forest margin shapes responding to the visual forces creating a direct relationship between the forest cover and the landscape. (h) The effect of visual forces can be seen in this example at Ratagan where effects of grazing and burning have restricted the woodland to the lower slopes and valleys. © Crown Copyright, reproduced with permission of the Forestry Commission.

redesign to change the original monoculture, even-aged plantations into something more diverse and attractive.

The forest design planning system follows the well-established design process drawn from landscape architecture. Step 1 is to set objectives. These are not solely for visual quality but also for all the other resource values (this emphasizes the integrated character of this approach compared with the single focus on scenic aesthetics of many others). Step 2 is landscape survey (or inventory) where all the information needed for forest planning is collected. Step 3 is analysis. One key type of analysis is that of landscape character, using perspectives as well as plans (*see* **Landscape and Planning**: Visual Analysis of Forest Landscapes). This analysis is carried out by applying design principles as descriptors, especially focusing on the main components of the landscape and on the visual problems associated with the existing forest. Step 4 is to develop a design concept, which describes the overall strategy for redesign and the desired future character of the forest. Step 5 is more detailed design, where options for dividing the entire forest into coupes/cut blocks and for replanting it over time are developed and evaluated. The final design is presented using computer-based graphic simulation and submitted for approval in Step 6 (**Figure 8**). Steps 7, 8, and 9 are implementation, revision, and monitoring.

The idea of proactive design has also been tested and developed in British Columbia into a complementary method by which to ensure that the VQOs are being met. A program of training was undertaken to support this and a manual published to demonstrate the process. The design approach also expanded the scale from the single cutblock to the entire forest, looking into the future, so that anticipated changes over time and any unforeseen problems caused by cumulative effects could be tested (**Figure 9**). This developed into a much more integrated design method similar to that used in Britain, with the added element of a more comprehensive ecological analysis, based on work developed in the US Forest Service by Nancy Diaz and Dean Apostol, where the proactive design approach was also tried out (see below).

A similar program to that of British Columbia was developed in the Maritime and Atlantic provinces of Canada (Labrador, New Brunswick, Newfoundland, Nova Scotia, and Prince Edward Island) and Ireland. The integrated model was also applied, looking at the whole landscape over time.

Elsewhere, similar design approaches have been developed over the years. In the 1970s and 1980s a method was established in New Zealand and some regional guidance booklets were produced by Clive Anstey and Steve Thompson. In France researchers at CENAGREF, a government forest research agency, also looked at the British model and developed similar guidance for French foresters. Expansion of forestry in Denmark led to guidelines being produced on forest location and design, while researchers in Sweden have also produced a book which seeks to integrate ecology and aesthetics. In Latvia the design approach was also developed, based on the use of a simpler landscape character system and aimed largely at new afforestation, partly in response to the need to replace the Soviet system and also to reflect the change in land ownership and the abandonment of farmland to natural forest regeneration.

Privately Owned Forests

In countries where the forest area comprises the holdings of many small landowners, the kind of broad-scale assessment and design models described above are less easily applied. In Finland, guidance for forest owners considers three key objectives: paying attention to the regional characteristics of the Finnish forest landscape, harmonizing forest management measures with the long-range panoramic views of the landscape, and preserving the pleasant impression of the close range, or feature view. The design of felling coupes is also considered.

Assessing the Success of Visual Resource Management

There has been little recent scientific evaluation of the success of the approaches described above. Casual observation of the US national forests suggests that the VRM approach was successful at directing where logging took place but was unable to exert much influence on the design of individual cutblocks, let alone their cumulative impact. In British Columbia the introduction of design was largely in response to the perceived weakness of the VRM system in this area. Studies have taken place to test whether the expert-led system is supported by the public, for example in the degree of tree growth and stocking densities needed to deliver visually effective ‘green-up’ following logging.

In Britain two routes have been used to validate and test the design-led approach. Several studies have been carried out from the 1980s through to the present to validate the design principles used in the various guidelines and these broadly show public support for the proactive design approach. Secondly,

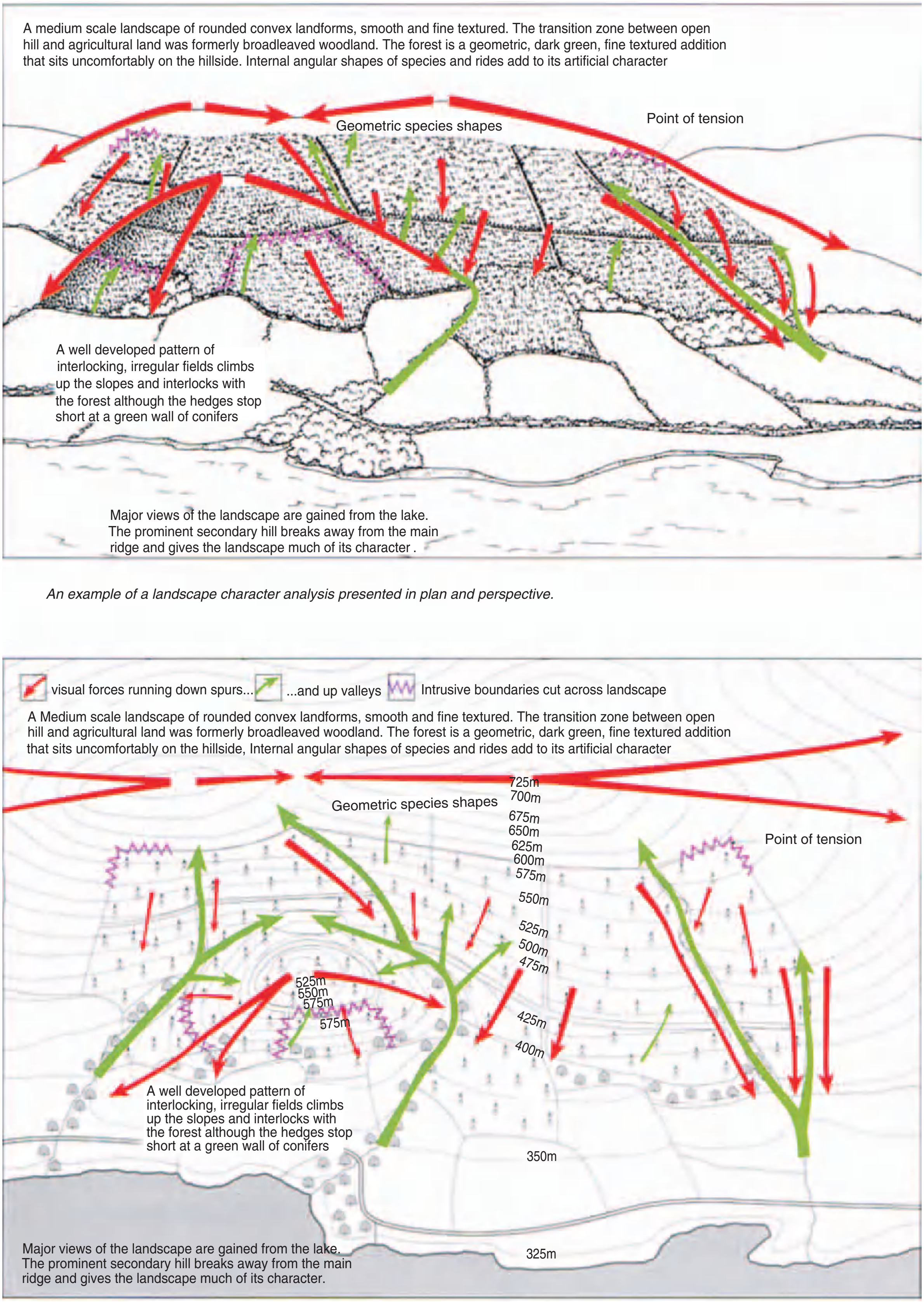
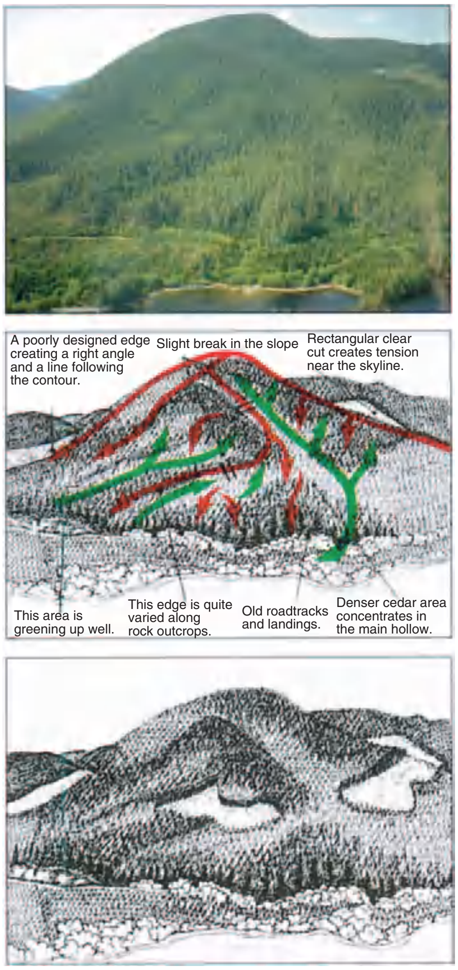


Figure 8 An example showing a detailed landscape character analysis, part of the forest design planning system. © Crown Copyright, reproduced with permission from the Forestry Commission.



A landscape of rounded landforms, mainly convex but with some useful valleys. Older logging varies between poorly designed and acceptable. Any logging should avoid the upper slopes where the hilltop caps should be retained at a sufficient scale (2/3 of the depth). The main valley may need to be retained for riparian protection purposes. Vancouver Island, Vancouver Forest Region.

The following examples demonstrate how units can be fitted into a range of different landscapes using sketches and photographs.

Landform and land feature analysis.

Two clear cuts are proposed and shown as their basic shapes, which are designed to reflect those in the landform-flowing and curvilinear. They are positioned asymmetrically, one bigger than the other. Implicit in their design is the possibility of further units and unfelled areas. To reduce the contrast, the edges should be thinned and stable trees left within the units toward the edges.

Figure 9 A cutblock design example from the British Columbia Visual Landscape Design Training Manual. From British Columbia Ministry of Forests.

in 1999 a monitoring project across the UK assessed the extent to which the upland conifer plantation forests had reached an acceptable standard according to the guidelines. The results were mixed but showed that most of the design plans would, over time, meet the standards; one of the problems is the long timescale of forest design implementation. Also in 1999 some evaluation of pilot forest designs was carried out in New Brunswick and Nova Scotia, Canada. These had been developed with public participation so it was possible to find out how well the communities thought that the designs were being implemented and what they thought of the processes used. The results were positive.

As yet, aesthetics has not been well integrated into systems of sustainability criteria and indicators as used in certification programs. There are now a large number of completed projects where forests are being managed for timber, visual landscape, biodiversity, and other resources in an integrated way, avoiding the trade-off problems between aesthetic and biodiversity values found in the earliest US Forest Service planning systems. These will not demonstrate fully their effectiveness in comparison to other systems for some years yet, although the application of adaptive management may help to uncover any problems fairly early on.

Conclusions and Trends

With the increased interest in biodiversity, sustainable forest management, and ecosystem management, it would seem that the impetus for visual resource management of forests has to some extent seen its period of popularity pass by, although it remains in routine use. In fact, while the VRM approach has seen little development since the 1995 revision of the US system, the proactive design approach has continued to develop and to be fairly widely applied in some countries.

The main areas of development have been in the approach to holistic or integrated forest landscape design, where the design process as based on landscape architectural models has been refined to incorporate a wide range of objectives, including visual quality but especially aspects of applied landscape ecology.

The advent of GIS, computer aided design, sophisticated visualization methods (*see* **Landscape and Planning**: The Role of Visualization in Forest Planning), and computer modeling has enabled designers and managers to plan and design the visual resource far more effectively. While many studies of public perceptions and preferences for forest landscapes have been undertaken over the years, recent public preference studies have been used to calibrate design guidance (see above) but more such studies need to be done.

The use of landscape character criteria to develop local design guidance also means that visual landscape issues can be demonstrated to be important and that they can be incorporated into forest planning without serious conflict with other resources, without practical problems, or at unrealistic cost. With the increasing importance of community participation in forest planning, visual quality issues come to the fore once more, but this time require understanding of locally perceived landscape and aesthetic values and expectations for the forest.

See also: **Landscape and Planning**: Perceptions of Forest Landscapes; The Role of Visualization in Forest Planning; Visual Analysis of Forest Landscapes.

Further Reading

Anstey C, Thompson S, and Nichols K (1982) *Creative Forestry*. Wellington, New Zealand: New Zealand Forest Service.

Bell S (1993) *Elements of Visual Design in the Landscape*. London: E & F N Spon.

Bell S (1994) *Visual Landscape Design Training Manual*. Victoria, Canada: Ministry of Forests of British Columbia Recreation Branch.

Bell S (1998) *Forest Design Planning: A Guide to Good Practice*. Edinburgh, UK: Forestry Commission.

Bell S and Nikodemus O (2000) *Forest Landscape Planning and Design*. Riga: State Forest Service of Latvia (in Latvian).

Crowe S (1978) *The Landscape of Forests and Woods*. Forestry Commission Handbook no. 44. London: HMSO.

Forestry Authority (1994) *Forest Landscape Design Guidelines*, 2nd edn. London: HMSO.

Forestry Commission of Tasmania (1990) *A Manual for Forest Landscape Management*. Hobart, Australia: Forestry Commission of Tasmania.

Gustavsson R and Ingelog T (1994) *Det Nya Landskapet*. Jönköping, Sweden: Skogstyrelsen.

Hauninen E, Oulasemaa K, and Salpakivi-Salomaa P (1998) *Forest Landscape Management*. Helsinki: Forestry Development Centre Tapio.

Litton RB (1968) *Forest Landscape Description and Inventories*. US Department of Agriculture Forest Service Research Paper no. PSW-49. Washington, DC: US Department of Agriculture.

Lucas OWR (1991) *The Design of Forest Landscapes*. Oxford, UK: Oxford University Press.

Ministry of Forests, Forest Practices Branch (2001) *Visual Impact Assessment Guidebook*, 2nd edn. Victoria, Canada: Ministry of Forests, Forest Practices Branch.

Province of British Columbia (1981) *Forest Landscape Handbook*. Victoria, Canada: Ministry of Forests.

US Department of Agriculture Forest Service (1970) *National Forest Landscape Management*, vol 1. Washington, DC: US Department of Agriculture Forest Service.

US Department of Agriculture Forest Service (1995) *Landscape Aesthetics: A Handbook for Scenery Management*. Washington, DC: US Department of Agriculture Forest Service.

Perceptions of Nature by Indigenous Communities

P Maiteny, South Bank University, London, UK

Introduction

The purpose of this article is to provide an overview of how indigenous communities perceive and relate to the bio-ecological contexts of which they are part and on which they depend. The main message is that there is much more to learn from them than information about plant resources or methods to enhance Western-style conservation management. The forest is only one such context and it is possible to discern principles that also apply in others.

There are two possible approaches to take in this article. The first is to compare and contrast particular beliefs, values, and meanings that different peoples ascribe to their surroundings. This is analogous to drawing up inventories of species or habitat types that can then be used as resources to further existing purposes – be they commercial or for conservation – and management methods. However, this approach does little to challenge underlying assumptions or encourage learning from primary cultural perspectives. Einstein once said that problems cannot be solved through the same type of thinking as caused them in the first place. He was referring not to a need to accumulate greater quantities of information but to the need to see and analyze the situation in a qualitatively different way. This entails bringing different meanings, values, beliefs, and theoretical perspectives to bear on the problem rather than assuming that more data applied in essentially the same ways will resolve it.

Evidence of continuing failures in stemming the tide of ecological disintegration in forested and other environments suggests that Einstein was right. It therefore becomes necessary to ask what it is about humans that seems to make us unwilling or unable to act in a way that regulates rather than damages the ecological systems on which we depend. This article argues that the root causes are less to do with quantity of factual knowledge – this will always be incomplete. More significant are the underlying meanings, interests, purposes, and priorities that shape what we decide about the relevance of those facts and how we use them. Understanding our own cultural assumptions and their flow-on effects is therefore as important as gathering indigenous knowledge – perhaps even more so.

For these reasons, this article goes a step further than providing accounts of values and perceptions. Instead it offers a framework developed in ecological anthropology for comparing different cultural views and logics on a level playing field – particularly Western and indigenous – on the basis of whether the behaviors they generate are more or less likely to result in sustaining the ecological contexts on which they depend. Such an approach requires that we step back from the beliefs, assumptions, and cultural interpretations of mainstream science to ask what benefits for forest management might be learned from longer-established indigenous world-views and beliefs. Although the latter inevitably differ in their details, an underlying shared orientation to nature is discernible as expressed through the different beliefs and practices.

There is often a temptation to idealize indigenous peoples as 'noble savages.' That is not the intention here. This article does, however, echo indigenous peoples' views of the world in recognizing that cultural beliefs, values, and meanings are intrinsic parts of ecological systems, not separate from them. This is necessary for a truly holistic approach to ecology. It is also logical, especially now that humans have a more powerful ecological influence than any other species. This influence is shaped by the cultural meanings we ascribe to our relationship with nature, as expressed through decisions and behavior.

The article describes how different types of meaning underpin different orientations to nature and how, in turn, these take the form of human choices and actions that may be adaptive or maladaptive in relation to the ecological processes on which humans depend. It articulates the dynamics of how this occurs. Aspects of Western tradition that retain perspectives more akin to 'indigenous' perspectives are also described. Finally, implications and potential learning for forestry management are considered.

Definitions

Homo sapiens is a species that necessarily lives according to meanings that it itself must invent. Culture is the name we give to the 'screens,' or 'lenses,' of beliefs, knowledge, values, and meanings that are shared by any given group of people, and through which they see and interpret the world. It is the domain of meaning-making. As such, it informs human behavior, interactions, and relationships – social, economic, and ecological. Other terms used more or less synonymously with culture are 'world-view' and 'cosmovision.'

To understand culture entails understanding symbols which, in simple terms, are signs that represent and are associated with something else according to the conventions of the culture concerned. Humans live in cultural – and therefore symbolic – environments. It is in and through symbols that meaning is encapsulated, expressed, and conveyed. Words are relatively simple symbols but they are still symbols. Others are more complex and abstract – for example, notions of the 'invisible hand' of economics, the 'superego' of psychoanalysis, or 'the divine,' conceived in some way by most cultures that have existed. Symbols – meanings – do not only reflect or approximate those aspects of the world that exist independently of humans. Humans, through their symbolic meanings and corresponding actions, also participate in its construction. Humans are physically made of the physical elements of nature. However, we also make ourselves through symbols and cultural meanings that we ourselves conceive – cosmologies, customs and norms, institutions, values, rules, and so forth. In turn, this also contributes to constructing the outside world – to the 'state' of the world. The extent to which nonhuman dimensions of the world – such as ecological 'life-support systems' – are incorporated into representations of them differs from one set of cultural meanings to another.

A key distinction – and relationship – to make in understanding culture in an ecological context is between physical phenomena and the meaningfulness that is ascribed to them. The two are frequently conflated. As anyone involved in participatory decision-making will know, the same external situation is actually many situations when perceived (and felt) through the cultural screens of various stakeholders. A forest, for example, is a source of timber or of other commercial products, an ecological life-support system, a wilderness or collection of species to conserve, a home, a tourist playground, and as many other things as there are interests in it. The same goes for something as simple as the color red. Individual and group insistence that they see a particular external situation in the 'truest' possible way results in conflicts with others who are equally convinced of their versions of the situation, their 'realities.' This has less to do with the facts of the situation than their interpretation by interested parties. It can be painful to admit that others' perspectives on a situation are as valid as one's own. Yet it is impossible to enter into the logic of other outlooks, such as those of indigenous cultures, without doing so.

Another difficulty Westerners face in entering into other cultural logics concerns the whole subject of religion. All societies are shaped by cultural belief, and most have had some form of religious belief at their foundations. This need not be a worry, especially if we think about religion simply as belief that articulates how a given people see themselves as embedded within a bigger context than themselves alone. Other philosophies and ideologies serve the same purpose. 'Secular religions' such as humanism, Marxism, nationalism, capitalism and, as some would include, scientism provide overarching frameworks that provide a context within which adherents can find a sense of purpose and belonging. The key difference is that, unlike spiritual religions, these secular religions do not conceive of anything beyond the human. It is often argued that they are more rational. However, one of the fundamental lessons of anthropology is that all cultures have an internal logic and that they may well seem illogical and erroneous to each other when viewed from outside.

The cultures of so-called indigenous peoples are generally contrasted with those of Western economistic, industrialized society. Other equivalent terms, such as 'vernacular,' 'first,' and 'primary' refer to the fact that these peoples were living successfully in their ecological contexts long before contact with Westerners. Literally, they were there first. The fact that these peoples have lived for so long in these places suggests that their cultures served them well in adaptive survival terms. In this very practical sense, 'primary cultures' are part and parcel of local ecology as, of course, all human culture is part of global ecology. Humans could not exist without it and we have a profound impact upon it. To distinguish the meaningful and the physical does not mean that they are separate or separable. On the contrary, it is to articulate more clearly how, and through what medium, humans interact with the physical realities they depend on. Although all humans perceive nature through cultural lenses and act in terms of these, we do nevertheless act on physical nature, manipulating, using, and managing it. In turn, physical nature acts upon us 'responding' ecologically and reflecting back the consequences of what we do to it. There is a feedback relationship between culture and nature in any given ecological situation. Anthropologists have used the terms 'cultural ecology' and 'human ecology' to emphasize this systemic interrelatedness.

Some Western scientists, foresters included, often assert that their work is value-free; that their aim is simply to understand forest dynamics and processes in objective terms. So long as this work remains purely descriptive, this is a valid claim. However, there is a fine line between objective description and a values-based assessment. Any assessment, and subsequent decision about a desirable course of action, is inevitably based on values, interests, and purposes that are deemed to be desirable from a particular perspective. The purpose of a forest, for example, might be construed to be timber or non-timber production, natural heritage, conservation of species, habitat, genes, or indigenous cultures amongst others. Such purposes are rooted in foresters' perspectives, beliefs, values, and norms that express their professional and/or societal culture or subculture. Furthermore, choices about what is important to research are also culturally influenced.

All this is not to say that the research, interpretations findings or implications for action are inherently wrong – that would itself be a cultural value judgment. It is simply to illustrate the often fuzzy boundary between science – as a descriptive, explanatory activity – and culturally defined prescriptions about the implications of findings for decision making. Assessments of indigenous cultural views of forests as being 'unrealistic' or 'counterproductive' must be seen in the light of various, and often conflicting sets of values and interests. Conversely, so must indigenous assessments of the appropriateness of modern methods of managing forests or other ecosystems. Each perspective may have much to learn from the other. If mutually respectful dialogue can be achieved, new synthesis could emerge that provide benefits for all stakeholders groups concerned.

As ecological anthropologist Roy Rappaport emphasizes, the logical – and critical – bottom-line test for human ecological sustainability is not so much whether any particular cultural approach is good or bad in its own terms but the extent to which the practices and behaviors it generates support or undermine physical life-sustaining processes, without which all human futures are jeopardized. This perspective is critical of cultural relativist positions that emphasize the equal legitimacy of world-views in their own terms without taking into account their impacts on ecological life-support systems.

As should now be clear, an underlying theme of this article is the role of culture in adaptation and sustainability. A definition of adaptation in relation to human ecology is therefore warranted. A particularly apt one has been formulated by Rappaport:

> The processes through which living systems of all sorts – organisms, populations, societies, possibly ecosystems or even the biosphere as a whole – maintain themselves in the face of perturbations continuously threatening them with disruption, death or extinction.

Successful adaptation ensures sustainability and, in human systems, cultural beliefs and practices are pivotal to adaptive processes.

Cultural Meaningfulness and Physical Law

As mentioned already, it is salutary to remember that before modern industrial–economistic culture arose, primary societies had existed successfully for thousands of years. Though small scale, this suggests that they were rather good at regulating their ecological relations. Logically, it also suggests that the cultural lenses through which they mediated these relationships were resonant with – or at least not overly antagonistic to – physical life-support necessities. By contrast, the scale of ecological problems precipitated by Western industrial society suggests such a degree of dissonance between our culturally mediated behavior and sustainability of ecological necessities that we are now feeling its consequences at a global level. This global predicament is, of course, the cumulative result of the smaller-scale activities of individuals, collectives, and professions of all sorts.

Dissonances between physical laws on which humans depend and the maps of meaning that we live by inevitably give rise to behavior that, in the long term, is damaging both to those physical systems and to ourselves. Furthermore, as technological power increases, so does the impact of these context-destroying meanings. Rappaport has warned that humanity's 'most profound problems flow from discontinuities between law and meaning... There is nothing in the nature of human thought to prevent it from constructing self-destructive or even world-destroying errors' – except, that is, the choices, priorities, and values that human thoughts and feelings produce. This, in a nutshell, describes a root cause of ecological problems and the source of their possible resolution.

There are always exceptions, but a certain resonance between the meaningful and physical necessity does seem to characterize many primary cultures. It may be argued that this is illusory and due to the fact that populations were too small and/or their technology too simple to put any great pressure on ecological processes, biodiversity, and so forth. Perhaps, given their populations and technologies, these peoples would have acted in analogous ways to Euro-Americans. Such a perspective neglects the possibility, however, that different cultural meanings themselves bring different priorities to bear on the development and use of technology.

Behaviors that support, or at least do not undermine, physical ecological necessities are not always consciously planned and, as such, can appear irrational in Western scientific terms. Though not based on precise understandings of ecological processes, the traditional beliefs and ritual cycle of the Maring people in the forests of New Guinea, for example, have been shown to generate behaviors that effectively constrain human activities from putting ecologically unsustainable pressures on the environment. Such matching between cultural practices and ecological sustainability is by no means inevitable, however, as illustrated in various Western contexts.

Decisions and behavior, then, are never wholly rational but generated by meaningful beliefs and purposes that are always emotionally charged. Meaningfulness is, after all, a felt experience and the more experiential and emotional it is, the more meaningful. This applies as much in Western contexts, including the meanings we apply to science, as in indigenous contexts. In both cases, it is meaningfulness, and therefore emotional attachment, that drives behavior more than purely descriptive scientifically derived information. This is the main reason for focusing this article on types of meaning: so as to shed light on the motivations underlying human impacts on nature in different cultures, and whether they are contextually adaptive or maladaptive.

The rest of this article describes three basic types of meaning that humans experience. They are described with reference to examples of beliefs from both primary and Western cultures. Their significance to the peoples concerned in terms of how they view human–nature relations is described, as are their implications for ecologically adaptive behavior.

Meaningfulness and Traditional Ecological Knowledge in Primary Cultures

The term 'culture' refers to the way of life of the people of a given social grouping, to the foundations of that way of life in experience and to the frameworks of belief that give meaning to it. When scientists extract and build into databanks information about the distinctiveness of plant uses, habitat management techniques, and so on, they are harnessing only one of the benefits to be derived from primary peoples' knowledge. It is the tip of the iceberg of what could be learned from them. This, however, is bound to be the case so long as the information extracted is interpreted solely in terms of their own cultural meanings and applied to their predefined purposes. The legitimacy of other possible meanings and purposes can be obscured, or actively rejected, when they do not correspond with Western goals and priorities.

Compared with Western culture, primary peoples tend to see the particular 'parts' of, for example, a forest in the broader context of the forest (or other environment), perceiving, making sense of, and therefore experiencing them as dimensions of a whole system. A systematic analysis of a forest or other ecosystem must recognize human cultures as intrinsic dimensions of these ecosystems. In acknowledging this, the typology of meaning described below can help us to expand our cultural perception of indigenous cultural knowledge as merely sources of 'useful information' for our databanks. It can thereby help us expand the range of what we could learn from people about environments as whole systems, in the process learning more about ourselves and our human–nature relations.

The typology describes meanings that range from the descriptive, quantitative, and analytical – where the emphasis is on discerning differences and creating categories – through more qualitative, conceptual, inclusive, and experiential forms of meaning through which humans discern the similarities and connections underlying distinctions. These more synthesizing forms of meaning are necessary to begin answering questions such as 'What does it all mean?' It is these forms, therefore, that are more influential in shaping behavior. Analysis is necessary for this but not sufficient on its own.

Logically, qualitative meaning always encompasses and forms the context for the quantitative. To quantify is to translate qualitative values into measurable criteria. Qualitative appreciation of value is always prior to quantitative measurement of it. Analogic sound exists before its digitized equivalents, not vice versa. Meaning is always prior to evaluation.

On the other hand, the existence of quantitative criteria of value always implies a qualitative context of value and meaning in the background that is assumed and often remains unstated. Hence, economic criteria such as growth in gross domestic product are used as measurements of increasing human development and well-being. This assumes and indicates a cultural world-view that increases in material consumption and accumulation are the most important factors in enhancing quality of life and developing a fairer, more fulfilling and generally better society.

The suggestion in this article is that, by entering empathically into the logic of other cultures, improving our understanding of them and comparing their logics with our own, Western natural scientists could interpret the data they collect in a more meaningful, contextualized way, and potentially learn new ways of perceiving ourselves and our purposes that are more adaptive in relation to how we engage with our own and others' environments.

Type 1 Meaning: Distinction and Classification

The first type of meaning emphasizes the need to make distinctions between one thing and another. It is the sort of meaning that classifies and categorizes, a process that is necessary to all people in order to function. Types of tree must be distinguished and defined as being useful in different ways. Human needs are distinguished from those of other species and villages from the surrounding forest or other ecosystems.

In Mali, as elsewhere, different ethnic groups have specialized in complementary subsistence strategies corresponding with particular ecosystem types. The Bozo live by rivers and their main traditional activity is fishing. The Bambara and Songay cultivate the more fertile land and forests. The Fulani pastoralists graze their animals on the lowlands. The Tuareg are traditionally more nomadic transhumant pastoralists, traveling great distances with their livestock to make the most of what vegetation is available in the more arid regions. None of this would have been possible without the essentially quasiscientific capacities of observation and discrimination.

Similarly, the Mende people in the Gola forest, Sierra Leone, traditionally distinguish between the 'red' forest which is wild and uncontrollable, 'white' homes and villages that are tame, and transitional areas such as ruined villages and farmland.

This type of meaning is often focused on identifying what is necessary to serve particular human interests. It is essentially self-orientated, be it towards the person, family, community, or ethnic group. Awareness of the impact of one's actions on other people and wider contexts is of relatively minor importance at this level of meaning. Such awareness comes into the picture with the meaning types 2 and 3.

Much professional interest in forestry is focused on tapping into this type of meaningfulness through building up inventories of species, identification of food, medicines and other materials, cultivation of plants with commercial, consumeristic potential, and biodiversity surveys to assess conservation value. Such activities must be seen in the context of Western society's prevailing norms, interests, and priorities, as expressed, for example, by commercial desires to patent plant material and ancient knowledge as intellectual property. Traditionally, such knowledge has not been seen in Western terms of ownership. Recent threats to limit access have started to change this.

Primary knowledge is therefore not only of value in identifying or extracting commercial or other benefits, outside the original ecological and cultural contexts. Beyond methods, knowledge, and management practice, there is also much to be learned about how relations between humans and nature are construed. This, too, is primary knowledge that has served people well for thousands of years. Evidence is emerging, for example, of conceptual understanding and application of sustainable principles, indicators, environmental education, and other practices that would be recognizable to ecological, forestry and other natural resource professionals. Such practices, however, are framed by, emerge from and are still embedded within traditional beliefs and worldviews. These have been termed 'traditional (i.e., primary) ecological knowledge' (TEK) and have been found to add to Western professional knowledge. To understand the contexts of belief and world-view in which knowledge and practices are grounded is itself of great benefit to management and policy, especially when it is recognized that these, and not information and practices *per se*, have a far greater regulating influence on behavior. This leads on to considering the next type of meaning.

Type 2 Meaning: Synthesis and Continuity

This type of meaning-making is about synthesizing and theorizing. People develop their understanding by creating frameworks, discerning similarities, patterns, and relationships between facts and information to form a bigger picture. This constitutes the cultural worldview or 'cosmovision' of the more technical type 1 meaning. It is through type 2 meaning that the world and everything in it becomes emotionally meaningful and therefore a greater influence on behavior. Human existence comes to be seen – and experienced – not only in a self-interested way but also in the context of a 'wider scheme of things.' This may extend to experiencing being part of this larger whole – of a sense of place – and of having a role to play within it. *Homo sapiens* becomes just one species amongst many, all of which have their place within the larger 'being.' Individuals feel a belongingness, connectedness, and purpose within their various contexts – family, community, society, and nation, forest and nature in general and, beyond that, the biggest possible context that is described in terms of sacred Ancestor Spirits, the Divine Creator and Sustainer, and other abstract concepts. The Islamic prayer, 'Allah-u-akbar' gives a flavor of this, when translated as 'God is Big' (to avoid the coercive connotations of the usual translation 'God is Great').

In more familiar terms, the emotional satisfaction when an understanding or discovery falls into place for a scientist gives a flavor of how type 2 meaning is experienced. The scientist feels they have contributed something to their professional context and will be recognized for this. They feel they have fulfilled part of their role in their professional community and, perhaps, in society generally. Some have even described a sense of awe in tapping into something that is much greater than themselves of which their particular discovery is a tiny part.

Primary worldviews warn against seeing the world solely in terms of dichotomies (i.e., distinctions) between, for example, nature and culture or mind and matter, whilst recognizing the need for them in day-to-day life. More often than not ecosystems are seen as encompassing humans in a way that informs the meaning of human life. This links with another feature of type 2 meaning: the meaning that comes from a sense of continuity between human generations, and between humans and nature. Understanding of ecological and other cycles is, for example, often expressed in traditional myths.

The Mende classification of the forest into wild, tame, and transitional areas was mentioned earlier. These distinctions are related aspects of a wider symbolic view of forest–human relations whereby different qualities of the forest are symbolized by spirits. The two transitional areas – ruined villages and farmland – are respectively associated with the dominance of nature over people and the control of nature by people. Since the latter always requires effort, nature is ultimately dominant, encompasses humans and is, therefore, to be respected. Forest spirits are uncontrollable and dangerous, though under certain conditions, they can proffer powers on people who are then also feared by others. Spirits symbolizing the village–forest boundaries such as Ancestors and the original forest people ('pygmies') who pre-dated the Mende also command respect. They are both of nature and of culture and, in some sense, represent the relationship and continuity between the two.

In Zimbabwe, Ndebele people – and they are by no means unique in this – actually define culture as continuity that is essential to survival and well-being; continuity of identity, belief, knowledge, skills, and trades passed from one generation to the next. There is a special power in its continuity which, if lost, will also result in loss of cohesiveness and an inability to survive in the long term, especially in times of hardship.

This continuity is often construed as being 'intended and approved by God and the ancestral Forebears.' Problems will arise if it is lost because 'you have done something against God's will.' Losing it will bring benefits in the short term but great problems later which 'you will not know how to deal with because the solutions are embedded in your culture.'

Similar thinking applies to the importance of continuity between humans and nature. An old Malozi belief is that 'without nature there'll be nothing.' Many elders there, as in other cultures, understand that society is nested within and dependent upon nature, and this is given as meaningful a place as human well-being, *per se*. All cultures have it embedded in their beliefs in different ways. Cultural ecologists point out that the mere fact that traditional cultures have sustained societies and ways of life for thousands of years – longer than any urban-based civilization – suggests that they are ecologically (and socially) adaptive. Such ways of thinking are, however, becoming less significant under the influence of Western beliefs.

As mentioned, a lesson from primary cultures is that human–nature relations are influenced more by world-views and beliefs than by facts and information. In any culture, the latter are necessarily framed, interpreted, and applied in line with meanings, values, beliefs, and priorities. If these are only instrumental and utilitarian, without practical regard for ecological contexts – or traditional cultures that so often express understandings of them – the trajectory set is likely to be detrimental to those contexts. Later in the article we return to this problem. At this point it is worth mentioning that conceiving of oneself as one element in a wider context on which one also depends – familial, tribal, societal, ecological, and spiritual – is more likely than type 1 meaning to constrain behavior against excesses that would threaten that context. Some anthropologists have also convincingly demonstrated that the wider, more encompassing and, in some sense intangible and irrefutable is the contextual belief (as with strong beliefs in spirits and the divine), the more effective will they be in constraining damaging behavior. It is, of course, people themselves, acting according to the beliefs, who constrain their own behavior or that of others who are, as it were, overstepping the mark. Even when constraining mechanisms are conscious and deliberate, they are still belief-based. This is the case in Western societies too, except that social pressures here tend to have positive economic effects that are detrimental ecologically.

In sum, type 2 meaning extends beyond merely instrumental interest in what 'use' things are to 'me' or 'my community.' Rather, it is about feeling I have a meaningful place, and perhaps a role to play, within a bigger context. To live and take my role, I need to use resources from my environment. However, they are not seen as 'mine' and 'my interests' are not solely my own. In these senses, type 2 meaning is of more religious and philosophical than type 1 meaning. Indeed, it is often expressed through religious practice, ritual, metaphors, art, storytelling, and poetry.

Type 3 Meaning: Identification and 'Unification' with Context

Type 3 meaning deepens type 2 meaning but is much less widespread, especially in Western, scientistic cultures. It is also the type that provokes the most scepticism in Western society, although it is recognized by psychoanalysts and the mystical traditions of Western religions. All these may be reasons why it is so rarely written about even in the literature on indigenous culture. It cannot, however, be ignored because, first, it is a feature of most, if not all, primary cultures. Second, those who experience it carry a great deal of legitimizing weight in the cultures concerned. In this sense, it constitutes the strongest evidence for the truth or validity of the type 2 world-views that inform attitudes and behavior in the cultures concerned.

It is difficult to describe this type of meaning in intellectual terms, as it is not referential like the other two, is less intellectual, and more emotional and experiential. The experience results in 'esoteric' knowledge and is therefore associated with certain respected members of society, such as priests, holy men and women, shamans, and healers. It is grounded in profound all-encompassing feelings of identification, absorption or unification with context and, as such, might better be described as a state of meaning. This often occurs through the practice of religious ritual or devotion. The distinction between subject (person) and object (context) is blurred. It is the sort of experience depicted in feature films as possession by, for example, a totemic animal or a forest spirit. It can engender fear and awe in spectators as well as great respect for the 'object' of identification. In both these senses, it is taken as first-hand experiential evidence of the human–context relationship, a relationship that, in type 2 meaning, is construed more in terms of faith and belief. Those who can experience it directly in type 3 meaning are, for this reason, also held in particular esteem as they are deemed to have a direct link to the contextual 'forces,' and as being agents or vehicles through which they communicate. This, for example, is the case for those special people in the Gola forest who are proffered powers by the forest and transitional spirits.

All three types of meaning are interrelated but any one of them may be more evident at different times. All of them are also necessary. Although types 2 and 3 increase experience of meaningfulness, to see the world only in terms of synthesis or identification would obscure crucial distinctions, making it impossible for a person to live a normal life. On the other hand, a world seen only in terms of type 1 meaning (which is equivalent to uncontextualized information) encourages fragmentation, lack of relationship with and alienation from necessary social and natural contexts, with resulting tendencies towards divisiveness. Values, purposes, and action founded on types 2 and 3 are more inclusive, relational, and demanding of reflection than type 1 meaning. They are more likely to take wider systemic issues into account and to generate attitudes and behavior that are more conducive to ecological sustainability. The ultimate expression of the synthesis and relational wholeness to which they refer is often expressed in terms of sanctity and divinity. Particular behaviors deemed to be excessive or destructive are seen not only as corrupting or disrespectful to that divinity but also self-destructive, given that actors are themselves part of the wholeness it represents. Persons who live according to meanings and values of this sort, who are not motivated solely by instrumental and self-orientated interests, are therefore likely to be more conscious of the impacts of their actions on the wider, more tangible systems of which they are parts and on which they depend.

The Cultural Context of Western Forestry and Sustainability Science

This article has taken an unconventional approach focusing on the internal conceptual logic of indigenous culture. Implicitly, it has also highlighted a key source of difference between indigenous conceptions of the human–nature relationship and Western values that shape the behavior of individuals and collectives, including professions such as forestry. Considering the latter in the light of the typology of meaning, it is necessary to ask what is the most important contextual reference of Western culture. On the basis of observation, answers might include consumer democracy, the Western way of life, economic development or growth, the global market or market forces, the individual (as the basic economic unit whose interests the market is deemed to serve), and the invisible hand. All these 'ultimate' secular meanings share two important features.

First, the object they ultimately serve is human beings themselves. They are anthropocentric beliefs, self-referentially self-serving. There is no sense in any of them of a meaningful context – a bigger whole – from which human beings have emerged, that encompasses us, that would in some sense continue without us and within which we conceive ourselves as playing a role.

Second, the dominant way of assessing and assigning value, and making decisions in all of them is quantitative rather than qualitative – namely, through the metric of money. Money dissolves qualitative distinctions so making everything comparable with everything else on the basis of quantitative measures. In reality, the qualitative world on which the metric is imposed can, logically, never be as simple as the metric itself. The uses or commercial, monetary value of timber cannot ultimately substitute for the ecological processes of the forest. It is almost tautological to say so, but when a people loses touch with the qualitative ecosystemic processes and functions on which they depend, the logical and inevitable consequence is that they come to prioritize the maximization of value purely in quantitative terms – for the 'potential' of these processes once they have been converted into money. Hence, if all value is seen in terms of money then, logically, money itself comes to be seen as the ultimate value. The survival functions of forests themselves (and of other ecosystems) come a poor second place.

Seen in the light of the typology of meaning, both these features of Western culture elevate type 1 meaning to the status of type 2 meaning and subsume the qualitative, contextual dimensions of type 2 into it. The distinction between humans and the rest of nature has become more meaningful than recognizing ourselves as aspects of one synthesized and integrated system. The practical implications of this are that the interests of a special subsystem (humans and our creations) – and perhaps of other special interests within it (political, economic, commercial or ideological) – are given priority over the more general purpose systems that, in physical fact, do encompass us and on which we are inevitably dependent. Most importantly, decisions about policy, management, evaluation, and behavior are made on this basis.

In the context of the forestry profession, the pressure is always to underpin and justify all proposals and decisions in quantitative terms of monetary costs and monetary benefits, be it for commercial forestry or forest conservation. In the latter, there are pressures to couch arguments in terms of quasiquantitative 'biodiversity' rather than the more qualitative 'nature' or 'ecological processes' and to devise complicated surrogate evaluations of monetary costs and benefits. No amount of quantification will ever be able to provide a full picture of qualitative complexity. It is logically impossible.

All this is in stark contrast to primary worldviews where type 2 meaning remains qualitative and contextualizing of humans in a context that is bigger than them, rather than squeezing everything into a human context for human purposes. Far from devaluing human beings, such perspectives enhance their meaning by giving them a participatory role in the wider system. They also influence decision-making and behavior in such a way as to insure against disintegration of life-supporting contexts. Perhaps paradoxically, such world-views ultimately serve physical human purposes (i.e., ecological sustainability) but by way of emotionally meaningful belief systems that conceive of human lives being about serving something greater than themselves. Such perspectives also seem to provide an expanded sense of meaning and purpose for individuals themselves, one that is rooted in something other than maximizing material gain and consumption. Interestingly, some esteemed Western scientists have, for some years now, been advocating the need for a modern contextualizing world-view of this sort which is also scientifically rigorous and philosophically logical. Edward O. Wilson's 'Evolutionary Epic' and his Pulitzer Prize-winning book, *On Human Nature* (1978), Sir Julian Huxley's *New Bottles for New Wine* (1957 and see quotation below), and the emerging discipline of earth systems science (an alternative name for science informed by James Lovelock's Gaia theory) are important examples.

This article cannot offer recommendations about how to improve the effectiveness of forestry practice, within its existing parameters, assumptions, and priorities – that is, within the disciplinary culture according to which foresters currently operate. Plenty of other articles attempt to do this (*see* **Social and Collaborative Forestry**: Common Property Forest Management; Joint and Collaborative Forest Management; Social and Community Forestry). The purpose here has been to indicate how indigenous cultures, which are rapidly becoming extinct, quietly point to the need for changes to the basic meanings and orientations that inform Western attitudes and practices. It suggests that the existing disciplinary culture of forestry (amongst others) might benefit from being more receptive to learning from the perceptions and values of people who live – or used to live – in the places where foresters work.

It is appropriate to end by showing that perspectives described in this article are not limited to 'indigenous' primary cultures. The following quotations illustrate that, though neglected, they also exist in Western scientific and religious cultures. The final quotation is a contemporary native North American perspective.

First, from Sir Julian Huxley, originator of the International Union for the Conservation of Nature, first Director General of UNESCO and winner of the Royal Society's Darwin Medal:

> The universe is becoming conscious of itself, able to understand something of its past history and its possible future. This cosmic self-awareness is being realized in one tiny fragment of the universe – in a few of us human beings… On this, our planet, it has never happened before… It is thus part of human destiny to be the necessary agent of the cosmos in understanding more of itself, in bearing witness to its wonder, beauty, and interest… Most extraordinary in principle, it (evolution) has generated values… Evolution thus insists on the oneness of man with nature, not merely in respect of biological descent and chemical composition, but because nature is the indispensable basis of his material existence, and also the indispensable partner in his mental and spiritual achievements… For man to fulfil his destiny, he must think of himself as in partnership with the cosmos.

(From Huxley (1957) *New Bottles for New Wine*. London: Collin).

Second, a perspective from twentieth century Kabbalistic Judaism:

> Putting themselves in relation with all things, humans will then remember that in the deepest being of all that exists is hidden the Divinity to which they themselves feel 'connected' and by which they are conscious of being inhabited. They will feel that the *Shekhinah*, the Divine Presence, desires to dwell in them… Humanity and nature. Ecological necessity: Humans, humble in front of their Creator and recognizing Its goodness, regard nature with respect and come close to it without expecting gifts… Always, while contemplating these wonders, humans sense their Creator who reminds them: 'See how beautiful is My work!… Be careful not to corrupt it… because if you corrupt it no one after you will be able to repair it!'

(Author's translation from Safran A (1998) Florence, Italy: Giuntina, *La Saggezza della Kabbalah* transl. P. Maiteny).

Finally, there is a striking similarity of meaning between the above quotations and the following, written by contemporary native North Americans:

> For all the people of the earth, the Creator has planted a *Sacred Tree*… The life of the tree is the life of the people. If the people wander far away, if they forget to seek the nourishment of its fruit, or if they should turn against the Tree and attempt to destroy it, great sorrow will fall upon the people. Many will become sick at heart. The people will lose their power. They will begin to quarrel among themselves over worthless trifles. They will become unable to tell the truth and to deal with each other honestly. They will forget how to survive in their own land. Their lives will become filled with anger and gloom. Little by little they will poison themselves and all they touch. As long as the tree lives, the people will live. It was also foretold that the day would come when the people would awaken. They would begin to search again for the *Sacred Tree*.

(From Bopp J, Bopp M, Brown L, and Lane P Jr (1985) *The Sacred Tree: Reflections on Native American Spirituality*, 2nd edn. Alberta, Canada. Four Worlds International Institute for Human and Community Development.)

See also: **Landscape and Planning**: Perceptions of Forest Landscapes. **Social and Collaborative Forestry**: Common Property Forest Management; Joint and Collaborative Forest Management; Social and Community Forestry; Social Values of Forests.

Further Reading

Anderson EN (1996) *Ecologies of the Heart: Emotion, Belief and the Environment*. Oxford, UK: Oxford University Press.

Huxley J (1957) *New Bottles for New Wine*. London: Collins.

Nazarea VD (ed.) (1999) *Ethnoecology: Situated Knowledge/Local Lives*. Tucson, AZ: University of Arizona Press.

Posey DA (1999) *Cultural and Spiritual Values of Biodiversity: A Complementary Contribution to the Global Biodiversity Assessment*. London, UK: Intermediate Technology Publications, for United Nations Environment Programme.

Rappaport RA (1999) *Ritual and Religion in the Making of Humanity*. Cambridge, UK: Cambridge University Press.

Wilson EO (1978) *On Human Nature*. Cambridge, MA: Harvard University Press.

Urban Forestry

C C Konijnendijk and T B Randrup, Danish Forest and Landscape Research Institute, Hoersholm, Denmark

Introduction

Urban forestry is an integrated concept, defined as the art, science, and technology of managing trees and forest resources in and around community ecosystems for the psychological, sociological, aesthetic economic, and environmental benefits trees provide society. It emerged as a discipline in North America in response to better ways to deal with the growing importance of tree-dominated urban greenspace, as well as growing pressures on green areas. During recent decades an international urban forestry research community has developed, as has an increasing body of knowledge as well as new approaches and techniques. Urban forestry has close links to forestry, but tends to be more multidisciplinary.

Concept of Urban Forestry

According to the Society of American Foresters' *Dictionary of Forestry* (1998 edition), urban forestry is defined as 'the art, science and technology of managing trees and forest resources in and around urban community ecosystems for the physiological, sociological, economic, and aesthetic benefits trees provide society.'

The concept and scope of urban forestry is summarized in **Table 1**. Urban forestry has the urban forest as its domain. An urban forest is defined as

Table 1 The urban forestry matrix, representing the scope of urban forestry

	The urban forest		
	Individual trees		Urban woods and woodlands
	Street and roadside trees, and associated vegetation	Trees in parks, private yards, cemeteries, fruit trees, etc., and associated vegetation	(forests and other wooded land, e.g., natural forests and plantations, small woods, orchards, etc.)
Form, function, design, policies and planning			
Technical aspects (e.g., selection of plant material, establishment methods)		URBAN FORESTRY	
Management aspects			

comprising all tree-dominated green areas in and around urban areas. Thus it includes, according to Food and Agriculture Organization (FAO) definitions, forests, other wooded land, and trees outside forests, as long as these are situated in urban environments. The terms ‘woodlands’ and ‘woods’ are often used in an urban forestry context to distinguish between the wider urban forest resource and its components that have traditionally been defined as ‘forest.’ At a strategic level, urban forestry includes attention to the form and function of urban forest resources, as well as policies, planning, and design policies related to these. Urban forestry involves a range of techniques and approaches in terms of the selection and breeding of the right trees for urban environments and growing conditions, as well as tree establishment. Strategic and more operational aspects are brought together at the level of urban forest management.

The strengths of the urban forestry concept include the following characteristics:

- integrative, incorporating different elements of urban green structures into a whole (the ‘urban forest’)
- strategic, aimed at developing longer-term policies and plans for urban tree resources, connecting to different sectors, agendas, and programs
- multidisciplinary and aiming to become interdisciplinary, involving experts from natural as well as social sciences
- participatory, targeted at developing partnerships between all stakeholders, and aimed at multiple benefits, stressing the economic, environmental, and sociocultural benefits and services urban forests can provide.

Brief History of Urban Forestry

The earliest interest in trees and green areas at large as contributors to more attractive cities dates back to for example the ancient Greek and Roman civilizations. During the Middle Ages, many European cities took an interest in protecting the surrounding woodland resources, for example for providing food, fuelwood, construction wood, and fodder, as well as a reserve in times of war. Green areas inside the city walls often had a similar utilitarian role, being used as areas for agriculture, for example. Interest in the more aesthetic and recreational benefits of urban green space developed during the mercantilist and Renaissance periods. A new class of wealthy citizens emerged and showed an interest in estates, parks, and other green areas for leisure as well as for economic and prestige purposes. City authorities, often with the support of industrialists, took a greater interest in their green areas during the time of the Industrial Revolution. Large groups of workers had moved to the cities and needed to be provided with socially acceptable ways of spending their leisure time. Formerly closed-off royal and private parks and domains were opened to the public, and new green areas very much focused on active uses were created. Green space planning and management became more established parts of municipal activity during modern times (**Figures 1–3**).

With increasing urbanization and a growing demand for and pressures on urban green areas, the call for more comprehensive and integrated natural resource management emerged during the twentieth century. Various elements of urban green structures had traditionally been the domain of different professions. Individual trees along streets and roadsides had been given attention, for example through shade tree regulations in North America, and later became the domain of arboriculture. Horticulturists, landscape architects, and park managers had primarily been concerned with inner city public green space such as parks. Foresters, finally, had been hesitant to be active inside cities and remained at the urban fringe, where larger woodlands and other green areas are situated. A range of other professionals, including ecologists, biologists, and planners had also been involved.

The concept of urban forestry emerged in North America in response to increasing pressures on urban green spaces, and in recognition of the primary role trees play within urban green structures. Graduates of forestry schools were more frequently hired to manage municipal tree management programs because of their biological, quantitative, and

Figure 1 Street trees are an important element of the urban forest. Courtesy of Thomas Randrup.

Figure 2 Urban forests are among the most popular environments for outdoor recreation. Courtesy of Kjell Nilsson.

Figure 3 Trees alongside waterways are an important component of the urban forest. Courtesy of Thomas Randrup.

managerial skills. The term 'urban forestry' was introduced in 1965 as part of a study on the success and failures of a municipal tree planting program. In spite of initial resistance to the term and concept from both foresters as traditional urban green space professions, urban forestry gradually found wider scientific, political, and professional backing in North America. Other parts of the world, including Europe, took notice of the concept during the 1980s, but only during the past decade has a more established global research community within urban forestry emerged. Forestry has played an important role in the advancing of urban forestry, as have many other disciplines, including landscape architecture, landscape ecology, horticulture, arboriculture, soil sciences, as well as planning and social sciences.

Urban Forest Resources

Comprehensive assessments of urban forest resources have been scarce. Most assessments have been at the local level rather than national or international. Moreover, they have focused on only one or several components rather than the entire urban forest resource. While woodland data are often not very difficult to obtain due to existing inventories according to set definitions for 'forests' it remains difficult to assess the urban share of overall resources.

An exception has been the comprehensive assessment of national urban forest resources carried out by the US Department of Agriculture Forest Service. The study focused on tree canopy cover as the main indicator and combined methods using satellite imagery, existing statistics, and more detailed assessments at the local level. The assessment showed that about one-third of metropolitan areas defined in terms of administrative jurisdiction, in the adjacent USA is covered by tree canopy, i.e., approximately 8% of the entire country and about one-fourth of all US trees. When looking more narrowly at urban areas (cities, towns, and other built-up areas), urban trees still cover about 1% of the entire US land area. Less comprehensive assessments in Europe, often looking at land use categories rather than tree canopy cover, found green space cover of major cities to range from 5% to more than 60% of city area. Other comparative studies indicated a share of woodland within the municipal boundaries of larger cities to range between less than 1% to more than 40%. Although woodlands in and adjacent to urban areas mostly comprise a small percentage of the entire woodland base of a country, this still means several millions of hectares for Europe alone.

Urban Forest Functions

Social Benefits

The recreational values of forests, parks, gardens, and other urban green areas are especially well documented in the Western world. Urban woodlands in Europe, for example, attract as many as several thousands of visits per hectare per year, thus by far surpassing the average visitor number for woodlands. As people tend to prefer outdoor recreational areas close to their homes, urban green areas are the most popular outdoor recreational areas. Urban dwellers often form strong attachments to trees and green areas close to their homes, which often leads to controversy in cases of tree removal. Recently the health impacts of urban green space have also been studied. Urban green space can have a positive impact on physical and mental health, for example by providing settings for physical exercise, reducing ultraviolet radiation and air pollution, and reducing stress. By being actively involved in tree planting and management, local communities can be strengthened. In many developing countries, trees often have cultural and spiritual values that could assist new urban dwellers in finding their place in cities and towns. Urban forests also have high educational values by representing nature and natural processes in cities and towns, and they have often been used as testing and education areas for forestry and other disciplines.

Economic Benefits

Timber and other wood products from urban forests are in many Western countries often not very highly prioritized. But in other parts of the world they are crucial. Large parts of the urban population of Africa, for example, are still heavily dependent upon fuelwood. Systematic planting of street trees for timber production is widely practiced in countries of Southeast Asia; urban green areas, in which trees play an important part, provide non-wood forest products such as mushrooms, berries, medicinal herbs, rattan, and so forth. In addition, trees play an important role in urban agriculture, which provides an important source of livelihoods in developing countries. The focus in the Western world has been on additional economic values such as green areas contributing to more attractive cities for people to work, live and relax in. Studies in Denmark and Finland, for example, have shown the positive impact of nearby forests and green on house prices. Cities across the world have turned to planting trees and other greening efforts to attract investment and taxpayers.

Environmental Benefits

Trees and other vegetation intercept particles and gaseous pollutants. Moreover, they act as carbon sinks in the equations relevant within the context of global warming. Important in both the developed and developing world is the role urban vegetation plays regarding water. Trees reduce stormwater runoff and can assist with processing wastewater and minimizing air pollution and diseases from sewage water through its use for tree planting. Many cities have established and conserved forests for protecting their drinking water resources. Urban forests protect soils and moderate harsh urban climates, for instance by cooling the air, reducing wind speeds, and by giving shade. The shade effects of trees have proven to be significant in, e.g., the USA. Here shade provided by trees may result in building energy saving and lowering air conditioning cost. In arid regions, forest shelterbelts around cities help combat desertification. The level of biodiversity of urban green areas is often surprisingly high, representing nature close to where people live. Cities such as Rio de Janeiro and Singapore still have tracts of tropical rainforest within their boundaries. In Europe, national parks are found at the gates of large cities such as Warsaw, Moscow, and Vienna.

Pressures on Urban Forests

Urban forestry has to deal with growing trees in often very harsh urban environments. A first challenge is to protect green areas and trees against encroachment and annexation by other types of urban land use. The competition for land in and near cities is fierce. If urban forests can be conserved, they have to be protected against a wide range of biotic, abiotic, and anthropogenic stresses. Limited urban resources are very intensively used, and wear, tear, and ecosystem degradation by for example trampling, disturbance, and vandalism occur. Moreover, not all uses are easily accommodated and conflicts of interests are very common. Anthropogenic stresses are also caused by the presence of traffic installations and all kinds of infrastructure. Growing spaces for trees, and especially for those growing along streets, are limited. Levels of soil, water, and atmospheric pollution are often high, and climatic conditions can be harsh due to the artificial environment created by human structures. The use of deicing agents often has a detrimental effect on street and roadside trees. Consequently a large share of the trees planted in urban environments dies within the first years after planting. While pressures on urban forests in urbanizing societies are multiple, urban forest planners and managers are facing budget cuts and municipal reorganizations.

Urban Forestry Practice

Inventory and Evaluation

The starting point for urban forestry programs, policies, and planning is to assess the potential of the urban forest resource in terms of form and functions, as well as urban society's preferences regarding the benefits and services the urban forests should provide. Comprehensive urban forest resource and function inventories and monitoring are thus required to support decision-making. During recent years various (computerized) information systems to support policy-making and planning have been developed. A rapidly expanding body of research aims to assess the different social, environmental, and economic values urban forests can provide. In North America, for example, the environmental values especially of urban trees have been quantified in monetary terms, for example through assessing the cost avoided for air pollution reduction and cooling by using trees. Cost–benefit studies have shown that benefits of urban trees generally extend far beyond the cost of planting and management. This information is also very important for effective and efficient urban forestry. More efforts have also been made to determine what society's preferences are with regards to urban forests. Tools and procedures for public consultation and participation are increasingly used, in order to generate optimal benefits from a rather limited resource. Public participation is not only important at the strategic level, but also in establishment and management, for example to create a feeling of shared ownership.

Policies, Planning, and Design

One of the characteristics of the urban forestry concept is its strategic nature. Strategic programs and policies for urban forestry, however, are still not very common across the world. Exceptions are the Community Forests in the United Kingdom, embodying a long-term program aimed at generating socio-economic and environment regeneration of 12 urban agglomerations through forest and tree establishment and management. Another problem is the lack of integration of urban forestry with more general urban and regional policies and planning.

With only limited resources and a large societal demand, proper design of urban forests is crucial. Aesthetic aspects are of course important, as is the tradition in garden and landscape architecture, but design should also recognize the different roles urban forests play. Trees are living organisms, which requires a thorough knowledge of their development and possibilities as basis for design. Design has to build on strong links with future management, in order to develop a sustainable and multifunctional urban forest resource. The woodland part of urban forestry also requires extensive design, e.g., in terms of zoning different functions and providing attractive and safe environments for various forms of recreation.

Species Selection and Establishment

Urban conditions are very different than the conditions in rural or natural areas. Complex and often rather hostile urban growing conditions require a careful selection of the right tree species. There is a need for integrated focus on the identification and selection of cultivars and species for urban forestry, based on sound knowledge of site conditions and tree characteristics.

Urban trees have to endure a wide range of threats, as described before. As urban tree populations are often dominated by only a few tree species or families, the risks related to pests and diseases are larger. The dramatic impact of Dutch elm disease in North America and Europe is an example of this. In order to develop a more resistant urban forest resource, it is advisable to provide for sufficient variation regarding tree species, genus, and family.

The use of exotic versus native species has also been a topic of concern. Urban forests often include a high share of exotic tree species. There are several reasons for this, including the fact that some of these species might be better adapted to artificial environments, for aesthetic reasons, or interest in exotics as a result of the colonial era. The trend is towards increasing the use of native species, because of the demand for more nature-oriented management of green area's and interest in maintaining genetic resources.

The establishment of trees in urban environments often requires a major effort, especially when paved areas are concerned. Consideration should be given to the growing conditions below the surface, as sufficient space should be provided for root development. Special soil substrates have been developed for application in urban conditions. Sound establishment techniques are also needed in terms of planting holes, adequate water supply, protection against threats such as deicing salt, and proper staking if needed. Trees are often planted as part of construction and development schemes, so that the process of planting requires special care during the construction activities. In the case of woodlands, establishment of trees often is easier, although more difficult than in many rural forests due to higher trampling and compaction. Natural regeneration can supplement planting and sowing of seeds.

Management

The management of urban forests operates on different levels. At a more integrated and strategic level, management approaches should regard the urban forest as a whole, with linkages between its different components and its form and functions. Specific techniques are then also needed for the different components.

The management of single trees (arboriculture) builds on long tradition and experience. An important tree care activity is pruning, aimed at for example the training of young plants, maintenance of health and appearance (i.e., for aesthetic reasons), reduction of hazard, control of plant size, influence on flowering, fruiting, and vigor, and compensation for root loss. Different pruning approaches and techniques have been developed, but ‘modern arboriculture’ as developed in the USA during the 1970s is now widespread throughout the world. Modern arboriculture is based on a detailed understanding of tree biology, and the tree’s natural reactions to wounds, cuts, and so forth. Related to this is the discussion whether or not to treat wounds. The need to detect hazardous trees and assess tree vitality, however, is now becoming widely accepted as an important urban tree management feature.

Arboriculture also plays an important role in parks and gardens, but here management of other types of vegetation also comes in. More integrated approaches to the management of different park and garden elements are under development. Traditional forest management techniques are often not directly applicable to urban areas. Public scrutiny and different functions of urban woodlands require that management techniques have to be adapted. Education and awareness raising can enhance public understanding of management measures, thus reducing concern and the potential for conflict. Selection cutting methods are often seen as more appropriate for especially smaller-scale urban woodlands. Thinning regimes can be used to provide a greater diversity in urban woodland stands to meet, for example, urban demands for a wide range of recreational opportunities and experiences.

Management activities, just like policies and planning, should be based on detailed resource inventories and monitoring. These should not only provide basic information about the trees (species, age, height, and so forth), but also about vitality, special characteristics and their place in a wider urban forest context, not least related to human demands.

Urban Forestry Research and Education

By its very nature, urban forestry is an approach involving multiple disciplines and their specific body of knowledge and expertise. Urban forestry has also become recognized as a field of scientific relevance in Europe, and gradually an international research community has been formed. A survey of 20 European countries identified more than 400 recent or ongoing research projects on trees and/or forests in the urban environment. Many of these projects focused on only one element of urban forests, with about equal attention for street trees, trees in parks, and woodlands. The discipline of forestry had been involved in about half of all projects listed by national experts participating in the survey. Especially during recent years, however, more integrative research has been developed, focusing on the urban forest resource as a whole, as well as following a more multidisciplinary approach. Natural science gradually has become supplemented by social and planning sciences, although the natural science disciplines are still very dominant in urban forestry research in Europe, as well as in North America.

With growing scientific as well as practical interest, the need to develop urban forestry education also became clear. The USA hosts many degree programs in urban forestry. In Europe, higher education in urban forestry has been less developed so far. Recent years, however, have shown an increase in degree programs and student enrolment. Urban forestry education programs are also under development in other parts of the world, and most notably Southeast Asia.

See also: **Afforestation**: Species Choice. **Landscape and Planning**: Forest Amenity Planning Approaches; Perceptions of Forest Landscapes; The Role of Visualization in Forest Planning. **Recreation**: Inventory, Monitoring and Management; User Needs and Preferences.

Further Reading

Andersen F, Konijnendijk CC, and Randrup TB (2002) Higher education on urban forestry in Europe: an overview. *Forestry* 75(5): 501–511.

Bradley GA (ed.) (1995) *Urban Forest Landscapes: Integrating Multidisciplinary Perspectives*. Seattle, WA: University of Washington Press.

Bradshaw A, Hunt B, and Walmsley T (1995) *Trees in the Urban Landscape: Principles and Practice*. London: E & FN Spon.

Dwyer JF, Nowak DJ, Noble MH, and Sisinni SM (2000) *Connecting People with Ecosystems in the 21st Century:*

An Assessment of Our Nation's Urban Forests. Gen. Tech. Rep. PNW-GTR-490. Portland, OR: US Department of Agriculture Forest Service, Pacific Northwest Research Station.

Grey GW (1996) *The Urban Forest: Comprehensive Management*. New York: John Wiley.

Harris RV, Clarck JR, and Matheny NP (1999) *Arboriculture: Integrated Management of Landscape Trees, Shrubs and Vines*, 3rd edn. Upper Saddle River, NJ: Prentice Hall.

Hodge SJ (1995) *Creating and Managing Woodlands around Towns*. Forestry Commission Handbook no. 11. London: HMSO.

Konijnendijk CC (2001) Urban forestry in Europe. In: Palo M, Uusivuori J and Mery G (eds) *World Forests*, vol. 3, *World Forests, Markets and Policies*, pp. 413–424. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Konijnendijk CC, Randrup TB, and Nilsson K (2000) Urban forestry research in Europe: An overview. *Journal of Arboriculture* 26(3): 152–161.

McPherson EG, Simpson JR, Peper P, and Xiao Q (1999) Benefit cost analysis of Modesto's Municipal Urban Forest. *Journal of Arboriculture* 25: 235–248.

Miller RW (1997) *Urban Forestry: Planning and Managing Urban Green Spaces*, 2nd edn. Upper Saddle River, NJ: Prentice Hall.

Nilsson K and Randrup TB (1997) Urban and periurban forestry. In: *Forest and tree resources*. Proceedings of the 11th World Forestry Congress, 13–22 October 1997, Antalya, vol. 1, pp. 97–110.

Nilsson K, Randrup TB, and Wandall B (2001) Trees in the urban environment. In: Evans J (ed.) *The Forest Handbook*, vol. 1. and vol. 2, pp. 347–361 and 260–271. Oxford, UK: Blackwell Science.

Unasylva (1993). Special issue *Urban and Peri-Urban Forestry. Unasylva* 44(173).

Forest Amenity Planning Approaches

C Ward Thompson, OPENspace Research Centre, Edinburgh, UK

Introduction

This article begins by defining forest amenity planning and its relationship with other planning approaches. The benefits of forest amenity are explored in the context of a brief history of forest planning and design. Modern amenity planning is set against the international agenda for sustainability and recent legislation on forest and landscape planning. Examples of different approaches from North America, Europe, and Australasia are used to illustrate the way amenity planning has developed in different world regions, with a particular emphasis on innovative and integrated approaches to forest amenity in the context of broader landscape-planning initiatives. The conclusion points to areas of emphasis and challenge for the future.

Definitions of Amenity Planning

Amenity is generally deemed to refer to something pleasant as well as useful, often (but not always) associated with leisure. Forest amenity planning is therefore concerned with visual pleasure or attractiveness, often termed visual amenity (*see* **Landscape and Planning:** Visual Analysis of Forest Landscapes), but also with other aspects of the forest that make it a pleasant place to visit or to have as a nearby resource. Amenity planning thus places people rather than timber at its heart, and pleasure rather than economic return as its end; this sets it apart from planning for productivity, where the focus is on silviculture and the economic value of the forest products. Environmental impact assessment (EIA) requirements in the planning legislation of many parts of the world, including Europe and North America, tend to focus on the impacts of plans on soils, water, air, fauna, and flora, in other words, ecological and natural heritage, rather than cultural heritage, although this is beginning to change in some regions and countries. Amenity planning implies, at its ideal, an integrated approach to planning where aesthetic issues are combined with recreational and other social needs as part of a holistic planning process. In an increasingly globalized society, amenity planning is also an important tool in preserving the diversity and distinctiveness of different locations and landscapes.

Forest Amenity Benefits

There is a considerable range of potential amenity benefits that forests can provide for people who live or work near them, or who visit them for leisure activities. The amenity benefits that have been identified include functional aspects such as landscape enhancement (especially in areas of dereliction or abandoned agriculture); screening (for example, of mineral workings); noise reduction; dust filtering; summer shade; shelter; wildlife conservation and enhancement; providing the setting for buildings or groups of buildings in the landscape; and providing a location for many different kinds of recreation, from bird-watching and berry-picking to children's play and mountain biking. The perceptual and psychological benefits that are also important in amenities include: contact with nature and the seasons; peace and tranquillity; spiritual and emotional renewal; relief from stress and improved recovery from illness; improving the attractiveness of the living environment and the quality of everyday life; and raising a sense of pride of place and self-worth.

These benefits combine to create an economic argument for amenity forest planning, since attractive and pleasant forests can add to property values and tourism revenues, and attract other, appropriate development in some cases. There have been many attempts to place precise economic values on environmental amenities, including forests, although all have their limitations due to the intangible nature of many aspects of amenity. The economic approach has usually valued forest amenity based on 'willingness to pay' criteria. Hedonic pricing attempts to place a cash value on landscape elements by estimating the value of amenity benefits from the costs and prices of related market transactions, while contingent valuation of a particular change in the landscape uses 'preferred elicitation' models to distill the value of different preferences based on how consumers decide what to purchase. Such methods have been used to show that creation and management of farm woodlands or urban forests for amenity benefits can be profitable in economic terms. However, recent research in both Europe and North America has suggested that a combination of monetary and nonmonetary approaches to values needs to be adopted in coming to decisions on environmental decision-making.

Amenity is a culturally defined term. Cultural differences between countries and regions lead to variations in recreational use and access to forest resources. Berry and mushroom collecting are, for example, very popular in northern and Eastern Europe, as is skiing in winter, while in the UK and parts of central Europe, cycling is a popular tradition that is developing in new ways with the increasing interest in mountain biking. Forest amenity planning approaches should, therefore, define their aims in the context of determining appropriate cultural understandings, expectations, and aspirations on the part of local people and visitors. It is this cultural component which has often proved problematic to incorporate in practice and has led to a rapidly increasing interest in public participation and 'stakeholder involvement' in planning processes in the 1990s and early twenty-first century.

History of Forest Amenity Planning

Forests have been managed for amenity for as long as privileged members of society have had control over parkland and woodland to enjoy at will. The earliest records of hunting parks, e.g. from Assyrian Mesopotamia (thirteenth century BC), or late Shang dynasty China (sixteenth to eleventh century BC), suggest that they were managed to create a beautiful and pleasurable setting for recreational pursuits. While these forest lands were often the exclusive domain of the ruling classes, there is also a long history of more modest forest management for amenity, combining the practical and the pleasurable in local woodland economies. Western European forests in the early Middle Ages, for example, provided sustenance and pleasure for their inhabitants in many ways, from grazing for pigs to a source of berries, nuts, mushrooms, and honey for local people, quite apart from any economic exploitation of the timber itself. In England, the Norman invasion of 1066 brought an end to this in many parts with the creation of huge areas of special jurisdiction, known as 'forests' (not all were wooded), policed at the king's pleasure for the preservation of game. Thus the treatment of woodland as common land varied in place and time, depending on the extent of woodland coverage and the dominance of regulation and restriction over local cultural traditions at different stages in history. Their legacy remains reflected today in contemporary laws and the approach to forest amenity planning taken in different countries and regions.

The grand plans for royal and aristocratic hunting parks in seventeenth-century Europe were an extension of the Baroque articulation of space and visual order, culminating in designs such as André le Notre's plan for Versailles; this took a comparatively modest hunting lodge and set it in an extraordinary landscape of woodland articulated with geometric patterns of canals, allées, and rides which dominated the landscape to the horizon. This was amenity forest and landscape planning at its grandest and most autocratic, and led to a reaction in Britain from which the more curvaceous and undulating lines of the English Landscape style grew. In the eighteenth century, when these landscape designers were making their impact, there was considerable interest in tree planting for amenity as a part of estate improvements, and there was a lively discourse on appropriate species, planting style and management for beautiful, sublime, or picturesque effect, an aesthetic approach which has dominated the English landscape ever since. Such planting was still largely in the private domain of the landowner, however, and came at a time of the Enclosure Acts which removed much land from common use. In the nineteenth century, foresters were primarily concerned with gaining recognition for their role in their country's economy and amenity values were not a major concern. Germany led the way in developing academic institutions to train foresters and developed planning and management concepts such as the sustained yield system, which resulted in chessboard-pattern stands of single-aged trees in contrast to the more natural pattern sustained by selective felling. It was not until the twentieth century that forest amenity planning for the public at large and for local community enjoyment became a frequent duty of public authorities and philanthropic organizations. By the end of the century, nearly all developed countries were committed to sustainable, multiple-purpose forest-planning policies.

Early Amenity Planning – Examples from the UK

The British Forestry Commission, established in 1919 largely to secure a strategic home supply of softwoods, began to address amenity matters in the 1930s with the establishment of national forest parks, planned to provide for the integration of timber production and recreation. Visual amenity was addressed by avoiding straight outlines to plantations and introduction of species variety within plantations and at their margins. The first attempts to liaise with public opinion on amenity matters, through the Council for the Preservation of Rural England, were also made at this time. By the 1950s the Commission recognized that recreation provision should be an aim in all its state forests, wherever desirable and practicable. Sylvia Crowe initiated the integration of planning for nature conservation, recreation, and visual amenity, through her pioneering work as landscape architect and consultant to the Forestry Commission from 1963 to 1975, and the Commission has since been at the forefront of forest amenity planning throughout the UK and internationally.

In the 1990s, Forestry Commission initiatives to encourage planning of amenity forests in an integrated way included development of the concept of community forests and woodlands, supported by woodland grant schemes and community woodland design guidelines. The focus is on planning local countryside near towns and cities for the benefit of the whole community. The concept draws upon other European traditions, such as the Stadtwälder (town forests) of Germany, many of which were created over 200 years ago, and the 895 ha of new polder woodlands in the Bos Park on the outskirts of Amsterdam, created in the early twentieth century as a major recreational resort for the city. Such community woodlands are often developed as a way of reclaiming derelict land in a postindustrial age and so they have been particularly targeted at former mining and manufacturing centers. The National Forest, which covers 502 km^2 in the Midlands of England, and the Central Scotland Forest, covering 1600 km^2 in the central Scottish industrial belt between Glasgow and Edinburgh, are two such examples, initiated in 1994–1995.

North American Developments

Scenic amenity has been a consideration in US forestry planning since the early 1900s. The US Forest Service used landscape architect consultants to develop early guidance on wilderness preservation and recreation plans which recognized scenic values. However, their first official landscape management program was not developed until 1968, based on work done by R. Burton Litton Jr. and influenced by the work of Sylvia Crowe in the UK. This led to the development of visual management systems for scenic amenity and forest plans with scenic quality targets (*see* **Landscape and Planning**: Visual Resource Management Approaches). In 1995 a Forest Service handbook for scenery management entitled *Landscape Aesthetics* gave guidance on forest planning for visual amenity. This has been developed separately from guidance on ecosystem management and nature conservation and on provision for recreation. The social and cultural dimension of amenity planning is not well integrated, by contrast with European systems of amenity planning. The British Columbian Ministry of Forests, Canada, used concepts of landscape character and forest landscape management borrowed from the USA to develop their guidance on scenic amenity in the early 1980s. This has subsequently been refined into a visual landscape management process, with guidance from Simon Bell of the British Forestry Commission, who recommended a more integrated approach to amenity planning as a whole – total resource planning and design. This more integrated approach has been used in parts of British Columbia and the rest of Canada, where high-profile proposals have raised complex and sensitive issues.

The United Nations Conference on Environment and Development (the 1992 Earth Summit) embraced a statement of forest principles and helped define concepts of sustainability in the trio of economy, environment, and social equity, through Agenda 21. Social equity refers to social justice, the concept of equal access to facilities and benefits for all of society's members, and thus has implications for amenity planning. The Local Agenda 21 advice to local authorities supported the notion that global issues might best be tackled at a local level, taking into account cultural issues and the specificity of place. Yet forest-planning approaches in North America have not necessarily adopted a holistic approach that reflects this in practice. Planning for visual amenity, for biodiversity and nature conservation, and for recreation have tended to be undertaken as different exercises with separate goals, leaving out the local and the cultural dimension, but are integrated through subsequent multiattribute planning and decision-making approaches, such as the US Forest Service forest and resource management plans or decision support systems using diverse criteria and indicators.

The Council of Europe's European Landscape Convention

As agriculture in Europe at the turn of the twenty-first century has become ever more intensified, so a new interest in forests has grown: forests which will reclaim marginal agricultural land and create new kinds of amenity for rural and suburban populations. This creates challenges for planning and design as a more enclosed landscape is not necessarily always welcomed by local populations, and may be unfamiliar as a recreational environment. Equally, in a postindustrial age, there are many areas of landscape dereliction in and around major urban settlements, where forestry can make a contribution to improving the environment and reclaiming the land. This is particularly an issue for Eastern European countries whose economic base, agriculture, and heavy and extractive industries are changing more rapidly than elsewhere. As European society becomes more urbanized, the pressures on forests and green areas close to towns are increasing at the same time that land for other uses is being abandoned elsewhere.

The Council of Europe's *European Landscape Convention* was agreed in 2000 and aims to promote landscape protection, management, and planning, and to organize European cooperation on landscape issues. The convention recognizes in particular the importance of public interest in the cultural, ecological, environmental, and social roles of the landscape as a resource. It highlights the way that the landscape contributes to the formation of local cultures and asserts that the landscape is 'a basic component of the European natural and cultural heritage, contributing to human well-being and consolidation of the European identity.' In the light of the perceived acceleration of landscape change, in forestry as in other aspects, it seeks to 'respond to the public's willingness to play an active part in the development of landscapes and to enjoy high quality landscapes.' Signatories to the Convention undertake to establish and implement landscape policies aimed at landscape protection, management, and planning, to establish procedures for the participation of the general public, local and regional authorities, and other interested parties in the definition and implementation of landscape policies, and to integrate landscape amenity with any other planning policies.

Although the Convention does not recommend in detail approaches to landscape planning, it is of relevance to forestry because it sets out a pan-European approach to managing forests for visual, cultural, and social amenity. It points clearly to the need for public and community consultation and collaboration in developing amenity plans for the future of forests, and gives a perspective on the contribution that forests make to shaping people's lives and identities far beyond the economic value of its products.

The next section sets out some recent examples of innovative or distinctive approaches to forest amenity planning from different European perspectives.

Finland and the Nordic Countries

Forestry landscape planning in many Nordic countries focuses on visual amenity and on the local-scale integration of ecology and nature conservation with forest management. There is a legal right to roam in Finnish forests for everyone and thus the amenity of the forest is potentially available to all. One Finn in five is a forest owner, many on a small scale, and so forest amenity planning is often at the level of 'family forestry.' Some of the cultural traditions which used to be common across Europe remain, such as the gathering of berries, mushrooms, lichens, and hunting of game, as well as more modern enterprises such as ecotourism. However, for the forests in and around urban areas, which are often owned by municipalities, multipurpose planning objectives are often lacking. In a joint project a similar pattern of lack of strategic investment and failure to plan for urban forest amenity is seen across much of Europe.

Recent work in Finland and Sweden in the late 1990s has aimed at developing better ways of integrating environmental considerations and biodiversity with sustainable production of forestry, taking a landscape amenity perspective. In a joint project, a geographical information system (GIS) has been developed to provide an easy user interface for forest management planning, allowing for the notion of interactive communication and learning with forest owners over planning proposals. The GIS program divides the forest into management zones and can be used to calculate and analyze the influences of public participation and the requirements set by society on the economics of forest planning at landscape and estate level. It is still in development at the time of writing.

By contrast with Finland and Sweden, Denmark has a comparatively low level of forest cover but rationalization of rural land in response to EU agricultural policies has led to a desire to increase afforestation. In 1989, the Danish government committed to a doubling of forest land from 12% to 24% within a period of 80–100 years. In designating land for afforestation, local authorities were given the power to determine the priorities for criteria, particularly in relation to reduction in agricultural land, wildlife conservation, and outdoor recreation, for their county. The plans for each county, which are reviewed regularly, are now made available using GIS, via the internet, to all citizens, and this allows for an increasingly democratic involvement in amenity planning. Such electronic means of communication and participation are becoming commonplace across Europe and elsewhere, allowing local interests in and definitions of amenity to inform the planning process.

Southern Europe

Compared with northern and central Europe, few southern European countries have highly developed or integrated forest amenity planning strategies, although forests may still have an important cultural role. An example from Turkey illustrates the European Convention's statement on the importance of cultural identities: the forest lands around the Bosporus have, since the 1980s, been designated as public assets which must be protected as part of an initiative to preserve cultural, natural, and historic assets in the Bosporus zone. By contrast, and unlike many southern European states, Slovenia still has a considerable level of forest cover (57%), most of which is private, often in shared and highly fragmented ownership. Perhaps because of this, Slovenia is unusual in having a long-term strategy for forestry that extends to advice and guidance for a horizon of 100 years. However, larger forest owners have pressed in recent times for a reduction in freedom of public access, thereby threatening traditional enjoyment of forests for mushroom picking. The matrix of open fields and forest is also changing as agriculture is abandoned and fields are left to natural succession. Thus, there are new challenges for amenity forest planning in Slovenia as for many countries now entering the European Union.

The UK Forestry Standard

The UK Forestry Standard, published in 1998, sets out a vision for new woodlands that recognizes the need to plan for multiple benefits in an integrated and sustainable way. Of the seven benefits identified as arising from new woodlands, at least three are directly associated with amenity planning: (1) enhancing the beauty and character of the countryside, and contributing to the diversity and distinctiveness of rural and urban landscapes; (2) helping to revitalize derelict and degraded land; and (3) improving the quality of life, especially in and around towns and cities, by creating opportunities for recreation, education, and local community involvement.

The Forestry Standard aims to integrate physical, biological, human, and cultural resource planning, recognizing the importance of cultural heritage and landscape amenity in the last of these. The tools for this include the items identified in **Table 1**.

Assessment of landscape character (**Figure 1**) has been an important tool for planning and design of forests in the UK since the 1960s and was made explicit in design guidelines developed as part of Forestry Commission planning methodologies in the 1980s (*see* **Landscape and Planning**: Visual Resource Management Approaches). Such assessment has since been codified in generic guidelines for landscape planning across the UK, developed separately for Wales and for England and Scotland. Forestry planning now incorporates this assessment, which reflects an increasing understanding of the complex nature of the cultural landscape (**Figures 2** and **3**).

Landscape Character Assessment (UK)

Landscape Character Assessment, promoted in 2002 by the Countryside Agency in England and Scottish Natural Heritage, is an amenity-planning tool designed to serve a range of predominantly countryside planning purposes, including forestry planning. It recognizes the importance of people and place and the cultural/social, perceptual and aesthetic and natural elements of this interaction which determines what we call 'landscape.'

In developing the guidelines for landscape character assessment, a 'character of England' map was produced by the (former) Countryside Commission, building on previous work by English Nature and English Heritage. An equivalent exercise in Scotland produced the Natural Heritage Futures initiative, which promotes integrated management of the natural and cultural heritage. The Landscape Character Assessment Guidelines grew out of these exercises. Examples of the range of possible uses

Table 1 Sustainable forestry management in the UK: amenity and cultural resource planning

Criteria for sustainable forest management	*Source of national-level indicators*	*Forest management unit indicators*
Rural development Access and recreation Quality of life in and around forests Increased awareness and participation Community involvement Other land uses	Surveys of forestry employment Information on employment multiplier effects of forestry Rate of afforestation in areas of strategic importance for other land uses Surveys of visitors to forests, UK Day Visits Survey, Time Use research reports Monitoring of planting in sensitive areas as defined by Indicative Forestry Strategies Inventory–woodlands close to towns National opinion surveys Reports on public awareness and involvement in forest biodiversity conservation	Evidence that: • Access is available along public rights of way and permissive routes • Information is promulgated about recreational facilities and access • Opportunities for walking and other recreational pursuits in woodland are considered • Activities associated with recreation do not compromise unnecessarily any future benefits of forest products or nature conservation • Efforts are taken to mitigate the consequences of vandalism or other antisocial behavior in woodlands • Requests to use woodlands for environmental education have been reasonably considered • Consultations and involvement of communities are reasonably accommodated, especially in relation to work opportunities
Conservation of heritage features Landscape quality	Surveys and registers of ancient monuments Reports of damage to ancient monuments Woodland aspects of rural countryside character and landscape assessments Survey reports for special areas, e.g., national parks, moorlands, coastal plains	Evidence that: • Important sites are clearly recorded • Sound principles for integrating archeological sites in woodland are adopted • Archeological sites are protected and damage is avoided • Landscape principles of forest design are used • Cultural and historical character of countryside is taken into account when creating new woods and when making changes to existing woods

Adapted, with permission, from Forestry Authority (1998) *The UK Forestry Standard: The Government's Approach to Sustainable Forestry*. Edinburgh, UK: Forestry Commission.

for landscape character assessment in the planning process are shown in **Table 2**.

Landscape character assessment is seen as a two-stage process, the first a relatively objective one in which the landscape, at whatever level or scale is appropriate, is mapped, classified, and described in a (supposedly) value-free way – 'characterization' – and the second an evaluative process where judgments are made using approaches appropriate to different end-uses, e.g., woodland development. Judgments based on the landscape characterization are then available to help in the decision-making processes which lie beyond the landscape character assessment exercise. The main approaches to making judgments about landscape character are identified as:

- *landscape character and guidelines* which focus on the conservation and enhancement of the key characteristics of landscape character types and areas
- *landscape quality and strategies* which provide a strategy for the whole landscape character type or area based on considerations of landscape quality and the physical state of the landscape
- *landscape value and designation/recognition*, based on the relative value attached to the different landscape character types or areas and their ability to match with specific criteria
- *landscape sensitivity and capacity*, i.e., the ability of the landscape to accept change without adverse consequences.

The production of the Landscape Character Assessment Guidelines has been accompanied by a discussion on how stakeholders can help, recognizing the need to incorporate this dimension more fully in making landscape assessments. A discussion paper has identified:

- stakeholders that are 'communities of interest,' e.g., government departments and agencies or special-interest groups such as the Royal Society for the Protection of Birds
- stakeholders that are 'communities of place,' e.g., local residents.

There are a number of benefits to be gained from stakeholder participation in making judgments about the landscape and its future, not least in identifying what it is that particular stakeholders value in the landscape, and why (*see* **Recreation**: User Needs and Preferences). The 'globalized' aspects of landscape designation have involved communities of interest, by and large, in identifying what is valuable in the landscape. Assessments of this type have involved expert judgments on biological rarity and historical significance. The involvement of communities of place in identifying the value of landscapes must be, necessarily, a more local endeavor.

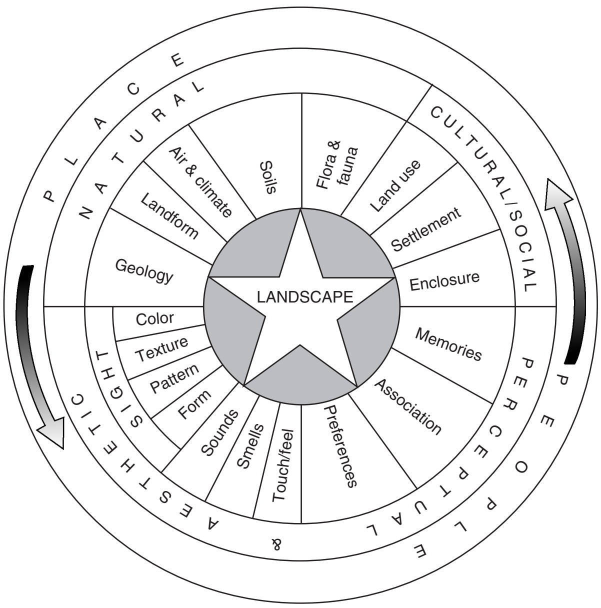


Figure 1 Landscape character. Adapted, with permission, from Countryside Agency and Scottish Natural Heritage (2002) *Landscape Character Assessment*, *Guidance for England and Scotland*. Wetherby: Countryside Agency Publications.

Australia and New Zealand

The New Zealand Forest Service of the 1980s, since disbanded, developed an early model for holistic forest planning, combining visual amenity with recreation and cultural provision that recognized the diversity of the landscape and the need for interpretation. Discussions of amenity planning approaches often focus on the challenge of defining amenity precisely; this has been particularly so in New Zealand and Australia. Amenity values have been defined as natural or physical qualities and characteristics of an area that contribute to people's appreciation of its pleasantness, esthetic coherence, and cultural and recreational attributes. Amenity planning policy in Australia aims to maximize the amenity enjoyed not only by the relevant property owners and occupiers, but also by neighbors and by the community at large. Social inclusion and planning for forest access for less mobile members of the community have become important issues here, as they have worldwide.

The original Landscape Character Assessment for the National Forest was central to the development of the Forestry Strategy. The consultation on the Strategy provided the opportunity for comment on the descriptive assessment and on the Forward Strategy for forestry creation based on the assessment. Consultation techniques included:

- written responses to the full strategy (220 replies)
- 1300 questionnaries returned by the general public from 18000 distributed summary documents of the strategy
- extensive media coverage – press, radio, and production of a video for loan to outside groups
- 30 talks to specialist stakeholder groups
- six public meetings and six day-long manned displays in local shopping centers
- watercolors commissioned to depict the changes in rural and coalfield landscapes over a 50-year period, for use in talks and exhibitions
- community views sought by interviewing six groups from within a typical coalfield village and an urban settlement from within the Forest

Source: Information supplied by the National Forest.

Figure 2 Landscape Character Assessment and Stakeholder Input in the National Forest. Adapted, with permission, from Countryside Agency and Scottish Natural Heritage (2002) *Landscape Character Assessment, Guidance for England and Scotland.* Wetherby, UK: Countryside Agency Publications.

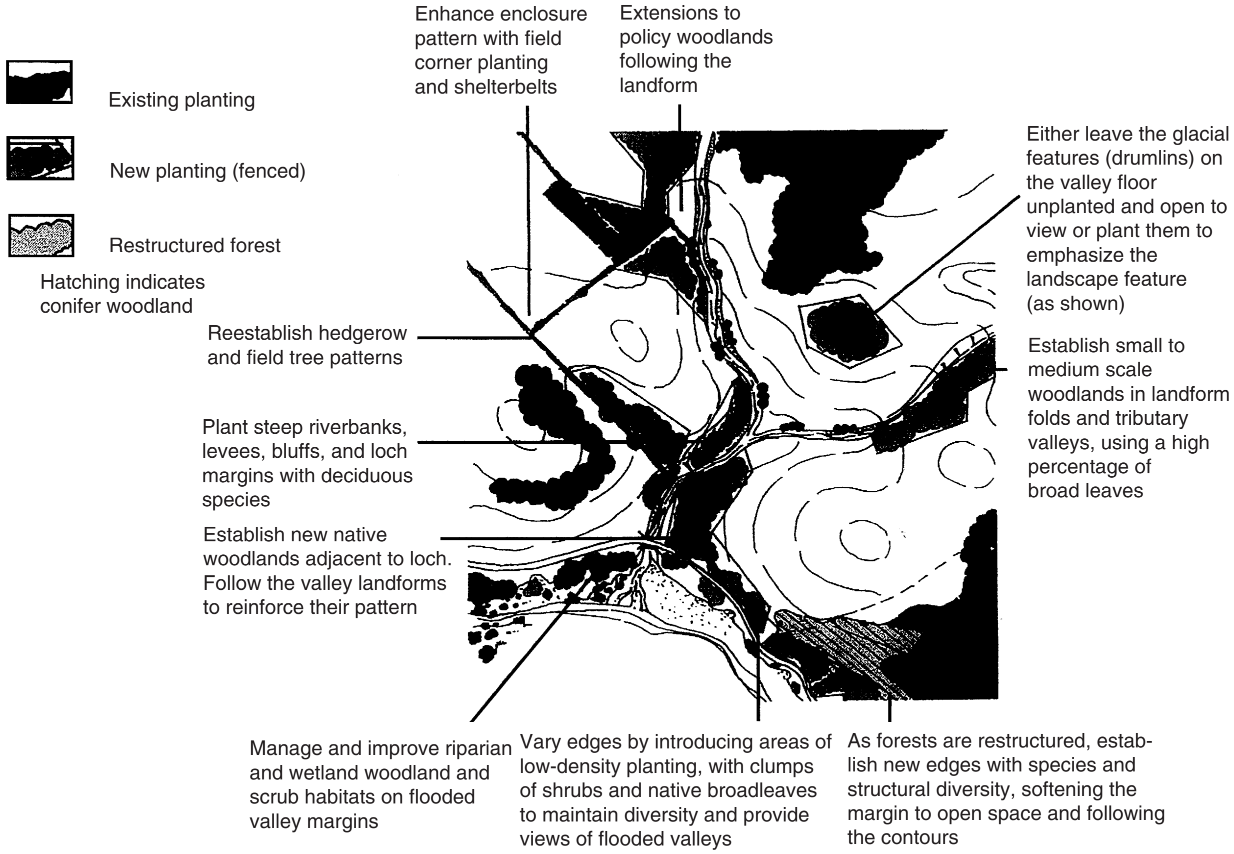


Figure 3 Landscape design guidance for forests and woodlands in Dumfries and Galloway. Source: ERM (1998) Landscape Design Guidance for Forests and Woodlands in Dumfries and Galloway. Forestry Commission, Dumfries and Galloway Council, Scottish Natural Heritage.

International Trends

On the international scene, amenity forestry planning must increasingly take into account the United Nation's Educational, Scientific and Cultural Organization (UNESCO) World Heritage Convention and the International Council of Monuments and Sites (ICOMOS), which advises UNESCO. The protection and conservation of archeological heritage in forest areas are concerns in many parts of the world, particularly where afforestation is increasing. Less attention has been paid to date to the concept of designating forests as cultural landscapes (as opposed to natural landscapes) in their own right but it seems likely that, in future, ICOMOS may designate world-class heritage landscapes on the basis of their cultural forest traditions. This is particularly likely as the European Landscape Convention and other initiatives across the world indicate a shift in emphasis on heritage value from monuments to people.

In some countries, forest planning may need to take into account the distinctive role that forests play in aboriginal cultural traditions. Forest planning in developing regions must also integrate amenity value in the context of subsistence economies and local ethnic communities' needs. Research has shown that recreational enjoyment of woodlands

Table 2 Landscape character assessment contributions to the planning process

Planning
- Capacity studies for different purposes, e.g., housing
- Expansion of settlements at the urban edge
- Input to environmental assessment of development projects

Landscape conservation and management
- Guiding land use change, e.g., woodland expansion

Landscape change for regeneration
- Community forests
- Reclamation and restoration strategies

Wider environmental initiatives
- Local agenda 21
- Environmental capital
- Environmental monitoring

Adapted, with permission, from Countryside Agency and Scottish Natural Heritage (2002) *Landscape Character Assessment, Guidance for England and Scotland*. Wetherby, UK: Countryside Agency Publications.

may often be restricted for women and young people, for older and disabled people, for those from ethnic-minority groups, and for socially disadvantaged groups. Amenity planning is increasingly required to take an inclusive approach which addresses these issues, although planning procedures which do so in practice are rare.

Conclusion

European traditions in forestry continue to provide a far-sighted model for the development of integrated amenity planning tools and multiple-use forest planning. Recent areas of interest in amenity planning in the UK include tranquillity mapping (mapping areas of countryside away from noise and visual intrusion) and mapping of areas free from light pollution, as well as focusing attention on the physical, mental, and social health benefits of living near woodlands, recognizing the potential for forests to improve people's quality of life. Nordic European countries such as Finland, with a different and more continuous tradition of living in and enjoyment of forest landscapes, have contributed to planning models which place an emphasis on the cultural landscape of forests. Early holistic approaches to forest planning in New Zealand have been matched by more recent innovative community-planning models in Australia. Worldwide, with the advancing urbanization of most nations and lifestyles, forest amenity planning has turned its focus increasingly on urban and urban periphery woodlands. For less developed countries, amenity planning for ecotourism is seen as a way to conserve forests while benefiting the local economy but requires strategies that are also compatible with the traditional dependence of local communities on forest resources for their way of life. This calls for integrated and holistic approaches to planning for multiple use that place a high value on social benefits, cultural contexts, and engagement of the community in the planning process.

See also: **Landscape and Planning**: Perceptions of Nature by Indigenous Communities; Urban Forestry; Visual Analysis of Forest Landscapes; Visual Resource Management Approaches. **Recreation**: User Needs and Preferences. **Social and Collaborative Forestry**: Joint and Collaborative Forest Management; Social and Community Forestry; Social Values of Forests.

Further Reading

Council of Europe (2000) *European Landscape Convention*, 20 October 2000, Florence. Available online at http://www.coe.int/t/e/Cultural_Co-operation/Environment/Landscape/.

Countryside Agency and Scottish Natural Heritage (2002) *Landscape Character Assessment*, *Guidance for England and Scotland*. Wetherby, UK: Countryside Agency Publications/Edinburgh, UK: Scottish Natural Heritage.

Crowe S (1978) *The Landscape of Forests and Woodlands*. London: Her Majesty's Stationery Office.

Forestry Authority (1998) *The UK Forestry Standard: The Government's Approach to Sustainable Forestry*. Edinburgh, UK: Forestry Commission.

Forestry Commission (1996) *Involving Communities in Forestry: Forestry Practice Guide*. Edinburgh, UK: Forestry Commission.

Forestry Development Centre Tapio (1998) *Forest Landscape Management*. Helsinki: Metsäteho Oy/Tapio, Finland: Forestry Development Centre.

Hodge SJ (1995) *Creating and Managing Woodlands around Towns*. London: Her Majesty's Stationery Office.

Miles R (1967) *Forestry in the English Landscape*. London: Faber & Faber.

National Board of Forestry Sweden (1990) *A Richer Forest: State-of-the-Art in the 1990s as regards Nature Conservation and Ecology*. Jönköping, Sweden: National Board of Forestry.

New Zealand Forest Service (1980) *Creative Forestry*. Wellington, New Zealand: Landscape Section Planning Division, New Zealand Forest Service.

Schama S (1995) *Landscape and Memory*. London: Harper-Collins.

Sievänen T, Konijnendijk CC, Lagner L, and Nilsson K (eds) (2001) *Forest and Social Services – The Role of Research*. Helsinki: Finnish Forest Research Institute.

Steiner FR (2000) *Living Landscape: An Ecological Approach to Landscape Planning*, 2nd edn. New York: McGraw-Hill Professional.

United States Department of Agriculture, Forest Service (1995) *Landscape Aesthetics: A Handbook for Scenery Management*. Agriculture Handbook Number 701.

The Role of Visualization in Forest Planning

S R J Sheppard and J D Salter, University of British Columbia, Vancouver, BC, Canada

Introduction

Modern techniques of computer visualization, involving three-dimensional (3D) modeling, computer animation, and virtual reality (VR), are taking their place among decision-support tools for forestry. This article focuses on the emerging role of visualization techniques that simulate the appearance of forested landscapes in forest resource planning, design, and management.

The Forest Planning Context for Visualization

It is increasingly recognized that sustainable management of forests cannot be effective without the integration of biophysical, socioeconomic, and cultural factors into the decision-making process. Public pressure for good stewardship of multiple forest resources requires more comprehensive and inclusive processes for decision-making. It is important that forest managers communicate with many stakeholder groups, with varying needs and degrees of knowledge on forest sciences. The complexity of these multiple demands on forest planning and management requires sophisticated decision-support techniques; this favors the use of visual communication techniques that can potentially simplify and explain complex information and improve the process of decision-making.

It is widely recognized that pictures can convey more information, more meaningful information, and more memorable information than other forms of communication. Visual information can also be interpreted by people from many walks of life. The general function of communicating scientific information can be achieved by what is called 'data visualization,' which comes in forms such as charts, diagrams, maps, graphics, models, etc. This can be helpful in explaining concepts, ecological processes, overall conditions, etc., which are not well expressed verbally, in text, or as data tables.

More specific forms of visualization, called visual simulation or landscape visualization, attempt to represent actual places and on-the-ground conditions in 3D perspective views, with varying degrees of realism (**Figure 1**). These convey detailed information on the expected future appearance of the landscape under certain forest conditions. Landscape visualizations offer potential to address social implications of site-specific management actions or scenarios, such as impacts on scenic quality, recreation, spiritual/cultural values, general quality of life, and property values. Furthermore, the general health of the forest is often judged by the public (and even experts such as forest certification panels) in part by what they see on the ground.

The two forms of visualization described above, data visualization and landscape visualization, can be combined in various ways. Showing spatial relationships (e.g., by mapping geographic information systems (GIS) data on to a landscape visualization) in the context of a recognizable place to which people can relate (**Figure 2**), can communicate complex information on ecosystem processes and patterns of resource values. This article will focus mostly on landscape visualization alone or in combination with data visualization.

It is widely believed within the forestry profession that the public often has little awareness of long-term landscape changes such as tree growth and death, and of temporal concepts such as succession and harvest rotations. Landscape visualization can depict both spatial and temporal variations in ecosystem conditions. It therefore offers the possibility of improving public knowledge regarding ecosystem management, and may perhaps help the public to strike a balance or trade-off in their own minds between short-term adverse effects on some values in return for long-term benefits to the ecosystem.

History of Landscape Visualization

Visual representations of existing landscapes and objects have occurred as art forms for millennia, with

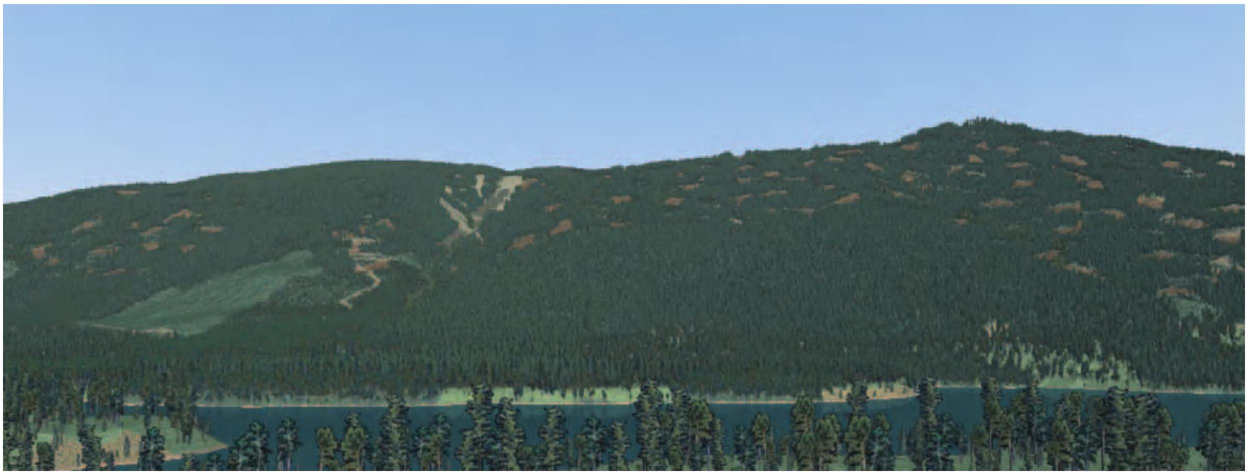


Figure 1 A fairly realistic computer-generated landscape visualization of a conceptual forest planning scenario in the Slocan Valley of British Columbia. Image by Jon Salter and Duncan Cavens, Collaborative for Advanced Landscape Planning (CALP).

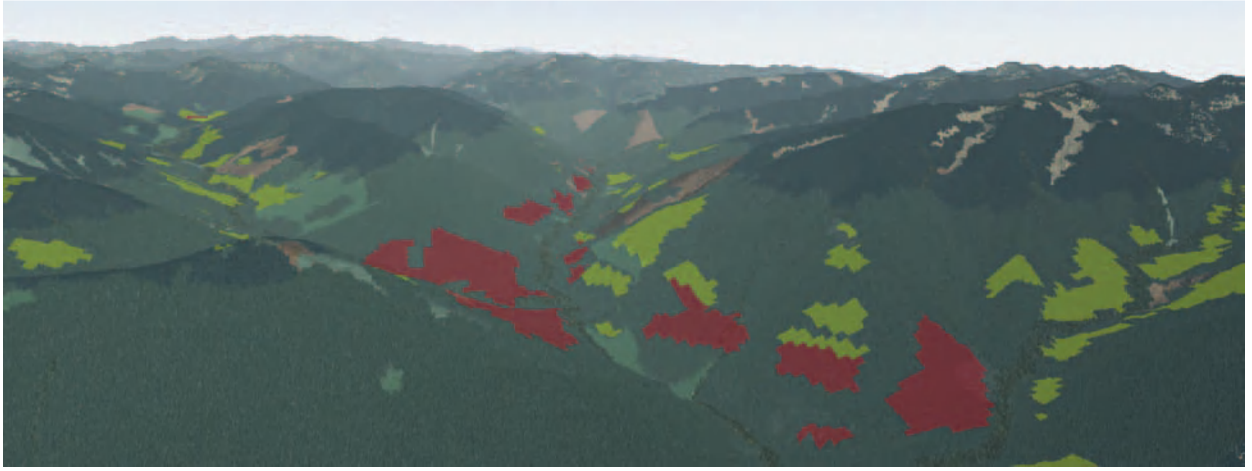


Figure 2 Overlay of habitat modeling results on to a landscape visualization of forest plans: red indicates high habitat value and green indicates moderate habitat value for a forest bird species. Image by Jon Salter, CALP and Ralph Wells, University of British Columbia.

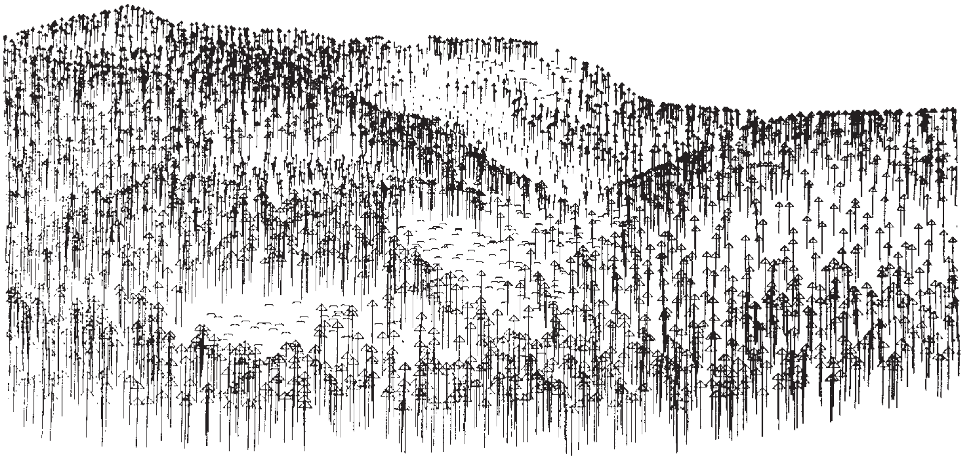


Figure 3 Example of a 3D modeling system used in the 1980s: 'wireframe' simulations from the PREVIEW program. Image by JA Wagar.

the rules of visual perspective developing during the Renaissance. Portrayals of future conditions or design proposals in perspective took a major step forward with the work of English landscape architect Humphry Repton, who presented his landscape design proposals in the form of 'before: after' paintings in the late eighteenth century. In the twentieth century, the emergence of land use planning and the design professions of architecture and landscape architecture led to standardized perspective simulations of proposed designs, initially in the form of scale models, line drawings, and color renderings. The availability of quality color photography led to techniques of photosimulation (i.e., photomontage and photoretouching), which were capable of delivering highly photorealistic landscape images many years before computers came into widespread use.

Beginning in the 1970s and 1980s, early computer-assisted or computer-generated visualization techniques were developed, initially for architectural projects, but these were soon expanded to engineering and forestry applications. Various software packages were developed in the 1970s and 1980s to model the appearance of changing landscape conditions. These 3D modelling systems used digital elevation models, building masses, and tree symbols to develop quantitatively accurate but rather abstract computer perspectives (e.g., 'wireframe' models) (**Figure 3**). These could be combined with traditional hand-rendering or photosimulation techniques to produce more realistic finished products. In the 1980s, the first image-processing techniques also emerged, allowing digital enhancement of scanned photographic images.

At the same time, the military and entertainment industries were developing more sophisticated computer-imaging techniques for modeling real or imagined landscapes. Some of these technological advances eventually contributed to the computer-based landscape visualization tools currently available commercially, including two-dimensional (2D) and 3D computer programs with a range of both abstract and highly realistic landscape imagery (see below).

Much of the visualization use in forestry has been associated with visual resource management (VRM) in Western nations, notably in North America (*see* **Landscape and Planning**: Visual Resource Management Approaches). The US Forest Service and other agencies have applied various visual simulation techniques since the early 1970s when the National Environmental Protection Act first mandated protection of aesthetic resources on public lands. These visualization techniques have been used mainly to support visual assessments and forest design, and are quite widely used for this purpose in several countries, such as the USA, Canada, New Zealand, Britain, and Finland.

In the 1990s, the development of spatially explicit stand modeling systems for mainly silvicultural purposes, such as the Stand Visualization System (SVS) at the University of Washington (**Figure 4**), SMARTFOREST at the University of Illinois, and MONSU in Finland, led to 3D visualizations of stand composition and structure, using increasingly detailed tree models. Developments in integrated decision-support systems using spatially explicit ecosystem modeling with multiple indicators are also beginning to link directly with visualization capabilities. Highly realistic viewers are also available to 'bolt on' to the outputs of various forest modeling systems.

Current uses of visualization in forestry can be broadly categorized as shown in **Figure 5**. This hierarchy illustrates the broader range of applications of visualization to research and education/professional extension activities, but consideration here is focused primarily upon practical use in decision-making where social values need to be integrated into the process. Because many forest management models and systems do not as yet explicitly incorporate social values into the process in a participatory way, the use of visualization in this context has not yet become commonplace.

Types of Visualization

This section presents a typology of landscape visualization techniques in current and emerging applications. Any typology in such a rapidly changing field cannot be all-encompassing or rigid in its definitions. It is important, however, to distinguish between the types of visualization models becoming available to generate visualization imagery, and the types of presentation formats through which the visualization products are delivered to their intended audience.

Visualization Models: Image Production

The following approaches to producing forest visualization imagery can be identified:

Geometric modeling This technique uses volumetric data (either from real-world inventory data or

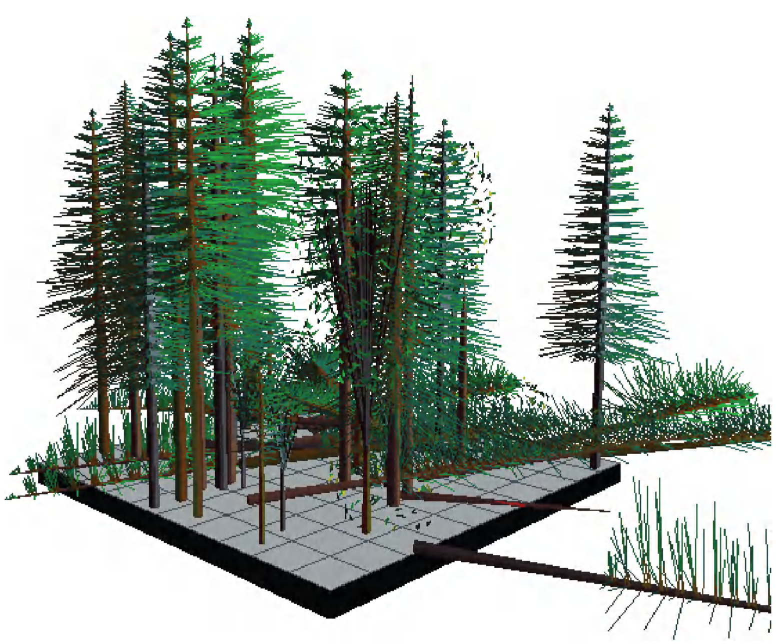


Figure 4 Example of a geometrically modeled stand with a moderate level of realism, from the Stand Visualization System (SVS). Reproduced from the SVS website. Image by Robert J McGaughey, USDA Forest Service.

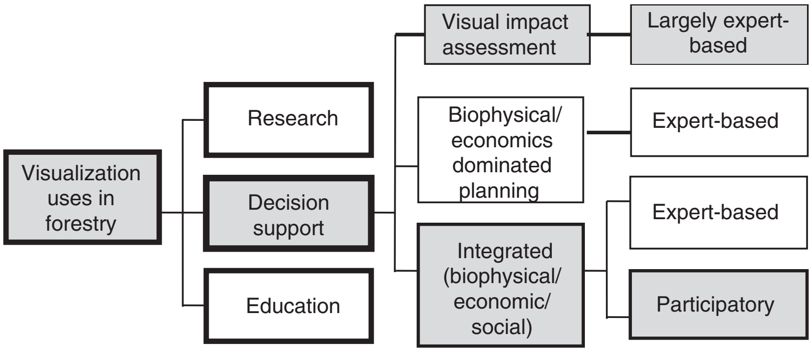


Figure 5 Hierarchy of visualization uses in forest ecosystem management. Shading indicates areas of concentration in this article. Reproduced with permission from Sheppard SRJ (2000) *The Compiler* 16(1): 25–40.

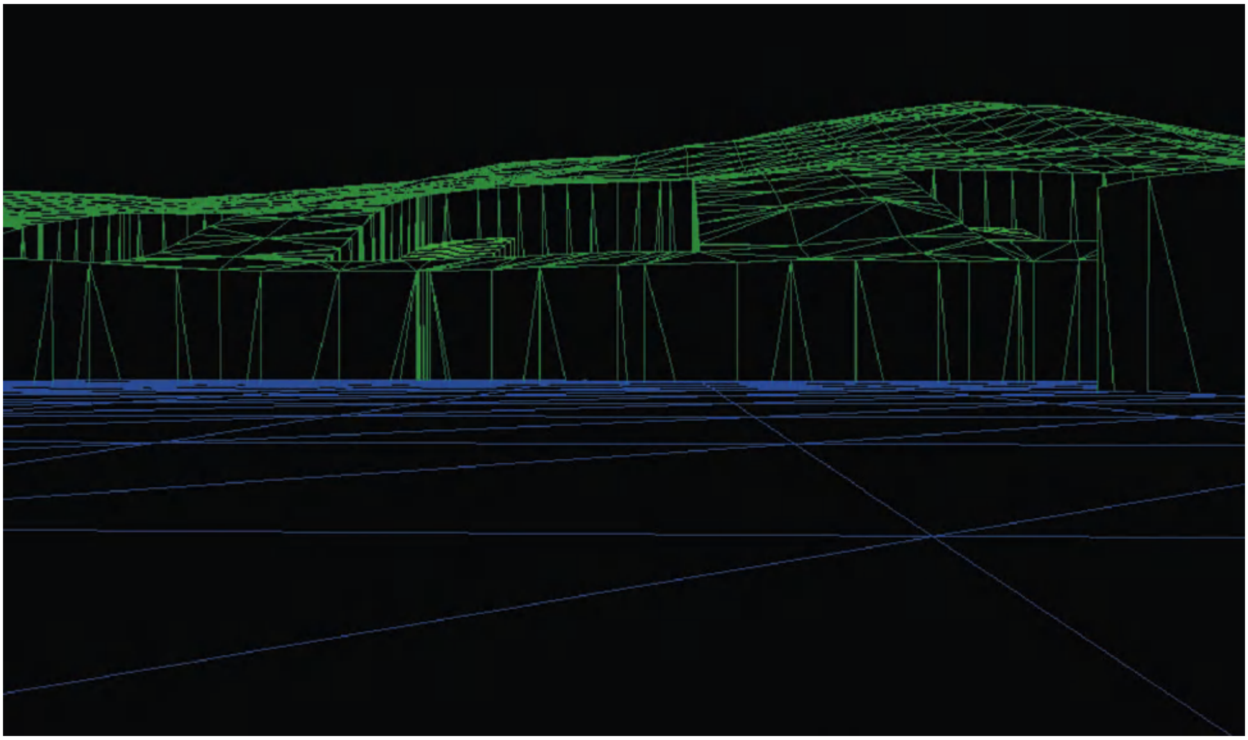


Figure 6 CAD-based 'wireframe' simulation of tree canopy and landform, showing proposed shelterwood harvesting at the Alex Fraser Research Forest, British Columbia. Image by John Lewis, CALP; Reproduced with permission from Sheppard SRJ and Harshaw HJ (eds) (2001) *Forests and Landscapes: Linking, Ecology, Sustainability, and Aesthetics*. Courtesy of CAB International, Wallingford, UK.

generated by predictive mathematical models) to construct digital 3D models of landscape forms. Ground surfaces or landforms can be constructed from surveyed elevation points or contour lines in computer-aided drafting (CAD) or GIS programs; vegetation can be generated from cruise data or ecological/growth models at the individual plant or stand level; and proposed roads or structures can be created from development plans. These models can range from simple wireframes (**Figure 6**) to more sophisticated solid models with synthetic textures and light sources (**Figures 4 and 7**). Geometric models may allow animation (dynamic motion or change over time). They can be considered as synthetic analogs of real world landscapes.

Photo-imaging (2D) The application of computer 'paint' programs to manipulate the pixel colors in digital 2D static photographs (**Figure 8**) is essentially artist-driven, but can be augmented by such tools as image element libraries (e.g., tree types, textures, etc.), 3D modeled perspectives to aid in element placement, and mathematical and/or survey techniques to improve image accuracy. Photorealistic images generally require skilled operators, and are too time-consuming for generation of large numbers of images, e.g., to show changing or alternative conditions over many time periods.

Hybrid geometric/photo-imaging Several techniques combine elements of the first two approaches to merge the synthetic elements of geometric models with photographic elements from photo-imaging. These fall into three main categories:

- 2D blend: views of 3D geometric models representing proposed management activities are placed into 2D static site photographs (**Figure 9**), precluding animation.
- Image draping/texture mapping: a 2D image or scanned texture map is draped on to a 3D model to represent surface features. This can be an aerial photo or satellite image draped on 3D terrain, or a texture image (such as grass or asphalt) mapped on to a landscape element. This technique is computationally efficient, and therefore is commonly used for animation and real-time applications. Its main drawback for forestry is that 2D image elements (e.g., an air photo) do not convey the 3D height effects of the trees (**Figure 10**).
- Photo-based objects: an extension of the draped texture map is the creation of discrete 3D objects which can be located with *x*, *y*, and *z* coordinates on a digital terrain surface, and upon which can be pasted individual photographic texture maps. For example, 2D or simple 3D tree models can be created and photographs of actual trees pasted on as 'billboards.' This technique can appear very lifelike, and allows animated travel through the forest model, though it is computationally very demanding because of the countless number of tree objects that need to be rendered (**Figure 11**).

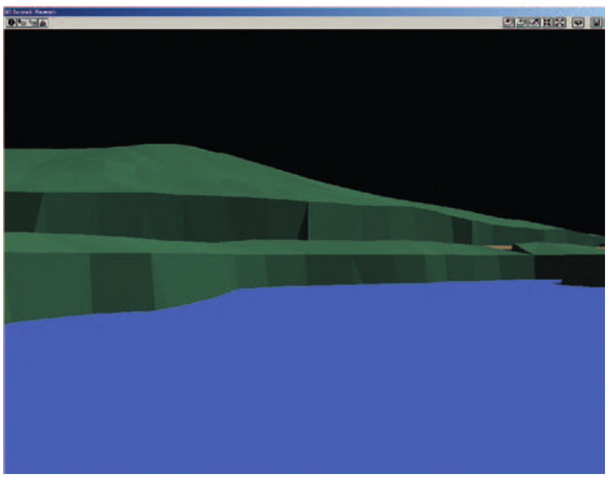


Figure 7 A digital solid model of proposed shelterwood harvesting at the Alex Fraser Research Forest, British Columbia; this model was constructed using ArcView 3D by ESRI. Image by John Lewis, CALP.

Viewing Formats: Image Presentation

Presentation formats for visualization can be classified by the degree of dynamism allowed in the delivery system, as follows:

- Static 2D images: hardcopy prints, on-screen images, or projected flat single images.
- Immersive static imagery: static images presented or projected in a 3D display, e.g., 'wraparound' projection screens or simulation booths which increase the viewer's sense of involvement in the simulated scene (**Figure 12**).
- Limited animation: allowing movement of the whole image to simulate changes in view direction or viewpoint, permitting the viewer to select different pre-prepared views of static digital

Figure 8 Photosimulation, created by 2D digital image manipulation using Adobe PhotoShop, of proposed shelterwood harvesting at the Alex Fraser Research Forest, British Columbia. Image by John Lewis, CALP, reproduced with permission from Sheppard SRJ and Harshaw HJ (eds) (2001) *Forests and Landscapes: Linking, Ecology, Sustainability, and Aesthetics*. Courtesy of CAB International, Wallingford, UK.

Figure 9 Hybrid image combining photographic elements with a geometrically modeled riparian corridor. Image by John Lewis, CALP.

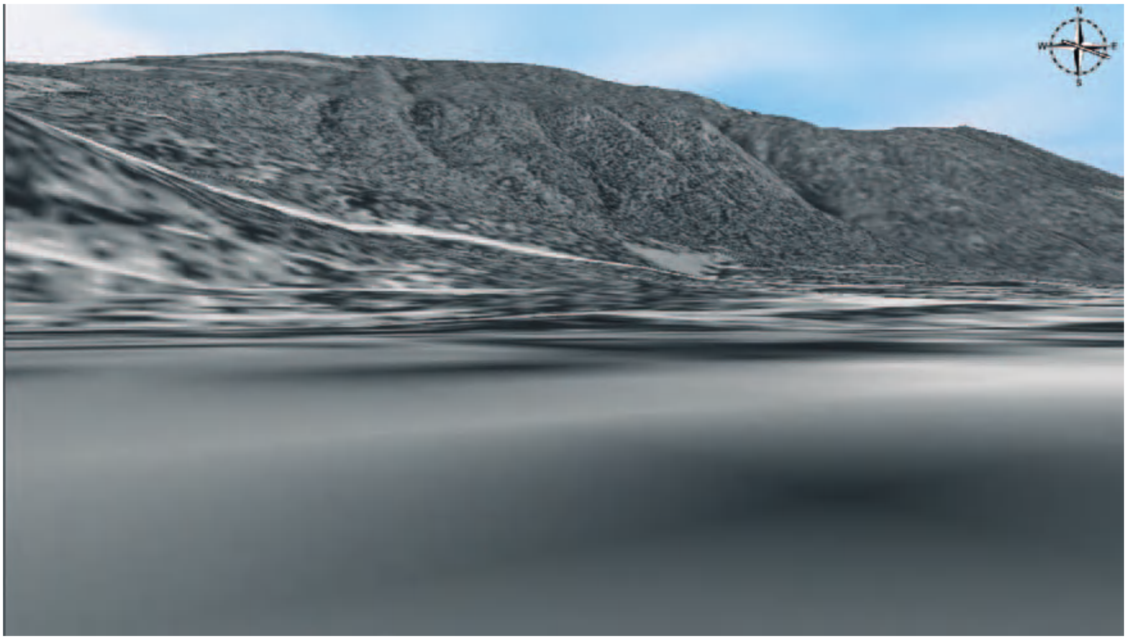


Figure 10 An orthophoto draped on a 3D model of a hillside in the Slocan Valley, British Columbia. Image by Jon Salter, CALP.

scenes arranged in viewing sequences or wrap-around panoramas.

- Animated viewpoints: allowing true dynamic simulation of continuous movement through a 3D model, along pre-prepared animation paths (i.e., the typical 'walk-through' or 'fly-through').
- Animated conditions: allowing pre-programmed continuous temporal/spatial change in simulated landscape conditions, e.g., trees growing (**Figure 13**) or a fire spreading.
- Real-time interactivity: allowing fuller interactivity between the viewer and the visualization system, whereby viewpoints, travel speeds, certain landscape conditions, etc., can be modified at will and in real time by user commands. Immersive VR systems allow the observer to experience virtual landscapes interactively as though they were within it, using headset systems or sophisticated forms of computer projection.

Assessing the Benefits and Limitations of Visualization in Forest Planning

Do these increasingly sophisticated and powerful visualizations live up to their promise? This section considers the advantages and disadvantages of established and emerging forms of landscape visualization in forest planning, based on research findings, current theory, and practice.

A limited amount of research on visualization methods in planning has been conducted since the

Figure 11 Hybrid image of proposed shelterwood harvesting on the Alex Fraser Research Forest, British Columbia, created with World Construction Set software and using 'billboard' 2D photographs of individual trees inserted into a digital 3D model. Image by John Lewis, CALP, University of British Columbia; reproduced by permission of Garten & Landschaft and CAB International, Wallingford, UK.

1970s, much of it grounded in the pioneering work of Donald Appleyard and colleagues at the University of California–Berkeley. The research comes from various disciplines, including urban and environmental planning, landscape architecture, computer science, graphic arts, information sciences, environmental psychology, social sciences, forestry, geography, and civil engineering. Implications for visualization in forestry have to be interpreted from the full range of applications. Some studies have evaluated the effectiveness of visualization media, but there have been few comprehensive experiments to assess the quality or validity of visualizations across multiple media or forest modeling contexts, and even fewer longitudinal studies relating predictive visualizations to actual landscape changes. The theoretical framework for landscape visualization is also very incomplete: the most cogent theories include communications theory, addressing the process of communications from source to receptor via certain channels; and various environmental psychology and aesthetic theories on human responses to the visual environment (*see* **Landscape and Planning**: Perceptions of Forest Landscapes). There is much anecdotal evidence to support the usefulness of landscape visualization in project-based decision support for forestry, but very little scientific documentation of real-world applications.

There is therefore considerable reliance on theoretical concepts and anecdotal evidence. The following sections summarize some key aspects of what is known and anticipated about visualization performance, and present a conceptual set of criteria for determining appropriate use of visualizations in the forestry context.

Performance of Landscape Visualization

The performance of visualizations can be thought of in terms of utility (practical usefulness or effectiveness) and quality (validity, reliability, realism, acceptability, etc.). The primary emphasis here is placed on the latter. Aspects of quality relate to the use of visualization to test observer reactions on the social acceptability of proposed forestry alternatives as well as on the acceptability of the visualizations themselves. Social responses can be obtained informally, through structured surveys of attitudes or judgments, or even through physiological measurements of pupillary excitation or stress levels. A variety of response types can be measured: responses can be categorized as cognitive (related to knowledge and

Figure 12 Immersive static image presented on three wraparound screens in the Landscape Immersion Laboratory of the Collaborative for Advanced Landscape Planning (CALP) at the University of British Columbia's Faculty of Forestry. Image by Jon Salter, CALP.

Figure 13 Visualization imagery showing ecological model-driven tree growth over three time periods, using CALP Forester experimental software. Image by Duncan Cavens and Jon Salter, CALP.

understanding), affective (related to feelings, perceptions, and emotions), and behavioral (related to changes in behavior of the viewer). Of these response types, little or nothing is documented scientifically on the effects of visualization on postexperiment behavior relevant to landscape management or forestry.

Specific advantages in utility believed to result from using landscape visualizations in a project planning context include: more meaningful participation of nonexperts in considering alternatives; more certainty for the project applicant and the affected community during the process; faster decisions as a result; better design of projects; less shock on the part of the public when visually disruptive changes occur on the landscape as a result of management; and in some cases an improved public image for the management agency. In theory, social response information can be fed back into the decision-support process to improve the basis of those decisions.

However, many visualization systems, and particularly the newer technologies such as animation and interactive VR, have very practical limitations associated with cost, availability of sufficiently powerful equipment, lack of appropriate data, availability of trained and experienced staff, and operational complexity.

Many of these factors are also believed to influence the quality of visualization. Quality also varies with the type of use or response sought from a given visualization set. With cognitive responses, adequate visualizations are generally understood to accelerate the mental processing of information, improve understanding, and place information in a context or perspective that allows broader interpretation of possible consequences. In practice, with site-specific landscape visualization, it is common that the process leads to new or modified conclusions on a project design or management action. Practitioners can often identify anomalies and errors in their data more quickly than in other ways. These cognitive benefits may be associated with abstract or conceptual (diagrammatic) data visualizations, realistic landscape visualizations, or hybrids of the two. However, there is a strong risk that visualizations may be cognitively misleading if they imply greater certainty than exists in future predictions of forest conditions.

Realistic ground-level views are often necessary for laypeople's fuller understanding of maps and plans. The more realistic visualizations also tend to evoke more affective reactions from viewers. Research shows that more abstract imagery (such as maps and simple computer modeling) provides less opportunity for people to respond to place-based cultural or quality of life issues such as aesthetics or acceptability of forest practices. Photographs and some forms of photorealistic visualization have been shown to replicate people's actual responses to real-world environments, which is the ultimate test of visualization validity (known as response equivalence). Most forestry studies with visualizations have tested responses on scenic beauty and/or acceptability of forest management; less is understood about validity on other questions.

However, visualizations have been criticized in terms of the following quality issues:

- Poor clarity of communication, leading to confusion and misinterpretation by viewers; this is understood to result from poor graphic presentation, too rapid animation speeds, overly complex information displays, etc.
- Low credibility of the visualizations to the audience; this can result from obvious errors, sloppy procedures, low realism, apparent bias in motivation of the preparer, etc.
- Actual bias (lack of response equivalence) in the responses arising from the use of the visualizations, as compared with the responses which would be expected from the corresponding real-world conditions if they were to be experienced. There is anecdotal evidence of misleading visualizations in practice, and some research measuring bias, though the causes are not fully understood.

Bias in responses to visualization can, in theory, be caused by deliberate manipulation (e.g., selective omission of landscape features), or unintentional inaccuracy. There is as yet no comprehensive evidence relating bias in responses to accuracy of the visualization. There is however a strong precautionary principle reflected in the literature, to the effect that, while accuracy may not be absolute or enough by itself to assure validity, it is risky to permit major inaccuracies in visualization content. Researchers such as Orland, Sheppard, and McQuillan have reinforced this view through their concerns about the ease with which realistic-appearing images can be created with today's technology, regardless of the accuracy of underlying data.

It is, however, known that responses to visualizations can be affected by factors other than image accuracy, such as the viewing locations chosen, accompanying information (e.g., verbal delivery or nonvisual data), and possibly the presentation format. Various studies have demonstrated the effects of using certain visualization media. Static imagery showing one or two 'snapshots' in time (e.g. 'before and after' an activity takes place) has been the predominant display technique for landscape visualization in forestry. Such methods offer a very limited window or slice of the information available: this places considerable reliance on the visualization preparer to select the appropriate view and conditions, in order to represent the universe of possibilities that exist over a long period of time, such as a forest rotation.

The general trend in emerging visualization methods appears to be towards more powerful and sophisticated animated graphics and VR displays, more realistic synthetic landscape models, more intuitive graphical user interfaces (GUIs), and wider access to these systems through means such as the Internet. However, the consequences of using this type of information have been tested in very few experiments. Even less information is available on the consequences of using VR techniques in practical resource management. Advanced techniques such as animation and interactive VR programs provide substantially more visual information and flexibility in viewing, and offer to overcome some of the limitations of previous methods. Much of this available visual information can of course be redundant, but there is also considerable potential for animation to provide new information through change of perspective. The ability for the user to control more aspects of the visualization also promises to reduce risks of bias from more limited or selective presentations.

Possible disadvantages associated particularly with newer methods of visualization include:

- The increased risk of raising unrealistic expectations of visualization accuracy, again because of its apparent realism.
- The risk of the novelty factor of dramatic visualizations overshadowing the content of the visualization message.
- The risk that the very sophistication, perceived expense, and 'high-tech' image of the emerging visualization media may cause a negative backlash in the public's mind, leading to rejection of the message regardless of its accuracy.
- The risk of excluding noncomputer-literate sectors of society from the decision-making process, through overreliance on digital media and access to online computer visualization techniques.

Indicators for Appropriate Use of Visualization

Given the incomplete state of our knowledge on visualization benefits and limitations, and the rapidly changing nature of visualization technologies, what guidance exists on the appropriate use of visualization for forest planning?

Previously elaborated principles and guidelines for valid and effective visualization can be used as a starting point, but needs to be extended and re-evaluated in the context of new techniques and modern demands on forest management. The following are principles for project-level landscape visualization where public (laypeople) responses may be expected:

- Representativeness: visualizations should represent typical or important views of the landscape.
- Accuracy: visualizations should simulate the actual appearance of the landscape (at least for those landscape factors being judged) (*see* **Landscape and Planning**: Visual Analysis of Forest Landscapes).
- Visual clarity: the details, components, and overall content of the visualization should be clearly distinguishable.
- Interest: the visualization should engage and hold the interest of the audience.
- Legitimacy: the visualization should be defensible and its correctness demonstrable; visualizations used should be driven by data, not by artistic license.
- Access to visual information: visualizations (and associated information) that are consistent with the above principles should be made readily accessible to the public via a variety of formats and communication channels.

These precautionary principles can be used to guide the ethical preparation and use of visualizations, the validity of which can ultimately be established only after the forest management actions have been implemented. It is therefore important to record

Figure 14 An interactive visualization system prototype (CALP Forester) that allows the user to prescribe management actions through a laser pointer interface and query the underlying model data. Image by Duncan Cavens, CALP.

and monitor the performance of the visualizations over time, so that the guidelines can be adapted as more hard information becomes available.

The current trend towards more public participation in forest management, and specifically toward the inclusion of social values in modern forest ecosystem management, calls for decision-support systems with more stakeholder involvement in and control over the development and evaluation of forest landscape choices. This can be translated into demands on visualization systems for:

- More intuitively understandable visualization methods.
- More transparent and accountable visualization processes/products.
- More involvement of the public in interrogating, interpreting, and even preparing visualizations which allow some user control over factors such as tree growth and management activities reflected in the visualization images (**Figure 14**).
- More choices of views, conditions, and alternatives visualized.

Conclusions

The science of landscape visualization is still young and evolving. There is much that we need to learn about how visualizations work in practice, and how emerging techniques will affect forest decision-making. While much more research is needed, the speed with which new visualization technologies are becoming available means that practicing forest managers cannot wait for research results, but must proceed under interim precautionary principles.

The power of the visual medium means that the preparer of visualizations carries a heavy responsibility to use that power appropriately. It must be recognized that all visualizations carry some inaccuracy, some bias in responses, and considerable uncertainty. This requires expectation management among users, and suggests that visualizations should not simply be plugged in and played without considerable planning and appropriate training for users. Updated guidelines and a code of ethics will be needed. Where possible, computer interfaces which provide access to nonvisual information about forest conditions should be provided, with built-in limitations on potential misrepresentation of data.

We can expect a new class of exploratory visualization tools to emerge that are more user-friendly, interactive, dynamic, and allow the user to navigate through the available 3D data to see forest conditions across space and time. Visualizations may move from being an end-product of planning activities or stand modeling exercises, to acting as a gateway to the planning or modeling process, through which new model runs or 'what-if' scenarios can be triggered directly and results browsed. The potential benefits are that it promises to provide easier and wider public access to the issues of forest management than has ever before been possible. The policy implications and procedural mechanisms to accommodate such public demands have yet to be thought through, however. It is also not clear whether the increasing choice and control by the viewer necessarily leads to greater validity and better decision-making.

In the long term, accumulating research and practice with visualization should fill out the theoretical framework for landscape visualization. Priorities for research include systematic evaluation of existing and experimental visualization techniques in laboratory conditions, and monitoring and evaluation of visualization techniques and effects in practical forestry applications.

Most forest managers are not well trained in methods of collaborating with the public, and often lack needed skills when dealing with affected communities. The use of credible visualization methods may ultimately help them to overcome these shortcomings, transform forest planning, and perhaps increase public understanding of forest sciences in management.

See also: **Landscape and Planning**: Forest Amenity Planning Approaches; Perceptions of Forest Landscapes; Perceptions of Nature by Indigenous Communities; Visual Analysis of Forest Landscapes; Visual Resource Management Approaches.

Further Reading

Appleyard D (1977) Understanding professional media: issues, theory, and a research agenda. In: Altman I and Wohlwill JF (eds) *Human Behavior and Environment*, pp. 43–88. New York: Plenum Press.

Daniel T and Meitner M (2001) Representational validity of landscape visualizations: the effects of graphical realism on perceived scenic beauty of forest vistas. *Journal of Environmental Psychology* 21(1): 61–72.

McGaughey RJ (1998) Techniques for visualizing the appearance of forestry operations. *Journal of Forestry* 96(6): 9–14.

McQuillan AG (1998) Honesty and foresight in computer visualizations. *Journal of Forestry* 96(6): 15–16.

Monmonier MS (1996) *How to Lie with Maps*. Chicago, IL: University of Illinois Press.

Muhar A (2001) Three-dimensional modelling and visualization of vegetation for landscape simulation. *Landscape and Urban Planning* 54(1–4): 5–17.

Orland B (1994) Visualization techniques for incorporation in forest planning geographic information systems. *Landscape and Urban Planning* 30: 83–97.
Sheppard SRJ (1989) *Visual Simulation: A User's Guide for Architects, Engineers, and Planners*. New York: Van Nostrand Reinhold.
Sheppard SRJ (2001) Guidance for crystal ball gazers: developing a code of ethics for landscape visualization. *Landscape and Urban Planning* 54(1–4): 183–199.
Tufte ER (1990) *Envisioning Information*. Cheshire, CT: Graphics Press.
Zube EH, Simcox DE, and Law CS (1987) Perceptual landscape simulations: history and prospect. *Landscape Journal* 6(1): 62–80.

Landscape Ecology, Use and Application in Forestry

N Brown, Oxford Forestry Institute, Oxford, UK

Introduction

Many ecological processes result in or are affected by spatial patterns. However, the relative importance of different processes is very sensitive to the scale of analysis. For example, at a very local scale, species diversity is often strongly affected by competition and trophic interactions between species. In contrast, at the regional scale species diversity is more strongly influenced by habitat dynamics and biogeography. The majority of ecological studies in the past has focused on local level processes, probably because they are less daunting to measure and are more amenable to experimental manipulation. The recognition that the important processes acting at a landscape level are often different from those at a local level has led to the development of landscape ecology as a distinct approach with its own paradigms and methodologies.

Ecologists have traditionally been interested in the spatial patterns of organisms. Charles Darwin's *On The Origin of Species* contains an entire chapter discussing the geographical distribution of species. However, the focus of his chapter, like much of the ecological literature since, is on the processes that create spatial patterns or biogeography. In contrast, an area of prime interest in landscape ecology is the way that spatial patterns affect ecological processes. This article reviews some of the ideas that this perspective has generated and looks at their relevance to forestry.

Why Landscape Scale?

The question of which is the appropriate scale for a particular analysis will largely depend on its objectives. Many issues in applied ecology and particularly those concerning environmental management are most appropriately addressed at a landscape scale. This is certainly true of forestry where many of the key management issues concern processes that operate over large areas. Environmental change, conservation, sustainability concerns, recreation, and public participation all involve considering forests in their landscape context.

The term 'landscape' has no precise definition. It implies an area that is perceived to have some coherence of natural or cultural entities. In practice the lack of a formal description of what constitutes a landscape is no more problematic than the similarly vague definition of the term 'population' in ecology. Both are useful because they demarcate biologically meaningful groups. Just like landscapes, populations can be identified at a scale that is appropriate to the objectives of the study.

The need for a large-scale perspective is not a new one but it is only recently that ecologists have acquired the tools that permit them to carry out this type of analysis efficiently. Remote sensing and geographic information systems (GIS) have permitted the collection and analysis of large quantities of spatial data. Although ecologists use experimental approaches more frequently than many environmental scientists, the possibilities for experimental landscape ecology research are severely limited. It is usually impractical to deliberately manipulate landscapes for experimental purposes and even in those situations where a treatment occurs as a consequence of other action it is usually impossible to replicate or control. Hence landscape ecologists typically measure rather than manipulate; patterns and processes are described rather than being experimentally controlled. Although purely descriptive studies in ecology are often criticized it is only by having accurate quantitative descriptions of landscape patterns that testable hypotheses can subsequently be developed.

Simulation modeling can be used as an alternative to the descriptive–inductive approach to landscape ecology. Aided by huge advances in computing, simulation modeling has permitted landscape ecology to throw off some of the constraints of studying region-specific, observable phenomena. Modeling has been used to identify the ecological implications of changing landscape patterns and of alternative management regimes applied to existing land use configurations. The combination of ecological models with GIS and, more recently, computer-generated visualization have provided a powerful planning tool.

One area that has proved to be a consistent challenge in landscape ecology has been the development of accurate, consistent, and ecologically meaningful measures of spatial pattern. The measurement of spatial pattern is often strongly scale-dependent. The types of pattern that can be recognized depend very much on the scale at which they are viewed. For example features that appear clustered at a small scale can be dispersed when viewed at a large one. Connectivity can change too. Small patches of woodland and wooded corridors between patches can disappear when a landscape is viewed at a small scale (**Figure 1**).

In 1967, Benoit Mandelbrot published a paper in which he concluded that the length of the coastline of Britain depended on the scale of measurement. He pointed out that each increase in scale reveals a new level of roughness and thus an increase in its length. He termed such patterns, which reveal greater complexity as they are enlarged, fractals. Many of the measures that are used to quantify shape and complexity in landscape ecology are similarly dependent on the scale of the analysis. This implies that it is crucial when investigating the impacts of spatial pattern on ecological processes to make sure that pattern is measured at a scale that matches the way the study organism perceives the landscape. A region in which woodland is highly fragmented from the point of view of a wood mouse (*Apodemus sylvaticus*) can be well connected for a more mobile organism like a jay (*Garrulus glandarius*). A further dimension to this problem is the difficulty of obtaining a consistent quality of information over space and time. Some types of measures of spatial pattern are sensitive to the quality of input maps. Very large differences have been found in a number of measures used to quantify landscape structure when the same region is analyzed on different map products.

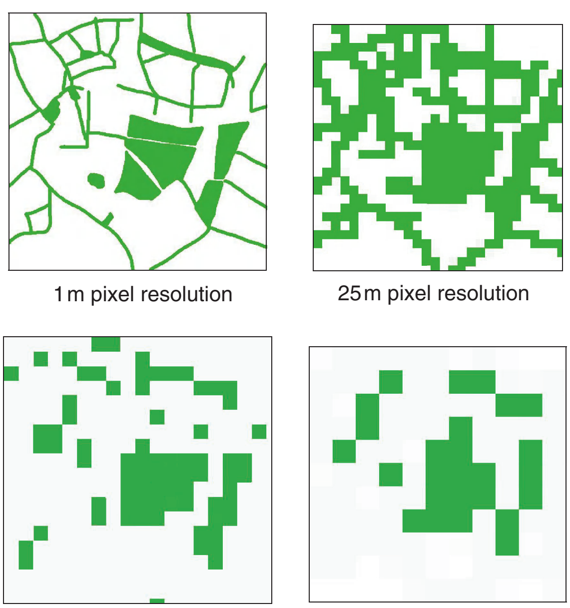


Figure 1 The connectivity of wooded areas in an Oxfordshire landscape changes with the resolution of the image used for the analysis.

Landscape Ecology and Forestry

Both forestry activities and deforestation alter landscape structure in ways that have significant effects on organisms. In many parts of the world different components of the landscape are managed virtually in isolation, with little or no account taken of surrounding land use or landscape context. Such components include forested blocks, agricultural fields, urban areas, and waterways. A consequence of this is that management objectives are often frustrated by the functional dependence of one land area on those around it. For example, recent research in Costa Rica has shown that the diversity of moths in sites outside forest is most correlated with forest cover within 1–1.5 km of the surveyed site. Fragmented management often results in resource use conflicts and environmental stress.

Growing interest in sustainable forest management systems over the last decade has resulted in efforts to apply ideas from landscape ecology to forest management practices, particularly timber harvesting and new woodland creation. A guiding principle has been the emulation of natural patterns. Landscape ecology provides useful ways in which natural patterns can be described and compared with those in the managed landscape.

There are four landscape characteristics that have important implications for forest management.

Fragmentation

Fragmentation occurs when a large area of forest is broken up into smaller, less connected patches. In many tropical landscapes fragmentation of natural forest is occurring rapidly and efforts to protect biodiversity and to understand the ecological processes that determine its survival are becoming increasingly important. In contrast, in many temperate countries, an excess of agricultural land and a concern to increase the area of woodland for aesthetic, conservation, and recreation reasons, have prompted interest in the potential benefits of defragmentation. There have been two types of approach to understanding patterns in fragmented landscapes; those that address issues of community composition and those that examine single species population dynamics. Here, both approaches are described.

The equilibrium theory of island biogeography (advanced in the 1960s by MacArthur and Wilson) has been a cornerstone of our understanding of the processes that determine community composition in a fragmented environment for nearly 40 years. Their theory proposed that the diversity of organisms on an island should decrease as its size decreases and isolation from the mainland increases. This concept has been widely applied to habitat fragments on the assumption that they function like islands surrounded by a 'sea' of more hostile environment. However, it has not generally proved to be a useful tool for predicting species diversity in habitat patches within a matrix of other land uses. This is because the community of species in a patch of habitat will be strongly influenced by the nature of the landscape around it and the sorts of species that inhabit that landscape. The management regimes used in open countryside have been found to influence both bird and invertebrate diversity in adjacent forest patches. Species that inhabit forest patches can be affected by competition and predation from species that inhabit surrounding land use types. For example, in the Midwest of the USA the replacement of forest by agricultural and suburban landscapes has resulted in a substantial expansion in the range of the brown-headed cowbird *(Molothrus ater)*. A relationship has been found between songbird nest predation and parasitism by cowbirds and the degree of forest fragmentation. The implication of studies such as this is that two fragments of forests may have identical areas and be equally isolated but their species composition may be very different as a consequence of their interactions with surrounding land use types.

Models of single-species population dynamics at a landscape level are a much more recent development. A variety of models has been formulated to describe the dynamics of a range of organisms with very different ecologies. Metapopulation theory envisages that a landscape is divided into habitable patches separated by unsuitable habitat and that as a consequence a species population will actually consist of a series of interacting local populations each occupying a patch. Changes that occur in one local population do not necessarily occur in other patches at the same time. This can mean that one local population may go extinct whilst others are thriving. Migration between patches can re-establish a local population should it go extinct. Metapopulation theory predicts that a threshold number of patches is needed in order that the species persists at a landscape level. The dynamics of the metapopulation are not simply a function of local population dynamics since larger-scale factors such as the distribution of patches in the landscape and migration rates between patches are important. The metapopulation concept has important implications for the management of fragmented forests. Silvicultural operations such as felling and coppicing can drastically alter habitat quality and unless there are enough similar habitat patches within migration distance it may be impossible for a local population to re-establish should it go extinct. Many rare UK butterflies are found exclusively in large and non-isolated habitat patches, while small or isolated patches of suitable habitat remain vacant. This distribution pattern is the result of local extinction and colonization processes and implies that long-term population persistence requires networks of suitable habitats, sufficiently close to allow natural dispersal. An extension of metapopulation theory considers the landscape to consist of habitat of variable quality rather than a simple division into habitable and uninhabitable areas. An area in which a species population thrives (with births exceeding deaths) may become a source of colonists whereas poor quality habitat may be a sink (deaths exceeding births). An important implication is that the decline of a local population in one forest may result in declines in adjacent forest patches as mobile species move out to recolonize vacant areas. This may make it difficult to diagnose the cause of a population decline and it emphasizes the importance of conserving habitat networks rather than focusing on the protection of a single site.

The fragmented nature of management planning in many patchy landscapes can make management of conservation networks difficult. Numerous owners and a variety of organizations may be responsible for taking decisions with the result that forest operations are planned on a case-by-case basis with no account taken of what is happening to adjacent forest areas. Landscape ecology has highlighted the importance of making sure that land use policies are aligned across owners and government agencies when sustainability is an essential goal.

Edge Effects

As patch size decreases so a progressively larger proportion of the remaining forest is influenced by edge effects. These can include increases in light and temperature and decreases in humidity. Increases in light have often been found to result in higher density and faster growth of natural regeneration of light-demanding trees along forest edges but also in the proliferation of herb and vine species. In tropical rain forest in the Brazilian Amazon significant increases in liana density have been detected up to 100 m from a forest edge. There is often an increased risk of windthrow on exposed forest edges. This has encouraged the development of special treatments for stand edges in areas that suffer from a high risk of wind damage. These include establishing shelterbelts of wind-resistant species or heavy thinning regimes to encourage well-tapered stems. It is also clear that the pattern of felling at a landscape level can have a significant effect on both the total length of exposed forest edge and wind turbulence.

Small woods have a high proportion of edge to core area. One reason for the creation of new forests in landscapes that have lost most of their forest area is to provide new niches that are not currently available. Large forests offer opportunities for species that require large forested territories, use large home ranges, or which thrive in forest interior habitats (i.e., are disadvantaged in forest edge habitats).

Connectivity

Connectivity refers to the degree to which habitat patches are linked so that organisms can move from one patch to another. Little is yet understood about colonization processes and rates and landscape use by many forest organisms but it is clear that connections in a landscape are organism-specific.

It has often been claimed that connectivity can be increased by the creation of habitat corridors. Strips of habitat connecting patches were assumed to facilitate migration and reduce the risks of local population extinction. However, empirical studies have shown that it is often the structure of the entire landscape matrix (the ‘habitat network’) that determines whether organisms can move. Many organisms can migrate through a landscape using a variety of habitats that they would not live in. Conversely, the provision of habitat corridors does not guarantee movement. Patches that are physically linked by a narrow corridor may not be connected for an organism that only occupies forest interior habitats. Indeed, it has even been proposed that corridors may facilitate colonization by invasive species and species tolerant of disturbed conditions.

Direct physical connections may be necessary for movement of organisms that inhabit old-growth forest and that have highly specific habitat requirements. Such species typically have extremely slow colonization rates. Even with an adjacent source of colonization, the number of such poorly dispersed species that will establish in newly forested areas may be low. Forest management systems need to be designed to maximize the opportunities for the dispersal of old-growth forest specialist species. This may include leaving substantial areas without any form of management intervention, avoiding excessive edge effects by minimizing the amount of harvesting around unmanaged core areas and distributing harvesting to ensure that regenerating forest is not isolated from old-growth areas.

Disturbance

Disturbance regimes determine the structure and composition of natural forests. Large or frequent disturbances (such as wildfires or hurricanes) create forests that have a uniform structure and a predominance of pioneer or colonizing species. In contrast, climax or shade-tolerant species will dominate forests that have only small or infrequent disturbances (such as those caused by the collapse of an old tree). As many of the organisms in a natural forest will be adapted to the prevailing disturbance regime, natural forest management systems that intend to sustain this biological diversity have attempted to match natural patterns. This includes matching the design of harvesting blocks to the pattern and distribution of natural disturbances across a landscape in terms of their size, shape, and frequency.

Natural forest management systems were abandoned during the twentieth century in many European and North American countries as markets for traditional woodland products declined. As a consequence, many seminatural forests have lost the diversity of ages and hence structures that management maintained and that were important for wildlife. There are a number of initiatives to bring neglected woodlands back into management with the primary objective of enhancing their wildlife value. Techniques such as thinning, coppicing, and the introduction of group selection felling systems have begun to re-establish a variety of woodland habitats. An important task is to decide how these different management regimes should be distributed at a landscape scale. Studies of natural disturbance regimes can help in the design of appropriate silvicultural systems but one of the greatest challenges remains the coordination of actions at a landscape scale particularly where this involves a number of different landowners.

See also: **Biodiversity**: Biodiversity in Forests; Endangered Species of Trees; Plant Diversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife; Natural Disturbance in Forest Environments; Plant-Animal Interactions in Forest Ecosystems. **Entomology**:

Population Dynamics of Forest Insects. **Environment**: Environmental Impacts. **Genetics and Genetic Resources**: Forest Management for Conservation. **Landscape and Planning**: Landscape Ecology, the Concepts. **Resource Assessment**: GIS and Remote Sensing. **Silviculture**: Natural Stand Regeneration.

Further Reading

Cissel JH, Swanson FJ, and Weisberg PJ (1999) Landscape management using historical fire regimes: Blue River, Oregon. *Ecological Applications* 9(4): 1217–1231.

Haines-Young R and Chopping M (1996) Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. *Progress in Physical Geography* 20: 418–445.

Honnay O, Hermy M, and Coppin P (1999) Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management* 115: 157–170.

MacArthur RH and Wilson EO (1967) *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Mandelbrot BB (1967) How long is the coast of Britain? Statistical self-similarity and fractional dimension. *Science* 156: 636–638.

Pierce AR and Ervin JB (1999) Can independent forest management certification incorporate elements of landscape ecology? *Unasylva* 196(50): 49–56.

Simberloff D, Farr JA, Cox J, and Mehlman DW (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6(4): 493–504.

Turner MG (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171–197.

Yahner RH (1988) Changes in wildlife communities near edges. *Conservation Biology* 2(4): 333–339.

Landscape Ecology, the Concepts

E A Simmons, National School of Forestry, University of Central Lancashire, Penrith, Cumbria, UK

Introduction

Landscape ecology is an emerging discipline that aims to understand the environmental processes and patterns influencing habitats and species beyond the site level. It arose independently in the latter part of the twentieth century in central and Eastern Europe and in North America as geographers, planners, and ecologists began to push the boundaries of their subject interests in the search for integrated approaches to land management of sensitive areas. They combined intellectual forces in the International Association of Landscape Ecology (IALE), formed in 1982.

Landscape ecology is based on the initial premise that a landscape can be viewed as a series of patches within an overall background matrix; taken together, patches and matrix make up a heterogeneous landscape mosaic. The significance for forestry is that it can take the focus up a level from the management of stands within a forest to forests within a landscape. Each forest or woodland can be viewed as a patch, within a matrix of other land use. The power of landscape ecology is that its principles can apply at vastly different scales, depending on the landscape or the research question. It has been used equally effectively by natural resource managers in conservation planning of large protected areas such as watersheds or national parks and by those undertaking local-scale restoration projects consisting of a few sites. In Europe the challenge is often to mitigate the effects of development, but landscape ecology can be used more proactively to design for conservation and related benefits. It is equally applicable to temperate and tropical landscapes, and although data constraints are significant, it is more often the speed of landscape change that prevents the full application of the discipline to landscape problems.

Landscape ecology is a broad discipline, with spatial planning at its heart, but it is much more than just mapping, as its twin concern is the time dimension of both natural and human-induced effects. Timescales from hours to years are used to understand more fully the effects of landscape-scale processes such as habitat fragmentation, loss, or restoration. In multifunctional landscape management many concerns can be taken on board in an approach based on landscape ecology, although there are criticisms that, because it is focused primarily on biodiversity issues, it currently fails to elaborate or model fully socioeconomic and cultural issues.

Underlying Thories

The patch/matrix model is in part an extrapolation of the theory of island biogeography in which the patches are islands in an archipelago, and their size and proximity to sources of biodiversity are critical factors in determining their own species load. Larger islands tend to contain more species than smaller islands and those nearer the mainland more than distant islands. Relative rates of colonization and extinction were invoked to explain these findings. It is now recognized that the theory is too simplistic for most landscapes as the critical factors for species and populations in land-locked patches are often more numerous and complex. Landscape ecology addresses the many variables involved, such as the composition of the patches themselves and the nature of the surrounding land use, which can be overriding factors in species dispersal in a landscape.

The notion of functional connectivity between patches, e.g., the flow of genes or energy, is still critical, as in island biogeography, but landscape ecologists consider this in a temporal as well as spatial context. Dispersal of organisms between habitat patches is explained in terms of metapopulation theory, dependent on identifying a series of interlinked subpopulations making up a functional population unit, and the related source–sink theory, in which patches are either net providers or net absorbers of migrating individuals.

Discrete landscape elements do not exist in isolation and there are different ways in which the linkages between elements can be understood. Hierarchy theory views the landscape elements as nested,

> Thus a forested landscape might be hierachically composed of drainage basins, which in turn are composed of local ecosystems or stands, which in turn are composed of individual trees and tree gaps. The landscape system is a nested hierarchy with each level containing the levels below it (Forman RTT (1995) *Land Mosaics*: *The Ecology of Landscapes and Regions*. Cambridge: Cambridge University Press).

The linkages that need to be understood between landscape elements are those disrupted, or created by changes in the processes and pattern in the immediate and wider landscape. They include those to landscape elements at the scale below and above the element under consideration and the landscape ecologist should consider these in addressing research or management questions (**Table 1**).

Interpreting Landscape Pattern

Landscape metrics are used to compare different landscapes or the same landscape over time (**Table 2**). It is important to remember that many metrics are correlated with or derived from each other, e.g., edge length and edge density, and care should be taken to choose a metric appropriate to available data and the conclusions or decisions that will flow from the data analysis. Knowledge of landscape structure and composition may become the basis for making assumptions about landscape-scale processes, e.g., erosion.

Issues of Scale

Selecting the appropriate scale at which to work is fundamental to the success of a landscape ecology approach. Anthropocentric bias must be minimized when considering scale. It is vital to acknowledge the scale at which the target organism(s) themselves are operating: is it tens of meters in the case of a woodland butterfly or is it kilometers in the case of a raptor? This leads us to an understanding that 'patches' overlap, and may even be nested, i.e., the patch for species A may be wholly incorporated within the patch for species B. It is likely that these species will be experiencing a different level of detail or grain in the landscape.

Data Constraints

The principal limitation to a more widespread application of landscape ecology is the availability of robust data sets at the appropriate scale. There are issues of comparability between data sets recorded at

Table 1 The landscape ecology approach

	Action	*Check*
Step 1	Crystallize the research or management need	Consult widely, with stakeholders, subject experts, and policy-makers
Step 2	Identify the appropriate scale at which to work	This must relate to the issue or species but is often dictated by data availability
Step 3	Define the landscape and the time frame	Make transparent the reasons for selection of both the landscape boundaries and the time scale
Step 4	Design optimum data capture strategy	Historical data Fieldwork at what scale and intensity? Design of geographic information systems?
Step 5	Gather date	Check scale and comparability of data sets
Step 6	Analyze data	Focus on identifying the spatial/temporal relationships between data sets
Step 7	Relate data analysis to research or management question and draw conclusions	Review limitations of data and analyses

Table 2 Landscape metrics

Metric	*Notes*
Landscape configuration metrics	
Patch size	The average size of a particular type of patch, e.g., woodland. In general, greater variability in patch size indicates less uniformity in landscape pattern
Patch core area	May be critical to certain species, e.g., those dependent on the more stable conditions in the interior of a forest patch
Patch shape = 0.25 perimeter/$\sqrt{\text{area}}$	With this equation a simple shape such as a square has a shape index = 1. A more complex shape has shape index > 1 Altering the shape of a habitat patch may influence many different processes within it, not least because edge and core measurements may change, and so may have advantages or disadvantages depending on the conservation priorities
For individual patches in the landscape: FD = 2(ln 0.25P/ln A)	Fractal dimension (FD) may also be used as a measure of shape complexity. FD = 1 for square and 2 for complex shape. FD can be computed for each patch and then averaged for the landscape. Because the patches are not usually equal sizes, this metric should be weighted, i.e., obtain the FD for each patch, then weight each value by the ratio of the patch area to the landscape area. This weighted average addresses patch evenness
Nearest neighbor = distance (m) to the nearest patch of the same type	This can be either to the patch perimeter or center
Edge metrics	If these are high it implies greater spatial heterogeneity
Total patch edge and patch edge density: these are not spatially explicit but fit best within landscape configuration	Changes in the total length of edge of an important cover type, e.g., forest, may be the most significant measure of fragmentation available. Many other metrics depend on edge or perimeter data. (In a raster GIS data set, the length of all edges is biased upwards because of the "stair-step" effect when the edge is composed of a series of squares. Edge indices change with the resolution of the image, with finer resolutions giving longer measures of edge)
Contagion If there are s cover types then the probability P can be calculated that in a raster data set, two randomly selected adjacent cells or pixels will belong to cover types *I* and *j* respectively	A high P-value indicates a clumped pattern of cover types over the landscape
Adjacency What is the probability that a grid cell of cover type *I* is adjacent to cover type *j*?	This can be calculated directionally – to find directionality in the pattern (anisotropy) or the average value calculated. High values indicate clumping of cells of the same cover type, i.e., they are likely to be found aggregated together
Landscape composition metrics	
This second group of metrics is concerned with the relative proportions of the patch types present and not with their spatial arrangement. However, taken together with the configuration metrics above, they help to explain landscape pattern	
Proportion of landscape	This is the proportion p of the landscape that is occupied by each cover type. p is used in other metrics which may then be correlated
Relative richness $R = s/s_{max} \times 100$	If there are data available for a similar landscape which allows one to estimate the maximum number of cover types present ($s_{\max}$) then it is possible to describe a second landscape with number of cover types s as having relative richness R
Diversity and dominance indices: dominance is the deviation from the maximum possible diversity for a landscape having s cover types; a high value indicates that the landscape is dominated by one or very few cover types	These are similar to the measures of plant and animal diversity. There are two parts to each index: richness, i.e., number of cover or patch types present, and evenness or the distribution of the total area among these different types. Different indices are more sensitive to one or other of these, e.g., the Shannon–Wiener diversity index which is more sensitive to richness than evenness, so rare cover types are disproportionately influential. A high level of the index H indicates high diversity in the landscape, although the absolute value is not meaningful except where appropriate comparisons are being made between landscapes These metrics are most useful when comparing change in a known landscape; even then, if the number of cover types and relative proportions remain the same, with a shift in the nature of the cover types between the proportions, then the indices will give similar values and be of limited value. Only one or other should be used as they give the same information about the landscape and they may not be useful where separate information is required on richness and evenness

GIS, geographic information system.
After McGarigal K (1996) *Fragstats Manual*. Corvallis, OR: Oregon State University, with permission.

different times and often for different purposes which are drawn on to cover as many variables as possible within the landscape. Analysis of such data sets has become possible with the advent of more user-friendly software tools applicable to natural resource management. Many ecologists, planners, and policy-makers now use geographic information systems (GIS) to analyze and present data and these support a variety of landscape ecology tools. Historic and contemporary maps of infrastructure, vegetation, or soils all provide a useful basis for understanding a landscape's structure but often the corresponding biotic data are lacking.

If, for example, the conservation of a particular forest bird species was paramount, data would be needed on the spatial and temporal variants in the life cycle of the bird, its population, and its habitat needs. It is unlikely that fully comprehensive data will be available to the forest manager but key facts on bird and habitat distribution, breeding cycles, and foraging patterns would be needed to implement landscape-scale management. The minimum level of data required will vary depending on the question addressed. To some extent, this single-species approach is the simplest application of landscape ecology but its success is still dependent on quality data.

At an early stage in a landscape ecological study the landscape boundary must be defined. There are parallels with the ecosystem approach – the concept of an ecosystem is itself abstract – and in some respects it is more straightforward to identify the boundaries of a landscape of interest, acknowledging that these might be arbitrarily influenced by landownership or management. The scale of the landscape however must be informed by the requirements of the target organisms.

A Key Challenge for Landscape Ecology: Reducing Fragmentation

Irreversible habitat loss is the greatest threat to biodiversity worldwide but this is closely followed by the fragmentation of habitats, and ecosystems, within landscapes. In the Brazilian Amazon it has been estimated in 2003 that the area of forest land affected by fragmentation was three times that which had been deforested. Combating fragmentation is a key action for biodiversity conservation both because many landscapes have become degraded as a result of habitat fragmentation and because many nature reserves and other important protected areas have become isolated fragments, with the associated pressures on the biodiversity under protection.

Fragmentation occurs when formerly extensive areas of natural habitat are divided into smaller fragments as a result of human activities, including the building of roads, railways, pipelines, and other communication lines. It may accompany larger-scale habitat destruction due to housing, industrial, or agricultural development. As a result, the remaining fragments of habitat may be separated by a highly modified or degraded landscape that may be inhospitable to species movements beyond or between fragments. As habitats become fragmented, the increased 'edge' is also exposed to a greater variety of microclimatic and biotic influences and human disturbance that typically have a detrimental effect on the remaining biodiversity. As patches of habitat become smaller, so the ratio of edge to interior, or core, increases disproportionately and edge effects may dominate the remaining fragment. The magnitude of edge effects is related to the nature of the matrix surrounding the habitat fragment. The greater the contrast in habitat type and structure, the greater the intensity of edge effect in most ecosystems. Thus an area of forest surrounded by scrubby vegetation is likely to suffer less severely from edge effects in comparison to a fragment surrounded by intensively managed farmland.

As well as the loss or reduction in movement of biota from and between fragmented habitats, the impact of external biota such as domestic stock, predators, or nonnative plant species may severely threaten the integrity of ecosystem fragments. These effects are typically strongest at habitat edges. For example, levels of nest predation by predators such as domestic cats, crows, squirrels, or oppossums on birds dwelling in forest fragments have been shown in a number of studies to be strongly linked to distance from habitat edge. Equally, increased light availability, nutrient enrichment and disturbance as a result of habitat fragmentation may encourage the colonization of invasive, often nonnative species at the expense of the less competitive native flora.

In forested landscapes roads are often a cause of fragmentation. The impacts have been shown to be highly significant for many organisms. Large mammals can be adversely affected by a reduction in the integrity of their domain; others, e.g., deer species, may exploit the increased patchiness of the landscape, and species operating at smaller spatial scales may be influenced by the change in the forest interior to edge ratio or by the fragmentation of other habitats around the wooded areas. Isolation may cause local extinctions within the metapopulation, which will be threatened if these subpopulations are not replaced. Overall, there is an increase in edge habitat and a reduction in core area – this may be offset by road closure when no longer needed but more often the cost of installing forest roads is so high they remain a permanent influence in the landscape.

Population Isolation and Barriers to Movement

The continued viability of populations in fragmented ecosystems may often be reliant on movement beyond the fragment to fulfill resource or habitat requirements (e.g., for hunting or seasonal feeding) and between fragments to maintain greater genetic diversity. Species' perception of 'barriers' will vary from species to species. For example, for small organisms such as invertebrates and some bird species, 100 m across an agricultural habitat may form a total barrier to dispersal, while for other bird species, small intervening areas of inhospitable habitat, such as a road or even a small development, may not radically affect movement between fragments. For small mammals, a road may form a significant barrier to movement due to road kills, while for larger mammals a fence may form a significant barrier to movement. A plant which is dispersed by wind or by birds may be able to disperse across small areas of inhospitable habitat, whereas a plant species with no such dispersal adaptations may be unable to disperse to other areas of suitable habitat.

If the surrounding matrix is an adverse environment for species dispersal, the landscape is described as 'resistant.' It is unlikely that the matrix is made up of one land use and so this heterogeneity must be analyzed to identify the key contributors to resistance where feasible. Resistance can potentially be improved by altering the intensity of the land use adjacent to the forest or by planting different vegetation between wooded patches, but often such intervention is outwith the scope of a forest manager.

The Role of Corridors

To ease the dispersal of organisms and to counteract the adverse effects of isolation, landscape ecologists often identify corridors in the landscape where they exist and propose them where they do not. The designation of corridors within a landscape is usually done in a spatial context and it assumes that linear movement is relevant to target organisms and other matter such as water. It is acknowledged that there are many assumptions made in identifying corridors, as there is little empirical evidence for their role in the majority of landscapes and for the majority of species.

In some landscapes potential corridors may be obvious; watercourses creating riparian corridors would be a good example of this. Corridors may actually have more functions than just acting as conduits (**Table 3**). It is also often forgotten that the corridor functions can vary considerably over different timescales, e.g., within a day, season, or year.

Unexpected effects of corridors can include the transport and spread of seeds by vehicles; this may be problematic if the species are invasive. Disease-causing organisms or pests, e.g., long-horned beetles, may be dispersed via corridors and a forester would need to assess the risk of increasing connectivity in a landscape-scale forest management scheme. It is also necessary to attempt to predict corridors that will be created – often unintentionally – from forest management practices.

Survival Within a Patch

When does a patch become too small or modified to retain its full range of species and habitats and to cease to function as a patch? Accumulating evidence shows that edge effects can significantly reduce the recruitment of new seedlings and aboveground biomass in small fragments drops sharply. Microclimatic changes and elevated wind turbulence are the most significant edge effects – posing a risk to large established trees as well as new recruits. Broken crowns and snapped trunks cause significant loss of biomass even in surviving trees, indicating that fragments may be less efficient as carbon sinks than previously predicted.

Bird richness and abundance also decline in small forest fragments, though guilds differ in their

Table 3 The functions of corridors between patches

Function[a]	
Conduit	Organisms or propagules move along or adjacent to the corridor
Barrier	Resists passage between patches
Habitat	Species, usually generalists or edge species, which use the corridor as habitat for part or whole of their life cycle
Source	A reservoir of propagules or organisms
Sink	Absorbs water, nutrients, and species from the matrix

[a] Function varies with species.

Adapted with permission from Forman RTT (1995) *Land Mosaics*: *The Ecology of Landscapes and Regions*. Cambridge, UK: Cambridge University Press.

response to fragmentation. In tropical forests this has been shown to be due to adverse impacts on food supplies; nectarivores such as hummingbirds may be less affected by fragmentation than insectivores or frugivores. Critical patch size varies as some species are better at exploiting the increased heterogeneity of a disturbed forest. The nature of the surrounding vegetation is critical to minimize edge effects; in some cases secondary growth creates effective links between forest patches.

Fragmentation therefore does not cause an immediate crash in overall biodiversity but it does affect the relative abundance of different species and endemics are particularly vulnerable to its adverse effects.

Woodland Planting to Counteract Fragmentation

What if you are considering planting to consolidate an existing woodland resource? How much is needed to maximize proximity and hence the interchange of species? Thirty percent woodland cover is currently suggested as an appropriate target based on a model which randomly added a 1 ha block to a landscape. However, it is not until this figure is doubled that a substantial increase in woodland core area occurs and this is highly relevant for the conservation of forest interior species (**Table 4**).

In the UK the Woodland Trust (the principal forest nongovernment organization) has considered the evidence for connecting ancient woodland sites to increase biodiversity but has concluded that there is less value in this than in consolidating the significance of individual sites by increasing their area. In turn, they considered the need to target areas where ancient woodlands are already concentrated for new planting of native woodlands to achieve 30% woodland cover. In such areas, the Trust recommended that this should be matched by 30% cover of seminatural habitats and a reduced intensity of management of the remaining land. The England National Forest also has a target of 30% tree cover but development pressure is such that it is not possible to match this with a similar area of seminatural habitat. The principle is sound however; woodland biodiversity gains are maximized when the adjacent land uses are benign.

Table 4 The effect on core area of adding 1 ha seminatural habitat blocks to a 2×2 km landscape

Cover %	*Cumulative core area (ha)*	*Critical threshold*
1	0	
10	10	
20	20	
30	40	Level at which connectivity is potentially optimal
40	60	
50	100	
60	220	Level at which core area significantly increases
70	260	
80	310	
90	355	
100	400	

Reproduced with permission from Buckley GP and Fraser S (1998) *Locating New Lowland Woods*. English Nature Research report no. 283. Peterborough, UK: English Nature.

The Challenge of Managing Whole Landscapes

Landscape ecology is only one component of an integrated landscape management approach. If applied to the exclusion of other interests, it will not provide sustainable solutions. However, its emphasis on spatial and time-related variables makes it a contender to provide the framework to integrate biodiversity conservation with socioeconomic and cultural concerns.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife; Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Population Dynamics of Forest Insects. **Environment**: Environmental Impacts. **Genetics and Genetic Resources**: Forest Management for Conservation. **Landscape and Planning**: Landscape Ecology, Use and Application in Forestry.

Further Reading

Bierregaard RO Jr, Laurance WF, Sites JW, *et al*. (1997) Key priorities for the study of fragmented tropical ecosystems. In: Laurence WO and Bierregaard RO Jr (eds) *Tropical Forest Remnants*, pp. 515–525. Chicago, IL: University of Chicago Press.

Buckley GP and Fraser S (1998) *Locating New Lowland Woods*. English Nature research report no. 283. Peterborough, UK: English Nature.

Dover JW and Bunce RGH (eds) (1998) Key concepts in landscape ecology. In *Proceedings of the 1998 European Congress of IALE*. Myerscough College.

FAO (2003) *State of the World's Forests 2003*. Rome: Food and Agriculture Organization of the United Nations.

Farina A (1998) *Principles and Methods in Landscape Ecology*. London: Chapman & Hall.

Forman RTT (1995) *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge, UK: Cambridge University Press.

McGarigal K (1996) *Fragstats Manual*. Corvallis, OR: Oregon State University.

Meffe GK and Carroll CR (1999) *Principles of Conservation Biology*, 2nd edn. Sunderland, MA: Sinauer.
Naveh Z and Liebermann AS (1984) *Landscape Ecology: Theory and Application*. New York: Springer-Verlag.
Peterken GF (2002) *Reversing Fragmentation: Habitat Networks as a Basis for Woodland Creation*. Edinburgh, UK: Forestry Commission Practice Note.
Woodland Trust (2002) *Space for Nature*: *Landscape-Scale Action for Woodland Biodiversity*. Grantham, UK: The Woodland Trust.

Spatial Information

T Tokola, University of Helsinki, Helsinki, Finland

Introduction

A common representation of forest characteristics within spatial analysis and geographic information systems (GIS) can often be found in native objects whose interactions are based on simple distance and connectivity relationships. The spatial description of forest objects can be understood as a continuous two-dimensional process as an intensity field, or a collection of discrete locations of spatial objects. Geometrical features, such as points, lines, polygons, and raster cells, are commonly used to describe real-world objects and their characteristics in computerized mapping systems. Data modeling is a process that simplifies and defines real-world objects as database objects. Further spatial analysis may be engaged in when database objects have sufficient characteristics for spatial analysis.

The quantification of heterogeneity in forest areas has long been an objective of forest inventory and management. Heterogeneity depends highly on scale. The spatial and temporal variation of the property that can be detected will often depend on the spatial and temporal scale at which the property was sampled, and the size of the mapping unit. The information levels used in forestry reporting are hierarchically divided into: (1) tree level; (2) stand level; (3) farm level; (4) region level; and (5) country level. The data collection is normally based on measured sample units or subjective field observations that come from reporting units. The spatial pattern of reporting units can be mapped using remote sensing techniques or field observations.

The relative spatial distribution of forests and trees varies, because of changing land use practices, differences in the fertility of soil, and the hydrology, competition, and size distribution of trees. It is well known that the spatial distribution of seedlings in stands of natural generation depends highly on the location of mother trees and soil preparation affects the probability of survival of seedlings. Spatial information is used in forest inventory planning, and the construction of growth models and problems relating to forest regeneration and thinning. For example, the predictors of a spatial growth model for drained peatlands normally include variables such as the distance between the tree and the nearest ditch. The optimal sampling design of forest inventory can be defined if a spatial pattern of large variation is known and the size of a sample unit can be determined when the probability of tree occurrence can be modeled. Different indices and techniques have traditionally been applied to seedling surveys, in order to find out if the spatial distribution of seedling and saplings is regular. In addition, the effectivity of thinning and stand growth estimates depends highly on spatial regularity.

There are many forestry variables that are spatially sparse and scattered. This is often the case when one is assessing coarse woody debris in managed forests, or surveying threatened species. The spatial description of sparse populations can also be problematic. On the landscape level, information about spatial distribution of different key habitats and areas with a high ecological value has also been used to assess the probability of existing rare species. Field data about indicator species and remote sensing data about landscape features are valuable a priori information for estimating the presence/absence probability and for stratifying areas of interest.

Spatiality of Trees

The simplest point process model that can be used for the spatial pattern of trees is the Poisson process, which is typically used to produce random Poisson forests and when there is no interaction between the locations of trees. There are several modifications that stem from the basic model, such as the inhomogeneous Poisson processes, the Poisson cluster processes, and the doubly stochastic Poisson processes. The location of seedlings after natural regeneration is often generated using the Poisson cluster processes. Lattice-based processes are suitable models for spatial patterns of trees in plantations. Pair correlation processes produce patterns in which points either ‘reject’ (regular) or ‘attract’ (clustered) other trees to each other. Hard-core processes reject other trees with such a high intensity that other trees cannot exist closer than the radius of the core area. The Markov point processes and the Gibbs process are often used as well, because interactions between trees can be sufficiently modeled and empirical data can be used to create a probability model.

Different kinds of indices can also be used to measure the deviation of the given tree pattern from the Poisson forest. These methods of analysis can be divided into three groups depending on the measurements done regarding the population:

1. Number of trees within plots are counted.
2. The distance from tree (or random point) to closest tree is measured.
3. All trees in the forest are mapped.

The methods of the first two groups are more suitable for field work, while the latter group gives detailed information about the underlying process, and allows for the estimation of parameters necessary to begin a selected point process. The known field methods include the index of dispersion and the distance-based indices. Ripley's *K*, Moran's *I*, and Geary's *C* are commonly used for testing randomness or clusterness of tree patterns, although Moran's *I* and Geary's *C* have mostly been used for characterizing the autocorrelation. When permanent sample plots of Finland were analyzed, 57% of the plots had a regular tree pattern, while 25% were random, and 18% were clustered. When the basic pattern of trees is identified, it can be utilized directly to determine the sampling unit and design.

One common example in forestry would be the stand representation of discrete forest patches, and the partition of forests into distinct classes or strata. The discrete model is usually adopted when the boundaries of units can be unambiguously delineated. This happens, for example, when there are sharp discontinuities in attribute values. The delineation of stands is typically guided by three criteria: (1) the forest characteristics in different parts of the stand should be similar; (2) the stand should be a practical management and harvesting unit; and (3) the stand should be identifiable to allow for the monitoring and updating of information. Because these criteria can be contradictory, one or more of them are often compromised, and an estimation of stand values is often based on the simple summation of sample data, an approach which sometimes masks substantial variations found within discrete forest stands. This spatial autocorrelation can be studied using a dense network of sample plots within an area of interests, and correlograms/semivariance of variable of interest can be estimated using localized sample plot data. The spatial autocorrelation within forest stands is larger in forests with regular tree patterns than it is in forests with random or clustered tree patterns. In Finland, some studies indicate that within stands, the autocorrelation for the basal area and growing stock volume of trees only exists within a 20–30 m distance, while 5–10 m distance intervals are used. The continuous description of forest characteristics has not received much attention in the forest resource inventory.

Spatiality of Landscapes

Habitat mosaics have been found to affect diversity and dynamics in both pristine and managed boreal forests, and many important processes have also been identified as being driven or affected by landscape heterogeneity. Efforts to quantify the spatial heterogeneity of landscapes began in the 1980s, but have accelerated in recent years, so that at the present there are hundreds of indicators that allow for some sort of quantification of various aspects of spatial heterogeneity at a landscape level. Thematic maps and satellite image-based products have also been used to estimate landscape indicators on a regional level.

Composition

Composition is typically indicated by the number of categories or classes in the map, the proportion of each class in the map, and the presence of diversity. Diversity measures typically combine two components of diversity: richness, which refers to the number of classes present, and evenness, which refers to the distribution of objects that are among the classes. Typical diversity indices are Shannon's and Simpson's.

Spatial Configuration

Spatial configuration of properties attempts to describe the spatial characteristics of individual patches, and the spatial relationship among multiple patches. Patch-based measures of pattern include size, number, and the density of patches. Useful edge information includes the perimeter of individual patches and various edgemetrics that incorporate the contrast between the patch and its neighbors. For example, there is less contrast between a mature forest stand and a young stand than there is between a mature stand and clear-cut areas. Patches can take a variety of shapes, making shape difficult to quantify. Most shape indices use a perimeter–area relationship. A widely used index related to both patch size and shape is the 'core area,' which is the proportion of a patch that is further than the specified distance from an edge. Patch cohesion has been proposed to quantify the connectivity of habitat as perceived by organisms dispersed among binary landscapes. Some pattern indices examine spatial neighborhoods, patch orientation, and isolation. These were developed primarily to predict the relative connectivity of habitat islands.

Contagion

Contagion is designed to quantify both composition and configuration. It measures the extent to which cells of similar classes are aggregated. It is calculated using the frequencies with which different pairs of classes occur as adjacent pixels on a map. This appears to summarize the overall clumpiness of areas of interest.

It has been shown that there are only five independent factors among 55 different landscape metrics. These are:

1. Number of classes.
2. Dominance.
3. Contagion.
4. Fractal dimension from perimeter/area.
5. Average patch perimeter/area ratio.

In Finnish forests, landscapes are transformed into a mosaic of managed forest stands of small size, in which species composition has become more homogeneous, and the age distribution of stands more even. Low values of contagion characterize the Finnish landscape, which is dominated by many small size-dispersed patches. The development of species occurrence and landscape level habitat models, based on National Forest Inventory (NFI) data and environmental information at the national level, highlight small variations among the indicators. This seems to have important implications for the spatial distributions of species. Landscape metrics has been proven to be an efficient method of monitoring forest characteristics, which might have important applications for management planning in order to improve forest biodiversity.

Spatiality of Regions

On a national level, both correlation and autocorrelation functions have been employed to study large structures of forest area, and volume of forests. In Scandinavian forests there is a slightly increasing autocorrelation almost until a 200 m distance, when larger distances are applied. This information is used to estimate the optimal distance between inventory tracts, the overall shape of the tract, and the distance between sample plots within tracts. To obtain a sufficient sampling set-up for the entire nation of Sweden, the country is divided into five regions with marginally diverse correlation functions for different variables.

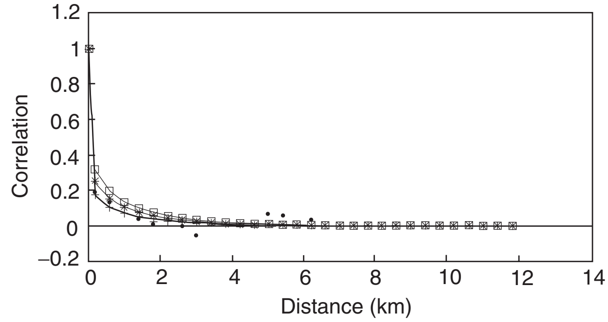


Figure 1 The estimated correlation function and empirical correlations for growing stock volume, as a function of distance between sample plots in three different areas. Reproduced with permission from Kangas A (1993) Estimating parameters of systematic cluster sampling by model based inference. *Scandinavian Journal of Forestry Research* 8: 571–582.

The final sampling design is based on their spatial characteristics and other practical considerations.

The correlograms (**Figure 1**) have also been used to estimate the standard error as regards large areas. The standard errors of systematic cluster sampling can be estimated using model-based estimators, which utilize the parameters of correlation functions. That way, the information about spatial dependency can be utilized in error estimation and spatial structure of forests is taken into account.

Border Effects in Spatiality

Spatial analysis is always connected to edge effects. In addition, edge effect correction methods are often used in inventory procedures, as well as in the analysis of limited empirical data sets. Four main methods are typically applied:

1. Plus sampling: additional data is measured, so that entire neighborhoods can be covered.
2. Minus sampling: buffer zones with a plot radius are generated for neighborhood calculation, and sampling is made in the core area only.
3. Toleroid edge correction, or mirror-sampling: an edge zone with plot radius is copied to the edge buffer, and the neighborhood is calculated from 'duplicated data.'
4. Weighting of observations: neigborhood data are weighted according to the probability of information existence.

Spatial Information in GIS and Remote Sensing

A forest information system contains information for decision-making in forestry, and forest inventory yields data for such a system. The initial and most

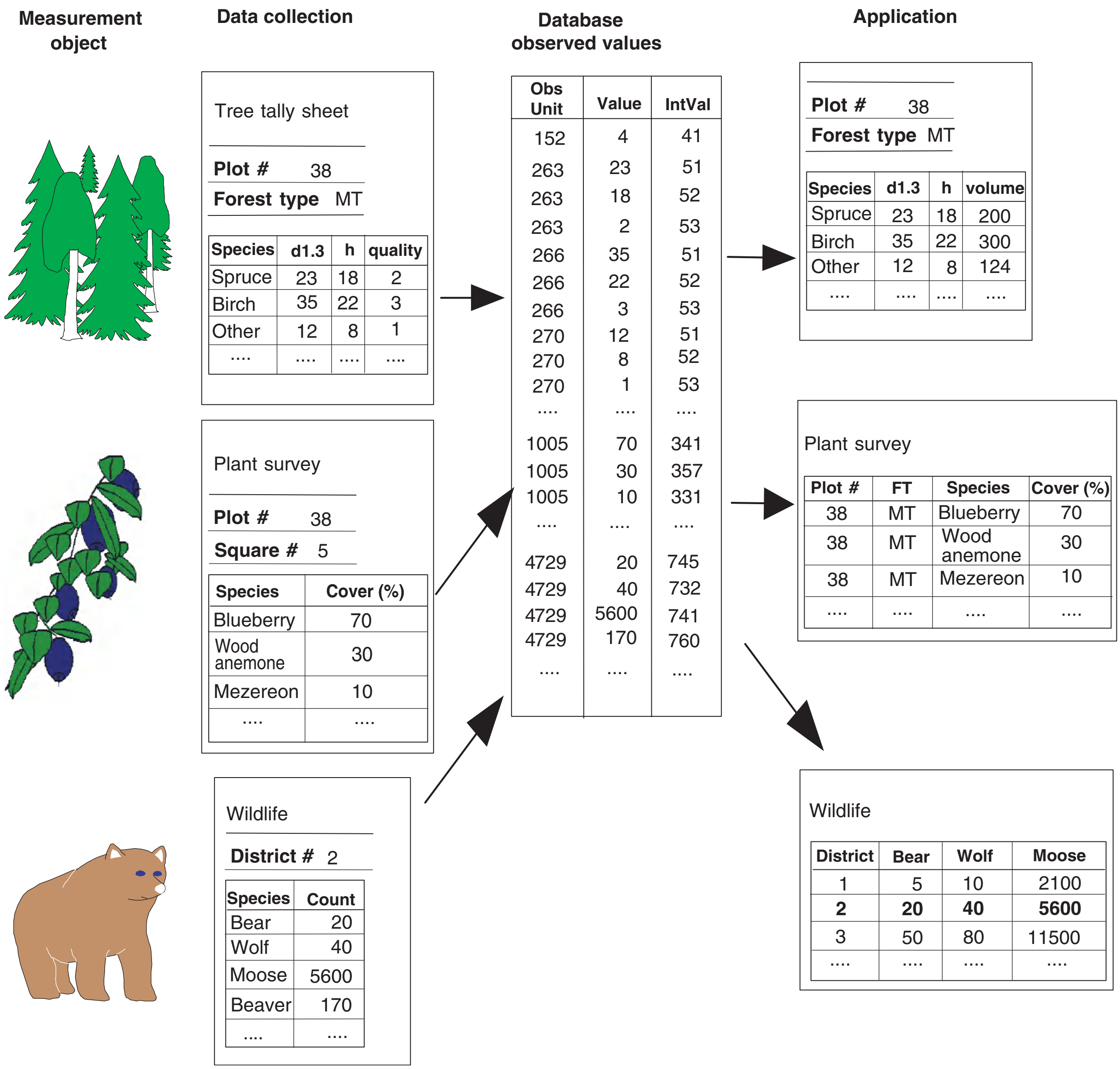


Figure 2 Storage structure for forest inventory attribute data. Reproduced with permission from Tokola T, Turkia A, Sarkeala J, and Soimasuo J (1997) Entity-relationship model for forest inventory. *Canadian Journal of Forest Research* 27: 1586–1594.

important phase of the forest database system design is the construction of a data model, which is primarily used to perceive, organize, and describe data in a conceptual schema. Real-world objects are defined in the data model in such a way that they can be described in databases (**Figure 2**).

Each observation and measurement in a system is linked to the geometry of GIS. The geometry of forestry objects can be presented using vector (point, line, polygon), raster, and dynamic segment-based models (**Figure 3**). Vector-based description is typically used for discrete phenomena (i.e., stand border maps) and raster-based systems (i.e., stratification of volume, elevation) do their best when continuous spatial surfaces are presented. Dynamic segmentation is used for objects which locate near line features, and can be located using the distance measure from known location along the line. Such a feature could be a hydrographic measurement unit along a river that has a particular distance from a known crossing.

The requirements for interoperable, computationally scalable software tools suggest the need for developing open software standards such as the Open GIS Consortium (www.opengis.org). The current Open GIS data model supports geometrical primitives, but requires application-specific definitions from the user side, as well as support for advanced analysis, which needs to be built externally.

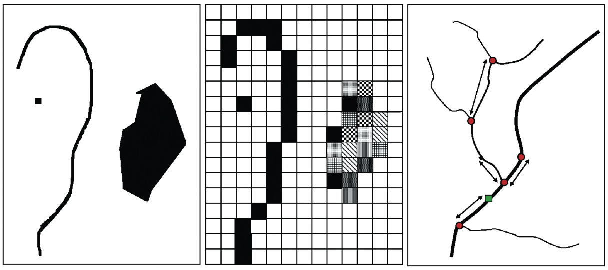


Figure 3 Vector-, raster-, and dynamic segmentation-based models are used to describe the geometry of real-world objects within global information systems. Reproduced from Tokola T and Kalliovirta J (2003) *Paikkatietoanalyysi*. Publications 34. Helsinki, Finland: Department of Forest Resource Management.

Remote sensing is considered to be an efficient tool for data acquisition and the updating of information into forestry GIS system. Yet, the remote sensing sensors can vary a lot, and it is important to realize that the spatial dependency of forest objects also affects the data collections phase.

When the pixel size is larger than the forest objects, information is perceived to be lost because the spatial resolution of images is so low. In contrast, when very-high-resolution images are used, adjacent pixels give the same information, because it is highly probable that they are taken from the same object. Another drawback of high-resolution data is that the amount of data soon becomes too enormous to compute. A worst-case scenario occurs when the use of unsuitable resolution results in erroneous image interpretation, due to the spatial autocorrelation of neighboring pixels. Good examples are the Landsat MSS images which have strong positive autocorrelation between neighboring pixels. It has been found that there are three reasons for this phenomenon: (1) a natural continuity of land cover, compared to the spatial resolution of the imaging system; (2) a positive correlation caused by the imaging system itself; and (3) image processing algorithms such as resampling. Studies with Landsat MSS images have indicated that the radiance of one pixel can affect the radiance of surrounding pixels that are 4–6 pixels apart. With higher-resolution systems like Landsat TM and SPOT, the positive autocorrelation can be even higher. The autocorrelation of pixel gray values in a forest environment is usually clear, and depends on the crown sizes and crown cover proportions of the trees. When semivariograms derived from aerial photographs have been studied in boreal areas, spatial resolution in which the variance was maximized was 2–4 m. Principally, such results have indicated that the local variance curve maximum is dependent on the object size, and a maximum is reached when the resolution is somewhat smaller than the object size. Nowadays, single tree-based digital delineation techniques are often used in various remote sensing materials, and 0.5 m resolution image material is generally used during these interpretation processes.

Satellite image-based surveys often utilize distant field sample plots from target areas. Normally, the margin of error increases when distant field sample plots from existing field samples are used. In one study, the best results were achieved when plots were within a 20-km range. Stand margin areas are also critical in remote sensing. The accuracy of growing stock volume estimation near a stand edge can be much lower than it will be inside the stands.

Simulated Forests

Simulation models of landscape levels are needed to understand large-scale variation, as well as predict the development of forests under different management schemes.

Alternative sampling designs for forest inventories can be evaluated through several means. One way involves carrying out actual manual inventories in the target forest. Computer-simulated samplings offer a cheaper and more flexible option for this. Following the first inventory round, it is possible to use remote sensing data to create a computerized depiction of the selected target area. The main advantages of such a simulation are that by manipulating input variables, a process of controlled experimentation and sensitivity analysis can take place. In spite of certain disadvantages, a simulation approach provides a flexible method for experimentation with prospective sampling designs, and is free from the restrictions associated with the analytical error propagation methods.

Using simulated sampling designs, changes in the sampling error of the estimate can be examined, and one can discover the best cluster design. In the simulation approach, all local small-scale characteristics of spatial variation can also be included in the analysis. In numerous other studies, entire spatial variation has been described by using the average covariance function. Certain simulation models use satellite image-based simulated models of forests. These models normally show a moderate fit with the field data. This type of model can also be used to test different sampling designs for carrying out forest inventory, and seemed to be representative in terms of the sampling error of estimate when compared to the overall structure of the spatial distribution of a given forest.

The standwise interpretation result of small-scale remote sensing materials does not vary within forest stands, and the correlation between neighboring satellite image pixels is relatively high. This correlation is caused by observation characteristics of the satellite sensor. While the small-scale accuracy of Landsat TM interpretation is low, and the tree-level information is missing, the main focus of this type of inventory planning concentrates on the shape of clusters and distance between plots. If small-scale variation was available, it could also perhaps determine the size and shape of plots. Unfortunately, fairly detailed aerial photographs would be needed, if we wished to see a true realization of stand structure taken using remote sensing material.

Most approaches to creating spatially explicit simulations of forest landscapes have been developed in North America, yet a large amount of simulators are available for specific purposes. They have been used to demonstrate the effects of different potential disturbance regimes, and for planning alternative forestry management schemes. Trying to make predictions as regards landscape scale, one has to deal with all of the ecological site types and tree species as well as all possible stand development scenarios. In addition, landscape-level processes have to be incorporated. One solution to such difficulties has been to simplify the description of forest stands by discarding most of the quantitative attributes, such as stand basal area or size of trees, and to use a semiquantitative approach to describe tree stands by the age structure of each tree species. It is important to note that the purpose of simulation models is not necessarily to predict reality directly, but rather to reveal the logical consequences of the assumptions incorporated in the structure of application-specific computer models and parameter values. Complex spatial models are indeed hard to evaluate, because it is difficult to find sufficient empirical data sets, as well as to compare exactly which aspects of spatiotemporal patterns are crucial for either a correct simulation, or a future model application.

See also: **Inventory**: Forest Measurements; GIS and Remote Sensing; Large-scale Forest Inventory and Scenario Modeling; Multipurpose Resource Inventories.

Further Reading

Congalton RG (1988) Using spatial autocorrelation analysis to explore the errors in maps generated from remotely sensed data. *Photogrammetric Engineering and Remote Sensing* 54: 587–592.

Hyppänen H (1996) Spatial autocorrelation and optimal spatial resolution of optical remote sensing data in boreal forest environment. *International Journal of Remote Sensing* 17(17): 3441–3452.

Matern B (1960) Spatial variation. *Meddelanden fron Statens Skogsforskningsinstitutr* 49(5): 1–144.

Korhonen K and Maltamo M (1991) The evaluation of forest inventory designs using correlation functions. *Silva Fennica* 25(2): 77–83.

Riitters KH, O'Neill RV, Hunsaker CT, *et al.* (1995) A factor analysis of landscape pattern and structure metrics. *Landscape Ecology* 10: 23–39.

Ripley BD (1981) *Spatial Statistics*. New York: John Wiley.

Tomppo E (1986) Models and methods for analysing spatial pattern of trees. *Comunicationes Instituti Forestalis Fenniae* 138: 65.

Uuttera J, Haara A, Tokola T, and Maltamo M (1998) Determination of spatial distribution of trees from digital aerial photographs. *Forest Ecology and Management* 110: 275–282.

M

MEDICINAL, FOOD AND AROMATIC PLANTS

Contents

Medicinal Plants and Human Health

B K Tiwari, H Tynsong and S Rani, North-Eastern Hill University, Shillong, India

Introduction

Humanity's dependence on forests is probably as old as humanity itself. For most periods of 200 000 years of human existence on earth humans have been deriving all their material needs from the forest. During prehistoric days, virtually all human needs were met from non-wood forest products (NWFPs) except construction and energy. It was during industrial and postindustrial periods that we started looking at the forests as a source of timber, and NWFPs became minor and less important even though the variety and value of NWFPs have always been far greater than the woody forest products. Edible products and healing herbs have been the most important NWFPs since antiquity. Forests represent vast natural pharmacies by virtue of having an enormous stock of biological materials of which the indigenous populations had knowledge of the medical uses. Medicinal plants of forest origin constitute a vast undocumented and overexploited healthcare resource for a majority of the world's population. In the last few decades, due to the pressure of increasing population, the area under forests has been shrinking. Demand for medicinal and aromatic plants (MAPs) has been increasing due to the increased number of users and due also to a resurgence in interest in herbal medicines and cosmetics. The variety, tonnage, and value of medicinal herbs extracted from forests are enormous. For example, more than 10 000 plants are used as medicines by the people of India, 70% of which come from the forests. Almost all medicinal plants collected, either legally or illegally all over Himalayas or even other parts of Asia for various purposes, are collected from the wild and only a very small number of species is cultivated. The medicinal plant resource in forests and in the wild are depleting rapidly so that a number of medicinal plants are threatened with extinction. The extinction of medicinal plants presents a hidden health risk to both developing countries and industrialized societies.

According to an estimate of the World Health Organization (WHO), medicinal plants form the basis of traditional or indigenous healthcare systems used by the majority of the population of most developing countries. The increasing demand for medicinal plants in healthcare is putting pressure on wild sources of plants. The herbalists have to walk increasingly greater distances for herbs that once grew almost outside their courtyards. Disappearance or drop in availability of herbs is forcing more and more rural populations to switch to modern medicines which have not yet reached many rural areas in developing countries. For example, only 3–30% of rural India is covered by modern medical facilities, which is also true for most developing countries. Thus there exists a strong positive relation between availability of medicinal plants and human health. There cannot be two opinions that any reduction in the supply of medicinal plants will adversely affect the health and well-being of people across the world. In recent years however, there has been a phenomenal growth of interest in the conservation of medicinal plants; this has occurred partly due to the increasing demand for herbal medicines in North America and partly due to recognition of the value of biodiversity by governments, nongovernmental organizations (NGOs), and donor agencies particularly after the Rio Summit in 1992.

With tremendous advances in the area of modern synthetic drugs after World War II, the use of herbal medicines declined considerably and lost attention gradually. However, it is now realized that indiscriminate use of antibiotics and synthetic drugs may lead to health hazards owing to the toxicity associated with these drugs. Therefore, during recent times a new trend has emerged in the use of herbal preparations because it is believed that remedies of natural origin are relatively harmless to the systems of the body. Presently, a large number of herbal preparations are being produced in the pharmaceutical industries of developed countries. In America, Europe, and Japan the traditional herbal drugs of the Ayurveda, Unani, and Chinese systems are extensively used. More and more attention is being focused on the development of drugs from natural products, and many manufacturers of Western medicines are forging ties with traditional communities and herbalists for indigenous knowledge and exploring the world of biomedicines for development of new drugs particularly for emerging diseases like AIDS.

People have relied on plants for staying healthy and treating illness for millennia. In the New World tropics, for example, archaeological remains of plants used as medicine have been dated to 8000 BC. Extensive written lists of herbal medicines have survived since antiquity, including the *Pen Ts'ao*, written by herbalist Shen Nung in 2800 BC which lists 366 plant-derived drugs including the familiar *Ephedra*. The history of Western medicine begins with the Greek physician Dioscorides, who wrote *De Materia Medica* in AD 78, describing over 600 medicinal plants, including *Aloe* and *Opium*. The Swiss pharmacist–physician Theophrastus Bombastus von Hohenheim advocated the use of chemical remedies and originated the field of medicinal chemistry in the early sixteenth century; however, Dioscorides' writings remained the standard text until the early nineteenth century. In 1803 the German pharmacist Friedrich Wilhelm Adam Sertürner first isolated alkaloids from plants, a class of chemicals with many potent physiologically active compounds (including quinine, atropine, cocaine, and tubocurarine). In nations with rich botanically based medical traditions, such as India and China, plant medicines predominate. The earliest mention of the medicinal use of plants has been found in the *Rig Veda*, which were written between 4000 and 1600 BC. In the *Atharva Veda*, definite properties of plant-based drugs and their uses have been given in detail. *Charaka Samhita* is another earliest treatise on *Ayurveda* (600 BC) which lists a total of 341 plants and plant products for use in health management. *Susruta Samhita* also dealt with plants related to medicines. Subsequent authors of later treatises on ancient Indian systems of medicine have extended the list of plants to 600 species.

Traditional healers in India use more than 10 000 different plant species, out of which approximately 7500 are used in folk and tribal system, 1800 in Ayurveda, 500 in Siddha, 400 in Unani, and 300 in Amchi. In China where medicinal plant use goes back at least 4 millennia, over 5000 medicinal plants have been recorded, and about 1000 are used in current practice. In Western medicine, respect for the power of plants has largely been lost during the postindustrialization period but it is catching up very fast and today Europe and North America are emerging as the largest consumers of the medicinal herbs of South Asia.

In the remainder of this article, the use of medicinal plants in various health care systems will be described. Modern medicine, trade, threats, and conservation needs of medicinal plants are briefly discussed with the aim of elucidating the interactions among various factors affecting medicinal plants and human health.

Traditional Systems of Medicine

Over 80% of the world's population relies on traditional plant-based medicines for their primary healthcare needs. According to WHO traditional system of medicine refers to:

> the sum total of the knowledge, skills, and practices based on the theories, beliefs, and experiences indigenous to different cultures, whether explicable, or not, used in the maintenance of health as well as in the prevention, diagnosis, improvement or treatment of physical and mental illness.

In many developing countries, traditional and herbal medicines are very much indispensable. Traditional systems of medicine (TSM) may be classified into three broad categories:

1. Traditional medicine, which has written traditions of documentation of knowledge, pharmacopoeias for doctors, often known as *Vaidyas*, *Hakeems*, and *Amchis*, and institutions for their training. This system of medicine is especially concentrated in Asia. Some of the more widely familiar traditional medicine systems are Ayurveda,

Siddha, Unani, Chinese traditional medicine, Tibetan medicine, and Western herbal medicine.
2. Folk medicine. This is orally transmitted and associated with households, communities, or ethnic groups and is most prevalent among tribal and indigenous communities. The number of plants used in folk medicine is enormous, most of which still remains undocumented.
3. Shamanistic medicine. This system has a strong spiritual element and can only be applied by specialist practitioners (shamans/doctor–priests).

Ayurveda

The Ayurvedic system originated in India long back in pre-Vedic period which is believed to be 5000 years BC and is the earliest documented ancient Indian knowledge. Ayurveda recognized the medicinal value of plants and provided specific methods of treatments of several human ailments using plants. To cite one example, for at least 2500 years before the West recognized the medicinal properties of the *Rauwolfia* root, the Indian medicine men had been using it to calm violently disturbed patients. They called it snakeroot and used it to treat lunacy, and a whole range of afflictions, from snakebite to cholera. More than 1800 medicinal plants are used in Ayurveda. The important medicinal plants used in Ayurveda and their applications are given in **Table 1**.

Siddha

The Siddha system is one of the oldest systems of medicine in India. The term 'Siddha' means achievement, and the Siddhars were saintly figures who achieved results in medicine through the practice of yoga. Eighteen Siddhars seem to have contributed towards the development of this medical system. The Siddha system is practiced in Tamil-speaking parts of India, and its literature is in Tamil. The system is also called Agasthyar system in the name of its famous exponent sage Agasthya. This system of medicine developed within the Dravidian culture, which is also of the pre-Vedic period. The Siddha system is largely therapeutic in nature. According to this system the human body is the replica of the universe and so are the food and drugs irrespective of their origin. The Siddhars investigated and studied the causes of many diseases and the effect of many locally available plants and minerals on these diseases. About 500 medicinal plants are used in Siddha.

Unani

This is an age-old system that originated in Greece, from where it later spread to India through Arab and Persian traders. Hence it is also known as the Greco-Arab system of medicine. Indian physicians enriched this system with their local knowledge of indigenous herbs, their own observations, and their experiments to make it one of the nationally accepted systems of treatment. The drugs used are mostly of plant origin. The history of herbalism in Unani medicine goes back to the history of pharmacology. About 400–700 medicinal plants are used in Unani.

Chinese Medicine

The medicinal and pharmaceutical traditions of China have evolved over the centuries as essential parts of its civilization and are widely recognized today as representing its rich cultural and scientific heritage. As this medical knowledge and expertise were built on a land endowed with an abundance of varied flora, it is not surprising that medicinal plants play a central role in Chinese medicine and the country's achievement in the utilization of its native plants in healthcare delivery has been admired and acknowledged throughout the world. The total number of species of medicinal plants used in different parts of China adds up to over 10 000. The official Pharmacopeia of the People's Republic of China lists 709 different drugs. Among these only 40 items are animal and mineral products, the others all being derived from plant material. Plant material accounts for more than 80% of the drugs sold in the Chinese market. About 1000 species of plants are now commonly used in Chinese medicine and about half of these are considered as the main medicinal plants that are in particularly common use. Most plant materials used in Chinese medicines originate from wild sources.

Recent researches in this system of medicine have proved that a synergy between Chinese and western system of medicine can help in formulation of drugs for treatment of some presently almost incurable diseases like AIDS, cancer, and hepatitis.

Western Herbal Medicine

Western herbal medicine has traditionally been used mainly for treating specific conditions, such as headache, cough, arthritis, menstrual problems, skin sores, insect bites, colds, sore throat, etc. It is a curious fact that herbal medicine, as it seems to be most widely known in Canada and the USA, has been so little influenced by the great systems of herbal thought that once flourished in Asia. The use of herbs in the western hemisphere stretches back into antiquity well into the Paleolithic or Old Stone Age. The beginnings of organized study of herbal therapeutics in the West are in the ancient Mesopotamian, Eygptian, and later Greek civilizations. By

Table 1 Some medicinal plants commonly extracted from Indian forests for Ayurvedic medicines

Species	*Medical application*
Acorus calamus	Nervine, antispasmatic, sedative, stomachic, expectorant, emetic, laxative, diuretic
Artemesia absinthium	Anthelminthic
Artemisia vulgaris	Anthelminthic, expectorant
Asparagus racemosus	Galactogogic, antispasmodic, antidiarrhetic, demulcent
Azadirachta indica	Skin disease, blood disease, antibacterial
Bacopa monnieri	Nervine, tonic, diuretic, sedative
Boerhavia diffusa	Diuretic, expectorant, laxative
Boswellia serrata	Antiarthritic, analgesic, anti-inflammatory
Buchanania lazan	Skin disease, laxative
Butea monosperma	Diarrhea, flatulence, anthelminthic
Callicarpa macrophylla	Joint pain, skin disease, blood disease
Calotropis gigantea	Bronchitis, diarrhea, tonic, cancer (?)
Cannabis indica	Insomnia, cachexia, dysmenorrhea
Capsicum annum	Rubefacient, stimulant, tonic
Carum carvi	Flatulence, stomachic
Carum copticum	Spastic bowel, flatulence, dyspepsia
Cassia angustifolia	Constipation, liver disease, joint pain
Cassia fistula	Ringworm, constipation, fever, antibacterial
Cedrus deodara	Fever, diarrhea, urinary disorders
Centella asiatica	Tonic, sedative, alterative, anxiolytic
Cichorium intybus	Emmenogogue, digestive
Cinnamomum camphora	Diarrhea, nervousness, muscular pain, fever
Cinnamomum zeylanicum	Dyspepsia, flatulence, diarrhea, menorrhagia
Cissampelos pareira	Bowel disease, uterine prolapse, alterative
Clitoria ternatea	Constipation, edema, anthelminthic, demulcent
Cocos nucifera	Fever, pharyngitis, skin disorders, alterative
Coleus aromaticus	Kidney stones, conjunctivits, spastic colon
Cordia myxa (obliqua)	Expectorant, colic, dyspepsia, ulcers, cough
Coriandrum sativum	Flatulence, colic, joint pain, antiseptic
Crinum deflexum (asiaticum)	Emetic, inflammatory conditions
Crocus sativus	Nervine, sedative, emmenogogue, aphrodisiac
Cuminum cyminum	Diarrhea, dyspepsia, antiseptic, hookworm
Curculigo orchiodes	Hemorrhoids, asthma, kidney stones, skin disease
Curcuma longa	Arthritic pain, anti-inflammatory, skin disease
Curcuma zedoaria	Cough, asthma, leukorrhea, tonsillitis
Cynodon dactylon	Diuretic, styptic, hematuria, hemorrhoids
Cyperus rotundus	Antiinflammatory, flatulence, fever, estrogenic
Datura metal	Antispasmodic, jointpain, asthma, dysmenorrhea
Dolichos biflorus	Edema, kidney stone, asthma, dysmenorrhea, tumors
Eclipta alba	Hepatic deobstruent and tonic, alterative, emetic, purgative, antiseptic, antiviral
Elettaria cardamomum	Bronchitis, flatulence, dyspepsia, hemorrhoids
Emblica officinalis	Fruit: cooling, laxative, stomachic, tonic, diuretic
Evolvulus alsinoides	Anxiety, diarrhea, bronchitis, memory loss, fever
Ferula foetida	Flatulence, cough, constipation, palpitations, aphrodisia
Ficus religiosa	Ulcers, skin disease, diabetes, constipation
Ficus racemosa	Diarrhea, hemorrhoids, bleeding disorders, antiseptic
Foeniculum vulgare	Cough, flatulence, dysmenorrhea, hookworm, edema
Gmelina arborea	General tonic, to increase strength, antiviral, indigestion
Grewia hirsuta	Diarrhea, wounds, heart disease, fever
Gymnema sylvestre	Diuretic, astringent, hypoglycemic, refrigerant, stomachic
Hemidesmus indicus	Excellent alterative, to increase appetite, cough, skin
Holarrhena antidysenterica	Diarrhea, dysentery, amebiasis, anthelminthic
Hyoscyamus niger	Chronic dementia, hysteria, palpitations, asthma, sedative
Hyssopus officinalis	Cough, asthma, bronchitis, amenorrhea
Ipomoea digitata	Cough, hoarseness, respiratory stimulant, tonic
Justicia adhatoda	Bronchitis, asthma, jaundice, antispasmodic
Linum usitatissimum	Cystitis, bronchitis, boils, expectorant, demulcent
Luffa acutangula	Splenomegaly, emetic, excellent for skin disease, expectorant
Madhuca longifolia	Tonsillitis, cough, rheumatic joints, diabetes, appetizer
Michelia champaca	Gastritis, chronic arthritis (?), emmenagogue, diuretic, colic
Mimosa pudica	Menorrhagia, hemorrhoids, skin wounds, diarrhea
Mimusops elengi	Tonic, cardiotonic, urogenital disease, snakebite, skin sores

Table 1 Continued

Species	*Medical application*
Morinda citrofolia	Acne, eczema, hyperlipidemia, brochitis, diarrhea
Moringa oleifera	Source of vitamin C, colds, boils, fever, joint pain, gout
Mucuna pruriens	Nervine tonic, aphrodisiac, parkinsonism, hypercholesterolemia
Nardostachys jatamansi	Nervousness, anxiety, dysmenorrhea, insomnia, hair tonic
Nelumbo nucifera	Refrigerant, sedative, demulcent
Nyctanthes arbortristis	Liver diseases, constipation, anthelminthic, antihistaminic
Ocimum sanctum	Demulcent, expectorant, anticatarrhal, antispasmodic, anthelminthic
Paederia foetida	Rheumatic joint pain, edema, bladderstones(?), inflammation
Papaver somniferum	Anxiety, diarrhea, aphrodisiac, sedative
Peucedanum graveolens	Flatulence, colic, abscesses, digestive
Phyllanthus fraternus	Jaundice, liver disease, fever, genitourinary disease, edema
Picrorhiza kurroa	Hepatitis, asthma, anorexia
Piper nigrum	Dyspepsia, cough, pharyngitis, headache, diarrhea
Plantago ovata	Constipation, colitis, irritible bowel, cystitis
Premna integrifolia	Flatulence, fever, arthritis, liver deobstruent
Pterocarpus santalinus	Skin tonic, liver disorders, fever
Punica granatum	Anthelminthic (esp. tapeworm), diarrhea, dyspepsia
Randia dumentorium	Fruit and rind are emetic, diaphoretic, and antispasmodic; bark is sedative and nervine calmative
Rauwolfia serpentina	Hypertension, anxiety, insomnia, colic

3000 BC the Egyptians and Sumerians had written traditions of systematic herbal use, and by 400 BC there were numerous medical schools in Greece practicing various forms of natural medicine, including herbology, cupping, and progressive open-air sanitoriums for the mentally ill. In modern times, since the scientific revolution of the nineteenth and twentieth centuries, Britain and Germany have rich traditions of herbal medicine use.

Tibetan Medicine

Tibetan medicine (Amchi) originated with the local folk tradition (known as Bon) that dates back to about 300 BC and was formally recorded by Xiepu Chixi, the physician to the Tibetan King Niechi Zanpu, in 126 BC. Aspects of both the traditional Chinese and Indian (Ayurvedic) medical systems were added later. Ayurveda has had the most profound influence on Tibetan medicine. The medicine of India was introduced to Tibet as early as AD 254, with the visit of some Indian physicians.

Tibetan medicine has been practiced also throughout Central Asia since at least the eighteenth century. The concepts are deeply grounded in the concept of universal compassion associated with the local religions of Buddhism and Bompo; the latter is the ancient religion of Tibetan. Historically, most Amchis (Tibetan medicine men) belonged to a lineage of healers and were taught medicine by their fathers or other elder male relatives. For them the healing value of plants and their precise identification is crucial. Tibetan herbal formulas they brought with them have been available as pharmaceutical products in Europe since 1980.

The modern Materia Medica of Tibet is derived from the book *Jingzhu Bencao* (The Pearl Herbs), published in 1835 by Dumar Danzhenpengcuo. This text has been compared to the famous Chinese herbal *Bencao Gangmu*. Its format includes two sections, one being in the style of the Buddhist sutra with praise of the medicines, and the other being a detailed classification of each substance, giving the material's origin, environmental conditions where it is found, quality, parts used, and properties. The text included 2294 materials, of which 1006 are of plant origin, 448 of animal origin, and 840 minerals. About one-third of the medicinal materials used in Tibetan formulas are unique to the Tibetan region (including the Himalayan area in bordering countries), while the other two-thirds of the materials are obtained from India and China. Although Tibetan herbal medicine includes the use of decoctions and powders, for the most part, Tibetan doctors utilize pills that are usually made from a large number of herbs (typically 8–25 ingredients). In general, Tibetan remedies emphasize the use of spicy (acrid), aromatic, and warming herbs. About 300 medicinal plants are used in Tibetan traditional system of medicine.

Folk Medicine

This system of medicine is very diverse and each type is specific to its own ecosystem and ethnic community. It is an oral tradition purely empirical in nature that exists in all rural, indigenous, and tribal communities of the world. Folk medicine knowledge is considered to be the most valuable asset of human civilization. Some folk medicine practices are described below.

Folk Medicine in India

This is widely practiced throughout the length and breadth of India. Its practitioners include housewives and village elders, herbal healers, bone setters, and 'Visha vaidyas' (poison healers). Almost every hamlet in rural India has a medicine man. An estimate suggests that more than 7500 plant species are used by folk medicine practitioners of India. Several Indian folk medicine plants or their extracts have already been adopted by Western modern medicine, e.g., *Psyllium husk* for bowel problems and *Cassia fistula* for antibiotic activity.

Northeastern India has rich knowledge of folk medicines. Meghalaya, a small state with 2 million population has thousands of traditional herbal practitioners.

Folk Medicine in Africa

People in rural Africa depend almost entirely on folk medicine. Traditionally, rural African communities have relied upon the spiritual and practical skill of traditional medical practitioners, whose botanical knowledge of plant species and their ecology and availability are invaluable. This dependence has led many medical scholars to believe that Africa, the cradle of humanity, is the birthplace of traditional methods of treatment. Folk medicines, as well as traditional practitioners, enjoy a special status in African societies.

There are hundreds of thousands of traditional healers in Africa, e.g., 900 000 in Nigeria, 700 000 in South Africa, 50 000 in Zimbabwe, and 450 000 in Senegal. Traditional healers use powders and other forms of medicines mainly extracted from plants, as well as superstitious practices, such as necromancy.

Folk Medicine in Other Parts of the World

As stated earlier folk medicines are known to almost every community of the world. The traditions of folk medicine are strong in Russia, Central Asia, Iran, Afghanistan, Mongolia and Manchuria. Equally, herbal medicines are an integral part of Brazilian folk medicine. Folk medicines are also popular in primary healthcare in several developed countries like Belgium, France, Germany, and the Netherlands.

Modern Medicine

Homeopathy

Homeopathy is based on the principle that substances that are poisonous in large doses can be very beneficial in small doses. Homeopathy is a form of medicine that treats the body as a whole and helps it to heal itself. Most homeopathic medicine preparations are partly or fully plant based. According to a recent estimate 482 medicinal plants are used in homeopathy. The applications of the drugs used in homeopathy are given in **Table 2**.

Allopathy

Allopathic system of medicine is also known as 'modern,' 'western,' or 'scientific' medicine. It is firmly rooted in the products of synthetic chemistry, as its drug arsenal. Nevertheless, in the developed world, 25% of all medical drugs are still plant-based and in the developing world this is closer to 75%. Allopathy will continue to depend on plants for its drugs and this dependence is more likely to increase rather than decrease. A large number of modern drugs have been derived from plant products, e.g., morphine, steroids, quinine, artemisinin, etoposide, taxol, etc.

Medicinal Plants in Modern Medicine

Modern pharmacology recognizes the therapeutic effects of plants: over 25% of all prescriptions in Western Europe and North America and up to 60% of those in Eastern Europe consist of unmodified or slightly altered higher-plant products. More than 40% of the industries producing modern medicines use plants as their active ingredient, although generally in a synthesized and more concentrated formula. The active ingredient in aspirin, for example, was originally found in the bark of willow trees (*Salix* spp.).

Western medicines produced from medicinal plants include contraconceptives, steroids (e.g., prednisone), and muscle relaxants for anesthesia and abdominal surgery; quinine and artemisinin against malaria; digitalis derivatives for heart failure; and the anticancer drugs vinblastine and vincristine, etoposide and taxol. These cannot be fully synthesized in a cost-effective manner. Therefore their production requires reliable supplies of plant materials, either from cultivated plants or from the wild. These few examples suggest how modern drug delivery depends on continuing availability of raw materials and how vulnerable it is to the exhaustion of natural resources.

Pharmaceutical industries look at biodiverse forests of tropics as an unmatched source of chemicals with potential for new drug development. Several national laboratories in North America, Europe, and Asia and drug industries are actively engaged in screening of plants for medicines. Quite a few

Table 2 Some medicinal plants collected from Indian forests for use in homeopathy

Species	*Application*
Abroma augusta	Diabetes mellitus, dysmenorrhea
Aconite sp.	Pain of abdomen, retention of urine, coldness, respiration, etc.
Azadirechta indica	Malarial fever, liver and spleen enlarged, skin diseases, leprosy
Berberis vulgaris	Peptic and renal disorders with pain in liver and abdomen with gravel in the kidney
Cannabis sativa	Gonorrhea, inflammation of the bladder, thin scanty pus, intense burning and pain, asthma
Desmodium gangeticum	Fever, burning in palms, soles, eyes, and face
Dioscorea	Biliary colic, flatulent colic, flatulent despepsia, gastralgia
Drosera sp.	Whooping cough
Eupatorium sp.	Snake bites, bleeding from lungs with cough, dysentery, etc.
Equisetum sp.	Enuresis
Ficus indica	Profuse mucus and blood in acute dysentery stools, emission of blood followed by evacuation of faccus with colic and tenosmus
Geranium maculatum	Hemorrhage from lungs and stomach
Gynocardia odorata	Leprosy, secondary syphilis, rheumatism, scabies, eczema, cutaneous eruptions
Hypericum perforatum	Injury of nervous tissue, spinal injury, shocks, gunshot wounds, etc.
Jacaranda caroba	Warts, redness after the syphilitic ulcer is cured
Lobelia inflata	Headache, nausea, vomiting
Momordica charantia	High temperature developed due to smallpox, measles
Nyctanthus sp.	Fever with vomiting, constipation, diarrhea, etc.
Passiflora incarta	Tetanus, dysmenorrhea, asthma
Ricinus communis	Stimulates the secretion of the mammary glands
Rauwolfia serpentina	High blood pressure, insanity
Tinospora cordifolia	Chronic malaria, especially after abuse of quinine with enlarged spleen and liver, yellowness of conjunctiva, diarrhea, vomiting
Tribulus terrestris	Impotence, gonorrhea, mental, nervous and physical weakness
Viscum album	Gonogorrheal rheumatism of joints and glands, especially in women

companies have made formal agreements with local indigenous communities and medicine men for the collection of medicinal plants on the basis of sharing of profits.

Trade

The world market for medicinal plant based products is estimated to be US$60 billion year^{-1} with a growth rate of 7% per annum. In Germany and France many herbs and herbal extracts are used as prescription drugs, while in USA herbal drugs are sold in food stores with turnover of US$4 billion in 1996, which was expected to double by the year 2000. The herbal medicine trade is booming business worldwide. In India, for example, there are 46 000 licensed pharmacies manufacturing traditional remedies, 80% of which come from plants. It is estimated that India expected to export crude drugs worth US$600 million in the year 2003 which may grow to US$2000 million by 2010. China exports crude drugs worth US$4400 million and Thailand worth US$2000 million. Europe is the major trading center for medicinal and aromatic plants globally, with imports into one European country or another amounting to 440 000 tonnes in 1996. There are at least 2000 MAPs marketed in Europe, which originate from over 120 countries. In 1999, the world market for herbal remedies was calculated to be worth US$19.4 billion, with Europe in the lead (US$6.7 billion), followed by Asia (US$2.2 billion), North America (US$4.0 billion), Japan (US$2.2 billion) and the rest of the world (US$1.4 billion). Hong Kong is claimed to be the largest market in the world, importing MAPs worth over US$190 million annually. A list of the leading countries exporting MAPs are given in **Table 3**.

Table 3 Twelve leading exporting countries of medicinal plants, according to export volumes (1992–95)

Country	*Export volume (tonnes)*
China	121 900
India	32 600
Germany	14 000
Singapore	13 200
Egypt	11 250
Chile	11 200
USA	10 150
Bulgaria	7 800
Morocco	6 850
Mexico	6 300
Pakistan	4 800
France	4 700

Threats to Medicinal Plants

The increasing population, desire to earn more money, and increasing acceptability of herbs as medicine are among some of the factors responsible for rising trade and increasing threats to the medicinal plants in the wild. Earlier, the harvesting of medicinal plants was the domain of specialist herbal healers but now harvesting has become the domain of uncertain and often indifferent commercial gatherers leading to a decline in wild stock.

The international herb trade, which has grown into a multi-billion dollar business, is depleting the local stock of the medicinal plants. International and national demands have changed a local harvesting pattern to commercial gathering without any regard to the regeneration of species for future yields. Most of Europe and North America's herbal medicine needs are fed from unsustainable wild collections in South Asia. There is a vast, secretive and largely unregulated market of medicinal plants sourced mainly from forests and the wild. The size of the market is growing dramatically, leading to depletion of resource base and making the species vulnerable to extinction.

The total number of plant species estimated to be threatened by IUCN is about 36 000, of which about 10 000 are medicinal plants (**Table 3**). The most serious threats to medicinal plants generally are habitat loss, habitat degradation, and overharvesting. The threats from overharvesting are also due to collection for purposes other than medicinal; for example, the African trees *Acacia sebegal*, *Boswellia papyrifera*, and *Pterocarpus angolensis* are often harvested for timber. Another reason why medicinal plants have become increasingly threatened has been the weakening of customary laws traditionally regulating the management and use of natural resources. The collapse of customary institutions has been connected directly to changes in the ways that medicinal plants were exploited and this has become a widespread phenomenon. Different countries may have different factors which result in the loss of medicinal plants; for example, in Pakistan a majority of medicinal plant species is facing severe threats from extraction, grazing, cutting, deforestation, unawareness, and misuse by the local vendors who are making key traded species vulnerable. In northeastern India and Nepal, deforestation, forest fires, shifting cultivation, overgrazing, and overharvesting have significantly eroded the medicinal plants resources.

Conservation Needs

Considering the importance of medicinal plants for human health and well-being, there is an urgent need for their conservation. Some countries have laws that regulate the commercial collection or trade of medicinal plants. For example, Poland lists species of medicinal and aromatic plants that cannot be

Table 4 Some endangered plants of actual or potential use in traditional medicine

Species	*Family*	*Threatened range*	*Use*
Acorus calamus	Araceae	India	Sedative
Alpina galanga	Zingiberaceae	India	Drug
Arbutus canariensis	Ericaceae	Canary Islands	Vitamin C
Artemisia granatensis	Asteraceae	Spain	Infusion
Catharahthus coriaceus	Apocynaceae	Madagascar	Alkaloids
Commiphora wightil	Burseraeae	India	Drug
Dendrobium nobile	Orchidaceae	India	Dendrobine
Dendrobium pauciflorum	Orchidaceae	India	Alkaloids
Dioscorea deltoidea	Dioscoreaceae	Afghanistan to Vietnam	Cortisone
Diplomeris hirsuta	Orchidaceae	India	Alkaloids
Dracaena draco	Liliaceae	Canary Islands, Cape Verde Islands, Madeira	Gum resin
Gentiana kurroo	Gentianaceae	India	Drug
Lodoicea maldivica	Arecaceae	Seychelles Islands	Drug
Nelumbo nucifera	Numphaecaceae	India	Drug
Paeonia cambessedesil	Paeoniaceae	Balearic Islands	Epilepsy
Panax quinquefolius	Araliaceae	US	Tonic tea
Paphiopedilum druryi	Orchidaceae	India	Alkaloids
Pelagodoza henryana	Arecaceae	Marquesas Islands	Endosperm
Podophyllum hexandum	Berberidaceae	India	Drug
Rauwolfia serpentina	Apocynaceae	India	Drug
Rheum rhaponticum	Polygonaceae	Bulgaria, Norway	Medicine
Rumex rothschildianus	Polygonaceae	Israel	Medicine
Ruta pinnata	Rutaceae	Canary Islands	Balsma-like properties
Santalum album	Santalaceae	India	Drug
Saussurea lappa	Asteraceae	India	Various
Siscymbrium cavanillesianum	Brassicaceae	Spain	Mustard-like properties
Toxocarpus schimperianus	Adelepiadaceae	Seychelles Islands	Pharmacology

collected without a permit from the department concerned. An Italian law of 1931 stipulates that permits for the commercial collection of species that are listed to be of medicinal value will only be issued to people who have degrees in herbalism from any recognized school of pharmacy. Bulgaria has established a quota system for the gathering of certain MAPs that is reviewed annually; they also ban export, as did the Government of India in 1994 for 50 species believed to be endangered in the wild. Nepal's Forest Act of 1993 provides power to ban collections of forest products. Enactment of such laws and their enforcement may go a long way in conservation of medicinal plants.

Botanical gardens and seed banks offer a more attractive way of storing *ex situ* the genetic diversity of the MAPs. However, medicinal plants are poorly represented in seed banks. A major task for conservationists is to create opportunities for the sharing of knowledge to encourage learning, or else there is a risk that much of folk medicine knowledge will be lost. Efforts should be made to document and integrate indigenous knowledge on MAPs, vegetation and forest management, NWFPs, agroforestry, homegardens, and biodiversity. Huge quantities of MAPs collected from the wild are lost during harvest, storage, and processing. The involvement of all stakeholders, i.e., collectors, traders, manufacturers, and consumers, through sharing of benefits can help a great deal in conservation of this resource so vital for human health and survival. Appropriate management and harvesting methods need to be developed to allow regeneration and maintenance of viable population of medicinal plants in natural habitats including forests. Full participation of local communities in conservation and management of MAPs is desirable. Multinational pharmaceutical industries and drug manufacturers need to invest part of their income in conservation and management of MAPs. There is a need for more work to ensure that the benefits from new drugs or botanicals developed and manufactured using indigenous knowledge are fairly and equitably distributed, as required by the Convention on Biological Diversity. (**Table 4**)

See also: **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest; Forest Biodiversity Prospecting; Medicinal and Aromatic Plants: Ethnobotany and Conservation Status; Tribal Medicine and Medicinal Plants. **Non-wood Products**: Resins, Latex and Palm Oil; Rubber Trees; Seasonal Greenery. **Silviculture**: Bamboos and their Role in Ecosystem Rehabilitation; Managing for Tropical Non-timber Forest Products. **Sustainable Forest Management**: Definitions, Good Practices and Certification.

Further Reading

Bhatt KKS (2003) Medicinal plant information databases. In: *Non-Wood Forest Products for Rural Income and Sustainable Forestry*. pp. 1–18. Rome: Food and Agriculture Organization.

FAO (2003) *Non-Wood Forest Products for Rural Income and Sustainable Forestry*. Rome: Food and Agriculture Organization.

Organization (2002) *Regional Workshop on Wise Practices and Experiential Learning in the Conservation and Management of Himalayan Medicinal Plants*, 15–20 December 2002, Kathmandu.

Rana AK (2003) Indian medicinal and aromatic plants special – I and II. *The Indian Forester* 129: 1–297.

Sharma R (2003) *Medicinal Plants of India – An Encyclopedia*. Delhi, India: Daya Publishing House.

Shankar D and Majumdar B (2003) Beyond the Biodiversity Convention: the challenges facing the biocultural heritage of India's medicinal plants. In: *Non-Wood Forest Products for Rural Income and Sustainable Forestry*. Rome, Italy: FAO.

Tiwari BK and Tynsong H (2003) *Medicinal Plants of Meghalaya, India*. Unpublished Technical Report. Shillong, India: Centre for Environmental Studies, North-Eastern Hill University.

Medicinal and Aromatic Plants: Ethnobotany and Conservation Status

N Bhattarai, Government of Nepal, Kathmandu, Nepal
M Karki, Medicinal and Aromatic Plants Program in Asia, New Delhi, India

Introduction

Ethnobotany is a multidisciplinary science involving the traditional use of plants by human beings. Billions of people in the world rely chiefly on herbal medicines. The great majority of medicinal and aromatic plants (MAPs) used locally or entering into trade and herbal industries comes from wild sources and constitutes the source of livelihoods of millions of people.

Ethnobotanical information and knowledge are believed to have contributed to the development of close to 30% of modern medicines. In recent years, the increasing demand for herbal medicines in industrialized countries is being fueled by a growing consumer interest in natural products. As international trade in medicinal and aromatic plants has grown to a multibillion dollar industry, local harvesting patterns have shifted from subsistence local collection to commercial 'mining.' The continued growth in the global raw-material market of MAPs has largely contributed to this trend.

Assessment of the conservation status of MAPs involves consideration of different threat factors including biological and socioeconomic issues such as destructive harvesting, habitat change, species extinction and loss of livelihoods of locals that have contributed towards disturbing trends in species loss. The conservation and management measures adopted so far have proved to be grossly inadequate. Tangible improvements in the livelihoods of local communities and inculcation of conservation values in the minds of people may be more sustainable measures for long-term conservation of MAP diversity and associated ethnobotanical knowledge systems.

Ethnobotany

Plants have been the basis of life on earth. The identification of plants useful to human beings from natural stands commenced in prehistoric times. Experiments and trials were the two main ways through which humans have learnt the various uses of plants. Only a few of the useful plants have so far been domesticated, while a majority of them are still used from the wild. With the advancement of civilization, the plants found in nature have been put more to use in various ways. The importance of plants as a means to fulfill the basic requirements of human beings can be keenly observed in the rural and remote areas of the world.

Harshberger in 1896 coined the word 'ethnobotany' to denote the study of plants used by people living in traditional societies. Later various workers defined ethnobotany variously. Despite considerable variations in definition, almost every worker has accepted the subject of ethnobotany as dealing with the relationship between human societies and plants. Ethnobotany, therefore, has a broad coverage including any traditional use of plants and plant products. The subject is multidisciplinary, involving many interrelated subjects such as history, anthropology, culture, literature, etc.

Ethnobotany being a use-group of plants by human beings, any traditional use belongs to the ethnobotanical discipline. On the basis of variety of uses, ethnobotanical studies may belong to various use-categories (**Table 1**).

Documentation of ethnobotanical information has mostly been based on archaeological sources, oral folklore, and other mythologies, literature sources, study of reference specimens in herbaria and museums, etc. Field-based study is, however, the most popular.

Table 1 Common ethnobotanical uses of plants and plant products

Agricultural implements
Beads and rosaries
Beverages
Ceremonial uses
Condiments
Containers
Cultural uses
Detergent
Dye
Edibles
Equipment
Essential oil
Fatty oil
Feed and fodder
Fiber
Fish-poison
Fragrances
Gum
Incense
Insecticide
Insect repellent
Intoxicant
Manure
Medicine
Musical instruments
Religious uses
Resin
Spices
Tan
Tools
Toxicant
Weapons

Medicinal and Aromatic Plants (MAPs)

'Medicinal plant' is not a taxonomic but a use-group of plants. Any plant when used in medicine or for medicinal purposes, whether in modern or in organized systems of traditional medicines like Ayurveda, the Unani system, homeopathy, etc., or the widespread indigenous and folk systems, can be categorized as a medicinal plant. 'Aromatic plants,' on the other hand, are those plants containing essential oil, mostly having an aromatic flavor, which may be, but is also not only limited to, medicinal plants. Both the two groups are these days collectively termed as medicinal and aromatic plants (MAPs).

Traditional Medicine and Traditional Healers

In the beginning all drugs were natural, such as vegetable, animal, and mineral products in their crude forms. Until the beginning of the twentieth century all medical practice was what we now call traditional. Traditional medicine is, therefore, used mainly to distinguish the ancient and culture-bound healthcare practices, which existed before the application of science to health matters in official modern scientific medicine or allopathy. Some frequently used synonyms are indigenous, unorthodox, alternative, folk, ethno, fringe, and unofficial medicine and healing.

A large number of individual therapies are currently in practice in different parts of the world, many of them increasingly employed for self-medication accompanied by faith and confidence with considerable extent of effectiveness, with or without the services of the traditional healers (**Table 2**).

The World Health Organization (WHO) has defined traditional medicine as:

> the sum total of all the knowledge and practices, whether explicable or not, used in diagnosis, prevention and elimination of physical, mental or social imbalance and relying exclusively on practical experience and observation handed down from generation to generation, whether verbally or in writing. Traditional medicine might also be considered as a solid amalgamation of dynamic medical know-how and ancestral experience.

Table 2 Some of the well-known individual therapies

Acupressure
Acupunture
Allopathy
Anthroposophical medicine
Apitherapy
Aroma therapy
Astrological diagnosis
Autogenic training
Ayurveda
Breathing
Clay and mud therapy
Color therapy
Dance therapy
Faith healing
Fasting
Flower remedies
Herbalism
High-fiber diet
High-protein diet
Homeopathy
Hot-spring bath
Hydrotherapy
Hypnosis
Magic
Medication
Monodiets
Moxibustion
Music therapy
Naturopathy
Osteopathy
Raw food therapy
Siddha system
Sun baths
Ultra-violet radiation
Unani system
Urine therapy
Vegetarianism
Witchcraft
Yoga

> In its *Traditional Medicine Strategy* (*2000–2005*), WHO has defined traditional medicine as a comprehensive term used to refer both to traditional medical systems such as traditional Chinese medicine, the Indian subcontinent's Ayurveda and Siddha, and Arabic Unani medicine and also to various other forms of indigenous medicine.

Various traditional medical systems, with varying theories and formalities, are currently fulfilling the primary healthcare needs of more than three-quarters of the population of the developing world. Considering the coverage and effectiveness of these systems of traditional medicine throughout the world, the Alma-Ata Declaration of the WHO proposed the theme 'Health for all by the year 2000' in 1978. The commitment was reaffirmed by the International Consultation on Conservation of Medicinal Plants, organized by WHO/IUCN/WWF in Chiang Mai, Thailand, popularly known as the Chiang Mai Declaration (1988). It put emphasis on the primary healthcare approach and the principles of conservation and sustainable development, outlined in the World Conservation Strategy. In view of these facts, the World Health Assembly in May 1976 first discussed seriously the contribution that traditional healers make to the healthcare of communities worldwide.

The African Expert Group has defined traditional healer as:

> a person who is recognized by the community in which he (or she) lives as competent to provide health care by using vegetable, animal and mineral substances and certain other methods based on the social, cultural and religious background as well as on knowledge, attitude and beliefs that are prevalent in the community regarding physical, mental and social well-being and the causation of disease and disability.

In almost every part of the world traditional healers are practicing means of healthcare coverage that is culturally acceptable to the local population, dealing more or less satisfactorily with many of their health problems. Conducting religious ceremonies, preaching of supernatural powers and evil spirits, psychotherapy, cauterization, prevention, surgery, use of animal and mineral products, etc., are the important basis of most folk therapies. Herbal medicine is, however, the most popular.

Ethnobotany of Medicinal and Aromatic Plants

Health issues have always been of prime importance for humankind since the very beginning of civilization. The use of plant resources for medicinal purposes is one of a number of practices developed by ancient people. The early use of plants as medicine must have been learnt and developed by humans through constant trial and error, probably at the cost of many lives and sufferings. People adopted various herbs that exhibited curative properties. Due to lack of communication, and varying ways of life, many of these earlier remedies survived only by word of mouth from generation to generation. These remedies not only exist but also are being largely practiced in most parts of the world, particularly in rural and tribal societies. The absence of acculturation has, in many instances, helped in the preservation of this knowledge in almost original form. In most developing countries, the indigenous modes of herbal treatment are a part of the culture and the dominant method of therapy. These remedies, with a considerable measure of effectiveness, are socially accepted and economically viable, and are often the only available source to the rural poor.

Ethnobotanical studies have mostly been employed to study the medicinal uses of plants in general, involving a range of disease and ailments. Medicinal plants used to treat a particular category of health problem have become increasingly popular, e.g., to treat skin diseases, to heal wounds, to kill intestinal worms, to treat digestive and other abdominal complaints including diarrhea and dysentery, to treat amoebic and respiratory diseases, to treat malaria and other types of fever, to treat venereal diseases, to induce antifertility effects, to terminate pregnancy, to regulate fertility, to treat reproductive disorders, to treat cancer, etc. Consequently, ethnomedicobotanical studies have recently been focused on some more specialized health disciplines, e.g., papers have been published under the discipline of ethnonarcotics, ethnopediatrics, ethno-obstetrics, ethnogynecology, ethno-veterinary medicine, etc.

Conservation Status of Medicinal and Aromatic Plants

Estimation and monitoring of the conservation status of medicinal and aromatic plants, in general, is an important but challenging issue that can be realized only after identifying the various threat factors and their extents including use and trade as well as by evaluating the conservation measures and management practices adopted so far.

Medicinal and Aromatic Plants in Folk Medicine

The great majority of species of medicinal plants which are the dominant mode of therapy in almost all developing countries and that are used in folk or ethnomedicine, are collected from the wild. The WHO has listed 20 000 medicinal plants used in different parts of the globe. Other estimates indicate the number to range between 35 000 and 70 000 worldwide.

An estimated 70–80% of people worldwide rely chiefly on herbal medicine to meet their primary healthcare needs. In south Asia only, over 800 million people rely on herbal medicine. In China, 40% of urban patients and more than 90% of rural patients depend on plant-based medicine. Some 10 000–11 250 species are used in ethnomedicine in China, 6000–7500 in India, 2237 in Mexico, 2572 traditionally by North American Indians, and 1600 species in Nepal. Considering the extent of fieldwork ongoing in different parts of the developing countries among various tribes, ethnic groups, and other indigenous communities generating additional information on indigenous medicinal plants, the number of plants known to be used in human medicine is likely to increase considerably in the future.

Medicinal and Aromatic Plants in Organized Systems of Traditional Medicine

Many countries, especially in Asia and Africa, have officially recognized the use of plant-based traditional medicine in their healthcare delivery systems. These organized traditional medical systems employ relatively few species, viz. 500–600 in traditional Chinese medicine, 1106 in Tibetan medicine, 1250–1400 in the Ayurveda, 342 in the Unani, and 328 in the Siddha systems.

The value of traditional medicines in China is estimated at US$571 million per year. In 1995, according to the State Administration of Traditional Chinese Medicine, the countrywide sale of crude plant drugs was at US$2.3 billion. China's demand for medicinal plant material has grown at an annual rate of 9% over the last two decades. In India, there are 7843 registered pharmacies of ISM and 851 of homeopathy and a large number of non-registered small-scale production units. About 240 000 tonnes of crude herbs, representing about 10% of the quantity collected from the wild, are processed per annum by the Indian herbal pharmacies. The herbal product market in Germany in 1989 was estimated at US$1.7 billion. In the urban areas of contemporary Africa, there is a burgeoning demand for herbal-based traditional medicines. The same tradition is active in many South and Southeast Asian countries such as Bhutan, India, Myanmar, Nepal, Thailand, and Vietnam.

Herbal medicine is becoming even more popular in richer countries, a market sector that has grown at 10–20% annually in Europe and North America over recent years. In industrialized countries, the demand is being fueled by an outburst of consumer interest in natural products. The extent of interest on the part of the general public is demonstrated by the fact that in 1990 the trade in herbal remedies in the European Union has been valued at over US$1000 million and rising at 13% year^{-1}. Similar growth rates have been recorded and are expected to continue in rich countries like Canada, the United States, Germany, Japan, and others. In Japan, pharmaceutical expenditures for Kampo medicines (adopted from Chinese traditional medicine) in 1983 was US$150 million.

Medicinal and Aromatic Plants in Modern Medicine

A large number of drugs of the modern system or allopathy were discovered from plants based on their ethnobotanical uses (**Table 3**). Further, many other pure constituents obtained from plant sources are used as drugs in modern medicine (**Table 4**). Today, there are approximately 119 pure chemical substances extracted from higher plants and in use in modern medicine throughout the world. Out of these, more than 90 chemicals have been isolated from plants having ethnic uses; others are either from random screening or screening certain plant families that are known to be rich sources of biologically active compounds.

Approximately 25% of all prescriptions dispensed from community pharmacies in the USA between 1959 and 1973 contained one or more ingredients derived from higher plants. It has been estimated that the total economic value to the USA from plant-derived pharmaceuticals is the total sale of US$12 400 million year^{-1}. Financially, the retail sale of plant-based pharmaceutical products was estimated at US$80–90 billion globally in 1997, with medicinal plants contributing very significantly.

Medicinal and Aromatic Plants in Trade

In many parts of the world there is virtually no cultivation on any significant scale, including for example in Albania and Turkey in Europe, Pakistan, Bhutan, and Nepal in Asia, and most countries in Africa. Large quantities of MAPs are traded into urban centers from rural areas in developing countries, and also regionally and internationally. The global demand for medicinal plants and herbal medicine is very large, estimated at US$40–60 billion year^{-1}, and still growing.

China's output of medicinal plants from cultivated and wild harvested sources, considered together, was 1.6 million tonnes in 1996, with a total value (excluding exports) in terms of finished products of US$3.7 billion. The reported annual global imports of MAP material during the 1990s amounted to an average of 400 000 tonnes, valued at US$1.2 billion, showing a 100% rise from 1991 to 1997. The three leading exporting countries are China (140 000 tonnes year^{-1} over 1991–1997), India (50 000 tonnes year^{-1}), and Germany. Hong Kong is considered the largest herbal market in the world, importing in excess of US$190 million per year. Europe, especially Germany, is the major trading center for MAPs globally, with imports into one European country or another amounting to 440 000 tonnes in 1996. The WHO had estimated the world trade of medicinal plants at US$500 million in 1980.

India exports large quantities of Ayurvedic and Unani herbs and preparations over a very wide geographical area including Bangladesh, Japan, Nepal, Pakistan, Saudi Arabia, the UAE, Russia, and USA, and accounts for 12% of global herbal pharmaceutical trade. The annual herbal medicine sales in Eastern Europe, Asia, Japan, and North America are US$6000, US$2300, US$2100, and US$1500 millions respectively with a total derived from higher plants amounting to US$11 billion. In 1999, the world market for herbal remedies was calculated to be worth US$19.4 billion, with Europe in the lead (US$6.7 billion), followed by Asia (US$5.1 billion), North America (US$4.0 billion), Japan (US$2.2 billion), and finally the rest of the world (US$1.4 billion).

Habitat Degradation and Loss due to Commercialization

The great majority of the medicinal and aromatic plants used locally or entering into trade and used in herbal industries comes from wild harvesting. In China, the annual demand of plant materials for traditional as well as officially decreed medicines has been reported to exceed 1.6 million tonnes, more than 80% of which come from wild sources. More than 95% of the medicinal and aromatic plants of Nepal out of 10 000–15 000 tonnes that enter into trade annually are harvested from wild sources. In India, 90% of the medicinal and aromatic plants that enter into trade and industry are harvested from wild

Table 3 Important drugs discovered from ethnobotanical leads

Drug	*Medicinal use*	*Plant species*	*Family*
Ajmalin	Heart arrhythmia	*Rauwolfia canescens*	Apocynaceae
		Rauwolfia serpentina	Apocynaceae
Aspirin	Analgesic, anti-inflammation	*Filipendula ulmaria*	Rosaceae
Atropin	Ophthalmology	*Atropa belladonna*	Solanaceae
Benzoine	Oral disinfectant	*Styrax tonkinensis*	Styracaceae
Caffeine	Stimulant	*Camellia sinensis*	Theaceae
Camphor	Rheumatic pain	*Cinnamomum camphora*	Lauraceae
Cascara	Purgative	*Rhamnus purshiana*	Rhamnaceae
Cocaine	Ophthalmologic anaesthetic	*Erythroxylum coca*	Erythroxylaceae
Codeine	Analgesic, antitussive	*Papaver somniferum*	Papaveraceae
Colchicine	Gout	*Colchicum autumnale*	Liliaceae
Demecolcine	Leukemia, lymphomata	*Colchicum autumnale*	Liliaceae
Deserpidine	Hypertension	*Rauwolfia canescens*	Apocynaceae
		Rauwolfia serpentina	Apocynaceae
Dicoumarol	Thrombosis	*Melilotus officinale*	Fabaceae
Digitoxin	Atrial fibrillation	*Digitalis purpurea*	Scrophulariaceae
Digoxin	Atrial fibrillation	*Digitalis purpurea*	Scrophulariaceae
Emetine	Amoebic dysentery	*Cephaelis ipecachuanha*	Rubiaceae
Ephedrine	Bronchodilator	*Ephedra sinica*	Ephedraceae
Eugenol	Toothache	*Syzygium aromaticum*	Myrtaceae
Gallotanins	Hemorrhoid suppository	*Hamamelis virginiana*	Hamamelidaceae
Hyoscyamine	Anticholinergic	*Hyoscyamus niger*	Solanaceae
Ipecac	Emetic	*Cephaelis ipecacuanha*	Rubiaceae
Ipratropium	Bronchodilator	*Hyoscyamus niger*	Solanaceae
Morphine	Analgesic	*Papaver somniferum*	Papaveraceae
Noscapine	Antitussive	*Papaver somniferum*	Papaveraceae
Papain	Attenuates mucus	*Carica papaya*	Caricaceae
Papaverine	Antispasmodic	*Papaver somniferum*	Papaveraceae
Physotigmine	Glaucoma	*Physostigma venenosum*	Fabaceae
Picrotoxin	Barbiturate antidote	*Anamirta cocculus*	Menispermaceae
Pilocarpine	Glaucoma	*Pilocarpus jaborandi*	Rutaceae
Podophyllotoxin	Vermifuge, Cancer	*Podophyllum hexandrum*	Berberidaceae
		Podophyllum peltatum	Berberidaceae
Proscillaridin	Cardiac malfunction	*Drimia maritima*	Liliaceae
Protoveratrine	Hypertension	*Veratrum album*	Liliaceae
Pseudoephedrine	Rhinitis	*Ephedra sinica*	Ephedraceae
Psoralen	Vitiligo	*Psoralea corylifolia*	Fabaceae
Quinidine	Cardiac arrhythmia	*Cinchona pubescens*	Rubiaceae
Quinine	Malaria prophylaxis	*Cinchona pubescens*	Rubiaceae
Rescinnamine	Hypertension	*Rauwolfia canescens*	Apocynaceae
		Rauwolfia serpentina	Apocynaceae
Reserpine	Hypertension	*Rauwolfia canescens*	Apocynaceae
		Rauwolfia serpentina	Apocynaceae
Sennoside-A	Laxative	*Cassia angustifolia*	Caesalpiniaceae
Sennoside-B	Laxative	*Cassia angustifolia*	Caesalpiniaceae
Scopolamine	Motion sickness	*Datura stramonium*	Solanaceae
Stigmasterol	Steroidal precursor	*Physostigma venenosum*	Fabaceae
Strophanthin	Congestive heart failure	*Strophanthus gratus*	Apocynaceae
Teniposide	Bladder neoplasms	*Podophyllum hexandrum*	Berberidaceae
		Podophyllum peltatum	Berberidaceae
THC	Antiemetic	*Cannabis sativa*	Cannabinaceae
Theophylline	Diuretic, asthma	*Camellia sinensis*	Theaceae
Toxiferine	Surgery, relaxant	*Strychnos guianensis*	Loganiaceae
Tubocurarine	Muscle relaxant	*Chondrodendron tomentosum*	Menispermaceae
Vinblastine	Hodgkin's disease	*Catharanthus roseus*	Apocynaceae
Vincristine	Pediatric leukemia	*Catharanthus roseus*	Apocynaceae
Xanthotoxin	Vitiligo	*Ammi majus*	Apiaceae

sources. An estimated 99% of the 400–550 species currently sold for use in traditional medicine in South Africa originate from wild sources. Only 130–140 of the 1200–1300 species that are both traded in, and native to, Europe are derived predominantly from cultivation. An estimated 70–90% of the medicinal

Table 4 Some pure constituents from plant sources as useful drugs

Drug	Medicinal use	Plant species	Family
Ajmalicin	Antihypertensive, tranquilizer	*Rauwolfia canescens*	Apocynaceae
		Catharanthus roseus	Apocynaceae
Ajmaline	Antihypertensive, tranquilizer	*Rauwolfia serpentina*	Apocynaceae
Artemisine	Antimalarial	*Artemisia annua*	Asteraceae
Digoxin	Cardiotonic	*Digitalis lanata*	Scrophulariaceae
Diosgenin	Induces sterilization	*Dioscorea deltoidea*	Diodcoreaceae
Emetine	Antiamoebic	*Psychotria ipecacuanha*	Rubiaceae
Gossypol	Male contraceptive	*Gossypium herbaceum*	Malvaceae
Hyoscyamine	Anticholinergic	*Atropa belladonna*	Solanaceae
		Datura stramonium	Solanaceae
		Hyoscyamus muticus	Solanaceae
Ipecac	Induces vomiting	*Cephaelis ipecacuanha*	Rubiaceae
Khellin	Vascodilator	*Ammi visnaga*	Apiaceae
L-DOPA	Antiparkinsonian	*Mucuna pruriens*	Papiloinaceae
Marsilin	Sedative, anticonvulsant	*Marsilea minuta*	Marsileaceae
Pseudo-ephedrine	Central nervous system stimulant	*Ephedra sinica*	Ephedraceae
Rutine	Decreases capillary fragility	*Ruta graveolens*	Rutaceae
Taxol	Overian cancer, breast cancer	*Taxus brevifolia*	Taxaceae
		Taxus wallichiana	Taxaceae
Theobromine	Diuretic, myocardial stimulant, vasodilator	*Camellia sinensis*	Theaceae
Theophylline	Cardiac stimulant, vasodilator, smooth muscle relaxant	*Camellia sinensis*	Theaceae

plant material imported into Germany, the third largest importer, is wild-harvested and only 50–100 species among these are currently propagated on a large scale. The commercial sector of medicinal and aromatic plant is, therefore, facing serious problems due to the excessive dependency of users on resources sourced from the wild.

In addition to factors lying beyond human control, viz. landslides, flood, fire, etc., the most serious proximate threats to plant resources in general and medicinal and aromatic plants in particular are habitat loss, habitat degradation, and overharvesting. Forests are home to more than half the world's terrestrial species, but population pressure and the proportionately increasing demand for forest products are causing a rapid depletion of habitats in almost every part of the world. As the result, more than 50% of the world's original forest cover has already been wiped out and each year alarmingly big areas are cut, bulldozed, or burned. Poor people in the developing countries such as Bangladesh, Bhutan, India, Laos, Mexico, Myanmar, Nepal, the Philippines, and Vietnam, among many others, are pushed to destroy forests in desperate efforts to raise living standards. As a result, countless plant species including medicinal plants are facing considerable danger of extinction due to loss of habitat or its degradation.

Extensive destruction of medicinal plant-rich habitats such as tropical forests, wetlands, Mediterranean ecosystems, parts of the arid zone, etc., are enhancing the rate of extinction of biodiversity including medicinal and aromatic plants. Ninety-three percent of the original primary forest in Madagascar has been eliminated. It has been estimated that 12 000 plant species and probably around 190 000 animal species have been lost in Madagascar. All the forests of Western Ecuador have been destroyed to make way for banana plantations, oil wells, and human settlements, destroying almost 200 000 species of plants and animals.

Worldwide, the verdant tropical forests that existed in 1985 covered only 900 million ha out of 1.5–1.6 billion ha that once existed. Between 7.6 million and 10 million ha are eliminated each year and at least a further 10 million ha are grossly disrupted annually. Like other natural resources the forests of the world are being sacrificed on the altar of development. By giving the definition that affluence is development, the rich countries have set an unsustainable path to achieve human prosperity. Human activities, under the so-called development initiatives, have posed considerable threats to habitats and ecosystems, thus threatening biological diversity, in general. Major human impacts includes a significant lowering of the upper timberline, conversion of forest to arable land, commercial timber cutting, excessive use of timber for domestic purposes, construction of roads, dams, and canals, high-tension electricity cables, etc. One glaring example is the Amazon forests, when Brazil decided to construct a highway in 1970, and deforested an area almost equal to that of India.

It has been estimated that the average background rate of extinction has been roughly 2–3% $year^{-1}$.

Current species extinction rates are estimated at approximately 10 000–20 000 year^{-1} or between 1000 and 10 000 times faster than the natural rate or maybe 1 million times faster than the rates of speciation. This increased rate of plant extinction means loss of immense biodiversity much before these species are properly understood.

Conservation and Management of Ethnobotanical Resources

In some communities, women play a significant role in medicinal plant conservation and cultivation, e.g., the women herbalist in Kabale, Uganda grows most of her herbs in her home compound. The same trends have recently evolved in certain localities of Bangladesh and India. Valuing the forest as a source of medicine, in Manongarivo, a tropical rainforest area in northern Madagascar, the local community has preserved an area of forest as a 'green pharmacy' that, otherwise, would have been slashed and burned for subsistence agriculture. In the same line, sacred groves, which are patches or pockets of climax vegetation preserved on religious grounds by the local communities, are still found scattered in different parts of India, Nepal, and Sri Lanka.

Many countries have little or no regulations controlling the collection of plant material from the wild. In India, however, 29 species of medicinal plants, thought to be threatened in the wild, have been restricted from collection. Nepal has, likewise, imposed different levels of restriction on the harvesting and trade of 16 medicinal and aromatic plant species including 10 species of trees. These restrictions are mainly aimed at protecting the wild flora and encouraging their cultivation practices.

Medicinal and aromatic plants are important components of the local flora, and valuable parts of the ecosystem. However, these ecosystems and communities are being degraded and destroyed and species are being driven to extinction, thus threatening the resource base of MAPs as well. Due to various human activities loss of biodiversity is occurring at all levels. Considering the importance of biological diversity, of which medicinal and aromatic plant resources are an important component, conservationists lay emphasis on the conservation of the entire habitat and the ecosystem to safeguard the biological resources and their inevitable interactions. With the aim of protecting representative samples of natural ecosystems, a number of protected areas of different status have been established in almost every country that cover a significant proportion of the earth's surface.

In India, 87 National Parks and 441 Wildlife Sanctuaries, respectively, cover 34 819 km^2 and 115 903 km^2 of the forestland. This accounts for 4.5% of the land of the country and 14% of the land under forest. In Nepal, 16.71% of the country's land has been brought under different levels of conservation and protection. In Bangladesh, 0.8% of the land of the country has been declared protected area. Bhutan has set aside 10 513 km^2 of its forestland under different types of protected/conservation areas including 535 km^2 as the 'buffer zone.'

The establishment of extractive reserves in Brazil is an important first step in resolving some of the problems like the development of viable extractive economies that is being hindered by destructive harvesting. In South India, a number of Medicinal Plant Conservation Areas (MPCAs) have been established that included the historically/traditionally known areas for rich medicinal plant diversity.

In Nepal, the management of the national forest is being systematically handed over to identified communities of users characterized by a comparatively high level of participation by women. As a group, they share the rights and responsibilities of using and managing the forest. So far, about 20% of the national forest including about 12 000 patches of forests have been handed over to the communities to manage. In most cases the communities have shown their efficiencies in terms of conservation, management, and development of the forest and the program in Nepal has so far been very successful. Many of them have started the commercial harvesting of MAP resources in a sustainable manner although in many cases they had to deal with severely degraded forest patches.

Discussion

Billions of people on earth depend chiefly on herbal medicines that have been significantly contributing to their primary healthcare needs. The curative properties of folk herbal medicines have always been a miracle and almost every folk remedy poses more questions than it answers. However, many of these questions are better answered today than in the past. Because so many people use medicinal plants, or plants as medicine, mostly collected from the wild, in the folk healing systems, it may be considered a serious threat to their conservation. But the problem, as usually repeated, is not always so severe, although it is critical indeed. So far as collection for medicinal purposes is concerned, there is general agreement that collection for household use is not overwhelmingly the problem. So many thousands of species are used in folk medicines, and just because a species has been used somewhere medicinally, it does not follow that it is so used everywhere and at all times. Its designation as a medicinal plant may carry little or no meaning to people living in the neighborhood. In several African, Asian, and some other countries wild harvesting for local requirements has not been experienced as detrimental to plant survival as the quantity collected tended to be small and also most of the material collected came from rather weedy species and common varieties. Ethnic medicinal plants can have other uses than as sources of medicines, and the threats from overharvesting may be due, or partly due, to collection purposes other than medicinal. There may be good reasons, for the purpose of genetic conservation, to conserve particular populations of medicinal plants, as many times a locally endemic or highly fragmented population of plants may have local uses.

The number of species used in herbal trade and industries is relatively small but this group of plants is most threatened in the wild. Despite efforts now under way, there remain many challenges in the conservation and sustainable management of wild medicinal plant resources, and it has now become inevitable to evaluate the threat status and conservation needs of the local and regional floras, more particularly the medicinal and aromatic plant resources. As it is unfair to tar every taxon with the same brush, the first and possibly the most desired step is to identify the potentially threatened species, assess them in terms of threat factors and conservation status, and carry out the recommended measures.

The IUCN-Species Survival Commission's Conservation Assessment and Management Planning (CAMP) exercise has recently been recognized as a suitable mechanism for using available information to assess possibly threatened taxa and to initiate adequate conservation and management planning. The five threat categories, involving evaluation of threat factors and conservation status are Critically Endangered (CE), Endangered (EN), Vulnerable (VU), Near Threatened (NT), and Least Concern (LC), based mainly on information on their distribution, regeneration potentials, productivity, use, interacting threats, etc. CAMP exercises have been successfully used to identify threat factors and to assess conservation status of some species of MAPs in different regions.

The collection of medicinal plants from wild habitats has long been a mode of self-employment for most rural people. Although the wild resource-based herbal trade and industries have remained functional for a long period of time, it cannot always serve as a model for the future. As international trade in medicinal and aromatic plants has grown to a multi-billion dollar industry, local harvesting patterns have shifted from subsistence local collection to commercial 'mining' without regard to the generation of species for future yields, in most cases. The growth in the alternative medicine market in industrialized nations is a significant contributor to this trend.

Because processing and marketing are mostly exogenous to the supply area, control of the system of gathering and trade also tends to be found mostly in the hands of people external to the region. When an outside interest dictates the volume and price of a resource, local biodiversity suffers irreversible harm. The marginalized and poor people generally take the view that 'If I don't pick what I can today, someone else will get it tomorrow.' Consequently, the local people are generally losing control over the conservation and management of their resources.

The threats caused due to overharvesting usually recover with time but the damage due to loss of habitat is irreversible. The loss or degradation of forests and grasslands worldwide has led to the habitats of medicinal plants shrinking in almost every country. This has affected not only the few hundred commercial medicinal plants but also many thousands having no commercial uses but still serving the medicinal purposes of billions of rural people who mostly have no other alternative facilities.

The conservation and management initiatives focused on medicinal and aromatic plants in various countries and among various communities, although laudable, appear highly inadequate to cope with the negative efforts in practice so far. The protected areas network worldwide represents various physiographic and climatic zones, admirably contributing to the conservation of biological diversity, and it is wise to continue to stress the future significance of these efforts. While the protected areas have assured protection of certain species, such protected areas, however, are usually surrounded by damaged habitats, making them habitat islands. Habitats outside protected areas are under continuous pressure from human activities which, mostly, have increased beyond the carrying capacities of the ecosystems. Many of them are degraded and converted into agricultural lands.

In most of the supplier countries, although there is considerable evidence of overharvesting of medicinal plants, quantitative analyses of the effect of extraction on natural populations are lacking. Without these analyses, it is not possible to assess the effect of harvesting on depletion of resources, nor is it possible to formulate appropriate conservation and management strategies.

Conservation of natural resources are necessary for future generations, and this need has been so often repeated that the phrase has almost lost its importance. There is no comfort in thinking that species extinction is a natural process and therefore inevitable for the organisms that are extinct or on the way to extinction. While natural processes are involved, the activity of human beings accelerates and multiplies the means by which extinction can occur. Once a particular species is extinct, literally millions of years of evolution become undone and nothing can retrieve the situation. In the plant kingdom, the time for warning has matured. The destruction of many wild habitats and their inhabitants has already taken place and continues.

In the developing countries that are the major suppliers of wild medicinal plant materials, the overwhelming concern of the majority of the population is meeting their immediate needs. It is, therefore, difficult to conserve and direct resources for the benefit of future generations. The overexploitation of wild medicinal plant resources by rural people is therefore not just a case of preference but also of a situation where there is no other option.

At the community level, local people are the true resource managers, with a vested interest in maintaining the natural resources on which they heavily depend. But poverty, and to some extent ignorance, has forced rural people to continue activities that help them survive in the present but which will cause more severe problems in the future. The conclusion is, therefore, a challenge. Our approach to conserving wild medicinal plants for sustainable exploitation should be targeted at different levels, from improving living standards to changing the attitude of the people.

See also: **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest; Forest Biodiversity Prospecting; Medicinal Plants and Human Health; Tribal Medicine and Medicinal Plants. **Non-wood Products**: Resins, Latex and Palm Oil; Rubber Trees; Seasonal Greenery; Seasonal Greenery. **Silviculture**: Bamboos and their Role in Ecosystem Rehabilitation; Managing for Tropical Non-timber Forest Products. **Sustainable Forest Management**: Definitions, Good Practices and Certification.

Further Reading

Akerele O, Heywood V, and Synge H (1991) *The Conservation of Medicinal Plants*. Cambridge, UK: Cambridge University Press.

Altuschul SVR (1973) *Drugs and Food From Little Known Plants*. Cambridge, MA: Harvard University Press.

Chaudhury RR and Rafei UM (2002) *Traditional Medicine in Asia*. New Delhi, India: World Health Organization, Regional Office for South-East Asia.

Cunningham AB (2001) *Applied Ethnobotany: People, Wild Plant Use and Conservation*. London: Earthscan Publications.

Honnef S and Melisch R (eds) (2000) *Medicinal Utilization of Wild Species: Challenge for Man and Nature in the New Millennium*. Hanover, Germany: WWF Germany.

IUCN (2000) *IUCN Red List Categories*. Prepared by the IUCN Species Survival Commission and approved by the 51st meeting of the IUCN Council. Gland, Switzerland: IUCN.

Jain SK (ed.) (1981) *Glimpses of Indian Ethnobotany*. New Delhi, India: Oxford and IBH Publishing Co.

Lange D (1998) *Europe's Medicinal and Aromatic Plants: Their Use, Trade and Conservation: An Overview*. Cambridge, UK: TRAFFIC International.

Marshall NT (1998) *Searching for a Cure: Conservation of Medicinal Wildlife Resources in East and Southern Africa*. Cambridge, UK: TRAFFIC International.

Martin GJ (1995) *Ethnobotany: A Methods Manual*. London: Chapman & Hall.

Schultes RE and von Reis S (eds) (1995) *Ethnobotany: Evolution of a Discipline*. London: Chapman & Hall.

Srivastava J, Lambert J, and Vietmeyer N (1995) *Medicinal Plants: A Growing Role in Development Agriculture and Natural Resources*. Washington, DC: US Department of Agriculture and Forestry Systems, The World Bank.

Tandon V, Bhattarai NK, and Karki M (eds) (2001) *Conservation Assessment and Management Plan Workshop Report: Selected Medicinal Plant Species of Nepal*. New Delhi, India: International Development Research Centre, South Asia Regional Office.

ten Kate K and Laird SA (1999) *The Commercial Use of Biodiversity*. London: Earthscan Publications.

Touchell DH and Dixon KW (eds) (1997) *Conservation into the 21st Century*. Perth, Australia: Kings Park and Botanic Garden.

Tribal Medicine and Medicinal Plants

S Vedavathy, Herbal Folklore Research Centre, Tirupati, India

Introduction

Nearly 80% of the world population is dependent on indigenous medicines for primary healthcare. Tribal medicine is an age-old system of health care practiced by aboriginals in remote villages and forests. Tribal remedies consisting of simple methods of treatment developed by trial and error hold an important place in almost all societies. The study of nature by forest-dwellers started out of necessity. Thus the first study of plants by ethnic communities was undoubtedly a practical study centered on the importance of plants as a source of food for human nourishment, of fiber for clothing the human body, of drugs for the treatment of human diseases, etc. As civilization advanced over centuries rational human beings with their probing intellect and reasoning faculties enquired, investigated, and discovered various biological processes and began to unfold nature's magnificent creations. Even after advancement people remained in remote forests and hilly tracks, far away from the so-called urban civilization, carrying out their existence meeting all their requirements from the environs of forests. As they live in small ethnic groups or tribes, they are nowadays called tribal people or aboriginals.

Religion, magic, and medicine were integral parts of life of prehistoric peoples. Any person in the community with religious bent and knowledge of diseases and spirits assumed the headship of the community or the village and performed the roles of priest, sorcerer, and physician. Apart from the treatment of wounds and broken bones tribal medicine was probably the most ancient aspect of the art of healing for primitive vaidyas (physicians) showed their wisdom by treating the whole man or woman, soul as well as body.

Similarly the ancient peoples in Mesopotamia, Egypt, Babylonia, Greece, and Rome all developed their respective indigenous medicines along the same lines of belief, religion, and experience from exploration of various medicinal plants. The ancient medicine of Mesopotamia was magico-religious, while Egyptian medicine was empirico-rational.

Ethnobotany

The study of the association, interaction, and interrelationships of ethnic human societies (especially tribal communities) with the surrounding flora is termed 'ethnobotany' or aboriginal botany. The term ethnobotany was coined in 1896 by Harshberger, one of the fathers of economic botany of America. Ethnobotany has more recently been defined as the study of the interrelationship of plant environment and primitive societies. There are many subdisciplines of ethnobotany dealing with various aspects of tribal plants such as ethnoagriculture, ethnotaxonomy, ethnomedicobotany, ethnoecology, ethnomycology, ethnogynaecology, ethnotoxicology, ethnopharmacology, ethnopharmacognosy, ethnophytotaxonomy, ethnoveterinary medicine, etc.

Ethnography and the Ethnobotanical Knowledge of Tribes

Plants have profoundly influenced the culture and civilization of tribes in many countries. Many wild plants are in use by tribes for various purposes and most of them have found a place in rituals and ceremonies and some have been accorded sanctity (sacred plants). Many of the practices developed by indigenous tribes are the result of novel experimentation and innovation by people from observing the medicinal herbs and animals.

India has an immense wealth of biodiversity. According to estimates there are about 45 000 species of wild plants, of which 7500 species are in medicinal use in indigenous health practices. The tribal peoples (some 60 million people in India) who depend on forest wealth are the custodians who have safeguarded the medicinal plants till now. The real danger for biodiversity is from the urban elite who destroy the forests for industrialization and for their own needs. In any country, forests should cover one-third of the total land, for the maintenance of biodiversity. Forest cover is far below the desired level in India; it is about 19.5% and the protected area in that is only 10%. Rapid deforestation caused by overharvesting and the exploitative trade in medicinal plants have significantly reduced the availability of medicinal plants. With deforestation the tribal peoples who live in harmony with nature are the most threatened, and the wonderful tribal medicine is also disappearing slowly.

Tribal medicine is not a codified system. Through experience the disease is identified and treated. Even the primitive surgery the tribal practitioners make is their own and is performed in their home setting. There is a strong belief in tribal medicine that the efficacy of the therapy is lost if it is revealed to strangers who have no belief and sympathy on nature and medicine. In the modern sense there seems little scientific or experimental basis to these claims. But the use of a plant for the same purpose in several societies or regions has been taken as one of the criteria for greater credibility in terms of Western science.

Tribal medicine has assumed a new significance in the field of science in the last three decades and has emerged into a new branch of ethnobotany called ethnomedicobotany. This deals with tribal medicine, methods of preparation, mode of administration and their values. The Botanical Survey of India (BSI) and the Council of Scientific and Industrial Research (CSIR) started organized fieldwork and other studies on this subject through their regional centers all over India. Ethnomedicobotanical studies have been established in some universities, and field study results, herbarium collections and literature are being built up (see Further Reading).

Types of Tribal Medicine

Not all the tribals are vaidyas (doctors). Only the people who are interested learn and practice this. In India, tribal therapy is of three types: (1) Raja vaidya (medical therapy), (2) Bhuta vaidya (Witch therapy), and (3) Rakshasa vaidya (fire therapy). These three types of treatments very often overlap and the third type is applicable to animals as well as human beings. The second type is called magico-religious medicine which in modern parlance can be equated with psychotherapy. Elderly members of the community are well versed in the knowledge of different herbs, roots, and plants and their practices i.e., materia medica of tribal medicine. Some of them also maintain small herb farms. Even the scientists depend upon them for the identification and supply of medicinal plants for their research and preparation of medicines. Whenever epidemics such as chicken pox, cholera, and flu breakout the bhuta vaidya who employs sorcery, magic formulae, talismans, and amulets for outward consumption, also uses herbal medicines secretly for arresting these epidemics. These practices become a boon not only to the patient but also to the entire village, as prophylactic measures. The talismans and amulets also contain some powerful herbs or minerals. These practices are in vogue for human beings as well as livestock, which are more important and valuable to the rural people. Mankind developed his own pharmacopeias by making his body as laboratory to experiment. The gradual process might have taken thousands of years to evolve but one thing is certain; this is passed on from one generation to other with refinement.

Contribution to Biodiversity

The concept of sacred groves and thereby preservation of biodiversity is another of the great contributions of the primitive people to modern world. In the same way, the belief that the misuse of nature results in punishment and curse became boon to conservation, in helping to preserve the snakes and other minor animals. Tribal people believe that if any one kills a snake he or she will become sterile and will suffer from chronic skin infections. Tribals never uproot trees and many trees are considered sacred.

Herbal Remedies

Tribal population have learnt to utilize local herbs in different ailments after centuries of trials. Some of the folklore medicines have proved efficacious after detailed pharmacological and clinical trials. *Rauwolfia serpentina* roots are a classical example. This is now prescribed as a remedy of high blood pressure and certain forms of insanity. The seed kernel of *Hydnocarpus kurzii* from the Assam and Tripura hills has proved useful in the treatment of leprosy and skin diseases. The roots of *Nardostachys grandiflora* have provided a safe sedative after detailed clinical trials. The kernel of *Entada pursaetha*, bark of *Premna latifolia*, base of rachis of *Angiopteris evecta* as subsidiary food; the use of powdered dry fruits of *Brucea mollis* in malarial fever; the leaf juice of *Clausena excavata* in muscular pain; and the root decoction of *Ixora acuminata* as a galactagogue by karbis of Assam are interesting. The traditional knowledge of Asurs of Netarhat plateau (Bihar) is significant. They have many herbal cures such as *Andrographis paniculata* for fever with chills, *Schleichera oleosa* for gout, *Iphigenia indica* for cough and asthma, *Anisomeles* sp. For snake bite and poisoning, *Grewia* spp. for debility, and *Celastrus paniculata* as an abortifacient. The tribes such as Kol, Saora, and Koudh from the state of Orissa use more than 100 plant species for various ailments. The Mundas, Orans, Santhals, Lodhas, Kondhs, Bhumjis, Hos, and Mechs of Eastern India have vast knowledge about the treatment of cattle and birds using locally available plants. The tribal peoples residing along the hilly region of the western Ghats in Maharashtra use more than 100 wild species as food. The Todas, Kotas, Irulas, Kurumbas, the Paniyars and the Kattu nayaks of Tamilnadu have rich traditional knowledge and hundreds of plants are used for various ailments. The Jarawas, the Sentinelese, the Onge, the great Andamanese, the Nicobarese, the Shompen, and the Burmans of the Andaman Islands knew many plants, though most of the tribes themselves have not been explored by Western scientists.

The tribal repository contains many medicines for the treatment of one ailment. The medicine varies according to the symptoms and secondary effects and with the tribe and place. For one disease many plants are used basing on the availability. Some therapies recorded during the survey of Herbal Folklore Research Centre, Tirupati, Chittoor district, Andhra Pradesh, India are given in **Table 1**.

Medicinal Plants Research

We already know that traditional medicine developed from clues from forest-dwellers and herders. Documentation of such knowledge has been going on for centuries, e.g., *Hortus Malabaricus* (seventeenth century). The earliest scriptures (4500–1600 BC) of

Table 1 Tribal treatments for various ailments

Ailment	*Plant*	*Part*	*Mode of administration*
Fever	*Asparagus racemosus*	Root tuber	Decoction
	Cyperus rotundus	Root tuber	Decoction
	Tinospora cordifolia,	Stem	Decoction
	Allium sativum,	bulb	
	Zingiber officinale	dried rhizome	
	Andrographis paniculata,	Whole plant	The decoction of garlic is
	Morinda tinctoria,	Root	mixed with the two herbal
	Allium sativum	bulb	powders and given to drink
Head ache	*Catunaregum spinosa*	Fruit	1–2 drops of the juice instilled in the eyes
Indigestion and dyspepsia	*Trachyspermum ammi*,	Seed	Seed powder of the two in
	Carum copticum	Seed	equal proportions mixed with a pinch of rock salt is given
	Ricinus communis/	Seed oil	If the problem is chronic, seed oil is given on empty stomach or fruit juice mixed with a pinch of cumin powder is given
	Tamarindus indica	Fruit	
	Cassia senna	Leaf	For chronic cases two to three teaspoons of leaf powder mixed with a pinch of salt are administered on empty stomach
	Cassia occidentalis	Leaves	Tender leaves are made into curry and used along with food
Eye infections	*Citrus limon*	Fruit	Juice is instilled in the eyes
	Allium cepa	Bulb	Juice of the bulb is put in the eyes
	Curcuma longa	Rhizome	One to two drops of fresh rhizome juice is instilled in the eyes
	Martynia annua	Leaf	Leaf juice is put in the eyes
	Acorus calamus and	Dried rhizome	Rhizome made into ash is
	Zingiber officinale	Fresh rhizome	mixed with ginger extract and two to three drops are instilled in the eyes
Liver disorders	*Cuscuta reflexa*	Plant	Paste made from the cooked plant is applied on the stomach
	Azadirachta indica	Gum	Gum mixed with opium is given
	Phyllanthus niruri	Tender twigs with leaves	Paste or powder is given with buttermilk
	Boerhavia diffusa	Whole plant	Decoction is given with toddy jaggery
Cough and cold	*Pongamia pinnata*	Fruit	Put as garland around the neck for the chronic cases
	Datura metel	Leaves	Inhalation of fumes
	Solanum surrattense	Root	Powder mixed with honey is given to lick
	Adhatoda vasica	Leaves	Decoction
	Ocimum sanctum	Leaves	Juice is given with long pepper powder
	Coleus aromaticus	Leaves	Leaves eaten directly or juice with black pepper
Cuts and fractures	*Ficus bengalensis*	Leaves	Leaves warmed under fire are bandaged
	Dodonaea viscosa	Leaves	Pounded leaves are bandaged on the fractured part using bamboo sticks
	Cassia spp.	Leaves	Leaf paste mixed with white yolk of the egg is applied and bandaged using bamboo sticks
Sexual potency	*Mucuna prurita*	Seed	Powder mixed with honey/jaggery is given
	Asparagus racemosus	Root tubers	Powder mixed with honey/jaggery is given
	Pedalium murex	Whole plant	Juice with sugar candy
	Corollocarpus epigeus	Root tuber	Powder with goat's milk

continued

Table 1 Continued

Ailment	*Plant*	*Part*	*Mode of administration*
	Curculigo orchioides	Root tuber	Powder with goat's milk
	Holostemma adakodein	Root tuber	Powder with goat's milk
	Portulaca tuberosa	Whole plant	Powder with honey/jaggery
	Pueraria tuberosa	Root tuber	Powder with jaggery
Toothache	*Calotropis procera*	Latex	Topical application
	Achyranthes aspera	Root	Paste for topical application
	Zanthoxylum armatum	Stem	Powder mixed with alum is applied on the affected part
	Azadirachta indica	Stem	For brushing teeth
	Pongamia pinnata	Stem	For brushing teeth
	Tridax procumbense	Leaf	Paste mixed with camphor is put on the affected part
For easy delivery	*Achyranthes aspera*	Root	Root paste applied on the abdomen and navel region
	Ricinus communis	Seed	Seed oil is applied on the abdomen and navel region
	Zingiber officinale,	Dried rhizome	Decoction made by mixing the
	Piper nigrum,	Seed	ingredients in equal proportions is given to drink to hasten the pains
	Brassica nigra,	Seed	
	Coriandrum sativum	Fruit	
	Bambusa arundinaceae	Leaves	Decoction of the leaves is given
	Boerhavia diffusa,	Root	A wick dipped in the root paste or seed oil or fruit juice is inserted into the vagina to hasten the pains
	Ricinus communis,	Seed oil	
	Sapindus emarginatus	Fruit	
	Moringa oleifera	Leaves	Juice mixed with a pinch of salt is given
	Calotropis gigantea	Flowers	Flowers fried in ghee is given at half an hour interval
To ensure complete discharge of the placenta after delivery	*Tephrosia purpurea*	Root	Extract is given two to three times for complete discharge
	Azadirachta indica	Leaf	Leaf extract
	Caesalpinia bonduc	Root	Decoction is given along with rice gruel
For expulsion of dead baby from the womb	*Bambusa arundinacea*	Leaves	Leaf decoction with asafetida, salt, and rice gruel is given; this facilitates the expulsion within half an hour
	Prosopis cineraria	Leaf	Decoction prepared by mixing with garlic, millets and black pepper
Snakebite	*Aristolochia indica*,	Root	Paste/powder given internally
	Andrographis paniculata	Whole plant	
	Alangium salvifolium	Bark	Paste/powder, given internally
	Corallocarpus epigeus	Root	Paste is applied on the part and given to lick/instilled in the nostrils if the patient is unconscious
	Strychnos colubrina	Bark	Paste/powder given to drink or instilled in the nose
	Marsedinia volubilis	Leaf	Paste/powder
	Cryptostegia grandiflora	Root	Paste/powder
	Celastrus paniculata	Root	Juice/paste, given to drink or two to four drops instilled in the nose
	Acalypha indica	Leaf	Leaf paste is given

the Hindus, the *Rigveda*, mentions the use of plants for curing various ailments. The history of early Indian medicine is covered elsewhere in this Encyclopedia (*see* **Medicinal, Food and Aromatic Plants:** Medicinal Plants and Human Health).

Importance of Tribal Drugs

Many drugs discovered recently are taking the lead from tribal medicine. The discovery of ephidrin from the Chinese herbal drug *mahuang* has attracted the attention of many. Egyptians have long used the fruit of *Ammi majus* in the treatment of leucoderma. Rutin, now a well-known glycoside originally obtained from *Ruta graveolens*, has been reported from 40 different species of plants and is now increasingly employed in the treatment of capillary fragility. Documentation of such knowledge is needed. Most of the primitive tribes do not accept any other medicine except the ones prescribed by their medicine men. Information on all such knowledge should be recorded, preserved, and scientifically tested for blending into modern-style health systems. More efforts are needed towards establishing an evidence-based approach to promote traditional medicine practitioners into community-based health activities (**Table 2**).

Recent Efforts Made to Document Traditional Knowledge

A new resource database on traditional knowledge has been developed at the University of Illinois at Chicago named 'Natural Products Alert' (NAPRALERT). This new resource contains the world literature on natural products. Comprising data from more than 80 000 scientific articles, abstracts, and books, the database contains a wealth of information primarily on the ethnomedicine, pharmacology (experimental), and chemistry of plants.

Institutional Roles in Protecting Traditional Knowledge

Coordinated efforts to preserve the rare and endangered genetic wealth are required. Not only preservation of plant wealth but also a knowledge base and natural pockets of vegetation such as sacred groves is necessary. If the tribal communities are involved in such activities, they may open up their thinking on positive lines and help in conservation of native plants and knowledge. The programs of tree planting and medicinal plants regeneration need vast quantities of seeds. Tribal peoples could be engaged in selection of the seed, trees, and seed production areas. They could also be engaged for collection of seeds from these known sources.

Patents

Traditional knowledge is easily available in the public domain through gene banks and digital databases. Hence biopiracy/bioprospecting cannot be prevented using the Access and Benefit Sharing (ABS) provisions of International Convention of Biological Diversity and its well-intentioned mandate of prior informed consent (PIC) of traditional practice contributors. Thus ABC conditions must now be imposed before granting intellectual property rights (IPR) to traditional innovations.

The CBD convention recognizes that traditional knowledge, innovations, and practices are of importance to the convention of biological and intellectual heritage in this age of biopiracy and require ownership. If the knowledge is novel, based on innovations and a product of biodiversity it comes under recognition and protection.

Areas that Need Attention

- The concept of the naming (local names) of the plants and any expression of such knowledge related to disease.

Table 2 Contributions of tribal medicine to modern medicine

Modern drug	*Ethnomedicinal use*	*Plant source*
Aspirin	Reduces pain and inflammations	*Filipendula ulmaria*
Codeine	Eases pain, suppresses cough	*Papaver somniferum*
Ipecac	Controls vomiting	*Psychotria ipecacuanha*
Pilocarpine	Reduces pressure in the eyes	*Pilocarpus jaborandi*
Pseudoephidrine	Reduces nasal congestion	*Ephedra sinica*
Quinine	Combats malaria	*Cinchona pubescens*
Reserpine	Lowers blood pressure	*Rauwolfia serpentina*
Scopolamine	Eases motion sickness	*Datura stramonium*
Theophyllin	Opens bronchial passages	*Catharanthus roseus*
Disogenin	Contraceptive	*Dioscorea floribunda*
Digitoxin	Dropsy, relieves heart congestion	*Digitalis purpurea*
Taxol	Wound healing	*Taxus brevifolia*

- Conservation practices of the tribe, the taboos associated with certain plants, and their impact on the ecosystem.
- Tribal peoples have some rules and regulations regarding the medicine practice such as age, gender, and background relating to plants and the reasoning behind the practice.
- The tattooing, painting, dancing, customs, foods need thorough local study for the development of ecocenters.
- Tribes have specific plants for various uses, and their use differs with the tribe; this needs greater attention where the cross-cultural study may lead to many revelations.

Conclusion

There is need for documentation of all tribal health practices and the plants used by them. Deforestation seriously affects the life of tribals who are the 'forest children.' Their health, wealth, and culture depend on the forest and no one can alienate them from nature and it is a crime to deprive their resource base. The elite society that thinks that these people are illiterate and ignorant and need modern medication and education should understand first the dynamic element of the systems before introducing any reform.

Further Reading

Alcorn J (1995) The scope and aims of ethnobotany in a developing world. In: Schultes A and von Reis S (eds) *Ethnobotany: Evolution of a Discipline*, pp. 23–39. Portland, OR: Dioscorides Press.

Chopra RN, Chopra IC, Handa KL, and Kapur LD (1958) *Chopra's Indigenous Drugs of India*. Calcutta, India: UN Dhur.

Jain SK (1991) *Dictionary of Indian Folkmedicine and Ethnobotany*. New Delhi, India: Deep Publications.

Joshi P (1981) The forest herbal resources and Bhil medicine. *Tribe* 13: 129–136.

Manandhar NP (1985) Ethnobotanical notes on certain medicinal plants used by Tharus of Dang-Deokhuri district, Nepal. *International Journal of Crude Drug Research* 23: 153–159.

Rama Rao N and Henry AN (1996) *The Ethnobotany of Eastern Ghats in Andhra Pradesh, India*. Calcutta, India: Botanical Survey of India.

Shah NC (1995) *Rauvolfia serpentina*: from folk medicine to modern medicine – some unknown aspects. *Ethnobotany* 7: 109–112.

Vedavathy S, Mrudula V, and Sudhakar A (1997) *Tribal Medicine of Chittoor district A.P.* Tirupati, India: Herbal Folklore Research Centre.

Vedavathy S (2002) Tribal medicine: the real alternative. *Indian Journal of Traditional Knowledge* 1: 25–31.

Forest Biodiversity Prospecting

S A Laird, University College London, UK
K ten Kate, Insight Investment, London, UK

Introduction

Forests have long been an invaluable source of medicines, foods, crops, and other products based on genetic resources. A wide range of commercial sectors is involved today in 'biodiversity prospecting' as part of research and development programs aimed at developing new products, processes, and ingredients. Although scientific and technological advances have changed the role of natural products in many industry research programs, they continue to contribute significantly to existing sales and new product development. Biodiversity prospecting takes place within a legal and ethical framework that has transformed in the last decade, in part as a result of the Convention on Biological Diversity and the International Treaty on Plant Genetic Resources for Food and Agriculture. Biodiversity prospecting partnerships must now incorporate requirements for prior informed consent, mutually agreed terms, and benefit-sharing with source countries and communities.

Sectors Involved in Biodiversity Prospecting

The collection and trade in genetic resources is as old as human civilization, but the term biodiversity prospecting (bioprospecting) was first defined in 1993 as 'the exploration of biodiversity for commercially valuable genetic resources and biochemicals.' Biodiversity prospecting involves a wide range of commercial industries including the pharmaceutical, biotechnology, seed, crop protection, horticulture, botanical medicine, cosmetic and personal care, and food and beverage industries. These sectors vary significantly in terms of size, and the role of genetic resources in research and development, and markets (**Table 1**).

In some sectors, such as the botanical medicine, horticulture, and agricultural seed sectors, commercial products are 100% natural products. In others, the contribution of genetic resources might be more indirect. For example, in the pharmaceutical, crop protection, and sometimes the cosmetic industry, genetic resources are screened for active compounds. The final commercial products might be chemically identical to the pure natural product, might start with a natural product that is then chemically modified, or

Table 1 Industries involved in biodiversity prospecting: comparison of size in 1998, and the role of genetic resources and traditional knowledge

Industry	*Size of sector (US$)*	*Average size of top companies (annual sales in US$)*	*Percentage of sales dependent on genetic resources*	*Use of traditional knowledge (importance: scale of 1–5)*[a]
Pharmaceutical	$300 billion	>$10 billion	25–50%	3–4
Crop protection	$0.6–3 billion	$2–3 billion	<10%	3–4
Agricultural seed	$30 billion	$500 million–$1 billion	100%	3–4
Horticulture	$16–19 billion	$200–500 million	100%	4
Botanical medicine	$20 billion	<$200 million	100%	2
Personal care and cosmetic	$75 billion	$5 billion	<10%	3–4
Biotechnology (other than agriculture and healthcare)	$60–120 billion	Great variation	100%	4

[a] 1, Very important, central to research strategy; 2, regularly used to identify, develop and market new products; 3, occasionally used to identify, develop, and market new products; 4, currently rarely used, but many products and the roots of the industry are based in traditional knowledge; 5, never used.

Source: ten Kate K and Laird SA (1999) *The Commercial Use of Biodiversity*. London: Earthscan Publications; Laird SA and ten Kate K (2002) Linking biodiversity prospecting and forest conservation. In: Pagiola S, Bishop J, and Landell-Mills N (eds) *Selling Forest Environmental Services*. London: Earthscan Publications.

might result when the parent structure comes from nature, but the final product is synthesized to a design based on a natural template. Interest in natural products has been cyclical over the last four decades in these industries, but naturally inspired compounds continue to contribute significantly to companies' profits. For example, 11 of the 25 best-selling blockbuster drugs in 1997, representing 42% of industry-wide sales and with a total value of US$17.5 billion, are biologicals, natural products or entities derived from natural products. Of the 87 cancer drugs approved by the US Food and Drug Administration between 1985 and 1995, 62% are of natural origin or are modeled on natural product parents.

Contribution of Traditional Knowledge

Traditional knowledge forms a component of some biodiversity prospecting discovery programs. In most cases, this is acquired through literature and databases, but traditional knowledge is also collected through ethnobotanical research with communities. Scientific and technological advances in recent decades have made the role of traditional knowledge more marginal than it once was, but all of the industries involved in biodiversity prospecting have their roots in this knowledge and many products continue to be marketed based on earlier research on traditional use (**Table 1**). For example, of the approximately 120 pharmaceutical products derived from plants in 1985, 75% were discovered through the study of their traditional medical use. In 1997 a study demonstrated that for the base compound in most of the top 150 plant-derived prescription drugs, commercial use correlates with traditional medical use.

Forest species that have been commercialized include the pharmaceuticals *Cinchona* spp. (which yield quinine) from South America; *Chondodendron tomentosum* (D-tubocurarine) from South America; *Rauvolfia serpentina* (reserpine) from Asia; *Pilocarpus jaborandi* from Brazil (pilocarpine), and *Camptothecen acuminata* (toptotecan) from China. Botanical and herbal medicines from forests with large international markets include *Uncaria* spp. (cat's claw) from Central and South America; *Prunus africana* (pygeum) from Africa; *Panax ginseng* and *P. quinquefolius* (ginseng) from Asia and North America respectively; and *Hydrastis canandensis* (goldenseal) from North America. By far the most commercially successful product to result from biodiversity prospecting in forests in recent decades is the case of the Pacific yew trees *Taxus brevifolia* and *T. baccata*, which yield anticancer compounds. Original collections of *T. brevifolia* were made in 1962 in the Pacific Northwest of the USA. Previously considered a waste tree following logging in the region, numerous groups struggled to develop large-scale sustainable supplies of raw materials once the commercial potential of this species became apparent in the late 1980s. By 2000, the commercial products derived from the Pacific yew tree had annual sales in excess of US$2 billion, making this one of the top selling drugs worldwide.

The Policy Context for Biodiversity Prospecting

In the last 15 years the ways in which biodiversity prospecting is viewed, and the ethical and legal framework in which it takes place, have transformed.

The Convention on Biological Diversity (CBD) sets out provisions according to which states should regulate access to genetic resources and associated traditional knowledge. It balances sovereignty and the authority of national governments to regulate access to their genetic resources with the obligation for them to facilitate access for environmentally sound purposes. Access to genetic resources is to be subject to governments' prior informed consent, on terms mutually agreed by the provider and recipient that promote the fair and equitable sharing of benefits. Similarly, subject to national law, access to the knowledge, innovations and practices of indigenous and local communities requires the prior approval of the holders of that knowledge and the resulting benefits should be shared fairly and equitably with the communities concerned.

The 186 Parties to the CBD are developing guidelines to spell out these provisions and translate them into action. When the Parties to the CBD met in The Hague in April 2002, they adopted the voluntary *Bonn Guidelines on Access and Benefit-Sharing* (http://www.biodiv.org). These provide operational guidance for 'users and providers' of genetic resources and serve as information for governments drafting national laws and for governments, communities, companies, researchers, and others involved in access and benefit-sharing agreements.

Figure 1 The Convention on Biological Diversity and 'Access and Benefit-Sharing.'

In particular, the Convention on Biological Diversity (CBD) (**Figure 1**), which opened for signature at the United Nations Conference on Environment and Development held in Rio de Janeiro in 1992, and the International Treaty on Plant Genetic Resources for Food and Agriculture (IT), finalized in Rome in November 2001, promote new principles of prior informed consent, mutually agreed terms, and benefit-sharing. At the same time, researchers and indigenous peoples' groups are exploring the parameters of what constitutes equitable research relationships, and have articulated appropriate terms for collaboration. A range of indigenous peoples' statements and declarations, researchers' codes of ethics, and institutional policies have been developed in response. All of this combines to create a new context in which biodiversity research and prospecting take place, in order to ensure source countries and local communities control and benefit from commercial use of their resources and knowledge.

Biodiversity Prospecting, Benefit-Sharing, and Conservation

The bulk of benefits for conservation and development resulting from biodiversity prospecting in recent years grew from the research process, and an increasing number of partnerships between companies and source countries. Benefits resulting from these partnerships include: information and research results, participation in the research process, technology transfer, training and capacity-building, and in some cases financial benefits in the form of fees, milestone payments, and royalties.

Benefit-sharing arrangements have improved significantly over the last decade, following entry into force of the CBD, and wider awareness of the issues raised by biodiversity prospecting. Benefits resulting from these partnerships can positively impact a country's capacity to undertake research and develop its own biodiversity, and lead to numerous spin-off benefits for research institutions, universities, local businesses and others. The direct impact of biodiversity prospecting on conservation remains modest in most cases, but can include capacity-building and support for biodiversity science; sustainable economic activities based on the supply of raw materials to industry; and in a few cases direct financial contributions to conservation programs and objectives. For example, in the case of INBio in Costa Rica, biodiversity prospecting is directly linked to building basic biodiversity science and management needs, like national inventories, and a financial contribution – 'conservation overhead' – for conservation areas is built into all commercial agreements.

Biodiversity prospecting can also pose dangers to the environment and can poorly serve local groups' interests. For example, poor collection of samples for research purposes can result in localized threats to populations of sought-after species. Unsustainable bulk collection of raw materials for manufacture can endanger species; this is a common concern for medicinal plants, many of which have landed on CITES Appendices as a result of overharvest in the wild (e.g., *Panax* spp., *Prunus africana*, and *Rauwolifa serpentina*). Inequitable relationships with local communities and source countries can mean that they benefit little from commercialization of resources and knowledge, and have limited or no control over the research and commercialization process.

In order for biodiversity prospecting to maximize its potential to positively benefit local groups and promote conservation, a number of basic steps and strategies are required. These include: effective national 'access and benefit-sharing' measures, growing from a solid national consultation process and a strategy addressing these issues; policies or guidelines for research institutions, protected areas, and in some cases local communities, to guide research collaborations; and a trust fund or guidelines for distribution of financial benefits to ensure equity and the service of national and local priorities.

See also: **Biodiversity**: Endangered Species of Trees; Plant Diversity in Forests. **Medicinal, Food and Aromatic Plants**: Medicinal and Aromatic Plants: Ethnobotany and Conservation Status; Medicinal Plants and Human Health; Tribal Medicine and Medicinal Plants. **Silviculture**: Managing for Tropical Non-timber Forest Products. **Sustainable Forest Management**: Definitions, Good Practices and Certification.

Further Reading

Balick MJ, Elisabetsky E, and Laird SA (1996) *Medicinal Resources of the Tropical Forest: Biodiversity and its Importance for Human Health*. New York: Columbia University Press.

Cox PA (1994) The ethnobotanical approach to drug discovery: strengths and limitations. In: Editor A (ed.) *Ethnobotany and the Search for New Drugs*. New York: John Wiley.

Cragg GM, Newman DJ, and Snader KM (1997) Natural products in drug discovery and development. *Journal of Natural Products* 60(1): 52–60.

Dutfield G (2000) *Intellectual Property Rights, Trade and Biodiversity: Seeds and Plant Varieties*. London: Earthscan Publications.

Farnsworth NR, Akerele O, Bingel AS, Soejarto DD, and Guo Z (1985) Medicinal plants in therapy. *World Health Organization* 63: 965–981.

Glowka L (1998) *A Guide to Designing Legal Frameworks to Determine Access to Genetic Resources*. Environmental Policy and Law Paper no. 34. Bonn: IUCN Environmental Law Centre.

Grifo F and Rosenthal J (eds) (1997) *Biodiversity and Human Health*. Washington, DC: Island Press.

Juma C (1989) *The Gene Hunters: Biotechnology and the Scramble for Seeds*. Princeton, NJ: Princeton University Press.

ten Kate K and Wells A (2001) *Preparing a National Strategy on Access to Genetic Resources and Benefit-Sharing: A Pilot Study*. Kew, UK: Royal Botanic Gardens.

ten Kate K and Laird SA (1999) *The Commercial Use of Biodiversity: Access to Genetic Resources and Benefit-Sharing*. London: Earthscan Publications.

Laird SA (ed.) (2002) *Biodiversity and Traditional Knowledge: Equitable Partnerships in Practice*. London: Earthscan Publications.

Laird SA and ten Kate K (2002) Linking biodiversity prospecting and forest conservation. In: Pagiola S, Bishop J, and Landell-Mills N (eds) *Selling Forest Environmental Services: Market-based Mechanisms for Conservation and Development*. London: Earthscan Publications.

Mugabe J, Barber C, Henne G, Glowka L, and La Vina A (1997) *Access to Genetic Resources: Strategies for Sharing Benefits*. Nairobi: ACTS Press.

Posey DA (1996) *Traditional Resource Rights: International Instruments for Protection and Compensation for Indigenous Peoples and Local Communities*. Gland, Switzerland: IUCN.

Reid WV, Laird SA, Meyer CA, *et al.* (1993) *Biodiversity Prospecting: Using Genetic Resources for Sustainable Development*. Washington, DC: World Resources Institute.

Rosenthal JP (ed.) (1999) *Drug Discovery, Economic Development and Conservation: The International Cooperative Biodiversity Groups*. Special Issue of *Pharmaceutical Biology*, 37.

Edible Products from the Forest

B K Tiwari and S Rani, North-Eastern Hill University, Shillong, India

Introduction

Forests are one of the major forms of natural landscape and are the most important natural resources of the world. The term 'non-wood forest products' (NWFP) has emerged as an umbrella expression for the vast array of both plant and animal resources other than wood derived from forests or forest tree species. The forests are important not only for their economic utility but they also influence the social and economic life of humankind. Forests are an important source of food; in fact people were dependent mainly on forest collected food when they were wanderers and the concept of cultivating food came in only after people started living in settlements. The cultivation of food items made life much easier for humans, who not only started cultivating food but also cultivated the selected ones they liked more. Thereby the number of plants that were included in the cultivated list was much less than the actual number of edible plants found in the wild. In the modern world people seem to have forgotten that all the edible things being used by them now are actually derivatives of those that used to grow in the wild once upon a time, and they also seem to be unaware of the fact that many such edible plants still exist in the wild which may be even more valuable and suitable nutritionally than the ones that are being cultivated. However, with increasing awareness of the natural environment people are becoming conscious and many have started exploring the wilds to find more plants that are edible. Eating wild foods has many nutritional benefits and can add another dimension to our diet as well as to our relationship to the natural world. Wild plants are nature's gifts to us and have high concentrations of vitamins, nutrients, and calories to make us strong and healthy. Edible forest products (EFPs) make a particularly important contribution to the nutrition of the tribal and rural poor, who more than others are likely to be dependent on trees for a significant part of their income and food supply. Forest-dwelling hunters and gatherers, the world's 300 million shifting cultivators, and millions of small-holders and landless households living near forests and in the savanna depend on forests for a significant part of their food. Forest foods can offer vital insurance against famine during times of seasonal food shortages or emergencies such as droughts, floods, and wars. It is very common for rural people to depend on forest foods between harvests, i.e., when harvested stocks have been consumed but the next crops are yet to mature. Women in particular count on these resources for supplementary nutrition, emergency foods, and many other important products they need to ensure the nutritional well-being of their families. Forest foods are traditionally used to supplement the staple diet, providing vitamins, minerals, and proteins that are lacking in starch-based cultivated crop food. In the subsequent part of this article various edible products from forests will be described. A few examples have been cited in each case and some data about edible forest products of India have been given in the tables. It was difficult to draw a line between 'wild' and 'forest' because at times these two terms have been used interchangeably. The groups of edible forest products included in this article and issues discussed are indicative only. The names of edible plants and animals listed in the tables or mentioned in the text are by way of an extended example.

Edible Products from the Forests

Any forest produce that can be consumed safely is classified as edible produce of the forest. In recent times wild edible products have gained considerable attention due to their ability to supplement the needs of the changing society. These wild edible products can be classified into various groups and subgroups:

- foods items (fruits and berries, vegetables, roots, rhizomes, bulbs and tubers, nuts, seeds and grains, resins, sap, gums, forest edibles of animal origin, honey, etc.)
- spices and condiments
- beverages
- health foods
- mushrooms
- medicinal plants
- edible oils.

Food Items

Fruits and berries The food items collected most frequently from the wild are fruits and vegetables. Fruits are undoubtedly humanity's oldest food. Before the start of organized agriculture, prehistoric nomads lived on wild game, wild fruits, and berries. When humans took to organized agriculture, they started cultivating grain crops, but surely they grew some fruits in the backyard too. Instead of the many varieties of fruits grown by humans there are still many others that have not yet been domesticated and are still found in the wild. These are the ones that are collected mostly by the forest-dwellers and rural people to supplement their diets, and they are definitely rich sources of many minerals and vitamins. Nutritionally, wild fruits are as rich in vitamins and minerals as cultivated fruits, lower in sugar and calorie content, and free of wax coating, chemical sprays, or artificial ripening agents. And they nearly always taste better than their cultivated counterparts. For example the fruit of baobab (*Adansonia digitata*) far surpasses the orange's famous vitamin C content of 57 mg per 100 g of fruit at 360 mg per 100 g, and one variety of jujube (*Zizyphus jujuba*) reaches levels as high as 1000 mg per 100 g.

In northeast India, which has a rich cover of forests, the locals are still very intimately related to forests and collect enormous amounts of edible fruits from the wild, the knowledge of which has been passed down the generations. For example fruits of wild trees like *Melodinus monogynus*, *Zizyphus mauritiana*, *Phyllanthus emblica*, *Myrica esculenta*, *Elaeagnus conforta*, *Emblica officinalis*, *Elaeagnus umbellate*, *Rubus ellipticus*, *R. niveus*, *R. moluccanus*, etc. are collected and consumed in large quantities. *Zizyphus mauritiana*, *Z. oenoplia*, prickly-pear (*Opuntia dillenii*), Cuddapah almond (*Buchanania lanzan*), Indian black plum (*Syzygium cumini*), Ceylon ironwood (*Manilkara hexandra*), wood apple (*Limonia acidissima*), Indian palm (*Borassus flabellifer*), Manila tamarind (*Pithecellobium dulce*), etc. are some of the common wild fruits used by the ethnic people of

Tamil Nadu in India. In Blue Creek, Belize the fruits of *Orbigyna cohune, Astrocayum mexicanum*, and *Bactris major* are collected from the tropical rainforests and consumed by the local people. Peaches, figs, mulberries, wine berries, chestnuts, ginkgo nuts, and chanterelles are the common wild edibles collected by people in Baltimore. In Ireland wild fruits like pine, hazel, strawberries, blackberries, cranberries, and rosehips are collected. In rural areas of Ethiopia, the most common wild plant fruits consumed are fruits from *Balanites aegyptiaca*, *Ficus* spp., *Carissa edulis*, and *Rosa abyssinica*. The list of wild fruits consumed by various communities can be enormous. The above examples are just indicative. Some more are listed in **Table 1**.

Vegetables Vegetables are also an important part of the diet and supplement it with various types of vitamins and minerals. They mostly comprise of the leafy parts of a plant, even though flowers and fruits are also included many times under this list. The vegetables that are collected from the wild include the leaves of trees and shrubs, leaves and twigs of herbs, or even the entire plant. The commonly used wild vegetables in northeastern India are *Amaranthus companulatus*, *Bauhinia variegate*, *Chenopodium album*, *Enhydra fluctuans*, *Ipomea repants*, *Elaeocarpus floribundus*, *Swertia chirayita*, *Parkia roxburghii* etc. *Allium acuminatum*, *Apocynum cannabium*, *Lewisia rediviva*, *Mentha arvensis*, *Scirpus acutus*, *Clintonia uniflora*, *Typha latifolia*, *Empetrum nigrum*, *Potentilla pacifica*, *Sedum divergens*, etc. are some of the herbaceous plants used by people of western Washington State, USA. Shrubs and trees used by them include *Berberis* spp., *Ribes* spp., *Rubus* spp., *Malus fusca*, *Mahonia* spp., *Prunus emarginata*, etc. *Myrica gale* and Sweet fern (*Comptonia peregrine*) are used as vegetables by people of Canada. In Belize *Sabal mexicana* and *Spondias mombin* are plants found growing abundantly in the rainforests,

Table 1 Names of some frequently collected edible fruit yielding wild plants of India

Sl number	*Wild edible plants*	*Family*	*Parts used*
1	*Polygonum chinense*	Polyganaceae	Ripe fruits
2	*Solanum surattense*	Solanaceae	Unripe fruits
3	*Ficus glomerata*	Moraceae	Fruits
4	*Ficus religiosa*	Moraceae	Fruits
5	*Ficus bengalhensis*	Moraceae	Fruits
6	*Ficus palmata*	Moraceae	Fruits
7	*Gnetum gnemon*	Gnetaceae	Fruits
8	*Grewia hirsute*	Tiliaceae	Fruits
9	*Phyllanthus acidus*	Euphorbiaceae	Fruits
10	*Calamus erectus*	Arecaceae	Fruits
11	*Solanum indicum*	Solanaceae	Fruits
12	*Solanum torvum*	Solanaceae	Fruits
13	*Solanum nigrum*	Solanaceae	Ripe fruits
14	*Berberis aristrata*	Berberidaceae	Fruits
15	*Cordia dichotoma*	Ehretiaceae	Ripe fruits
16	*Pyrus pashia*	Rosaceae	Fruits
17	*Madhuca butyraceoides*	Sapotaceae	Fruits yield butter
18	*Zanthoxylum aceanthopodium*	Rutaceae	Fruits
19	*Dillenia pentygyna*	Dilleniaceae	Fruits
20	*Bauhinia purpurea*	Caesalpinaceae	Fruits
21	*Grewia hirsute*	Tiliaceae	Fruits
22	*Mangifera sylvatica*	Anacardiaceae	Unripe fruits
23	*Prunus nepalensis*	Rosaceae	Fleshy fruit
24	*Myrica esculenta*	Myristaceae	Fruits
25	*Emblica officinalis*	Euphorbiaceae	Fruits
26	*Elaeagnus umbellata*	Elaeagnaceae	Fruits
27	*Elaeagnus pyriformis*	Elaeagnaceae	Fruits
28	*Elaeagnus parviflora*	Elaeagnaceae	Fruits
29	*Rosa macrophylla*	Rosaceae	Fruits
30	*Rosa moschata*	Rosaceae	Fruits
31	*Rubus elliptcus*	Rosaceae	Fruits
32	*Rubus niveus*	Rosaceae	Fruits
33	*Prunus armeniaca*	Rosaceae	Fruits
34	*Prunus communis*	Rosaceae	Fruits
35	*Prunus persica*	Rosaceae	Fruits
36	*Holoptelea integrifolia*	Ulmaceae	Fruits
37	*Madhuca longifolia*	Sapotaceae	Fruits

and their shoots and leaves are consumed raw as well as in cooked form. Wild greens (*Portulaca oleracea*), Capper bush (*Capparis zeylanica*), wild bittergourd (*Mimordica dioica*), poison berry (*Solanum indicum*), prickly amarnath (*Amaranthes spinosa*), Indian fig (*Ficus glomerata*), potato yam (*Dioscorea pentaphylla*), wild date palm (*Phoenix sylvestris*), Bermuda buttercup (*Oxalis corniculata*), heart's pea (*Cardiospermum helicacabum*), prickly leaved solanum (*Solanum trilobatum*), adamant creeper (*Cissus quadrangularis*), and mountain ebony (*Bauhinia tomentosa*) are some of the wild vegetables used by the tribals of South India (**Tables 2** and **3**).

Roots, rhizomes, bulbs, and tubers These are the underground parts, which are usually organs of perennation for the plants. Rhizomes are underground stems which grow beneath the surface of soil; they are frequently fleshy and serve as organs of food storage. Sometimes the rhizomes are condensed into solid swollen forms which are then known as corms. The tubers are also underground parts, which may either be modified roots or stems. They serve both as an organ of vegetative reproduction and storage organ. Rhizomes and tubers have high contents of carbohydrates, proteins, and minerals and are a very good source of food for humans. They have been used by humans as a source of energy to meet their dietary requirements since times immemorial. Tubers and rhizomes still constitute a significant part of human diet in many parts of the world.

Roots of knotweed (*Polygonum* sp.) and wild ginger (*Asarum canadensis*) are used by the people of Mound City, Ohio, USA. *Boerhavia chinensis*, *Pueraria tuberosa*, *Mauera oblongifolia*, *Dioscorea tomentosa*, *D. oppositifolia*, and *Cyanotis tuberosa*

Table 2 Names of some frequently collected edible vegetative parts yielding wild plants of India

Sl number	*Wild edible plants*	*Family*	*Parts used*
1	*Cassia tora*	Cesalpinaceae	Leaves and pods
2	*Polygonum chinese*	Polyganaceae	Leaves
3	*Solanum denticulatum*	Solanaceae	Leaves cooked
4	*Amaranthus spinosus*	Amaranthaceae	Young shoot
5	*Bambusa* spp.	Poaceae	Young shoot
6	*Cycas pectinata*	Cycadales	Young leaves
7	*Euphorbia hirta*	Euphorbiaceae	Young leaves
8	*Hygrophila salicifolia*	Acanthaceae	Leaves
9	*Oxalis corniculata*	Oxalidaceae	Leaves
10	*Polygonum* spp.	Polygonaceae	Shoot
11	*Phyllanthus acidus*	Euphorbiaceae	Leaves
12	*Allium tuberosum*	Liliaceae	Whole plant
13	*Amaranthus spinosus*	Amaranthaceae	Shoot
14	*Amaranthus viridis*	Amaranthaceae	Shoot
15	*Boerhavia diffusa*	Nyctaginaceae	Leaf and shoot
16	*Calamus erectus*	Poaceae	Shoot
17	*Centella asiatica*	Apiaceae	Whole plant
18	*Gnetum gnemone*	Gnetales	Leaf
19	*Ipomea aquatica*	Convulvulaceae	Leaf and shoot
20	*Oxalis corniculata*	Oxalidaceae	Whole plant
21	*Solanum media*	Solanaceae	Leaf and shoot
22	*Cassia floribunda*	Caesalpinaceae	Tender shoots and pods
23	*Cassia tora*	Caesalpinaceae	Tender leaves and pods
24	*Euphorbia royleana*	Euphorbiaceae	Pith of young shoots
25	*Polygonum orientale*	Polygonaceae	Leaves
26	*Bambusa tulda*	Poaceae	Young shoots
27	*Begonia palmata*	Begoniaceae	Young parts
28	*Ficus cunia*	Moraceae	Inner bark of stem
29	*Bauhinia vahlii*	Caesalpinaceae	Tender pods and stem
30	*Bauhinia malabarica*	Caesalpinaceae	Tender shoots and leaves
31	*Ficus virens*	Moraceae	Young shoots
32		Convulvulaceae	Whole plant
33	*Allium ampeloprasum*	Liliaceae	Young leafy shoots
34	*Alternanthera sessilis*	Amaranthaceae	Young leafy shoots
35	*Alternanthera philoxeroides*	Amaranthaceae	Whole plant
36	*Cassia sophera*	Caesalpinaceae	Stalks
37	*Cassia occidentalis*	Caesalpinaceae	Young leaves
38	*Cassia obtusifolia*	Caesalpinaceae	Young leaves
39	*Amaranthus spinosus*	Amaranthaceae	Whole plant

Table 3 Names of some frequently collected edible floral part yielding wild plants of India

Sl number	Wild edible plants	Family	Parts used
1	*Bauhinia acuminata*	Caesalpinaceae	Flowers
2	*Ipomea alba*	Convulvulaceae	Calyx
3	*Rhododendron arboretum*	Ericaceae	Flowers
4	*Bauhinia purpurea*	Leguminosaceae	Petiole
5	*Artemisia capillaris*	Asteraceae	Flower
6	*Bauhinia variegata*	Caesalpinaceae	Inflorescence
7	*Cassia fistula*	Caesalpinaceae	Flowers
8	*Amomum dealbatum*	Zingerabaceae	Petiole
9	*Musa glauca*	Musaceae	Flower buds
10	*Madhuca longifolia*	Sapotaceae	Spike

Table 4 Names of some frequently collected edible root, rhizome, bulb, and tuber yielding wild plants of India

Sl number	Wild edible plants	Family	Parts used
1	*Allium bakeri*	Liliaceae	Bulb
2	*Allium chinensis*	Liliaceae	Bulb
3	*Allium platyspathum*	Liliaceae	Bulb
4	*Asparagus racemosus*	Liliaceae	Root
5	*Habenaria grandifloriformis*	Orchidaceae	Rhizome
6	*Bombax ceiba*	Bombacaceae	Tuberous root
7	*Boerhavia chinensis*	Nyctaginaceae	Root powder
8	*Curculigo orchiodes*	Amaryllidaceae	Root
9	*Dioscorea oppositifolia*	Dioscoreaceae	Tuber
10	*Dioscorea tomentosa*	Dioscoreaceae	Tuber
11	*Dioscorea hamiltonii*	Dioscoreaceae	Rhizome
12	*Dioscorea bulbifera*	Dioscoreaceae	Tuber
13	*Dioscorea wallichii*	Dioscoreaceae	Rhizome
14	*Curcuma longa*	Zingerabaceae	Rhizome
15	*Purearia tuberosa*	Papilionaceae	Root

are some of the wild tubers used by tribals groups in India, e.g., Chenchus, Sugalis, and Yerukalsa of Andhra Pradesh. The roots of cattails (*Typha latifolia*), burdocks (*Arctium lappa*), and arrowheads (*Sagitaria sagittifolia*) are used frequently by people in Ireland. Cattails, thistle (*Cirsium* spp.) and *Bordiaea* are used by people of Pope Valley, California. *Ullucus tuberosus*, *Tropaeolum tuberosum*, and *Oxalis tuberose* are common tubers collected in Peru, Ecuador, and Bolivia (**Table 4**).

Nuts, seeds, and grains Nut is the popular name for many kinds of dry, edible seeds or fruits that grow in a woody shell. The word nut can refer to both the shell and the nutmeat, or kernel, inside or to the kernel alone. Botanists define a nut as a dry, one-seed fruit surrounded by a hard shell that does not open on its own. Prehistoric people probably ate nuts as a regular part of their diet. Some nutritionists believe that, because of food shortages, nuts will again become a widely used source of protein. Seed is the specialized part of a plant that produces a new plant and has a supply of stored food. Seeds serve as a major source of food for millions of people throughout the world. Nuts and seeds are good sources of fiber, protein, minerals such as iron, zinc, copper, magnesium, potassium, and calcium, vitamins such as vitamin E and phytosterols, and a variety of phytochemicals. Grains are the husked parts of inflorescences and are basically seeds of the Poaceae family. Wild grains, seeds, and kernels provide significant amounts of calories, protein, and oil. Their calorific value is frequently greater than that of the cultivated varieties. The results of analysis of the grass grains are impressive with a range of 310–391 kcals per 100 g which compares favorably with *Sorghum* sp. and maize (*Zea mays*) at 355 and 363 kcals per 100 g respectively. Names of some forest plants yielding edible kernels and seeds commonly collected in India are given in **Table 5**.

Forest edibles of animal origin Our ancestors were very much dependent upon wild animals for meeting their daily dietary requirements of protein, vitamins, and many minerals. These foods were not only capable of meeting their nutritional requirements but also gave them variety and taste. The various groups of animals found in the wild are not only eaten for their taste or nutritional value, but they have been

Table 5 Names of some frequently collected edible seeds and kernel yielding wild plants of India

Sl number	*Wild edible plants*	*Family*	*Parts used*
1	*Cycas circinalis*	Cycadales	Seeds
2	*Cycas pectinata*	Cycadales	Seeds
3	*Cycas revoluta*	Cycadales	Seeds
4	*Calamus erectus*	Arecaceae	Seeds
5	*Centella asiatica*	Apiaceae	Seeds
6	*Holoptelea integrifolia*	Ulmaceae	Seeds
7	*Solanum surattense*	Solanaceae	Seeds
8	*Bauhinia purpurea*	Caesalpinaceae	Seeds
9	*Bauhinia racemosa*	Caesalpinaceae	Seeds
10	*Bauhinia malabarica*	Caesalpinaceae	Seeds
11	*Bauhinia vahlii*	Caesalpinaceae	Seeds
12	*Cassia tora*	Caesalpinaceae	Seeds
13	*Cassia occidentalis*	Caesalpinaceae	Seeds
14	*Cassia obtusifolia*	Caesalpinaceae	Seeds
15	*Nymphaea stellata*	Nymphaeaceae	Seeds
16	*Vitex negundo*	Verbanaceae	Seeds
17	*Ocimum americanum*	Lamiaceae	Seeds
18	*Holoptelea integrifolia*	Ulmaceae	Seeds
19	*Prunus armeniaca*	Rosaceae	Kernel
20	*Juglans regia*	Rosaceae	Kernel
21	*Madhuca longifolia*	Sapoteacea	Seeds
22	*Nymphaea nouchali*	Nymphaeaceae	Seeds
23	*Buchanania axillaris*	Anacardiaceae	Seeds

Table 6 Names of some frequently collected edible wild insects of few selected countries of the world

Sl number	*Country in which used*	*Insects*
1	Indonesia (Bali)	Compost beetle larvae, palm weevil larvae, dragonfly, damselfly adults
2	Nigeria	Westwood larva, palm weevil larvae, termites, crickets, grasshoppers, caterpillars, compost beetle larvae, wasp larvae
3	Japan	Aquatic insect larvae, cicadas
4	Australia	Witchety grub, honeypot ants, bogong moths, beetle grubs, *Oecophylla* ant
5	Algeria	Desert locusts
6	China	Cicada nymphs, Wasp larvae/pupae, Ants, Locusts, Dragonflies, Scorpions, Diving beetles, Giant water bugs
7	Philippines	June beetles, grasshoppers, ants, mole crickets, water beetles, katydids, locusts
8	Ecuador	Dragonfly larvae, Cyclocephala beetles, Cicadas
9	Mexico	Cerambucid larvae, lemon ants, ants
10	Papua New Guinea	Grasshoppers, *Atta cephalotes*
11	Thailand	Walking sticks, leaf insects, *Apies florae*, *Apies dorsata*, *Apies cerana*, *Apies mellifera*
12	USA	Termite (*Macrotermes subhyanlinus*), caterpillar (*Usata terpsichore*), *Rhynchophorous palmarum*

found to be highly important medicinally too. Therefore, a wide range of insects, birds, and animals is collected from the forests along with the plants. The commonly collected mollusks in the UK are common mussel (*Mytilus edulis*), flat oyster (*Ostrea edulis*), common cockle (*Cerastoderma edule*), quahog (*Mercenaria mercenaria*), common razorshell (*Ensis ensis*), sand gaper (*Mya arenaria*). Hunting and gathering of animals from the forests is very common across the world, for example, in Kenya, Tanzania, Zimbabwe, Zambia, Malawi, Mozambique, and Botswana thousands of species of insects, birds, mammals, reptiles, mollusks, and amphibians provide a cheap source of protein and livelihood to poor communities that are struggling to survive. Bushmeat (mostly the meat of wild mammals) is sold in departmental stores and served in hotels and restaurants of many African countries. Similarly the Naga and Khasi communities of India also hunt and gather a wide variety of animals for food which include bat, barking deer (*Muntiacus muntjak*), porcupine (*Hystrix hodgsoni*), wild boar (*Sus scrafa cristatus*), mithun (*Bos frontalis*), unio, and fowl, frogs, snakes, etc. (**Table 6**).

Spices and Condiments

The term spices and condiments applies to 'such natural plant or vegetable products or mixtures thereof, in whole or ground form, as are used for imparting flavor, aroma and piquancy to and for seasoning of foods.' Spices may comprise different plant components or parts such as barks, berries, buds, bulbs, floral parts, fruits, kernels, leaves, rhizomes, latex, exudates, roots, and seeds. Spices are well-known appetizers and are considered essential in culinary art all over the world. They add tang and flavor to otherwise insipid foods. Some of them also possess antioxidant properties, while others are used as preservatives in some foods, e.g., pickles and chutneys. Some spices were used for preserving food like meat for a year or more without refrigeration as they contain chemical substances that inhibit the growth of microbes like bacteria. There are many spices and condiments that are collected from forests. Some wild plants used in India as spices are: *Acorus calamus*, *Thymus linearis*, *T. serphyllum*, *Eurya acuminata*, *Garcinia indica*, *Piper longum*, *Cinnamomum* sp., *Piper guineense*.

Beverages

Apart from the most popular beverages, viz. tea and coffee, there are many wild plants that are used as beverages by traditional societies. Leaves, twigs, or fruits of several wild plants are used for preparing beverages. For instance spearmint (*Mentha spicata*), sassafras, mitten tree, ague tree, or tea tree (*Sassafras albidum*), yarrow (*Achillea millefolium*), sweet fern, Labrador tea (*Ledum groendicum*), sagebrush (*Artimesia* spp.), and Mormon tea (*Ephedra* spp.) are widely used in eastern and western USA as beverages. Others include Coyote mint (*Monardella adoratissima*) and clover (*Trifolium* spp.).

Rubus allegheniensis, Fragaria virginiana, Vitis sp., etc. are used to prepare both tea as well as cold drinks, in Mound City, Ohio. The Saskatoon (*Amelanchiar alnifolia*) and pin cherry (*Prunus pennsylvanica*) is used by indigenous peoples of North America as soups and tea. Berries of sumac (*Rhus* spp.) are also used as tea. *Cassia occidentalis* and *C. tora* seeds are used as substitute for coffee in Africa and America. In India, *Albizia julibrissia*, *Coffea khasiana*, *Camelia kissi*, *Eschscholtzia cristata*, *E. polystachya*, *Taxus baccata* (bark and leaves), and *Cassia auriculata* are used as substitutes for tea and coffee, while berries like *Rubus* spp., *Fragaria* spp., and *Hemidesmus indicus* are used in preparation of cold drinks. *Madhuca indica*, *M. longifolia*, and some members of palm family are used in preparation of alcoholic beverages in India. The floral parts and leaves of *Cannabis sativa* is used for preparation of intoxicating drinks and stimulants.

Mushrooms

Mushrooms are yet another very frequently and commonly used products of forests. While most species of mushrooms are almost freely available to forest-dwellers and help them survive or supplement their diets, there are some wild mushrooms, viz., *Morchella esculenta*, which are amongst the most expensive edibles on earth. Indigenous collectors of the northwestern Himalayas sell these to middlemen at rates as high as US$100 kg^{-1}, and they pass it on to quality hotels and pharmaceuticals companies earning a profit of 35–40%.

Apart from adding variety to our diets mushrooms are also an important source of proteins and minerals. Hundreds of types of mushrooms are collected from the wild. While most of them are collected by the forest and forest fringe dwellers for their subsistence and as a food supplement, a small quantity is traded in local as well as regional and international markets.

Medicinal Plants

Since the beginning of civilization, people have used plants as medicine. It came into being when the earliest humans observed the animals mostly the apes and monkeys eating certain plants often to satisfy their hunger and at other times to heal their wounds and to alleviate suffering. This observation and the analysis of such observations probably led them to use plants for maintenance of life and alleviation of diseases. The earliest recorded uses have been described in the Vedic literature, roughly around 4500 BC. This traditional curing system is still being followed in India. In the recent years this practice has been rejuvenated and is being widely used over the other systems. A detailed account of medicinal plants can be found elsewhere in this Encyclopedia (*see* **Medicinal, Food and Aromatic Plants**: Medicinal Plants and Human Health; Tribal Medicine and Medicinal Plants).

Health Foods and Dietary Supplements

A large number of forest products of both plants and animal origin are believed to be beneficial in maintaining good health, as aphrodisiacs, and in increasing resistance to stress. They are probably the highest valued edible forest products on the market today. For example a digger of wild ginseng (*Panax quinquefolium*) in the USA can receive more than US$1000 kg^{-1} of dried root. There is a huge market for ginseng in Asia particularly in Taiwan and China. In 1997, the total export of wild-harvested ginseng from the USA was 191 500 kg worth more than US$32.4 million. Retail sale of *Ginkgo biloba*, another plant of this category, totaled US$90.2 million in 1997, while sales of *Hypericum perforatum* and *Podophyllum peltatum* plants growing in the forests of the USA yielding dietary supplements exceeded US$47 million and US$1.5 million respectively.

Edible Oils

Apart from the traditional uses of edible wild products there are some other ways in which the plants are used. In Brazil, people collect kernels from babassu plants (*Orbygnya phalerata*) which are a very rich source of edible oil, resembling coconut oil to some extent. Black walnuts are also a source of oil for the people of Brazil. In India kernels or seeds of *Prunus armeniaca*, *Juglans regia*, *Prinsepia utilis*, *Madhuca longifolia*, *Ventilago maderaspatana*, and *Fagopyrum esculentum* are used to extract edible oils and fats.

Social and Economic Issues

Wild edibles provide food security and livelihood to millions of rural poor people living around forests, and thus it plays an important role in the socio-economics of these communities. This is particularly important in Asia, tropical Africa, and South America. Forests also offer a great variety of food products of potential market value. The indigenous peoples of Amazon's State, Venezuela, have been selling their own native wild fruits. All indigenous peoples within Amazon's State have the right to hunt, fish, and collect wild products for their personal consumption; thus they have the right to continue their traditional lifestyles. Edible wild plant products are collected mainly for household consumption and for sale in the local market. Wild fruits and fish may be sold legally, but the sale of game animals, birds, and ornamental fish is strictly prohibited by law. The indigenous vendors and gatherers of forest edibles do not put up stalls, but instead sell along the pavement of weekly traditional markets. A similar situation is found in rural northeast India. In the Sudan, however, the perception of the economic importance of wild foods appears to be gender-specific. For women, these foods are an important source of income and with the small amounts of cash that they earn; they buy important non-food items such as soap. One reason that may lead outsiders to believe that there is not much trade in wild foods is that these foods are not usually sold in a prominent place in the market but on the periphery with a significant amount of barter trade being undertaken at village level. In Cameroon, hunting, trapping, and fishing from the wild accounts for an average 27% of annual income, while income from other forest products totaled some 30% of yearly earnings. Earnings from bushmeat are quite high in Peru; a hare hunter can earn the equivalent of US$1350 a month, compared with a laborer's typical wage of US$100 a month. People of Papua New Guinea's swamplands have virtually no saleable resources apart from the crocodiles that abound in these densely vegetated areas. A single skin of a mature crocodile can fetch around US$150. Other notable wildlife products obtained in various parts of the world and traded for high prices include snake venom and frogs' legs. The giant wild snail (*Achatina achatina*) is traded profitably in Côte d'Ivoire.

Cultural, Equity, and Gender Issues

In southern Sudan there is a social stigma attached with wild food items. Generally, male guests will be given sorghum because it is considered more prestigious while wild foods, and any other less prestigious foods are eaten by the women and the children of the household in a separate place. Allocating the best food to a guest is common to most cultures, but this does not mean that other household foods are nutritionally inferior or that they are not liked. There are some wild foods that have a high prestige value, such as the wild grass grains and rice which are particularly favored and will be given to the most important guests at ceremonies. Also, some wild foods are used to make relishes that give flavor and texture to other foods and are acceptable for male guests, e.g., fruits of *Tamarindus indica*, *Nauclea latifolia*, *Portulaca oleracea*, and *Gynandropis gynandra*. Female guests however tend to eat whatever the rest of the household eats. The collection of wild foods is mainly carried out by women and children. It does not necessarily involve expending a great deal of extra energy. Many foods are collected along the wayside whilst going about other chores, while wild leafy greens can be found growing (and are encouraged to grow) in the cultivated areas around the home. Collection of wild foods at a greater distance from the homestead will be undertaken by women who go in groups over a period of days, leaving their children in the care of a relative. These trips can become something of a social event for women, particularly for those who live on the more remote homesteads and have little time for visiting friends and relatives. Gathering some wild foods can be labor intensive, e.g., digging for wild tubers and for grain from termite stores, but people may choose to collect these foods even in normal years for the sake of dietary variety. Wild plant production only involves labor at the time of harvesting and may fit in well with other activities. In the case of grass grains, for instance, which start to ripen at a time when agricultural work is at a minimum, prior to the main crop harvest, there is little conflict of labor priorities. The collection of wild food may become burdensome when these foods become the major part of the diet, e.g., during periods of food scarcity and famine, especially when the foods need to be foraged for at great distances from the home. Whilst out on their errands children often forage for these foods. During this time they learn about the different wild foods and their availability which can stand them in good stead during periods of food deficit. Also, as growing children need food regularly throughout the day, wild foods can provide snacks between their main meals.

In Ethiopia also wild foods are often considered to be of low status, and their consumption is regarded as a source of shame. In normal times only children, youngsters, and the poorest families regularly collect and consume wild food. In Kayissa Kebele, wild food plant species are not consumed by the majority of the population except when there is a serious shortage of food affecting all strata of the population from the poorest to the richest. But for the poorest, collection and consumption of wild food may make up an important portion of their daily activity and dietary intake. Ethiopians generally are constrained to the consumption of the commonly cultivated crops and neglect wild plants like *Amaranthus* and *Solanium khasianum*. Strong traditions, beliefs, and religious taboos still obstruct people's willingness to domesticate and cultivate wild-food plants. In the southern part of Ethiopia, where there are many different tribes still living with their indigenous beliefs and traditions, there are fewer religious and external constraints than in other parts of the country. In these areas the daily diet of most people still comprises an element of wild food, both animals and plants, during certain periods of the year. Here mostly children collect and consume the fruits of wild plants. Other wild food and 'famine food' plants are collected by children and women and prepared by the latter. Women frequently collect wild food when they are on their way to fetch water, to collect firewood, or to the market, and when walking home from their fields.

Conservation Needs

As the area of the earth's surface under forest is shrinking at an alarming rate, so also is the availability of edible forest products. The natural forests of the tropics are the most important source of such products, both in terms of quantity and also in numbers of different edible species. Ironically these are the forests that are also facing the maximum anthropogenic pressures. Millions of rural poor look on the edible forest products as a source of food, researchers and scientists look on them as a possible source of germplasm for breeding, and the urbanites and rich often use them as a recreational food. Probably, it is not an exaggeration to say that modern humans are as dependent on the forest for food and healthcare as were the primitive humans. Also, the quantity and variety of edibles extracted from forests today far exceeds those extracted during remote past when all people lived in forests. For instance, in the past the collection of bushmeat from the African savanna would have been ecologically sustainable, but now it has far exceeded the carrying capacity of these ecosystems. Studies have revealed that at present trade in bushmeat is one of the main causes of falling animal populations in much of Africa, but bushmeat cannot be done away with as it provides a much-needed source of protein to the rural poor who cannot afford to buy farm-produced meat. However, conservation interests and food security interests must work together to balance food needs with long-term wildlife management.

Any strategy for sustainable management of EFPs will have to take a multilevel approach. It must cover documentation and identification of lesser-known EFPs, research on regeneration so as to decide about levels of extraction, improvement of methods of collection and harvest, ways to minimize loss during harvest, storage, and processing, research on substitution of products that come from endangered species, domestication and cultivation of EFP species, market research, resource accounting, education and awareness about conservation and management of EFPs and *in vitro* and *in vivo* conservation using modern biotechnological tools. Involvement of various stakeholders in formulating policies and enacting legislations favorable for EFPs conservation may also be desirable for evolving effective conservation strategies.

Conclusion

Forests are the source of huge quantity and enormous variety of edible products which are used by almost all sections of society through out the world. They provide subsistence to millions of rural poor and forest-dwellers as well as nutritious delicacies to the urban rich. They are a repository of germplasm of many food crops and farm products and a large number of them have potential for domestication and cultivation on commercial basis. Edible NWFPs received notable attention at the United Nations Conference on Environment and Development (UNCED) in Rio in 1992 and thereafter forest managers of several countries have recognized the importance to forest edibles in management of forests. However, there is conspicuous lack of understanding among resource managers and planners on sustainable harvest, value addition, equitable sharing of benefits, marketing, and conservation of these resources.

Further Reading

Chamberlain J, Bush R, and Hammett AL (1998) Non-timber forest products. *Forest Products Journal* 48(10): 9–19.

Cunningham AB (1997) Review of Ethnobotanical literature from Eastern and Southern Africa. *Bulletin African Ethnobotany Network, Bulletin* 1: 23–87.

Cunningham AB (2003) *Applied Ethnobotany: People, Wild Plant Use and Conservation*. London, UK: Earthscan Publications Ltd.

FAO (2003) *Non-Wood Forest Products for Rural Income and Sustainable Forestry*. Rome, Italy: Food and Agriculture Organization.

Jong W de and Campbell B (eds) (2001) *The Role of Non-Timber Forest Products in Socio-Economic Development*. Wallingford, UK: CABI Publishing.

Maheswari JK (2000) *Ethnobiology and Medicinal Plants of Indian Subcontinent*. Jodhpur, India: Scientific Publishers.

Oldfield M (1984) *The Value of Conserving Genetic Resources*. Washington, DC: US Department of Interior.

Shiva MP and Mathur RB (1996) *Management of Minor Forest Produce for Sustainability*. New Delhi, India: Oxford University Press.

Singh U, Wadhwani AM, and Johri BM (1996) *Dictionary of Economic Plants in India*. Delhi, India: Everest Press.

Sinha KR and Sinha S (2001) *Ethnobiology: Role of Indigenous and Ethnic Societies in Biodiversity Conservation, Human Health Protection and Sustainable Development*. Jaipur, India: Surabhi Publications.

MENSURATION

Contents

Forest Measurements

J P Skovsgaard, Royal Veterinary and Agricultural University, Forest & Landscape Denmark, Copenhagen, Denmark

Introduction

The field of forest measurements is concerned with measurement, sampling, analyses, and prediction of properties and characteristics of the forest, including trees as well as other components of the forest ecosystem. In general, the main objective of forest measurement activities is to provide quantitative and qualitative data for forest management, policy-making or research. Forest measurements thus contribute substantially to the basis of forest-related human activities. Often, data acquisition is carried out as part of a forest inventory, at estate, regional, or national level, or in scientific field experiments. Several forest measurement procedures can be used outside of the forest, for example in inventories of trees in urban streets and parks or in the landscape.

Forest Measurements

Historically, science-based forest measurement procedures were developed mainly for aboveground parts of the trees and with the main objective of quantifying the wood resource and its growth potential. Including the planning, performance, and analyses of measurements of tree and stand attributes, this is usually referred to as the discipline of dendrometry (i.e., tree measurement), forest mensuration, or forest biometrics.

In the classical sense, measurements tend to be at the macroscopic level and are often carried out in the field. Exceptions may be, for example, extracted wood cores that are taken to the laboratory for growth analysis, and the use of satellite, aerial, or other photographs for resource assessment. Carried out as part of a forest inventory and combined with land survey data, forest measurements provide information on individual tree properties as well as stand characteristics and overall forest structure for use in subsequent analyses and decision-making.

The Contemporary Context

Due to an increasing diversity of the forest policy agenda and of forest management objectives the field of forest measurements is developing to provide data for a broader range of forest and site characteristics and to adjust and refine measurement procedures accordingly. This includes, for example, assessment of forest operations performance, regeneration abundance and quality, forest health, carbon stock, biodiversity (fauna, flora, and fungi), habitat diversity, range land, water resources, light conditions, crop nutrient balance, soil characteristics, recreation opportunities, and cultural, heritage, and amenity values.

For many of these topics, sampling and measurement procedures have been developed in other branches of science. In the context of forest ecosystem management, the challenge is to combine these procedures cost-effectively with forest measurement practices. Many of the additional ecosystem attributes correlate well with individual tree properties, stand characteristics, or overall forest structure, and traditional forest measurements are often more cost-effective and versatile.

So, regardless of management objectives, the trees of the forest must be quantified for informed decision-making. Consequently, forest measurements maintain a strong focus on the aboveground tree components of the forest ecosystem.

Measurement, Sampling, Analyses, and Prediction

Forest measurement activities generally comprise direct and indirect measurement, sampling, analyses, and prediction. Obviously, mathematics, statistics, and computer science are fundamental to forest measurements, and several measurement techniques are borrowed or adapted from engineering, land surveying, photogrammetry, and other professions.

Due to the forest environment and the size of trees special instruments have been developed for field use. These include calipers to measure tree diameter, relascopes to measure stand basal area, hypsometers to measure tree height, and xylometers to measure wood volume.

In general, due to the huge number of trees present on most forest land, only a sample is measured. Sample values are then expanded appropriately to obtain estimates for the population of interest. General sampling theory provides the foundation, but several sampling techniques have been developed specifically to forest conditions.

Except for the purpose of timber trading, forest measurements are most often based on nondestructive sampling. Consequently, the prediction of quantities, qualities, and events other than those directly measured plays a major role for utilizing the potential of forest measurements. The prediction of stemwood volume is probably the most notable example. A more complex but equally important example is the prediction of forest dynamics in response to management actions. As a general recommendation, models should consider the simultaneous nature of state variables and account for relevant interactions as well as temporal and spatial correlations in data.

Overview

A comprehensive review of all methods used for forest measurements is beyond the scope of this contribution. Here, the focus is on general principles, definitions, variables, instruments, methods, and models that are widely used for the assessment of some basic tree properties and stand characteristics.

Following an introduction to general measurement definitions and principles and a summary of the history of forest measurements, the scope of dendrometry is outlined and forest measurement practices explained for variables age, stem number, diameter, girth and basal area, bark, tree and stand height, stem taper, form factor, and wood volume. More specific approaches and details, including remote sensing measurement techniques and forest modeling based on dendrometric data, are covered elsewhere in this Encyclopedia (*see* **Resource Assessment**: GIS and Remote Sensing. **Mensuration**: Yield Tables, Forecasting, Modeling and Simulation), in forest measurement and modeling textbooks, and in similar texts from other professions and sciences.

General Measurement Definitions and Principles

By facilitating comparison across time and space, consistent and objective measurement principles contribute to an unambiguous interpretation of observations which, in turn, may lead to an extension of human experience and knowledge. Measurements thus contribute to a huge variety of human activities and interactions.

Definition, Scales, and Units

In its broadest sense, measurement can be defined as the rule-based assignment of numerals to physical objects and natural phenomena. Numerical quantities can be assigned under different rules using different kinds of scales and different kinds of measurement procedures. Any scale of measurement may be classified as being a nominal, an ordinal, an interval, or a ratio scale.

A nominal scale is used for numbering or counting objects or phenomena of a certain identity (for example, number of live trees). An ordinal scale is used to express rank or position in a series (for example, numerical codes 0, 1, 2, 3, or 4 for tree sociological classes dead, suppressed, intermediate, codominant, or dominant, respectively). An interval scale includes a series of graduations marked off at uniform intervals from an arbitrary origin (for example, temperature). A ratio scale is similar to an interval scale, but implies an absolute zero of origin (for example, stem diameter, tree height, and wood cubic volume). Ratio scales are the ones most commonly applied in forest measurements.

The analysis and interpretation of observations must take into account the measurement scale. For example, the number and type of legitimate mathematical operations depend on measurement scale. Although different measurement units are used in different parts of the world, numbers generally follow the decimal system, while the SI system offers comparative advantages over possible local units.

Variation, Accuracy, and Precision

Variation caused by uncontrolled factors, both known and unknown, is called error. The main sources of variation include properties intrinsic to the measurement object as well as external factors in sampling, measurement, and analysis of data.

Any measurement is subject to error or, in other words, deviation from a true value which generally remains unknown. It is often useful to identify, estimate, and reduce this source of variation relative to other sources. Errors include systematic and random components and originate in measurements due to measurement object, instrument, procedure, or the imperfection of human senses.

Systematic errors are constant or functionally dependent on their cause. These should be identified and eliminated as far as possible. Random errors are normally and independently distributed with zero mean and common variance. They are due to several possible causes, none of which dominates the measurement process. Random errors account for unexplained variation and are inherent to any measurement.

For any application of measurements, results are only as reliable as the input. So, other things being equal, the measurement error should be minimized for increased accuracy and precision. Accuracy is a measure of reliability as indicated by the difference between the true value and the most probable value derived from a series of measurements. Bias is defined conversely of accuracy. Precision is a measure of repeatability and is the degree of agreement between individual measurements in a series of measurements of the same quantity. In practice, accuracy is often judged from precision although this may lead to misinterpretation.

History of Forest Measurements

Assessment of forest resources, including the production and harvest potentials, has probably been crucial for exploitation by people and land managers ever since trading of natural resource products began and has definitely played a vital role during history for central authorities of societies that depended on forest products. Although timber is useful or even a necessity for the construction of houses, fortifications, bridges, carriages, and ships, the forest also provides firewood, fencing material, berries, fodder, grazing, and a host of other commodities.

Scarcity of resources obviously provides an incentive to initiate forest measurements. It is known that early societies in many parts of the world developed local forest measurement practices and rules to ensure reliable estimates of forest resources. Some of these even took approaches that are very similar to modern scientific methods and principles.

The Scientific Approach

The scientific approach to forest measurements in a modern context began in Central Europe at the introduction of regular and planned forestry in the mid-1700s, coinciding with the advent of forest science and modern natural sciences in general. Early initiatives concentrated on the identification of key variables for estimation of wood volume and prediction of growth, and on measurement procedures (**Figure 1**).

The establishment of the German Federation of Forest Experiment Stations in 1872 furthered a major breakthrough which resulted in a common norm for tree and stand variables in Central Europe. Following the foundation of the International Union of Forest Research Organizations (IUFRO) in 1892 these recommendations have greatly influenced forest measurement developments and practices in other parts of the world. However, no internationally agreed standards have emerged (**Figure 2**), but there

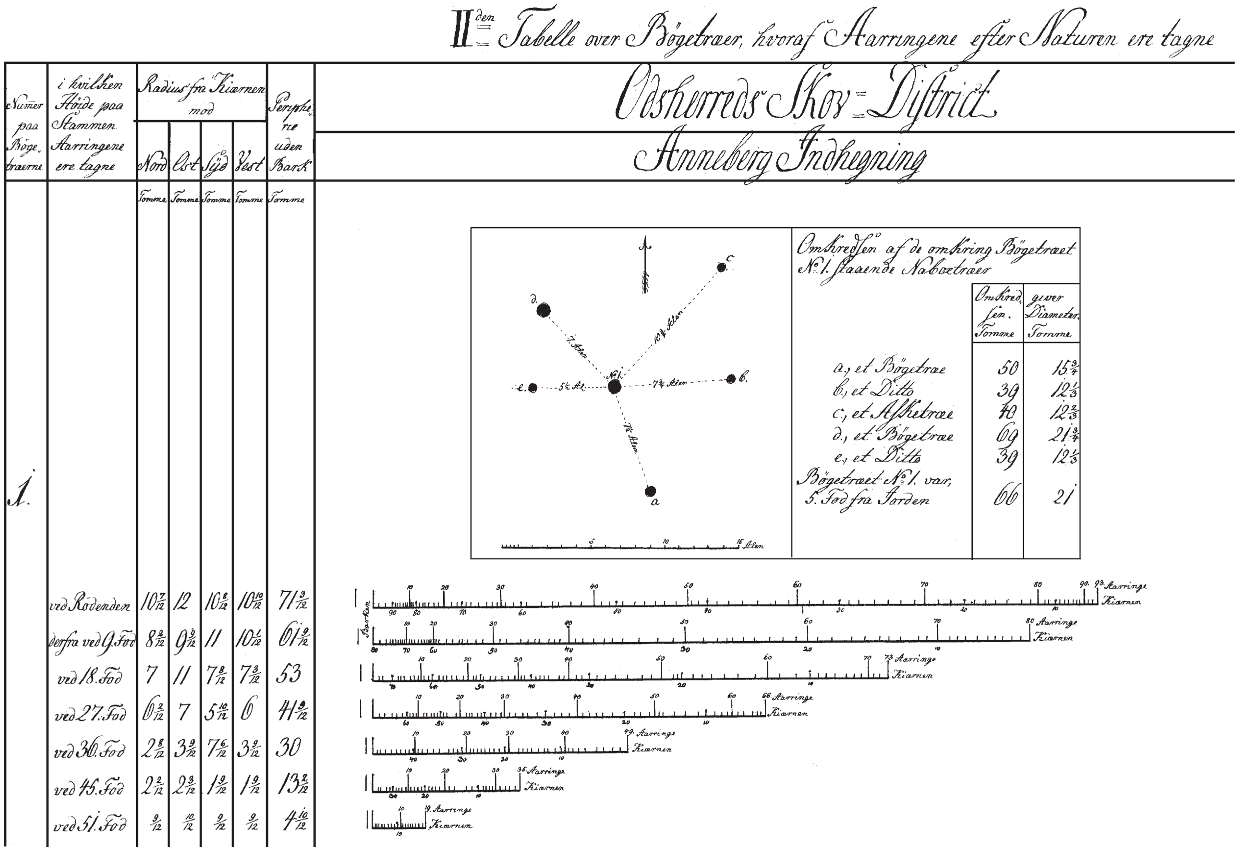


Figure 1 An example of early forest measurements to a modern scientific standard. In 1793, C.D.F. Reventlow initiated dendrometric measurements in stands of oak (*Quercus*) and beech (*Fagus*) in Denmark. Analyzing the size and past growth of trees in relation to the size of neighboring trees, he constructed accurate yield tables and prescribed economically optimal thinning practices that still prevail. Original record sheet for beech tree no. 1 in Anneberg Fenced Forest, Odsherred District. The sketch is a stem map for tree no. 1 and its closest neighbor trees A, B, C, D, and E, recording location, species, and circumference at the butt for each tree. Below to the left, measurements of stem radius (towards north, east, south, and west) and circumference of tree no. 1 at the butt and up the stem at regular intervals. To the right, measurements of annual rings at the same locations in the stem, indicating ring width and age. Number of years is counted from the center (right) as well as from the bark (left). From the archives of the Danish Museum of Hunting and Forestry/Society of Forest History.

appears to be a general consensus on some basic principles and variables. The most notable and universal key variable is diameter (or, alternatively, basal area) at 1.30 metres above ground level, often referred to as diameter at breast height (dbh).

Several of the historical forest measurement variables still prevail, although they were conceived during a period when the science of statistics was only emerging and calculations had to be carried out manually or using a slide rule rather than electronic data processing. Also, market demands for more uniform raw material due to the industrialization promoted a strong focus on timber production. An analytical, more holistic approach to classical dendrometry, unbiased by traditions of the profession and considering the range of issues in forest ecosystem management, would probably result in more comprehensive and statistically rigorous choices and definitions of variables and methods.

Dendrometry

The dendrometric components of a tree depend on measurement objectives and local traditions, but generally include stem, branches, foliage, bark, stump, and roots (**Figure 3**). Each of these may be measured with or without bark, individually or together, split in parts, or taken as a whole. Next, measurements may be carried out for standing trees, dead or alive, or for felled trees or wood products. Supplemented with area-based measurements, for example of sample plot area and stem number, measurement values for individual trees are expanded to obtain estimates at the population or stand level. Instruments for measuring or estimating dimensions of trees or forest products are collectively referred to as dendrometers.

Dendrometric measurements concentrate mainly on wood volume or, more precisely, measurements of

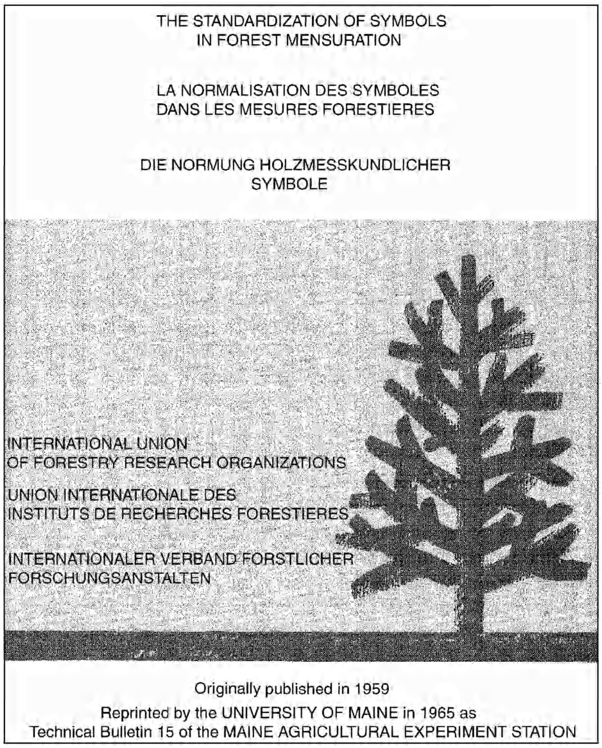


Figure 2 Forest measurement standards. Although seminal initiatives have been taken in Central Europe already in the late 1800s, no internationally agreed standards for forest measurements have emerged. Following approval from member organizations in 1956 IUFRO launched recommendations on the definition of variables and the standardization of symbols in forest mensuration. Although these recommendations were published simultaneously in English, German, and French, their use varies considerably between continents and countries.

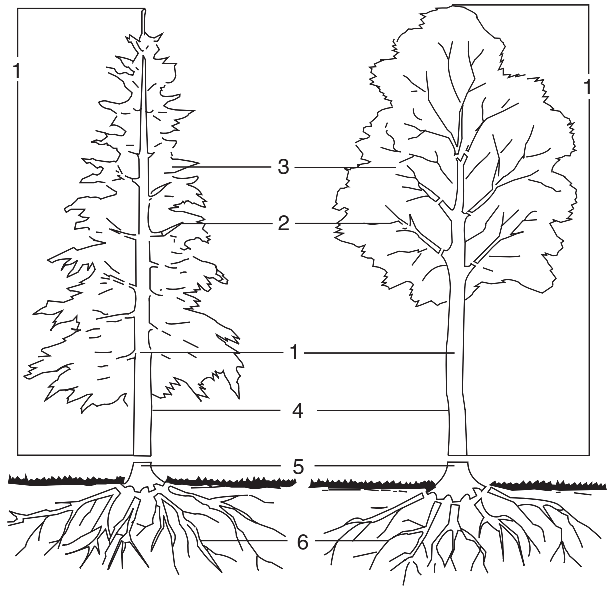


Figure 3 Dendrometric components of a tree: 1, stem; 2, branches; 3, foliage; 4, bark; 5, stump; and 6, roots. Depending on measurement objective and local traditions, measurements may exclude undersized material (size limit usually defined in terms of stem, branch, or root diameter), they may exclude or include bark, or bark may be measured separately. Generally, foliage is not considered except for scientific purposes, for health assessment, or in the case of whole-tree harvesting.

tree and stand attributes from which wood volume can be derived. For commercial purposes the main concern is merchantable volume of the main product, often one or more parts of the stem. Correspondingly, merchantable height (at which stem diameter or exterior wood quality is at its merchantable limit) is assessed directly in the field or derived from models of stem taper or total stem volume.

Due to different growth habits different tree species or species groups generally differ significantly in their dendrometric characteristics. This also holds for age, site, and stand treatment effects. Consequently, the identification of tree species or species group is often needed to capture and model the variation in tree sizes and shapes. However, in most situations, the volume of harvested products can often be assessed using general models that are independent of species or species group.

The most frequently used forest measurement variables include age, stem number, diameter, girth, basal area, bark thickness, height, stem taper, form factor, and volume at tree and stand level. In the following text, symbols for these and other dendrometric variables generally follow recommendations from IUFRO (**Figure 2**). By convention, uppercase symbols are used to denote stand values, whereas lowercase symbols refer to individual trees.

Age

For many practical and scientific purposes chronological time and age are considered fundamental variables for understanding and predicting the dynamics of tree and stand growth and other processes and events in the forest.

Definitions

By definition, the chronological age, t, of an individual tree is calculated from the time of germination of the seed or from the time of budding if the tree originates from a cutting or a sprout. Alternatively, age in a forestry context may be calculated from the time of planting or from the year in which the tree reached a certain reference height, for example 1.30 m above ground level. The latter is often preferred if early growth is hampered by browsing or severe weather such as drought or late frost. For coppiced trees, the age of stems may differ from the age of stools and roots.

In the case of strictly even-aged forest stands where all trees germinated, rooted or sprouted in the same year, stand age, T, is either known from management records or can be determined quite accurately from sampling. Otherwise, if a stand appears even-aged and the age of individual trees ranges within limits, stand age generally refers to some sample average. In the case of uneven-aged forest stands, age is hardly a main concern and is often disregarded.

Considering the longevity of trees, the scale of resolution for age is often 1 year, but any measure of time may be used.

Measurement Principles and Instruments

With distinct annual rings age is easily determined from counting on stumps or radial wood cores. Radial wood cores are extracted using an increment borer, a hollow auger that is screwed into the stem to remove a thin cylinder of wood. The main sources of error include incomplete, partial, and false growth rings, incorrect adjustment for age at the point of sampling, and failure to include the pith in core samples. The most reliable ring counts are made on complete cross-sections.

For some tree species, age may be determined alternatively from counting of branch whorls. In this case, errors may originate due to broken tops. Another important variation of the theme is dating of stumps to determine time and harvest volume of past cuts.

In the absence of seasonal growth rings and other reliable age indicators, age may be derived from observed correlation with other variables of the forest ecosystem. This method is subject to large variation.

Applications

Age determination of trees and stands is essential for even-aged forest management where age or, alternatively, a given period of observation, is often used in the prediction of growth, for site classification and for calculations leading to an optimization of economic return. For uneven-aged forest management age generally remains an inferior variable.

Stem Number

One of the most simple characteristics of a forest stand is the number of trees present, either dead or – more commonly – alive.

Definitions

In a forestry context, stem number is a more operational variable and frequently replaces the number of live trees. Generally, stem number is expressed in count per unit area. Sometimes, stem number refers only to trees above a certain size.

Measurement Principles and Instruments

Stem number at stand level, N, may be derived from stem counts, n, on sample plots or estimated based on counts at representative points in the stand.

For a plot, i, of known area, a_i, $N_i = n_i/a_i$. In the case of multiple plots per stand, the stand average may be weighted by plot area or another relevant factor. The number of plots needed to achieve a reliable stand level estimate depends mainly on the required precision, the stem number level, and its variation across the stand. Obviously, the error in determination of area propagates to stem number at stand level. When trees occur in rows spaced at regular intervals, counting may be carried out in a sample of these, and stem number at stand level derived from row length and sample fraction.

In dense stands, stem number can be pragmatically judged using a string of fixed length. Tied to a randomly located tree, the length of the string equals the radius of a circle of known area. For example, if the string is 3.99 m long, stem number per hectare equals stem count times 20. An alternative, pragmatic method is to measure the distance, k, from a sample point, i, to the nth nearest neighboring tree. Then, $N_i = 10^4(n - 1/2)/(\pi k_i^2)$. The efficiency and choice of these techniques depend on the pattern of variation in the stand and the ease of measurement.

Applications

Combined with other variables such as age or size of the trees, stem number provides an immediate impression of stand density for a given species or forest type. Consequently, stem number is widely used in forestry, for example in thinning decisions or in quality assurance of thinning operations. Stem number is also a significant variable in volumetric calculations.

Diameter, Girth, and Basal Area

Diameter, girth, or cross-sectional area of the stem or other woody parts of the tree is frequently used as an indicator of size, to calculate wood volume, or as a predictor of other tree and stand properties. This text mainly refers to measurement of the stem of standing trees, but similar principles apply to any other measurement of diameter, girth, and cross-sectional area.

Definitions

For standing trees, the most widely used tree and stand characteristic is stem diameter, d, measured outside of the bark at breast height, often referred to as diameter at breast height (dbh). In countries that use the SI system breast height is generally located at 1.30 m above ground level. Alternatively, some other reference height may be used, for example 4 feet 6 inches.

Assuming that stems are circular, stem cross-sectional area or, in the forestry terminology, basal area, g, is calculated as $g = d^2(\pi/4)$. Alternatively, diameter and basal area may be derived from girth or stem circumference, c, as $d = c/\pi$ and $g = c^2/(4\pi)$.

At the tree level, stem diameter, girth, and basal area can be used interchangeably, but generally diameter is the preferred variable because it is easier to visualize. Stand basal area, G, i.e., total basal area per unit area of land, is a specific characteristic of stand density.

Obviously, the stem and other woody parts of a tree are generally not exactly circular in cross-section. Consequently, the objective of any tree diameter measurement is to obtain the diameter of a circle with the same cross-sectional area as the measured part of the tree. The deviation from the circle depends on tree species, terrain, and wind conditions. In the case of substantial and consistent deviations a model to adjust measurements may help provide reliable estimates of basal area.

Another problem is the universal reference level at breast height. This provides an apparently consistent standard and a convenient measurement height, but is biologically not well justified. In practice it is difficult or impossible to determine the exact location of ground level due to natural variations at the base of the tree, and for the individual tree ground level may change over time, for example due to subsidence, erosion, or changes in the amount of organic material. However, definitions such as the highest, lowest, or average point of the ground surface touching the tree are usually considered sufficiently accurate.

Depending on tree species, forest type, terrain, weather, and other conditions a number of irregularities may occur. The most common problems include stem swell, wound callus, forking, lean, and buttressing. Local stem irregularities may be circumvented by measuring above or on either side of the irregularity, and when trees fork below breast height each fork is usually considered an individual stem. Severe and frequent buttressing usually requires an alternative reference level above breast height.

For small trees, and especially those below breast height, another arbitrary reference may be used, for example 10 cm or a level consistent with measurement points for stem taper or form factor. However, measuring the diameter of trees shorter than breast height is generally only considered for scientific purposes.

Measurement Principles and Instruments

The diameter of stems, branches, stumps, and roots is most frequently measured directly using a caliper (**Figure 4**) or indirectly using a tape graduated in π units. Usually 100 cm is the size limit for caliper measurements. Reliable electronic calipers are now available and are widely used.

As an alternative to caliper and tape, indirect measurement may be carried out using a fork or a stick with two arms or sighting lines forming tangents to the stem and a scale graduated according to this geometry. A similar principle is used for remote, optical measurement of diameter. For scientific purposes, diameter and diameter change may be monitored on a continuous basis using a band dendrometer (periodic readings) or a dendrograph (continuous record) encircling the stem or a branch.

In the absence of previous measurements and when growth occurs in a traceable, seasonal, or annual pattern information on past dimensions and growth performance can be obtained from the analyses of growth rings, for example from extracted wood cores, cut trees or stumps (see section 'Age' above). This approach is sometimes used for inventory purposes, in scientific investigations, and for dendrochronological dating (*see* **Mensuration**: Tree-Ring Analysis). A main concern with this method is the representativeness of samples.

Errors in determination of diameter, girth, and basal area are mainly due to measurement object (the tree), instrument, class grouping, or observer. In general, the relative error is small compared to other forest measurements.

Obviously, diameter, girth, and basal area change throughout the growing season and for that reason time of measurement should be chosen consistently and considered in subsequent data analysis. Even in the case of a distinct growing season size during the rest period may fluctuate depending on weather conditions, but generally this does not produce error of any significant magnitude.

For convex as well as concave cross-sections, a calipered diameter is the directly measured distance between parallel tangents to the region of a convex closure, whereas a taped diameter is derived from a parametric measurement of the convex closure. By definition, the diameter of the measured cross-section should equal the average of diameters measured over all possible directions. Consequently,

Figure 4 The caliper is the most common instrument in forest measurements. It is used for direct measurement of diameter of stems, branches, stumps, and roots. The conventional forestry caliper consists of a graduated bar with two parallel arms at right angles; one arm is fixed on the bar, while the other slides on it. Calipers made of metal or carbon fiber are more reliable than those made of wood, because they are sturdy, weather-proof, and easy to clean for resin and dirt. Modern calipers operate electronically with data storage directly in the caliper or data transfer to a portable field computer.

taped measurements are more precise, but result in a slight overestimation of diameter and basal area. In contrast, the caliper is theoretically unbiased for direct distance measurement and the average error may be reduced through the use of random measurement directions.

Instrument error due to a loose caliper arm is likely to result in underestimation, whereas error due to natural fluctuations in the length of a tape is randomly distributed. Each of these can be reduced to a minimum through the use of properly manufactured and well-maintained equipment. For optical instruments the use of a calibrated prism, a magnifier, a split-image, and a tripod improves precision considerably. Generally, alternative instruments are less precise than caliper and tape.

When using an analog instrument diameter is often recorded to size classes. The error due to class grouping depends mainly on class width and the distribution of tree sizes. Except for very thin trees, the error for 1 cm classes is negligible.

Errors due to the observer include failure to identify breast height correctly or consistently, failure to measure perpendicular to the length axis of the tree, and varying or inconsistent contact pressure. The error due to incorrect measurement height may be one- or two-sided and depends mainly on stem taper. In the case of heavy snow cover, floodwater conditions, or similar irregularities, a stick may be used as a probe to locate true ground level. Tilting always results in overestimation of diameter and girth. The problem with contact pressure depends on bark characteristics. Special care should be taken for species with soft, scaly, or otherwise irregular bark.

If successive measurements are taken on the same tree, for example on continuous inventory plots or in scientific experiments, accuracy can be improved considerably by permanently marking the exact location of the breast height reference level. If a caliper is used, accuracy can be further improved by taking two perpendicular measurements and measuring in the same two directions on each measurement occasion (d_1 and d_2). Typically, basal area is then calculated based on the quadratic, arithmetic, or geometric mean diameter, where $\sqrt{(d_1^2 + d_2^2)/2} \geq (d_1 + d_2)/2 \geq \sqrt{d_1 \cdot d_2}$.

As a rule-of-thumb for trees with a "regular" cross-section, individual tree diameter can be measured to within $\pm 2.5\%$ of the true value when using a tape or two perpendicular caliper measurements. Often, diameter is recorded to the nearest 1 cm in forestry practice and to the nearest 1 mm in high-precision scientific investigations. As a rule of thumb stand basal area can be measured to within 1–2% of the true value.

As an alternative to diameter and girth measurements, stand basal area may be estimated directly using a relascope for angle count sampling. The relascope is used to discriminate between trees depending on whether or not the tree subtends an angle equal to or greater than that of the relascope gauge when viewed from the sampling point (**Figure 5a**). Counting from a random point the stems whose diameter at breast height exceeds a certain angle produces an estimate of stand basal area (**Figure 5b**).

A stick equipped with a notched metal plate at one end is an example of a simple relascope. More sophisticated versions include, in order of increasing precision, the wedge prism, the optical mirror relascope, and the telerelascope. In the absence of an instrument, the observer's thumb can be used to obtain a crude estimate of basal area, provided proper 'calibration' at an arm's length to a personal count factor.

Applications

Diameter at breast height provides an immediate impression of the measured object and is the most widely used general characteristic of standing trees and forest ecosystems. Often, diameter at breast height is measured for all trees of a sample, and several other tree and stand characteristics are then modeled based on this quantity. Derived properties commonly include height, stem form, wood volume, volume growth, and branch size. Models for each of these may be improved by including additional variables. For example, upper stem diameters for estimation of stem form and volume.

Full enumeration of individual tree diameters provides substantial information on the sociological structure of a forest stand, including the size class distribution (**Figure 6**). Commonly used stand variables includes arithmetic mean diameter, $\bar{D}$, and quadratic mean diameter, D_g. While the arithmetic

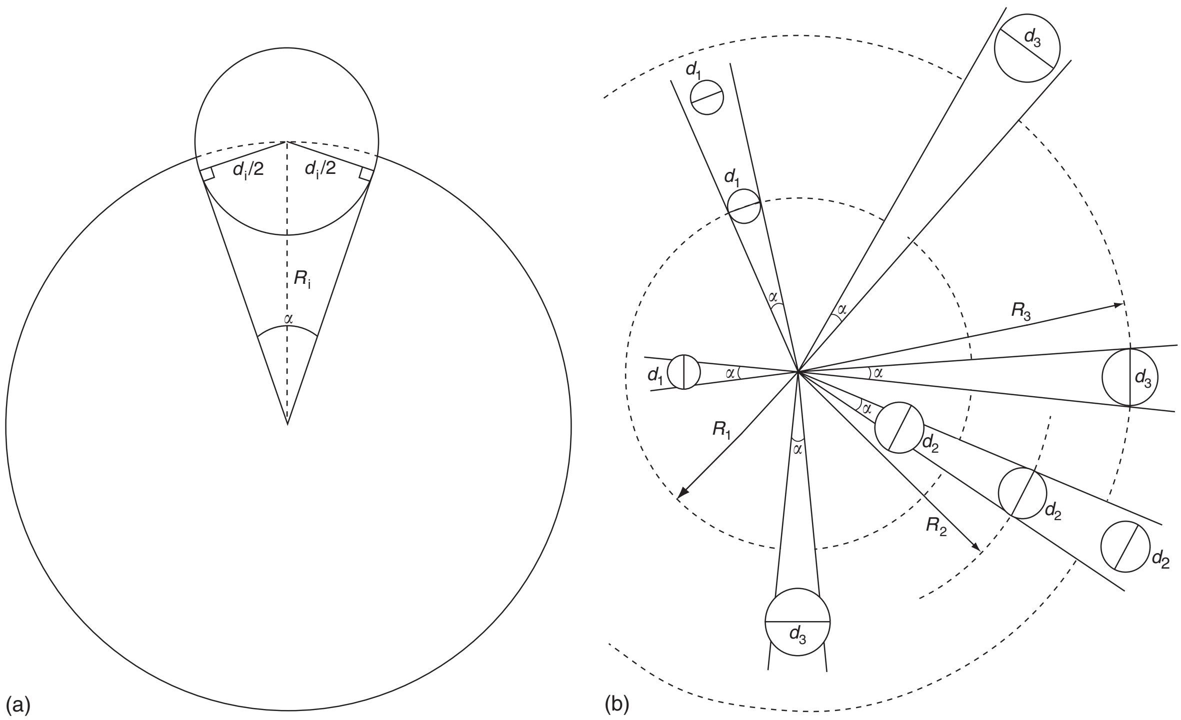


Figure 5 Angle count or point sampling. (a) Given a random point in a stand of trees of varying diameters d such that a particular tree of diameter d_i exactly subtends the relascope angle α when viewed from the random sampling point, the center of this tree is the distance R_i away from the sampling point, where $R_i = d_i/[2 \cdot \sin(\alpha/2)]$. The radius R_i describes a circle or sweep of area πR_i^2. (b) All trees of diameter d_i within this circle subtend an angle greater than or equal to α. The ratio of the basal area of these trees to the area of the circle equals $\sin^2(\alpha/2)$ independently of d_i. Consequently, a count n of all trees subtending an angle greater than or equal to α provides an estimate of the sum of basal area of these trees within each of their circles, i.e., $G\,\text{ha}^{-1} = n \cdot [10^4 \sin(\alpha/2)]$, where $[10^4 \sin(\alpha/2)]$ is called the count or basal area factor. Borderline trees exactly subtending the angle should be counted as $\frac{1}{2}$. For the example in Figure 5b n equals $4\frac{1}{2}$. Count accuracy is considerably improved by choosing an appropriate count factor, using steady instrument support, checking for hidden trees, inspecting the size of leaning and borderline trees, adjusting for slope in line of sight, and avoiding stand edges.

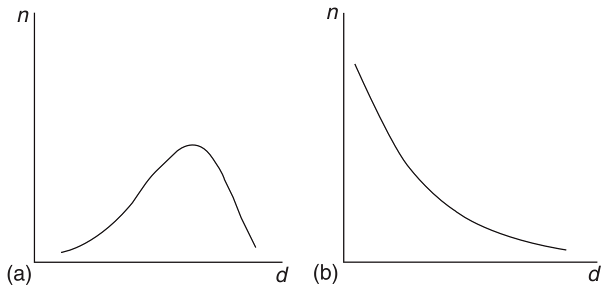


Figure 6 Smoothed diameter distributions (stem number, *n*, vs. diameter, *d*) for two different forest types. (a) An even-aged monospecific stand, and (b) an uneven-aged mixed species forest. The size class distribution is widely used in analyses of the sociological structure and dynamics of tree populations, and is a powerful tool for scenario modeling and decision-making in forest management. Commonly used models include continuous distribution functions as well as discrete functions and matrix models. Models may be univariate, as in this example, or multivariate, taking into account the simultaneous distribution of, for example, diameter and height of individual trees. For prediction and projection purposes parameter values are often recovered or predicted from relatively simple mensurational tree and stand characteristics.

mean relates immediately to the size class distribution, the quadratic mean is equal to the diameter corresponding to mean basal area. In forestry terms, the quadratic mean is often considered more meaningful because of its direct relation to basal area and, in turn, stand volume. Diameter enters quadratically into volume calculations, which are often based on either size class distribution or mean tree dimensions.

Stand basal area is an essential variable for forest management, for example for thinning decisions. In managed forests, individual tree diameter is strongly influenced by thinning practices, and stand mean values thus directly reflect management practices and their effects on growth. For a given forest type management guidelines are often based on an index or decision criterion that combines stand basal area with stand height, stem number (live trees), or mean tree size.

In addition to dendrometric tree and stand properties, diameter also serves as an input variable for harvesting criteria, assortment distributions, stumpage prices, forest valuation, and a range of other uses. Ultimately, through a number of model links, diameter at breast height is *the* key variable for decision-making in forest management, including ecological as well as economic and social aspects.

Bark

Measurement of bark thickness or bark volume may be needed to quantify bark for harvesting or to convert from over bark to under bark dimensions.

Definitions

Mensurationally, the bark comprises all tissues outside of the xylem, including the cambium. Bark thickness is generally defined as the difference in radius of two concentric circles, one defined by the bark surface, the other by the interior wood surface.

Measurement Principles and Instruments

On felled trees bark thickness can be measured at the cut ends or on bark samples that are cut off. On standing trees bark thickness may be measured using a probe or a gauge with a nail or a blade that is pushed through the bark, perpendicular to the stem periphery, to meet the wood surface. The depth of penetration is measured. Alternatively, bark thickness may be measured on extracted cores (see section ‘Age’ above) or on small pieces of bark that are cut off. Often, two or four measurements are made at diagonal points, and often at the points where the tree was calipered.

Measurements of bark thickness are often subject to large variation mainly due to irregular bark, difficulties in penetrating the probe or gauge exactly to the wood surface, slanted boring, and compression of the bark when using the instrument (probe, gauge, or increment borer). In the case of a distinct seasonal growth pattern, measurement accuracy usually deteriorates during the growing season.

When bark is a main commercial product more accurate methods may be needed. This normally implies cutting out samples of bark, for example squares of $20\,\text{cm} \times 20\,\text{cm}$, to determine thickness, volume, or weight. These may also be used for assessment of bark quality. The size and distribution of samples should be optimized based on statistical correlation with harvest quantities.

Bark volume may be derived from thickness or measured directly using a xylometer. Xylometry is also used for direct measurement of wood volume (see section ‘Volume’ below). The bark (or another object) is submerged into water to determine water displacement or buoyancy. If the bark is highly irregular, sample volumes measured by xylometry may underestimate stacked or piled volume.

The weight of bark is easily measured directly. Due to large variation within and between trees and seasonal fluctuations in moisture content, objective measurements require that the bark has been dried to a specified level. For operational purposes, the bark may be allowed to dry in open air for a given period to achieve equilibrium moisture content before being measured.

Applications

Bark thickness varies with tree species, genotype, site conditions, age, stand treatment, tree size, growth rate, health, height above ground, and geographic orientation. For many species, the average volume of bark ranges from 5 to 20% of the over bark volume.

When trees are measured over bark, bark measurements may be needed to estimate diameter, basal area, or volume under bark. This is essential mainly when sale of commercial timber is based on under bark dimensions, or when growth estimates are based on extracted wood cores or stem cross cuts. In the latter case, bark growth should also be considered. Often, bark volume or under bark wood volume is calculated based on the simple model $b_v = ((d_{\text{ob}}^2 - d_{\text{ub}}^2)/d_{\text{ob}}^2) \cdot v_{\text{ob}}$, where b_v is bark volume, d_{ob} is stem diameter over bark, d_{ub} is stem diameter under bark, and v_{ob} is volume over bark.

When bark is a main product, requirements on accuracy of measurements and models obviously relate directly to the commercial value of the bark. Bark is often traded by weight, which may be measured directly or predicted from other dendrometric variables.

Height

The height of individual trees as well as stand height are widely used in volume calculations, in the estimation of site productivity, and for a range of other objectives. Height measurement is more demanding and less precise than measuring the length of felled trees or wood products.

Definitions

The height of a standing tree, *h*, may be defined in different ways, depending on usage and measurement traditions. For total height, two slightly different definitions prevail: the shortest distance either between base and top of the tree, or between ground level and top of the tree. These definitions result in different measures of height only for leaning trees. The first definition may be preferred because it is often compatible with the length of felled trees and a consistent measure for volume calculations, whereas the second definition may be generally more practical. Other height definitions may refer, for example, to merchantable parts of the tree.

Another problem with definition of tree height is the exact location of ground level and of the base and the top of the tree. The principles for location of ground level and tree base is similar to those used to define the location of breast height (see section 'Diameter, girth, and basal area' above). Except for trees with a very distinct tip, it can be difficult to locate the top. This may be due to deliquescent growth, drooping branches, an irregular crown, or crown dieback. Consequently, the top of a standing tree is often defined as its highest growing point.

Measurement Principles and Instruments

Tree height and any other measure of height along the stem may be determined by direct or indirect measurement. Instruments for measuring the height of standing trees are collectively referred to as hypsometers. Several such instruments have been developed specifically for use in the forest.

Due to poor sighting conditions and the time needed for instrument handling it is generally slow work to measure tree height and a much smaller sample is measured than for diameter or basal area. Sampling principles and sample size should be determined based on requirements for end-use precision balanced with measurement costs. As an alternative to measuring standing trees, height estimates may be obtained from the length of felled trees that are sampled for this purpose.

Depending on tree size and stand density direct height measurement may be carried out using a graduated rule, stick, or pole. Extendable poles may be equipped with an engraved or colored scale on the outside or a self-winding tape measure in the inside. Generally, direct measurement is practical only for trees shorter than 10–15 m, and often indirect measurement is used even for these.

Indirect height measurement is based on geometric or trigonometric principles (**Figure 7**). The geometric principle relies on the use of similar triangles, whereas the trigonometric principle makes use of trigonometric functions. In both cases, the accuracy and precision of hypsometers generally depend more on construction details and fine mechanics than on measurement principle. However, with the advent of electronic hypsometers based on high-precision angle measurement combined with acoustic or laser technology for distance measurement, the tendency is that trigonometric hypsometers prevail. This technology has increased reliability of height measurements considerably, but not to a standard similar to that required in land surveying.

In the absence of previous measurements and when height growth occurs in a traceable, seasonal, or annual pattern, information on past height and growth performance can be obtained from measuring back to the terminal bud in previous years (see section 'Age' above). For species without annual whorls, reasonable estimates of height growth can be obtained from counting growth rings at intervals along the stem. If diameter growth is also analyzed

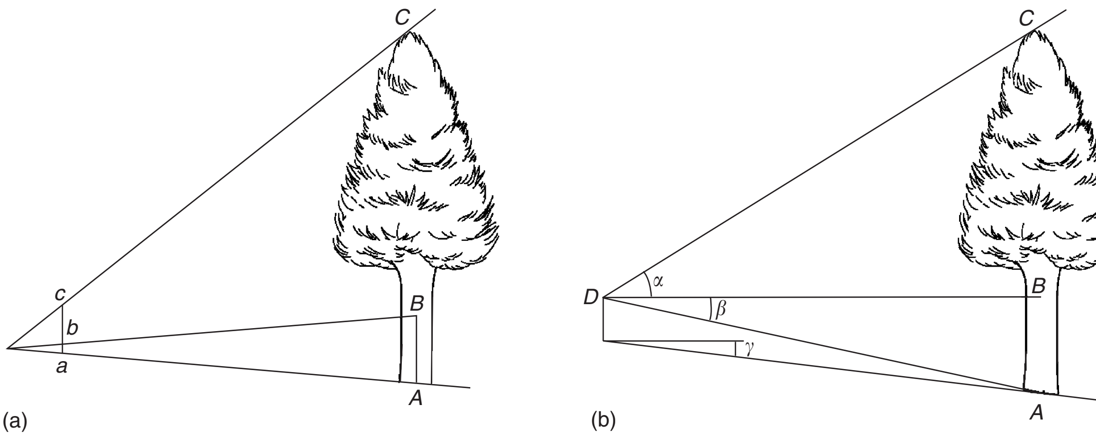


Figure 7 Indirect height measurement based on geometric or trigonometric principles. (a) The geometric principle relies on the use of similar triangles. In this example, a vertical ruler on the hypsometer is adjusted to fit the reference measure $|ab|$ with the length $|AB|$ of a pole at the base of the tree. Next, total tree height $|AC|$ is read directly off a scale which is graduated according to the known proportion between $|ab|$ and $|AB|$, i.e., $|AC| = |ac| \cdot |ab|/|AB|$. (b) The trigonometric principle relies on the use of trigonometric functions. In this example, the angles α and β are measured with the hypsometer, while the horizontal distance $|BD|$ between tree and observer is determined independently. Total tree height $|AC|$ equals $|BD| \cdot (\tan\alpha + \tan\beta)$. If horizontal distance is not measured directly the distance between tree and observer needs adjustment for terrain slope γ by a factor $\cos\gamma$. The angle scale of the hypsometer may be replaced by a nonequidistant tangent or percentage scale, so that tree height is easily calculated directly from hypsometer readings.

this may provide a complete record of past growth. This method is known as stem analysis.

Errors in height measurement are mainly due to measurement object (the tree), instrument, or observer. The most common field problems include leaning trees, parallax error in sighting, and incorrect identification of the tree top. While the latter can be avoided by careful observation, the effect of these problems is essentially similar: sighting is not done to a point located vertically above the geometric center of the base of the tree.

Generally, only a small fraction of trees is measured for height, so trees that lean severely can be avoided. Otherwise, simple geometry and trigonometry can help provide an estimate of tree height that is close to the true value. When parallax error is not due to hypsometer construction this can be avoided by careful observation.

Instrument errors originate in the construction or calibration of hypsometers. Whereas bias in analog hypsometers is often one-sided, more subtle but significant patterns may originate with electronic hypsometers. Outdoor work conditions and the sensitivity of mechanical and electronic components is a critical combination that stresses the need for regular test and calibration.

The random error in height measurement depends highly on tree species, forest type, hypsometer quality, and whether instrument support is used. As a rule of thumb individual tree height can often be measured to within $\pm 2.5\%$ of true height, but measurement errors of up to $\pm 5\%$ or more may occur. Electronic hypsometers and the use of instrument support may help increase precision. Often, individual tree height is recorded to the nearest 10 cm.

Applications

Tree and stand height as well as their distribution and growth provide essential information on forest and stand conditions and are used for a range of different objectives. For example, height is used in the estimation of wood volume, volume growth, stem form, and site and stand productivity, and it is incorporated in more complex models of forest dynamics. Height is also used more directly for management decisions, for example as a criterion for thinning of conifer plantations at a high risk of windthrow.

The potential uses of tree height depend highly on forest type. For even-aged forest individual tree height is often modeled as a static, age and stand specific function of diameter at breast height (**Figure 8a**). For uneven-aged forest interpretation of the relationship between tree height and diameter is less straightforward due to a more complex stand structure, and mathematically more flexible models are needed.

Different indicators of stand height may be derived from the model or directly from sample values. Commonly used indicators of stand height include arithmetic mean height, $\bar{H}$, height corresponding to mean basal area, H_g, mean height weighted by basal

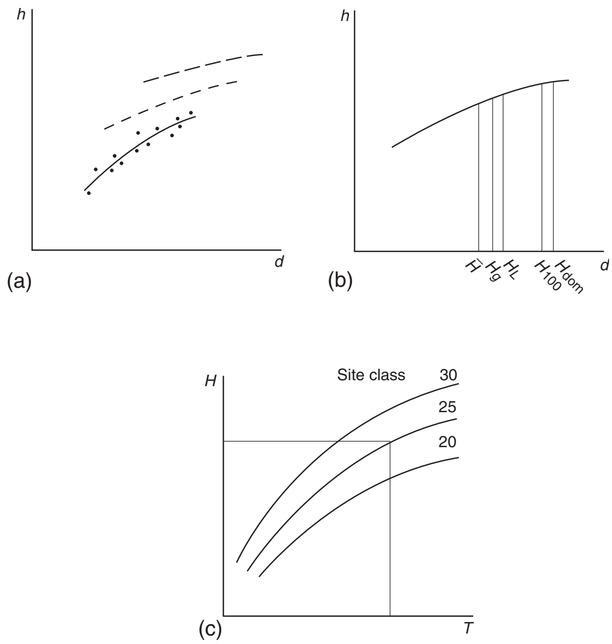


Figure 8 Tree and stand height in an even-aged, monospecific forest. (a) Individual tree height, *h*, as a function of diameter, *d*, at breast height (full line). If remeasurements take place, for example as for continuous forest inventory plots or scientific experiments, a family of curves (dashed line) may be derived that reflects site characteristic height growth for a given stand treatment. In this example there are three remeasurements, with individual observations (•) included only for the first one. (b) The relative position of different indicators of stand height ($\bar{H}$, H_g, H_L, H_{100}, H_{dom}). For readability, labels for stand height appear on the *d*-axis. (c) Classification of site and stand productivity by age, *T*, and stand height, *H*. In this example, the typical height–age development has been shown for three site classes (stand height 20, 25, and 30, respectively, at a given reference age), and a stand has been classified.

area, H_L, top height or average height of 100 thickest trees per hectare, H_{100}, and dominant height or average height of sociologically dominant trees, H_{dom} (**Figure 8b**). Historically based on arguments of computational ease rather than statistical rigor, each of these was conceived for specific purposes, generally aiming to reflect an 'average' property of the forest. Except for stands that are thinned from above the dependence of stand height on stand structure and thinning practices decreases through the progression $\bar{H}$, H_g, H_L, H_{100}, and H_{dom}. Consequently, $\bar{H}$, H_g, and H_L are mostly useful for volume calculations, while H_{100} and H_{dom} are better suited for classification of site and stand productivity (**Figure 8c**).

Volume

Volume is the most widely used measure of wood quantity. For some purposes, however, dry matter production is a more informative variable, but because volume is more easily determined, dry matter content is usually derived from volume estimates. Alternatively, fresh weight may be used to quantify wood or dry matter, with or without adjustment for moisture content and wood density.

Definitions

The wood volume of a tree includes stem, branches, stump, and roots (**Figure 3**). For standing trees, aboveground volume production is generally calculated on stemwood volume for conifers, but may include branch volume for broadleaved tree species. Depending on measurement objectives and local traditions measurements or predictions of wood cubic volume may refer to, for example, total stem volume, v, total tree volume (stem and branches), v_b, or volume above a certain merchantable limit ($d \geq a$), v_a. Volume estimates may exclude or include bark (disregarding the fact that anatomically bark is not a wood component) and, for aboveground estimates, exclude or include stump.

Measurement Principles and Instruments

Wood cubic volume may be determined by direct or indirect measurement. Direct methods are based on the principle of water displacement or pycnometry, while indirect methods are based on geometry. Indirect methods prevail because these are often more practical.

Generally, due to the tedious work, a much smaller sample of trees is measured for volume than for diameter and height. The volume of remaining trees is subsequently derived based on general or stand-specific models. Choice of sampling principles, sample size, and volume function should be based on requirements for end-use precision balanced with measurement costs.

It is relatively easy to sample and measure for stem volume, more tedious for branches, and quite difficult for stumps and roots. Stem volume can be measured on standing as well as felled trees, branch measurements are most often carried out on samples from the crown of cut trees, while stumps and roots that need excavation are only rarely measured. Consequently, and because of the commercial importance, methods and models for volume estimation mainly consider stemwood and other traditionally merchantable wood products.

Direct volume measurement is carried out using a xylometer, which is essentially a water tank in which the wood is submerged. The principle of water displacement requires that the xylometer is equipped or used with a suitably graduated volume scale. The cubic volume of wood equals the volume of water and wood minus the volume of water. Pycnometry requires that the wood is weighed before and during submersion, for example on a scale beam or in a sieve bucket. The cubic volume of wood equals the apparent difference in mass.

In principle, both approaches are accurate, but their precision depends strongly on a suitable graduation of measurement scales (i.e., relative to the size of the piece of wood being measured). Except for very small pieces of wood, measurement error due to air bubbles and the effect of water temperature is negligible. With pycnometry it is important that the water is still.

Direct volume measurement obviously requires destructive sampling. In scientific investigations it may be useful for measuring irregularly shaped parts of the tree and for testing the quality of indirect volume measurements. Often, branch wood is weighed as a substitute for xylometry. Commercially, direct volume measurements are used at some industrial-scale sawmills and plants, for example for scaling of pulpwood.

Indirect volume measurement relies on geometrical models of stem, branches, stump, and roots and may be carried out for felled as well as for standing trees. Due to differences in taper and shape different models are usually required for different parts or segments of the tree. The exact location and number of segments depend on measurement objective, species characteristics, tree size, and local measurement traditions. When felled trees are measured for total (aboveground) volume, for example for the construction of a volume function, the volume of under-cut and back-cut should be included or adjusted for.

In practice, the cubic volume, v_s, of each segment of a sample tree is calculated from the product of its cross-sectional area, g, and length, l_s (**Figure 9a**). Three formulae are commonly used for this purpose: Huber's formula with $v_s = l_s \cdot g_m$, Smalian's formula with $v_s = l_s(g_1 + g_2)/2$, and Newton's formula with $v_s = l_s(g_1 + 4g_m + g_2)/6$, where subscript m refers to the middle and subscripts 1 and 2 to one or the other end of the segment, respectively. The accuracy of each of these formulas depends on the shape of the segment (see section 'Form factor, stem taper, and volume models' below). Huber's formula provides relatively robust volume estimates for long logs and is often used in timber trading.

Most indirect volume measurements on felled trees are carried out using a caliper and a tape measure. Depending on circumstances, an optical caliper and a hypsometer may be better suited for standing trees. The measurement principles that apply to these instruments therefore also apply to the determination

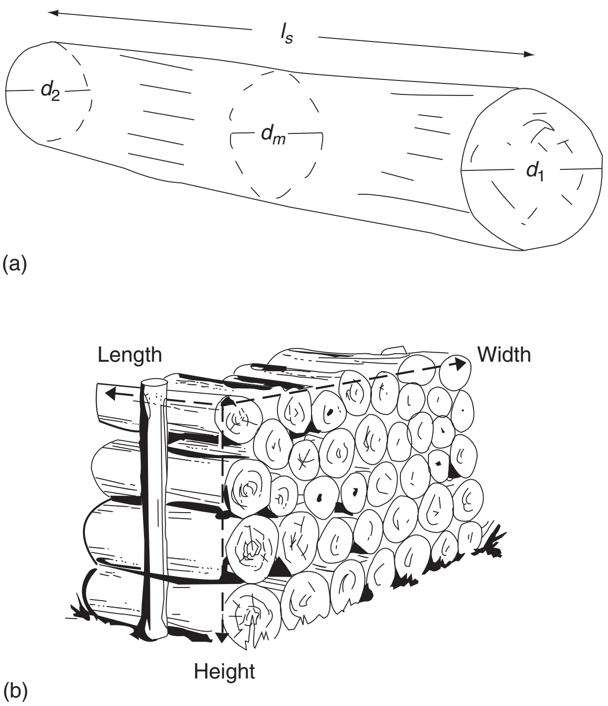


Figure 9 Measuring the cubic volume of wood and wood products. (a) Solid cubic volume is generally derived from measurements of diameter (d_1, d_m, or d_2) and length (l_s) of logs and pieces of wood. (b) Stacked wood is often measured for stacked volume, whether in a regular stack (as here) or in an irregular pile (as for example a heap of wood chips). Stacked volume is the total space occupied by a stack or a pile of wood, as determined by its external dimensions. Solid wood content is calculated using a conversion factor that adjusts for open space in the stack.

of wood volume, and potential measurement errors compound to the calculation of cubic volume. Next, apart from sampling error, error in volume estimates may be due to the models used and, for volume at stand level, error that originates in determination of plot and stand area.

The measurement of trade volume for wood products depends on local customs and trade agreements. The trade volume of logs that are measured individually generally refers to solid wood content. Stacked wood is often sold by stacked volume and solid wood content derived using a conversion factor that adjusts for open space (**Figure 9b**). In both cases, trade customs often prescribe rounding down of measurements. Alternatively, wood products may be traded by weight, with conversion to volume or dry matter based on estimates of moisture content and wood density.

Form Factor, Stem Taper, and Volume Models

The volume of stems, branches, stumps, and roots is modeled in numerous ways, using a range of different predictor variables. Here, three different approaches to modeling stem volume serve as examples.

In its simplest formulation, the classical approach to estimation of volume, v, is based on three volume factors: basal area at breast height (or at another nominated reference level), g, total tree height, h, and a form factor, f (**Figure 10**). The product of basal area and height ($g \cdot h$) yields the volume of the so-called reference cylinder. The form factor is a reduction factor, by which reference cylinder volume is multiplied to obtain the volume of wood. Thus, wood volume is calculated as $v = g \cdot h \cdot f$. Alternatively, diameter or circumference may enter the volume equation directly.

As a second example, volume may be estimated directly from dendrometric variables such as diameter and height. Classical volume models include the so-called combined-variable equation, $v = \alpha + \beta \cdot d^2 h$, and the more general model, $v = \alpha \cdot d^\beta h^\gamma$, where in both cases α, β, and γ are coefficients and other symbols are as usual. The latter model is often used after logarithmic transformation, $\log v = \log \alpha + \beta \log d + \gamma \log h$, where estimates of β often approach 2 while estimates of γ approach 1.

Choice of model may depend on modeling objective, data used in the estimation of coefficients and on error structure. Both models may be expanded to account for effects of, for example, age, site, and stand treatment. Apart from stand variables, the inclusion of an upper stem diameter often improves model performance. As an advantage, variation within stands can be quantified separately from variation between stands, and the accuracy of volume estimates improved. This requires, however, that there is no significant interaction between variables which determine volume level as this could result in ambiguous predictions due to lack of parallel response planes.

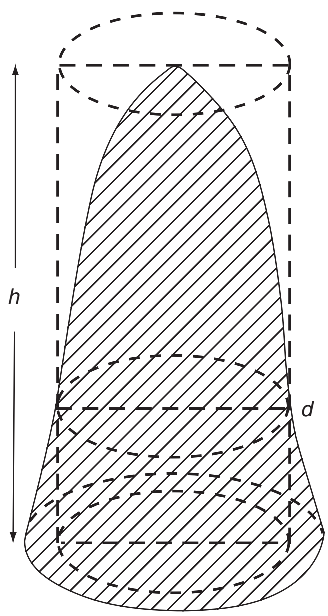


Figure 10 The form factor, f. In one number, the form factor summarizes the volume of a tree relative to its height and its diameter or basal area at breast height, viz. $f = v/(h \cdot d^2 \pi/4)$. Counterintuitively, the form factor is not a characteristic of stem form. The form factor is generally influenced by tree species, age, site, and stand treatment. Because the reference point, for example 1.30 m above ground, is chosen arbitrarily rather than relative to tree size, f is called the artificial form factor. For conifers f usually refers to stemwood, whereas for broadleaved tree species f often includes branches.

The classical form factor and volume equations can be used for individual trees as well as for stand values. Stand values are calculated by summation of individual tree or size class volumes, or a model tree is assumed. The model tree is sometimes referred to as the mean tree. Model tree dimensions reflect an 'average' tree of the stand in question. For example, with diameter corresponding to some stand average and height corresponding to some indicator of stand height. To obtain total stand volume, model tree volume is multiplied by stem number. Interestingly, the sum of individual tree volumes is identical to stand volume according to the mean tree method, when models of the combined-variable equation type are used with quadratic mean diameter, D_g, and stand height weighed by basal area, H_L.

As a third example, stem taper and stem volume may be modeled jointly, resulting in compatible estimates of volume and diameter at any height along the trunk. In the compatible system of stem taper and volume functions, the solid of revolution of the stem taper equation equals the volume according to the stem volume function.

Assuming circular cross-sections (see section 'Diameter, girth, and basal area' above) the cubic volume of the stem or any segment of the tree can be calculated based on the general taper equation $y = k\sqrt{x^r}$, where y is the radius at any point along the length axis x, and k and r defines the rate of taper and the shape of the solid, respectively (**Figure 11**).

In forestry terms, the classic stem taper equation is often expressed as $d_l^2 = 4p(h - l)^r$, where d_l is the diameter at a given height l (above ground), h is total tree height, $p = k^2 > 0$ and $r \geq 0$; r is called the form exponent. The solid of revolution, i.e., the stem volume, is thus

$$\begin{aligned} v &= \pi \int_0^h p(h - l)^r dl = \frac{\pi p}{r + 1} h^{r+1} \\ &= \frac{\pi}{4} d_{1.30}^2 \frac{1}{r + 1} h \left(\frac{h}{h - 1.30} \right)^r \end{aligned}$$

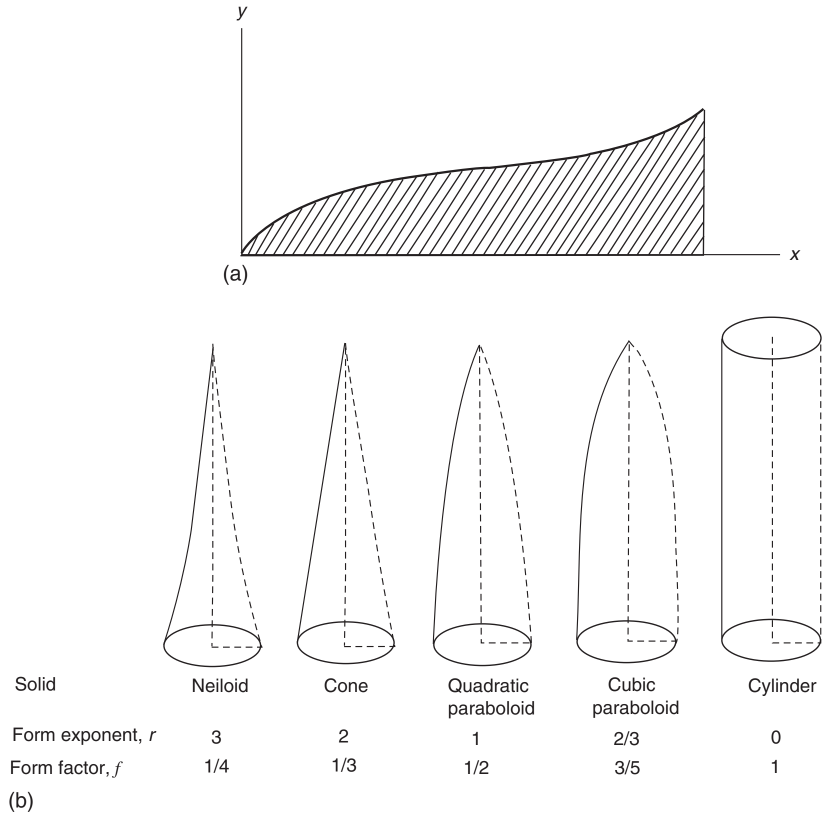


Figure 11 The classic stem taper equation and its solids of revolution. (a) The stem taper equation $y = k\sqrt{x^r}$ provides a general model of radius, y, at any point along the length axis, x. (b) Resulting solids of revolution depending on the form exponent, r. The form factor, f, given for each solid refers to a cylinder of identical diameter at the base.

where v is cubic volume and other symbols are as just described. Combining these equations yields

$$d_l^2 = \frac{4v}{\pi h}(r+1)\left(1 - \frac{l}{h}\right)^r$$

When using the model in practice, some restrictions may be desirable. Apart from compatibility, predicted diameter at breast height should equal the measured diameter, predicted diameters should decrease with increasing height along the stem, no diameter predictions should assume negative values, predicted diameter at the tip of the stem should equal zero, the derivative of the stem taper function with respect to l should equal zero at the tip of the stem, and first derivatives should agree at points of transition along the stem.

With this model the stem volume is explicitly expressed in the stem taper function and it is possible to adjust estimates of the stem taper curve to a specific stand volume level, thereby accounting for the effects of age, silvicultural practice and site on stem taper. Compatible systems may be taper-based or volume-based, depending on which function is derived first.

When the value of r progresses from 0 to 3 the solid of revolution progressively changes from a cylinder ($r=0$) through a cubic (2/3) and a quadratic (1) paraboloid to a cone (2) and a neiloid (3) (**Figure 11b**). Generally, stems approximate the shape of a truncated neiloid at the butt end, one or more truncated paraboloids in the middle, and a paraboloid or a cone towards the tip. Merchantable logs often falls between the frustum of a paraboloid and the frustum of a cone.

Considering the accuracy of indirect volume measurements (see section 'Measurement principles and instruments' above), all three commonly used formulas are accurate when $r=0$ (a cylinder) and when $r=1$, and Newton's formula is unbiased for all of the geometric solids concerned. When $r>1$ Huber's formula overestimates volume, while Smalian's formula underestimates volume; vice versa when $r<1$. In practice, a stem and even a short wood segment may be an irregular composite of different geometric solids whose real shape usually remains unknown. Consequently, the theoretical bias should be interpreted with care.

The volume of branches is often modeled for whole trees at a time (rather than at a more detailed level). Roots generally vary considerably and are very difficult to model.

As a rule of thumb individual stem volume can be estimated to within $\pm 7.5\%$ of the true value and stand volume to within $\pm 5\%$. Often, the volume of individual trees is calculated to the nearest $0.001\,m^3$ ($0.0001\,m^3$ for very small trees) and at stand level to the nearest $0.1\,m^3\,ha^{-1}$ for research plots and $1–10\,m^3\,ha^{-1}$ in operational forestry.

Applications

Quantification of wood volume and volume growth is one of the most important forest measurement activities. The wood volume of a tree or a forest stand is an integral measure of solid substance for a major component of the forest ecosystem and a potential basis for estimates of tree biomass, dry matter production, and carbon storage. Furthermore, trading of wood products is often based on their cubic volume, and standing volume and volume growth are significant decision variables in forest management. Importantly, the magnitude and quality of growing stock is closely correlated with the economic potential of the forest as well as with its biological and social value. At the national level, accurate inventory information on volume, volume growth, and their distribution to owner categories, growth regions, forest types, species groups, etc., is a basic requisite for suitable, well-targeted, and efficient forest policies.

As forest management objectives gradually change over time and may vary considerably from place to place, it is becoming increasingly important that forest measurement variables can be used purposefully for a wide range of different aims. It is easy to invent new and unproven variables, but hard to think of any variables that are more robust and less expensive to measure than those from which wood volume is derived. Although dendrometry rarely provides causal models for science or for forestry, it certainly should continue to provide suitable measurements for the sustainable management of our forests.

See also: **Biodiversity**: Biodiversity in Forests. **Experimental Methods and Analysis**: Biometric Research; Design, Performance and Evaluation of Experiments; Statistical Methods (Mathematics and Computers). **Health and Protection**: Diagnosis, Monitoring and Evaluation. **Inventory**: Forest Inventory and Monitoring; Large-scale Forest Inventory and Scenario Modeling; Modeling; Multipurpose Resource Inventories; Stand Inventories. **Landscape and Planning**: Spatial Information. **Mensuration**: Growth and Yield; Timber and Tree Measurements; Tree-Ring Analysis; Yield Tables, Forecasting, Modeling and Simulation. **Plantation Silviculture**: Stand Density and Stocking in Plantations; Sustainability of Forest Plantations. **Resource Assessment**: Forest Resources; GIS and Remote Sensing; Non-timber Forest Resources and Products; Regional and Global Forest Resource Assessments. **Tree Physiology**: Shoot Growth and Canopy Development.

Further Reading

Avery TE and Burkhart HE (2002) *Forest Measurements*, 5th edn. Boston, MA: McGraw-Hill.

Bitterlich W (1984) *The Relascope Idea*. Slough, UK: Commonwealth Agricultural Bureau.

Husch B, Beers TW, and Kershaw JA (2003) *Forest Mensuration*, 4th edn. New York: John Wiley.

Loetsch F, Zöhrer F, and Haller KE (1973) *Forest Inventory*, vol. 2. Munich, Germany: BLV Verlagsgesellschaft.

Philip MS (1994) *Measuring Trees and Forests*, 2nd edn. Wallingford, UK: CAB International.

Prodan M (1965) *Holzmesslehre*. Frankfurt am Main, Germany: J.D. Sauerländer's Verlag.

Schreuder HT, Gregoire TG, and Wood GB (1993) *Sampling Methods for Multiresource Forest Inventory*. New York: John Wiley.

Soest J van, Ayral P, Schober R, and Hummel FC (1965) *The Standardization of Symbols Used in Forest Mensuration*. International Union of Forestry Research Organizations. Approved by IUFRO 1956, originally published 1959, and reprinted 1965 by University of Maine as Technical Bulletin no. 15 of Maine Agricultural Experiment Station.

West PW (2004) *Tree and Forest Measurement*. Berlin, Germany: Springer.

Timber and Tree Measurements

C L Brack, Australian National University, Canberra, Australia

Introduction

Trees are complex three-dimensional structures that are very difficult to quantify or measure accurately. To overcome this complexity, the practice of tree measurement is generally to assume that portions of tree resemble simple shapes like cylinders, spheres, etc. A lot is known about these simple or Euclidean shapes, and this knowledge includes relationships between specific variables (e.g., radius of a sphere and the volume or surface area of that sphere). The closeness of the assumed shape to the real shape will partially control the closeness or the errors in estimating the quantity or size of a tree based on measurements of the simple variables. The study of the lengths, areas, and volumes of simple geometric shapes is called *mensuration*.

Forest mensuration is 'the art and science of locating, measuring and calculating the length of lines, areas of planes, and volumes of solids; and the appropriate application of these calculations to trees and forest stands.'

A tree may be divided into various components that may be quantified in various ways. The most appropriate quantification will depend on the reason why the quantification is required.

Definitions

Bole/Trunk

This is the main woody part of a tree, which is the major source of woody products derived from a tree. It is a three-dimensional object with a cross-sectional area that decreases progressively with increasing height. The bole may be quantified by its volume, height/length, or size at a reference height. The number or volume of standard wood products also often quantifies the bole.

Bark

The bark is the outer sheaf of the bole, branches, and twigs. Bark provides protection for the tree and may be harvested for horticultural, agricultural, or medicinal purposes. The thickness of the sheaf varies with height and position, and whether the bark is persistent or deciduous. Volume or thickness at specific positions may quantify this component.

Leaves/Needles/Crown/Branches/Twigs

The branches and twigs of the crown support the display of the leaves or needles to capture radiant energy for photosynthesis. This component may be harvested as fodder or horticultural products. It is also strongly correlated with growth of the tree. Quantification can include measurements of volume or mass, depth/length of the crown along the bole, and size at a reference height.

Roots

Tree roots provide anchorage and storage (large roots) and access to water, minerals, and other elements in the soil (fine roots) and may be harvested for agricultural or medicinal purposes. Quantification is relatively rare, but is normally mass.

The following sections outline the issues and practices involved with measuring these tree components.

Bole/Trunk

Reference Height (Breast Height)

To allow measurements of bole size to be compared, a standard point on the trunk is defined. It is important that this point is at a convenient height near the ground and that it can be reliably located (and relocated) by different measurers. This standard height is termed *breast height*.

The actual location of breast height varies slightly between some countries. In continental Europe, South Africa, Australia, the UK, Canada and some former members of the British Commonwealth, breast height is defined as 1.3 m above the ground. The breast height convention in the USA, New Zealand, Burma, India, Malaysia, and some other countries is measured at 1.4 m (or 4′ 6″) above ground.

Breast height is a convention with a long history of use within forestry practice. However, other standard heights are also used. Some researchers in grazing and agriculture use bole size at 0.3 or 0.7 m above the ground as their standard height. This reference height is used because it has a strong relationship to the grass/crop/tree competition measurements. Researchers studying tree volume have also found very strong relationships between volume and the size of the bole at a relative height (e.g., 5% of the total tree height up from the ground). However, while 5% of a 30-m tall tree is only 1.5 m above the ground and therefore easily within reach, it is difficult to reach the same relative height on a 60-m tall tree.

Measurement at breast height (or other nominated height) may not always represent the appropriate size of a tree. For example, the volume of the tree bole may not be correlated with a measurement at a height that corresponds to a fork in the tree or a fire scar. Typical causes of unrepresentative points include:

- branches or forks
- nodal swellings
- malformations of the trunk due to genetics or disease
- wounds
- insect attacks.

Special rules apply where a tree forks near breast height. For example, if a fork is below breast height, the tree should be treated as double- or multi-stemmed (i.e., more than one tree). If the fork is above breast height, treat the tree as a single stem with multiple leaders. When swelling at breast height occurs due to multiple leaders, the breast height measurement is conventionally taken where the bole diameter is smallest below the swelling.

Special instructions are also necessary where buttressing and fluting are common. Measurement is commonly made above the influence of the buttress or fluting. Where this influence extends well up the bole, an arbitrary height is specified.

When repeat measurements on the bole are expected (e.g., permanent samples), the actual height of measurement should be clearly marked.

The representative size of the bole at a nominated height may be estimated by two common techniques:

1. Take two measurements equally distant above and below the nominated height. If there is little difference between these measurements, take the mean value as the representative size. If the difference in bole diameter at these two heights is relatively large, then a quadratic mean may be more appropriate.
2. Subjectively select a representative point and take measurements at this point. Although quicker than the above method, this approach may lead to bias.

Consistent definition of ground level is essential to maintain precision of measurements. Ground level generally excludes loose leaves and litter that is not incorporated into the soil. Clear this loose material away before taking measurements of height. Sloping ground presents another problem for consistency of measurement. Conventionally, ground level on sloping ground is taken to be the uphill side of a vertical tree, however the mid-point between the uphill and downhill side is used in some countries. If a tree is leaning, imagine which would be the uphill side if the ground were rotated to make the tree vertical. Thus, on flat land, ground level would be defined from the underside of a leaning tree.

Size at a Specified Height

Measurement of a tree bole at a specified height would be easy if the bole corresponded to a simple geometric shape. For example, if we could assume that the bole cross-section was like a circle, then we could measure the radius (r), diameter (d), circumference (c), or area (a). We can calculate all the other variables once we measure any one of them.

$$c = \pi \times d = 2 \times r \times \pi$$

$$d = c/\pi = 2 \times r$$

$$a = \pi \times r^2 = \pi \times d^2/4$$

where $\pi = 3.14159265\ldots$

However, the tree bole is rarely circular (or any other simple geometric shape) and the use of the above equations will only provide approximate estimates. The selection of which parameter to measure will depend on: (1) the use of the measurement; (2) the resources and tools available; (3) tradition; and (4) the acceptable error.

Radius (r): length from the center to the outside of the bole The radius is rarely measured in forestry. Radius cannot be measured on standing trees because the center of the tree needs to be accurately located. Because a bole is not circular, different measurements of radius are possible.

Diameter (d): length from the outside of the bole, through the center, to the opposite side Diameter is commonly measured in forestry. Again, because tree boles are not circular, different measurements of diameter are possible.

Diameter at breast height (dbh) is probably the most common measurement made on a standing tree.

Direct measurement of diameter commonly measures two different axes:

- the diameter of the maximum and minimum axis of the bole on trees that are clearly elliptical
- the diameter of the maximum axis and the axis at 90°
- the diameter of any two axes at 90° to each other.

The two diameter measurements are averaged using an arithmetic mean (most common) or a geometric mean (for highly elliptical boles).

The measurement of diameter on one axis is often acceptable when the data are only being used to group trees into diameter classes for a stand table.

Circumference (c): the length around the outside of the bole Circumference, also known as girth, is commonly measured in forestry, but usually it is then used to estimate bole diameter. If the bole were circular, diameter can be estimated as circumference divided by π. However, if the bole deviates from this ideal shape, then this calculation will overestimate the diameter. The size of this bias is not constant and will vary with the degree and type of deviation. However, this bias is rarely considered significant.

An advantage of measuring the bole girth is that there is no sampling error involved. Unlike diameter measurements, the result does not depend on which axis was selected to measure. This leads to an increase in measurement precision. In addition, if a tree bole changes by 1 cm in diameter, the girth measurement changes by 3.1415... cm (π). Thus, finer readings of the change can be read.

Sectional area (a): the area of the cross-section of the bole This parameter is very important in forestry. The sectional area at breast height is used in many relationships and is called basal area (g).

Sectional area could be directly measured using a planimeter, but this is rarely done. Instead, sectional area is calculated from diameter after assuming that the bole has a circular shape. If the diameter is estimated from a measurement of circumference, then the basal area estimate will be an overestimate (positively biased). If the diameter is estimated from the mean of measurements on one or two axes, then an over- or underestimate of the sectional area is possible. The geometric mean of the maximum and minimum axes is less biased than other approaches.

Height

Total tree height may be defined as the distance along the axis of the bole of the tree from the ground to the uppermost point (tip). In trees with a single, straight stem, this corresponds to the total length of the stem.

The total height (or potential height) of a woody plant is used to distinguish shrubs from trees. For example, a woody plant, usually with a single stem, that is more than 5 m tall may be classified as a tree. Tree height is also well correlated with other important tree and stand parameters.

On leaning trees, height may also be expressed as the:

- vertical component – the vertical distance from the ground to the uppermost point of the tree
- slope or linear component – the length from the base of the tree along the axis of the bole to the uppermost tip of the tree.

The linear component will always be greater than the vertical component for leaning trees. However, unless the lean is severe, the difference is rarely critical. The tree must be leaning by more than 18° off vertical before the difference exceeds 5%. A lean in excess of 15° looks severe.

The vertical component (V) can be calculated from the slope (S) height (and vice versa) if the horizontal distance (H) from the base of the tree to the point directly beneath the tip is known.

$$S = \sqrt{H^2 + V^2}$$

Merchantable height Merchantable height may be defined as the distance from the base of the tree to the first occurrence of either:

- the highest point on the main stem where the stem diameter is not less than some specified value or
- the lowest point on the main stem, above the stump, where branching or other defect limits utilization of the stem.

Merchantable height is used to predict conventionally merchantable woody material. Unfortunately, it is a variable quantity that depends on the specification of the merchantable products at the time of measurement.

Shape (Form)

The diameter of a tree bole generally decreases or tapers from the base to the tip. The way in which this decrease occurs defines the bole form. This taper can occur at different rates and in different ways or shapes. Tree form is complex; however, portions of the tree bole may approximate general geometric shapes like cylinders, conoids, and truncated paraboloids and neiloids. The base of the tree tends to be neiloid while the tip tends to be conoid. The main part of the bole tends to be paraboloid. The points of inflection between these shapes however are not constant. Species and genotype predispose the bole to certain forms, but a wide range of environmental and contextual factors will influence this form.

There is a complex interaction between the bole form and the tree crown. Thus, any factor that influences the crown may also influence the bole form. Different parts of the bole grow at different rates as environmental and other factors affect the crown and the way photosynthates are distributed. The major theories that attempt to explain the shape of the bole may be grouped into three general types:

1. Mechanical: argues that the bole shape corresponds to the most economical shape of a beam of uniform resistance to bending anchored at the base, and functioning as a lever arm. If the tree were firmly anchored, the most economical shape for this beam would be a uniform taper similar to a truncated cubic paraboloid. However, if the tree stem were not firmly anchored to the ground, a quadratic paraboloid shape would be more consistent with the mechanical needs imposed by this assumption.
2. Transportation: based on ideas that deal with the movement of liquids through pipes – tree bole shape is related to the need of the tree to transport water or nutrients within the tree (water-conducting theory and nutritional theory of stem form respectively).
3. Hormonal: growth substances, originating in the crown, are distributed around and down the bole to control the activity of the cambium. These substances would reduce or enhance radial growth

at specific locations on the bole and thus affect bole shape.

Overall or average shape is in some cases quantified as an index of a nominated bole dimension to a reference shape or dimension. Two common indices include:

1. Form factor: the volume of the stem compared to the volume of a standard geometric solid of the same diameter at the base and total height. The most common form factor is the breast height form factor, which is defined as the ratio of the bole volume to a cylinder of the same height as the bole and with a sectional area equal to the sectional area of the stem at breast height. Specific breast height form factors suggest general stem shapes: 0.25 neiloid; 0.33 conoid; 0.50 quadratic paraboloid; 0.60 cubic paraboloid; and 1.00 cylinder.
2. Form quotient (FQ): the ratio of the diameter at some point above breast height to the diameter at breast height. The absolute FQ is used to group trees into form classes. This quotient is calculated by measuring the diameter at a height halfway between breast height and total tree height. This diameter is then divided by the diameter at breast height and expressed as a decimal. Absolute FQs also suggest general stem shapes: 0.325–0.375 (FQ class 35) neiloid; 0.475–0.525 (FQ class 50) conoid; 0.675–0.725 (FQ class 70) quadratic paraboloid; 0.775–0.825 (FQ class 80) cubic paraboloid.

More precise quantification of bole shape is now commonly achieved through the development of mathematical equations that predict the diameter or sectional area of the bole at any height up the tree. These mathematical equations, called taper equations or taper models, use polynomial, exponential, and other types of mathematical structures to relate diameter or sectional area at nominated points up the bole to a reference diameter (diameter at breast height), total tree height, and the relative height where the prediction is required.

Volume

Stem volume is a function of a tree's height, basal area, shape, and, depending on definition, bark thickness. It is therefore one of the most difficult parameters to measure, because an error in the measurement or assumptions for any one of the above factors will propagate to the volume estimate.

Volume is often measured for specific purposes, and the measurement and interpretation of the volume estimate will depend on the units of measurement, standards of use, and other specifications. For example:

- Biological volume is the volume of stem with branches trimmed at the junction with the stem, but usually excluding irregularities not part of the natural growth habit (e.g., malformation due to insects, fungi, fire, and mechanical damage).
- Utilizable or merchantable volume excludes some volume within irregularities of the bole shape caused by normal growth in addition to those irregularities not part of natural growth. For example, the volume contained in the swelling around a branch node may be excluded because this volume could not be utilized (by a nominated user).
- Gross volume estimates would include defective and decayed wood.
- Net volume estimates would exclude defective and decayed wood.

Thus, the type of volume measured must be reported for reliable interpretation. For example, the net merchantable volume of sawlogs in a tree will be significantly different from the gross biological volume.

Calculations of merchantable volume may also be based on true cubic volume or product-oriented volume. Product-oriented volume is the volume of a nominal product that could be cut from the log or stem under specified conditions and assumptions.

Direct and indirect methods for estimating volume are available. The direct methods tend to divide the stem into theoretical or actual sections and measure the volume of these sections:

- Fluid displacement: essentially, the tree stem is cut into manageable sections and immersed in a bath. The amount of water displaced equals the volume of the section. Also called xylometry, this approach most accurately measures gross biological volume.
- Graphical method: measurements of sectional area are made every 1–2 m up the tree bole and then plotted against height (in meters) on a scaled graph. Freehand lines join the plots, and then the area under the curve is equivalent to the cubic volume of the bole.
- Standard sectional method: the main stem, up to merchantable height, is theoretically divided into a number of (mostly) standard length sections. The standard length is normally 3 m (10 ft). The exception to the standard section is the odd log – a section less than the standard length that fits

between the last standard section and the merchantable height. These sections are assumed to be second-degree paraboloids in shape. The bole from the merchantable height to the tip is assumed to be conoid in shape. Equations to predict the volume of second-degree paraboloids and conoids from measurements of length and sectional area are then used to estimate the volume of each section.

The indirect methods include:

- Volume tables: a tree volume table is a statement of the expected volume of a tree of nominated dimensions in a particular stand or population. The number of measurements or dimensions determines the number of entry points or ways into the table. For example, a one-way table normally uses dbh or basal area as the only measurement; a two-way table may use dbh and height; while a three- or more way table would include measurements that correspond to bark thickness or taper.
- Volume equations: volume equations are a mathematical statement of the expected volume of a tree of nominated dimensions in a particular stand or population. The input variables to the equations can also include diameter (at breast height and other heights), height, taper, and interaction terms.
- Integrating taper equations: where a taper function is continuous and able to be integrated, the volume of the bole can be determined by integration. Where this is not feasible, the equation can be used to predict the sectional area at 1- or 2-m intervals up the tree, and volume can be calculated as for the graphical method.
- Variance reduction methods (e.g. importance sampling and centroid sampling): variance reduction methods use the knowledge contained in taper functions to improve the precision and cost of estimating sample tree volume. Essentially, a taper model predicts tree shape and hence sectional area and cumulative volume at any height up the tree. A sample height on the tree is selected and the bole measured. The difference between the measured and predicted size at that height is used to correct the volume estimated from the original taper equation. Various methods differ in the way the sample height is selected and the way the original estimate is corrected.

The volume of wood contained in a tree bole is of primary interest to sawmillers and these millers are interested in the quantity of product they can extract from the bole or logs cut from the bole. Therefore, product-oriented volume definitions rather than the true volume estimates of the three-dimensional shape are of more direct interest. Log rules are a common attempt to estimate volume that is of direct interest to these wood-processing industries.

A log rule is a table or formula showing estimated volume, in standard units, for various log diameters and lengths. During the 1900s, at least 100 log rules were devised. Several sets of these rules are widely adopted throughout the USA, but have not become common in other regions of the world.

The major log rules in the USA predict the production of the board foot. A board foot is equivalent to a plank 1 in. (2.5 cm) thick and 12 in. (1 ft: 30 cm) square; it contains 144 cubic in. (900 cm^3) of wood. However, none of these rules can accurately predict the mill output of boards, except when near-cylindrical logs are sawed according to rigid assumptions on which the rules are based.

Bark

Bark is the outer sheath of the tree. Some trees annually shed bark, while others have persistent bark. The inner bark transports photosynthates from the crown, while the outer bark has a major protective role. The bark protects the bole from insects and damage from physical abrasion. It is also important for fire resistance. Bark thickness normally decreases from the ground to the tree tip. This decrease may be related to the rate of taper of the bole, but there are often irregularities and anomalies. Bark thickness varies with species; genetic constitution; site; tree age, health and size; rate of growth; bark persistence; and position along the bole.

On felled trees and logs, bark thickness can be directly measured at the cut ends. A small chip of bark can also be cut and the thickness measured. However, cutting the chip with an axe may compress the bark and provide biased estimates. Where a ring of bark can be removed, the diameter overbark and diameter underbark can be measured. Bark thickness is one-half of the difference between overbark and underbark diameter.

On standing trees, bark thickness is measured indirectly. A probe is pushed through the bark to meet the wood interface and the length of penetration is measured. Because bark varies around the bole, an average of four measurements (evenly spaced or where the caliper arms contact the bole) is normally required.

Bark sectional area is normally calculated as the difference between overbark and underbark sectional area. Similarly, bark volume is the difference between overbark and underbark volume, where volume is by the standard sectional or other technique. Thus diameter overbark and bark thickness, at a number of heights up the bole, needs to be determined.

Many hardwood trees maintain a reasonably constant ratio of diameter underbark to diameter overbark along the tree bole. Thus diameter underbark at any point along the tree may be calculated by multiplying overbark diameter by the ratio of under- to overbark diameter at breast height.

For many other tree species, particularly conifers, the under- to overbark diameter ratio increases with increasing height along the bole. That is, the relative bark thickness decreases. A few rare species have a decreasing ratio of under- to overbark diameter.

Where the ratio of under- to overbark diameter is not constant, statistical equations may be developed to predict bark thickness from measurements at ground level.

Leaves/Needles/Crown/Branches/Twigs

Crown Diameter

The width of a crown can be measured by projecting the edges of the crown to the ground and measuring the length along one axis from edge to edge through the crown center. Unless the crown has a regular shape, the width measured will depend on the axis selected for measurement. If the crown width is being used to estimate sectional area (used in crown surface area and volume calculations), two axes are normally selected and averaged.

Crown Depth (Length)

Crown depth is the length along the main axis from the tree tip to the base of the crown, where the base of the crown is defined by:

- the lowest complete branch whorl or major branch that forms part of the canopy (used in calculating upper crown length) or
- the lowest live branch, excluding epicormics or water shoots (used in calculating lower crown length).

The depth of the crown is often expressed as:

- crown length ratio (crown length divided by total tree height)
- green crown percent (crown length ratio expressed as a percentage of total tree height).

Crown Surface Area

Crown surface area is a surrogate for the area available for leaves to capture radiant energy from the sun or atmospheric gases and pollution. As the most actively photosynthetic leaves are the young leaves near the crown periphery, crown surface area is a useful index of growth. Crown surface area is calculated by assuming the crown is a solid geometric shape (e.g., conoid, paraboloid, or hemisphere) with a measured crown depth and crown width.

Crown Volume

Crown volume is calculated in a similar way to crown surface area. It is normally estimated from the crown width and crown depth after assuming a regular geometric shape.

Crown Mass

The only direct way to determine crown mass is to fell the tree. Once felled, the leaves, twigs, and branches are separated into discrete pools and the fresh or green weight of these components is determined. The dry weight (and mineral content if required) of a subsample of components is also determined. The ratio of dry-to-fresh weight is used to estimate the original crown's total mass. A variety of sampling approaches has been designed to estimate an unbiased ratio of dry-to-fresh weight.

Indirect approaches to estimating crown mass include the development of statistical equations of the correlation between the expected mass of a tree crown or branch of nominated dimensions in a particular stand or population.

Roots

The measurement of mature tree roots is difficult and rare. The mass of smaller, pot-grown roots is determined by washing away the potting material and direct measurement. The mass of the large roots for mature trees may be estimated by digging a trench around the tree and then pushing the tree over. Many of the major roots will stay attached to the pushed bole. These roots can then be detached and weighed.

Indirect approaches to estimating root mass include the use of estimated root : shoot ratios and the development of statistical equations of the correlation between the expected mass of the roots and dbh or basal area.

See also: **Mensuration**: Forest Measurements; Growth and Yield; Yield Tables, Forecasting, Modeling and Simulation. **Resource Assessment**: Non-timber Forest Resources and Products. **Solid Wood Products**: Lumber Production, Properties and Uses.

Further Reading

Avery TE and Burkhart HE (1983) *Forest Measurements*. McGraw-Hill series in forest resources. New York: McGraw-Hill.

Clutter JL, Fortson JC, Pienaar LV, Brister GH, and Bailey RL (1983) *Timber Management: a quantitative approach*. New York: John Wiley.

Lund G (1998) *IUFRO Guidelines for Designing Multiple Resource Inventories*. Vienna, Austria: IUFRO World Series.

Schreuder HT, Gregoire TG, and Wood GB (1993) *Sampling Methods for Multiresource Forest Inventory*. New York: John Wiley.

Research Working Group #2 (1999) *Code of Forest Mensuration Practice: A Guide to Good Tree Measurement Practice in Australia and New Zealand*. Available online at: http://sres.anu.edu.au/associated/mensuration/rwg2/.

Growth and Yield

R Matthews and E Mackie, Forest Research, Farnham, UK

The Purpose of Forest Mensuration

Forest mensuration (the study of measurement) is the research discipline that develops and evaluates both the theoretical basis and practical application of systems for assessing the growth and yield of trees and forest stands. Originally subjective assessments and qualitative systems were used for characterizing the productivity of forest stands; however, methods of mensuration developed over the past 200 years have allowed the adoption of a strictly quantitative approach.

Forest inventory techniques are underpinned by a substantial body of research on measurement methods, and on approaches for the processing of measurements to derive summary results that provide an indication of current and potential future yield. Often the term mensuration is also used to describe the conventions adopted in standardized procedures used by forest industries for quantifying forest resources and as part of production forecasting.

A comprehensive forest mensuration research program involves developing and evaluating:

- measurement instruments and conventions for their use
- procedures for quantifying the structure and yield of forest stands
- descriptions and analyses of tree and stand growth patterns
- relationships between potential stand yield and site factors
- mathematical models of forest structure, growth and yield.

Measurement Variables, Instruments, and Conventions

The essential endeavour of mensuration involves working out how to measure variables relevant to the growth of trees and forest stands. Traditionally measurements are taken of external physical characteristics of a tree or sample of trees that are easy to measure and obviously related to growth. Notable examples of tree growth variables include:

- total height
- stem diameter, circumference, or cross-sectional area
- stem volume
- gross dimensions of the crown.

Sometimes more complex measurements are included as part of mensuration procedures, for example involving detailed assessments of tree and stand architecture. A variety of methods exists for measuring and describing the architecture of individual trees or stands, such as based on:

- the shape and size of crown(s)
- the detailed disposition of branches, foliage, and roots
- the distribution of tree species and size classes in a stand.

A wide range of instruments has been applied to the measurement of growth variables of trees as illustrated in **Table 1**.

Conventions and standards for the measurement of growth and yield variables are very important in order to ensure consistency. These need to cover not only the typical trees in a population but also give clear rules for the measurement of unusual trees (**Figure 1**). Conventions are also required for the measurement of felled trees and any cut produce such as roundwood. Consistency is important if measurements and derived results are to be repeatable. This is essential in the forest industries when buying and selling of quantities of wood. It is also important in a research context when the growth of trees or stands needs to be monitored over time, for example to find out if production is consistent with growth.

An important function of measurement conventions is to prescribe levels of accuracy for measurement. For

Table 1 Examples of tree growth variables and instruments used for their measurement. Common units of measurements are also indicated for each variable

Variable	*Examples of measurement instruments*	*Units*
Tree height	Graduated poles (on smaller trees)	
	Simple hypsometer (geometric principles)	m
	Clinometer (trigonometric principles)	
	Ultrasonic or laser-based combined range-finder and hypsometer	
Tree diameter	Tape measures (which may be calibrated in terms of diameter of an equivalent circle)	cm
	Pair of calipers (which may include digital recorder)	
	Optical dendrometer (for out-of-reach diameters)	
	Laser-based, optical scanning systems (under development)	
Tree basal area	Calculated from diameter assuming circular cross-section	m^2
Stand basal area	Sum of cross-sectional areas based on diameters of individual trees	$m^2\,ha^{-1}$
	Relascope (optical device which may include digital recorder)	
Tree stem volume	Sum of volumes of short sections of tree stem calculated from the measured lengths and diameters of sections	m^3
Stand volume	Measurement of a sample of tree volumes as above; establishment of correlation between tree stem volume and diameter; sum of individual tree stem volumes based on correlation with tree diameters	$m^3\,ha^{-1}$

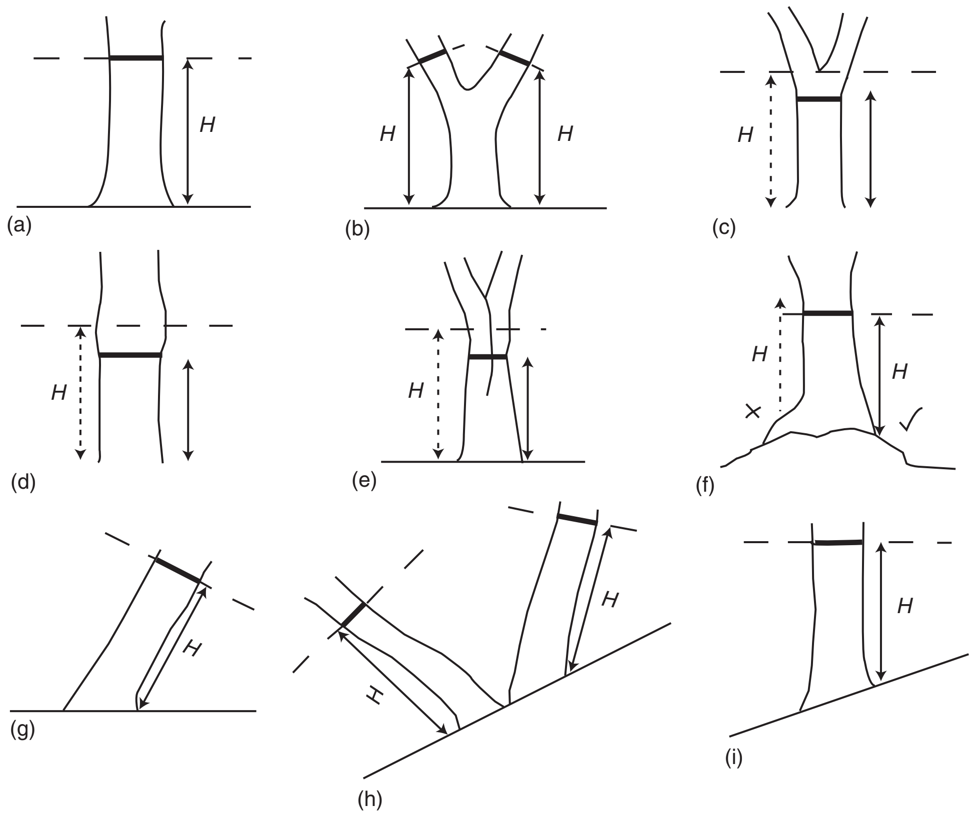


Figure 1 Illustration of conventions that may be adopted to determine a point above ground level (*H*) for measuring tree diameter. (a) Measurement of upright stem on flat ground; (b) stem forked below *H* – measure both diameters; (c) stem forked at *H* – measure diameter at smallest point below fork; (d) swelling at *H* – measure diameter at smallest point below swelling; (e) forks have fused up to and above *H* – measure diameter at smallest point below; (f) planted on plowed or uneven ground – measure from base of stem, not root buttress; (g, h) on leaning stems – measure diameter at *H* on underside of stem with smallest angle to the ground, diameter should be measured perpendicular to long axis of stem; (i) on sloping ground measure diameter at *H* on upslope side of stem.

example, a convention may require the height of a tree to be rounded down to the nearest 0.1 m to reflect the accuracy of the measurement instruments in general use.

Quantifying Stand Structure and Yield

One important aspect of mensuration methods is the requirement for efficient and cost-effective methods of measurement. For example, one of the most important variables used in describing forest growth and yield is tree stem volume which is time-consuming and expensive to measure directly. In particular, inventory systems rely on relatively quick, cheap, and reliable methods for assessment of stand structure and potential volume yield. The forest industry also uses a suite of simple mensurational methods for deciding if, when, and how to carry out thinning or harvesting of stands, as a basis for sale of timber, for planning forest operations, and ultimately as part of the development of forest design plans. These methods are thus essential tools for supporting and demonstrating the sustainable management of forest estates.

Mensuration researchers develop protocols for the assessment of stands that aim to minimize the intensity and complexity of measurements needed to obtain yield estimates of different levels of precision. Where stand structure and volume need to be quantified to high accuracy, an intensive procedure may be specified involving for example:

- counting all the trees in the stand
- measurement of a large sample of tree stem diameters
- measurement of a smaller sample of tree stem volumes.

Tree stem volumes may be measured by climbing or felling trees, or using an optical instrument such as a dendrometer.

Standardized statistical computations can be specified for processing measurements into estimates of numbers of trees, tree size class distribution, and potential volume yield (**Figure 2**). It is also possible to use statistical theory to provide guidance on the size of samples of trees measured for diameter and volume needed to achieve a required level of precision.

Often forest inventories require relatively low resolution estimates of stand structure and yield over an entire forest estate formed of hundreds (sometimes millions) of hectares. In such situations, mensuration protocols are needed that are much

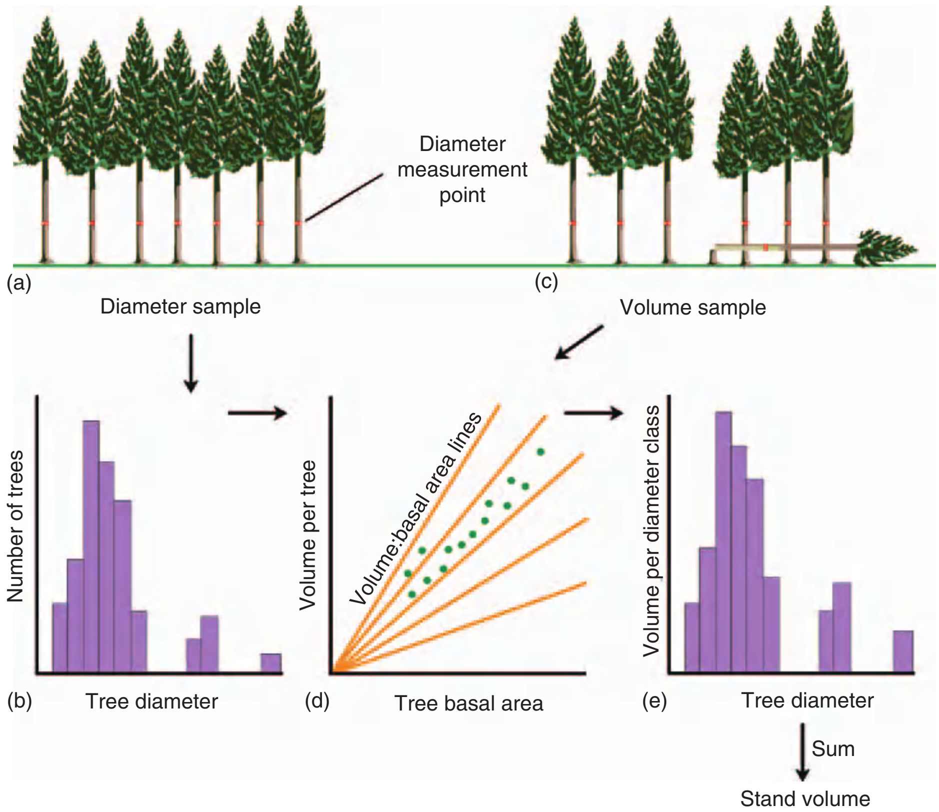


Figure 2 Illustration of intensive forest stand inventory procedure. (a) Count of all trees and diameter measurement of large sample of trees. (b) Construction of diameter frequency distribution based on diameter sample measurements and tree count. (c) Measurement of diameter and stem volume of small sample of trees (in this case by felling). (d) Measurements on volume sample trees are plotted as a scatter diagram of volume versus basal area (calculated from diameters). These are compared against a set of standard charts to determine a specific volume : basal area relationship for the stand. (e) The diameter frequency distribution is combined with the volume : basal area relationship to infer the stand volume in each diameter class, which can be summed to give total stand volume.

cheaper and more rapid to carry out than the sort illustrated in **Figure 2**. A diversity of such 'abbreviated' methods have been developed. The most obvious way is to restrict measurements (including tree counts) to small plots of known area rather than covering the whole stand. The plot level results are then scaled up to give a stand level estimate. Statistical theory can be used as the basis for guidance on the numbers of plots required to provide estimates of stand density, structure, and yield with target levels of precision.

The simplest and cheapest assessment methods dispense with plots, relying instead on 'point measurements' for example of basal area per hectare taken with an optical instrument such as a relascope. Alternatively stand density may be inferred from measurements of a limited number of measurements of distances between trees in the stand.

Simple mensuration protocols usually avoid involving intensive measurements of tree or stand stem volume. Instead these are estimated from measurements of basal area per hectare, individual tree diameters, or height by reference to standard tables or mathematical equations. Estimates may also be derived from yield tables or growth models.

As part of both simple and intensive protocols it may be necessary to estimate quantities of stemwood falling into different categories such as large diameter material suitable for sawlogs, small roundwood, and branches. Alternatively information about stand structure may need to be predicted from more simple measurement; for example, the distribution of tree diameters in a stand might be inferred using a table or statistical distribution function, selected by reference to measured stand mean diameter and assumptions about silvicultural practice. The development of reliable systems for deriving detailed estimates from more easily obtained summary measurements is one of the major tasks of mensuration research.

In all cases, the reliability of estimates derived from mensuration protocols depends crucially on the assumption that assessments are taken in a stand that is distinct in terms of area and uniform in terms of structure. The process of identifying distinct and uniform forest stands comprising a forest estate is known as stratification. Robust mensuration protocols include unambiguous rules for stratifying areas of forest.

Describing and Analyzing Growth

A significant aspect of the work of mensuration researchers involves describing and analyzing the patterns of growth exhibited by different tree species grown on different sites and according to different systems of silviculture.

Analysis of Growth Trajectories

Graphical analysis is a fundamental and frequently used technique which involves plotting sequences of measurements of selected growth variables (**Figure 3**). The sequential measurements, taken on the same tree or sample of trees over time, may be collected at intervals of less than a year or over several years, depending on the rate of growth and on the frequency of perturbations due to environment or management.

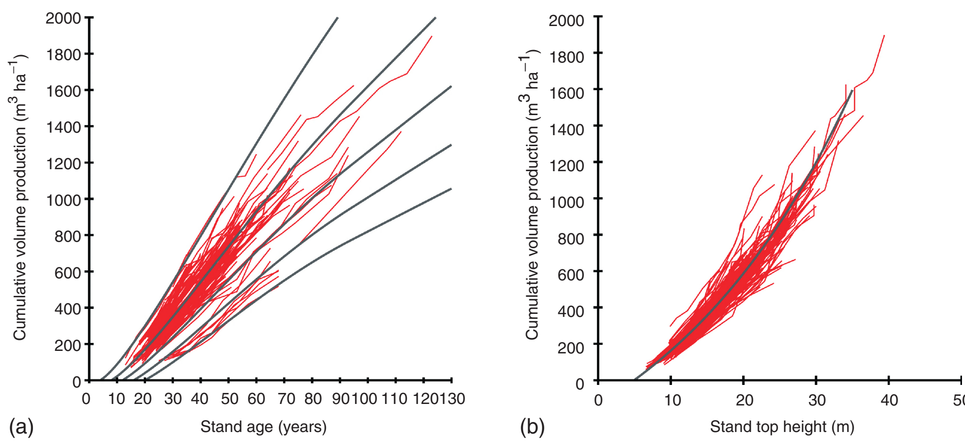


Figure 3 Examples of investigations of growth patterns by plotting trajectories. The graphs are based on assessments taken on stands of Corsican pine (*Pinus nigra* var. *maritima*) in Britain. (a) Cumulative volume production plotted against stand age. The red trajectories show sequences from different stands. The gray lines represent examples from a family of model curves describing the pattern of growth for different levels of productivity. (b) The same cumulative volume production data as in (a) but plotted against stand dominant or top height. Cumulative volume is observed to be more closely correlated with stand top height than with stand age. The gray line shows how the development of cumulative volume production might be described by a single curve with respect to top height. Mensuration researchers use results such as this to simplify the task of building growth models and yield tables.

A graph formed of lines joining the successive measurements of a given variable plotted against age is often referred to as a graph of trajectories. Trajectories may also be formed by plotting measurements of one tree or stand variable against another, in order to explore correlation between different growth variables. Tree level variables may be analyzed in this way but it is more common for growth patterns to be characterized graphically at the stand level. A range of variables may be analyzed, typically including:

- dominant or top height (the average height of dominant trees in a stand)
- mean height
- numbers of trees per hectare
- quadratic mean diameter (the diameter equivalent to a tree with average basal area in a stand)
- standing basal area per hectare
- standing (stem) volume per hectare
- cumulative basal area production
- cumulative volume production.

Traditionally, variables describing aspects of cumulative production, notably cumulative volume, are regarded as important, fundamental measures of growth performance. For an even-aged stand of trees, cumulative volume production is defined as the standing stem volume per hectare observed at a specified stand age plus the sum of all per-hectare volumes harvested as thinnings up to and including that age. Cumulative production has an obvious definition in even-aged stands but there is no widely accepted definition for application to uneven-age stands. Strictly speaking, cumulative volume production does not have any significance as a meaningful physical or biological variable, although it might be regarded as a rough indicator of ecosystem net primary production. The main applications of cumulative volume production are in economic analysis and in support of practical forest management. It has also proved useful in the theoretical development and practical construction of some types of yield models. In essence cumulative volume production represents the outturn of commercial stem volume from a stand up to a given year in the stand's development.

Construction of Growth Curves

Graphs of trajectories are used to construct curves describing the characteristic patterns of growth for the tree species, site types, and silvicultural regimes of interest. In certain circumstances, the shapes of these curves may be established directly by visual inspection of the data and by drawing curves freehand over the trajectories.

However, in the past 40 years mathematical expressions have been formulated for describing tree and stand growth patterns. Sophisticated statistical analysis techniques have also been developed which, when combined with computer software, can be used to calibrate mathematical growth curves based on data collected from trees or stands for the variables of interest.

Parameters of growth curves, estimated for different tree species and growing conditions, may be used as summary statistics indicating the potential growth and yield of different stands. The most common of these is a parameter generally known as the site index, which is usually based on curves describing patterns of height growth in dominant trees in stands (**Figure 4**). Dominant height (sometimes known as top height) growth is often favored as a variable for indicating the influence of site on stand productivity. This is based on the assumption that the growth of dominant trees is relatively unaffected by competition within the stand and not usually influenced by silvicultural interventions,

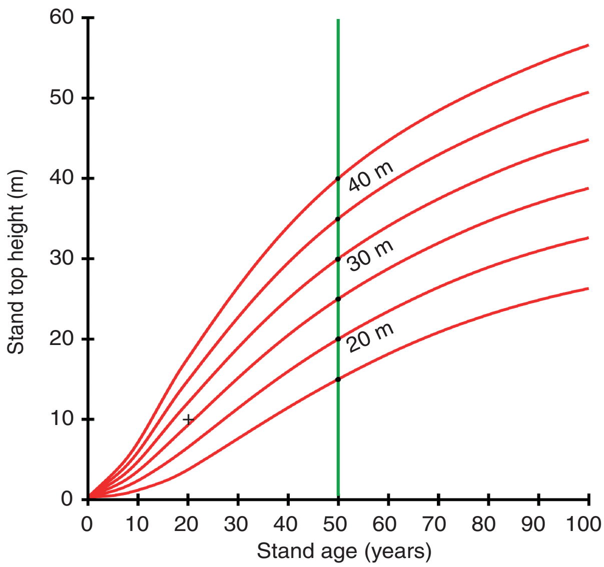


Figure 4 An example of a set of site index curves used for classifying the productivity of even-aged forest stands. The curves are based on observations of top height development with age in stands of Sitka spruce (*Picea sitchensis*) in Britain. Individual curves have been chosen to pass through specific values of top height at a 'reference' or 'base' age of 50 years. Each curve is separated at age 50 years by an interval of 5 m and the height attained at this age is referred to as the site index, for example the curve passing through 20 m represents site index 20. Measurements taken in stands of trees at varying stand ages can be compared to these curves to assess potential productivity. For example, suppose a stand of trees of age 22 years was measured and found to have a top height of 11 m, as illustrated by the black cross. This point is observed to be closest to the curve for site index 25; this curve could be used to forecast future growth potential of the stand.

notably thinning. Furthermore, the height growth of trees and stands has been observed to be much less dependent on stand density than variables such as diameter, basal area, and volume. It follows that height growth, in particular that of dominant trees, should be most strongly determined by the particular growth potential of the tree species comprising the stand in combination with site and other environmental factors.

Analysis of Increment

Mensuration researchers place emphasis on investigating increments of growth variables, indeed increments are among the most explicit representations of growth. They can be calculated for any variable of interest but cumulative volume production is often the focus of attention. Increments can be defined in different ways and three common measures are:

- current annual increment (cai)
- periodic annual increment (pai)
- mean annual increment (mai).

Current annual increment is the actual annual rate of growth of the variable of interest at a specified time. It is sometimes calculated as the difference of two values taken by a variable measured 1 year apart. Occasionally the slope of a curve fitted to a sequence of measurements over time is used to estimate cai. Alternatively periodic annual increment may be used as a surrogate. Records of cai may be used in the investigation of short-term growth trends, for example with respect to management interventions, fluctuations in climate, or episodes of pest infestation.

Periodic annual increment is the annualized growth rate of a variable over a period, typically 5 or 10 years. Measurements of pai are sometimes used in the analysis of forestry experiments for quantifying the growth response due to different experimental treatments.

Mean annual increment is probably the most important of the increment variables and is usually most relevant to the analysis of cumulative volume production. This may be defined as the average rate of cumulative volume production up to a given year. The development of mai follows a characteristic pattern with respect to stand age (**Figure 5**). In the early years of stand development, mai rises steadily from zero to a maximum value. From this point on mai declines steadily, although the rate of decline may be slight in the years immediately following

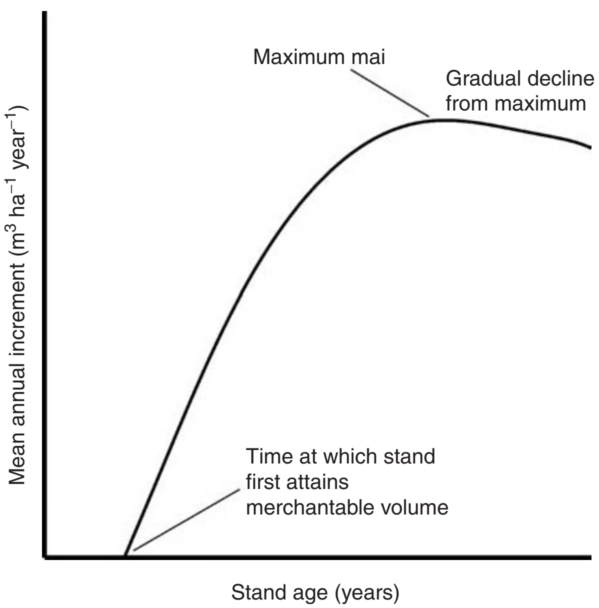


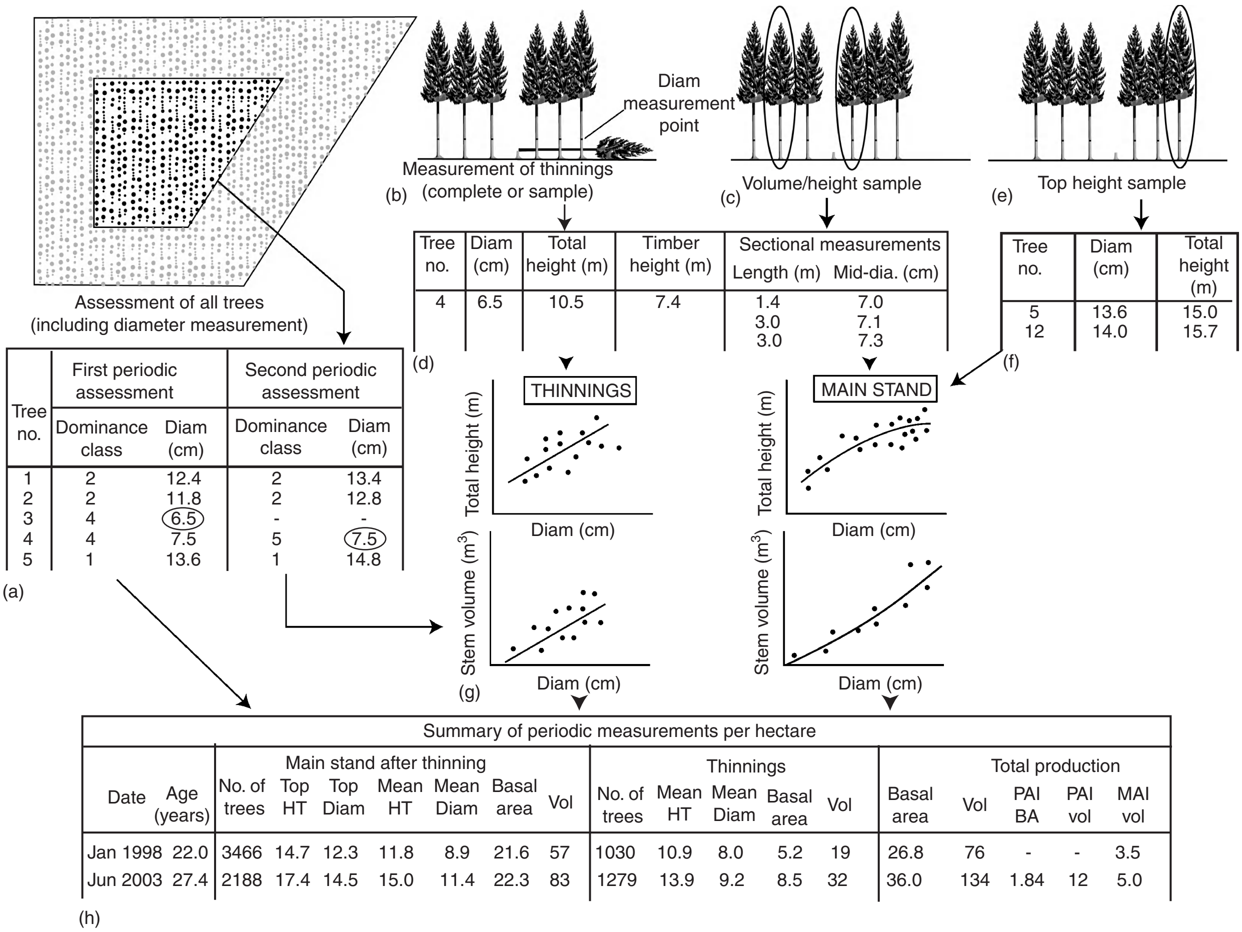
Figure 5 Illustration of the characteristic pattern of development of mean annual increment of cumulative volume production with respect to stand age in even-aged forest stands.

Figure 6 Measurements being taken in a mensuration permanent sample plot. Painted numbers identify the trees in the plot and allow successive measurements to be compared. The horizontal bands on the trees indicate the reference height at which diameter measurements should be taken. Sample plots have been a vital source of data on the structure, growth, and yield of forests. Courtesy of Forest Research Photo Library.

attainment of maximum mai. The existence of a stand age for which mai takes a maximum value may be regarded as being of great commercial significance in the management of even-aged stands particularly if the aim is to maximize sustainable volume production. Specifically, if the maximum value of mai occurs at a predictable stand age then a forest manager may choose to clear-fell the stand at this age. The average rate of volume production over the rotation period will then be equal to the maximum. The forest manager can then replant or regenerate a new stand on the clear-felled site. If this new stand is also grown over the same rotation period then average rate of volume production of the new stand will again be maximal, provided that the fertility of the site has not been depleted and environmental conditions have not changed. Clearly, managing a stand on this site using any other rotation period will result in a lower average rate of volume production.

Applications of Trajectory and Increment Analyses

Analyses of growth trajectories can be applied in some circumstances without further interpretation. For example, suites of curves describing cumulative production and the development of other growth



Tree no.	First periodic assessment: Dominance class	First periodic assessment: Diam (cm)	Second periodic assessment: Dominance class	Second periodic assessment: Diam (cm)
1	2	12.4	2	13.4
2	2	11.8	2	12.8
3	4	6.5	-	-
4	4	7.5	5	7.5
5	1	13.6	1	14.8

Tree no.	Diam (cm)	Total height (m)	Timber height (m)	Sectional measurements: Length (m)	Sectional measurements: Mid-dia. (cm)
4	6.5	10.5	7.4	1.4	7.0
				3.0	7.1
				3.0	7.3

Tree no.	Diam (cm)	Total height (m)
5	13.6	15.0
12	14.0	15.7

Summary of periodic measurements per hectare																			
		Main stand after thinning							Thinnings					Total production					
Date	Age (years)	No. of trees	Top HT	Top Diam	Mean HT	Mean Diam	Basal area	Vol	No. of trees	Mean HT	Mean Diam	Basal area	Vol	Basal area	Vol	PAI BA	PAI vol	MAI vol
Jan 1998	22.0	3466	14.7	12.3	11.8	8.9	21.6	57	1030	10.9	8.0	5.2	19	26.8	76	-	-	3.5
Jun 2003	27.4	2188	17.4	14.5	15.0	11.4	22.3	83	1279	13.9	9.2	8.5	32	36.0	134	1.84	12	5.0

Figure 7 Illustration of the types of measurements taken in mensuration sample plots and how they can be summarized. Standard protocols for measurement and calculation procedures are very important to ensure consistency and quality of data. (a) The sample plot is marked out on the ground with clear boundaries and protected by a marked surround of protecting trees. All trees in the plot are checked, and classified (for example for dominance or form), and diameter is measured. Standard forms or computer programs are used for collecting the assessments. (b) A sample of trees removed as thinnings is measured for diameter and stem volume. (c) A sample of trees remaining in the stand is measured for diameter, height, and stem volume. Measurements of crown architecture may also be collected. (d) The detailed measurements on sample trees are recorded in a standard format. (e) A sample of dominant trees (which may be used for establishing stand top height) is measured for diameter and height. (f) The measurements on the top height sample are recorded in standard format. (g) The detailed measurements of thinnings and standing trees are analyzed to establish correlations between key tree variables specific for the current assessment of the sample plot. For example, the correlation between tree stem volume and diameter is established separately for the standing trees and any thinnings. (h) The full diameter assessment and analyses of sample trees are combined in the calculation of summary estimates of key variables for the sample plot. Measurements taken at different stand ages can be displayed in a standard format and compared.

variables can be used to construct a range of simple yield tables for direct application to forest management. Summary parameters from these analyses, such as site index, can be used for classifying yield potential of real stands, either as part of stand management and production forecasting or as part of a more general inventory system. Sometimes, individual curves and equations developed to characterize particular growth variables are used to support inventory systems, for example in the form of volume tables or equations. Supplementary analyses may also be carried out that extend beyond direct assessment of stands, for example measurements of site index in stands may be analyzed with respect to site and environmental variables so that the potential growth of trees can be predicted for unplanted sites.

Models of increment are useful in a commercial context for very short-term forecasting. However, the main application of increment studies is in a research context, for example, for understanding relationships between tree and stand dynamics and environmental and management factors. As such, the study of increment has in effect developed into the science of dynamic growth modelling.

Sample Plots

Mensuration research depends on high-quality, comprehensive data on the growth and yield of forest stands. Internationally there has been considerable effort over the past 150 years to collect such data either as isolated assessments or through the long-term monitoring of research plots (**Figure 6**). Such research plots are generally known as 'mensuration sample plots' and are categorized as either temporary (one-off measurement) or permanent (repeated, long-term measurements). The data obtained from sample plots have been vital to the understanding of forest growth dynamics, for mensuration research and for development of models of stand structure and yield (**Figure 7**).

Future Developments in Mensuration Research

Although now a well established discipline, mensuration remains an important, arguably fundamental, element of forest research. Research will continue on development of inventory methods and growth and yield models but this is likely to be carried out in a more integrated context. For example, significant scope exists for integrating networks of mensuration sample plots with other forest monitoring networks addressing subjects such as forest condition, biodiversity, or carbon balance. Extension of the research to cover such integration would require the development of a more comprehensive range of measurement protocols and supporting equations and models. Rapid developments in the fields of geographic information systems (GIS) and remote sensing offer opportunities for combining traditional, intensive mensurational assessments with extensive, state of the art technologies such as satellite imagery.

See also: **Inventory**: Forest Inventory and Monitoring; Multipurpose Resource Inventories. **Mensuration**: Forest Measurements; Timber and Tree Measurements; Yield Tables, Forecasting, Modeling and Simulation. **Resource Assessment**: GIS and Remote Sensing.

Further Reading

Adlard PG (1995) Myth and reality in growth estimation. *Forest Ecology and Management* 71(3): 171–176.
Assmann E (1970) *The Principles of Forest Yield Study*. Oxford, UK: Pergamon Press.
Carron LT (1968) *An Outline of Forest Mensuration, With Special Reference to Australia*. Canberra, Australia: Australian National University Press.
Chapman HH and Meyer WH (1949) *Forest Mensuration*. New York: McGraw-Hill.
Hallé F, Oldeman RAA, and Tomlinson PB (1978) *Tropical Trees and Forests: An Architectural Analysis*. Berlin, Germany: Springer-Verlag.
Husch B, Beers TW, and Kershaw JA (2003) *Forest Mensuration*, 4th edn. New York: John Wiley.
Philip MS (1994) *Measuring Trees and Forests*, 2nd edn. Wallingford, UK: CAB International.
Tesch SD (1980) The evolution of forest yield determination and site classification. *Forest Ecology and Management* 3: 169–182.
Vanclay JK (1992) Assessing site productivity in tropical moist forests: a review. *Forest Ecology and Management* 54(1–4): 257–287.
Vanclay JK, Skovsgaard JP, and Pilegaard Hansen C (1995) Assessing the quality of permanent sample plot databases for growth modelling in forest plantations. *Forest Ecology and Management* 71(3): 177–186.

Yield Tables, Forecasting, Modeling and Simulation

A Kangas, University of Helsinki, Helsinki, Finland
J Kangas, Finnish Forest Research Institute, Joensuu, Finland

Introduction

Growth is usually defined as the net periodic annual increments of forest variables and the yield is their summation. Yield tables typically present the amount of forest variables from a given site, under certain prerequisities during a specific period. The period is usually the rotation, and the variables considered are basic forest parameters such as (mean) diameter, mean or dominant height, basal area, number of stems, and volume. Current and mean annual increment are also shown in a typical yield table, as well as yields obtained from thinnings, so that they should actually be called growth and yield tables. An example of a yield table is presented in **Table 1**.

Growth and yield predictions under different management options are a prerequisite in any forest management and planning task. The main purpose for developing the yield tables and yield equations has been to produce accurate predictions of forest yield to enhance decision-making. These models are typically empirical, based on observed development. Thus, although the object of all growth and yield studies is the past growth, their value lies in predicting the future development.

In this article, the historical development from first growth and yield tables to modern single-tree and projection models is briefly presented.

Predicting Forest Growth and Yield

Growth and Yield Tables

The very first growth and yield tables for pure stands were created in the late eighteenth and nineteenth century. In Germany, the number of publications about yield tables reached 1000 by 1880. An important type of table was the so-called normal yield table. In them, the yields of natural, fully stocked stands were shown. As most of the stands are not normal, they were utilized in yield predictions assuming that the relative density of the stand, compared to the normal stand, would remain the same. However, already in the 1930s this assumption was proved incorrect: the relative density was shown to approach that of the normal stands.

Empirical yield tables, on the other hand, presented the mean development of the stands with respect to age in cross-sectional (inventory) data for a large area. The measured stands were not required to be normal. In this way, the tables represent the development of average stands in the area. The tables were produced using graphical smoothing. They were not yet useful for planning the management of the stands, as they represented averages for different areas, sites, and treatment levels.

Later, site-specific yield tables were constructed from long-term experiments by grouping the observations according to site (**Figure 1**). However, site classification is a problematic field in itself. Climatic and soil properties are not easy to classify, and therefore, the observed yields are used as a measure of site quality. In early applications, quality classes based on mean height of the stands were commonly used.

Table 1 Example of yield table of Scots pine

T	H	N	G	V	$\bar{v}$	p_v	I_v	Y_v/T
20	5.6	1800	6.3	19.0	11	24.6		0.95
25	7.7	1800	11.1	42.4	24	14.7	4.7	1.70
30	9.7	1800	15.6	73.6	41	9.9	6.2	2.45
35	11.4	1800	20.0	110.2	61	7.4	7.3	3.15
40	13.1	1800	24.2	150.9	84	5.8	8.1	3.77
45	14.6	1800	28.2	194.5	108		8.7	4.32
45	14.6	1033	19.4	136.1	132	5.2		4.32
50	15.9	1033	22.9	171.4	166	4.2	7.1	4.60
55	17.1	1033	25.8	207.4	201	3.6	7.2	4.83
60	18.2	1033	28.8	244.2	237	3.1	7.4	5.05
65	19.2	1033	31.6	282.2	273		7.5	5.24
65	19.2	628	21.8	197.6	315	3.1		5.24
70	20.1	628	24.5	228.2	363	2.6	6.1	5.30
75	21.0	628	26.6	257.6	410	2.3	5.9	5.35
80	21.7	628	28.8	287.2	457	2.1	5.9	5.38
85	22.4	628	30.9	316.9	505	1.9	5.0	5.41
90	23.0	628	33.0	346.7	552	1.7	6.0	5.44
95	23.5	628	35.0	376.3	599	1.6	5.9	5.47

T, biological age (a); *H*, dominant height (m), *N*, number of stems; *G*, basal area ($m^2 ha^{-1}$); *V*, volume ($m^3 ha^{-1}$); $\bar{v}$, mean size of stems (dm^3); p_v, mean annual volume increment percentage of the future 5-year period (%); Y_v/T, mean annual volume increment up to the age in question ($m^3 ha^{-1}$).
Scots pine: $H_{100} = 24$ m, 100 years rotation, and two thinnings with 30% removal.
Reproduced from Vuokila Y and Väliaho HT (1980) Viljeltyjen havumetsiköiden kasvatusmallit. *Communicationes Instituti Forestalis Fenniae* 99(2): 271, with permission.

Nevertheless, other approaches, for example, based on mean annual increment were also applied. In recent years, the dominant or top height has been the most commonly used variable in quality classification (**Figure 2**). This is because it is assumed to be the stand characteristic least affected by thinning in the stands. In mixed and uneven-aged stands this might be a dubious assumption. For such cases, classification based on basal area index has also been proposed. In some countries, for instance in Finland, site classification based on ground vegetation has been used.

These provisional yield tables were density-free, meaning that an average intensity of thinning was assumed for all stands. Such tables could be used to compare managed and unmanaged stands, but for more detailed planning they were not very useful. In multiple yield tables, there might be two or three different management options, the yields of which could be compared.

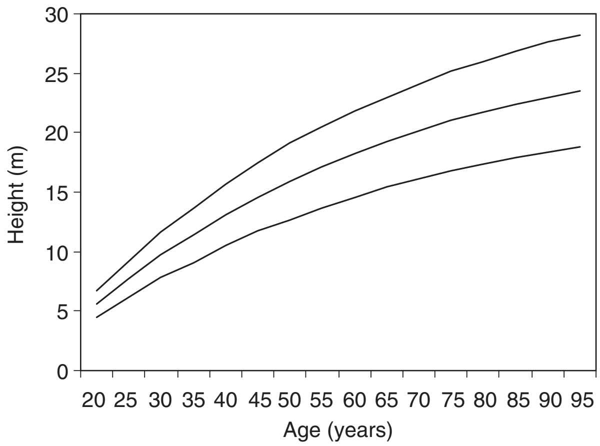


Figure 1 Example of height–age models for site classification.

Even these multiple yield tables are problematic in forest management planning, as they are restricted to the few specific management options. Therefore, variable-density yield tables were needed. These tables are based on statistical models that can simulate the development of the stand under different conditions. Another approach, used particularly in north America, was explicitly to model the change in relative stand density, and to use this information together with normal yield tables to produce growth and yield predictions.

The development of yield tables was quite straightforward as long as pure stands were considered. Such yield tables have been used until recently in most countries, and in tropical countries they are still used. However, mixed stands have always been a problem for both yield tables and equations. The yield tables and equations can only represent a restricted number of different conditions. Therefore, in order to utilize the stand level models, a huge number of parameterizations would be required for different species mixtures, making the practical usefulness of the yield tables for mixed stands very limited. However, examples of such tables can be found.

Growth and Yield Equations

For modeling the growth of stands, two types of models can be separated with respect to the time period considered. The first possibility is to predict the increment of basal area or volume in a period of a certain length, typically 5 years. The development is then calculated by summing subsequent predictions. This type is frequently used in Finland, for instance. Another possibility is to project the development of the desired variables, such as dominant height or basal area, for a desired time. These models, which

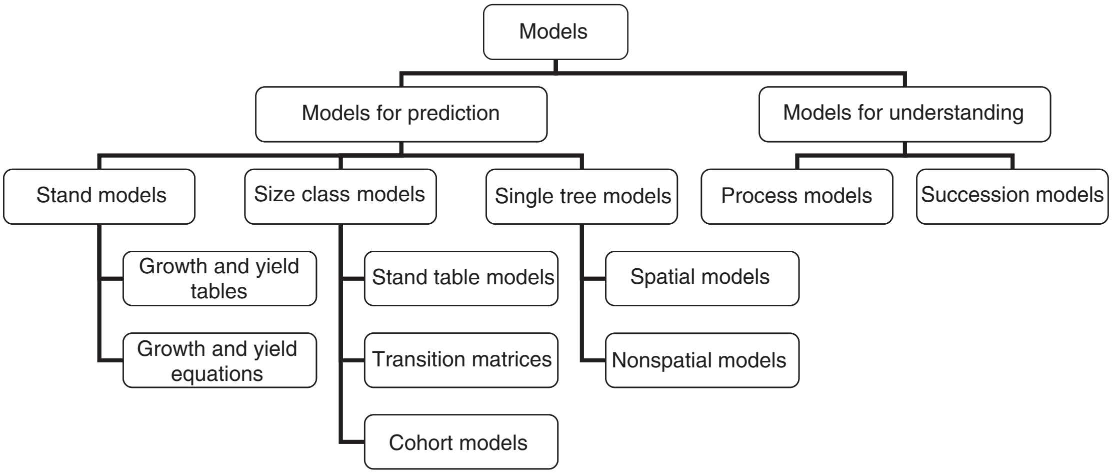


Figure 2 The model classification. Simplified from Porté A and Bartelink HH (2002) Modelling mixed forest growth: a review of models for forest management. *Ecological Modelling* 150: 141–148, with permission from Elsevier.

are called projection models, are commonly used in north America and in tropical forestry.

At the beginning, equations were mainly used to construct yield tables. The first models typically predicted yield as a function of age. Assuming that the parameters of yield models depend on site index and stand density, their effect could be accounted for in the model. Uneven-aged or mixed stands were analyzed, for example, by classifying the data according to species composition and silvicultural history, and by estimating a different parameter set for each group.

Nevertheless, yield equations always assume a certain management regime throughout the projection, but growth equations allow treatments to be defined as desired. The models published by Vuokila for Scots pine (*Pinus sylvestris*), for example, predicted the growth percentage of basal area, dominant height, and volume as a function of stand age, dominant height, basal area, percentage of basal area removed in thinning, and mean diameter. The growth percentage was defined for growth between two successive thinnings.

In those early days, growth and yield models were constructed independently of each other. Therefore, summing up the growths might not produce the predicted yield. To obtain compatible growth and yield estimates many forms of differential equations have been used. Such growth function can be integrated to obtain the yield and growth function can be obtained as a derivative of the yield function. An example of such models is the famous Chapman–Richards equation where growth is described by the equation:

$$\frac{\mathrm{d}x}{\mathrm{d}y} = k\left(\frac{A-y}{A}\right)y$$

and the yield by the equation:

$$y = B(1-\mathrm{e}^{-kx})^{1/1-m}$$

where k, A, B, and m are parameters. In this model type, only one independent variable can be included, typically the stand age.

Obtaining compatible growth and yield equations for several variables from multiple regression models was a challenge that has been tackled from the early 1960s. For example, the equation system proposed by Clutter is:

$$\begin{aligned} E[\ln(V_1)] &= \beta_0 + \beta_1 S + \beta_2 A_1^{-1} + \beta_3 \ln(B_1) \\ E[\ln(V_2)] &= \beta_0 + \beta_1 S + \beta_2 A_2^{-1} + \beta_3 \ln(B_2) \\ E[\ln(B_2)] &= (A_1/A_2)\ln(B_1) + \alpha_1(1 - A_1/A_2) \\ &\quad + \alpha_2(1 - A_1/A_2)S \end{aligned}$$

where V, B, A, and S denote volume, basal area, age and site index, respectively, and β and α are parameters. The subscript in stand variables denotes the time.

In order to obtain compatibility, the system of equations was solved so that $\ln(B_2)$ was substituted with $E[\ln(B_2)]$ in the function of $E[\ln(V_2)]$. Therefore, parameters for projecting the basal area could be solved from parameters of the volume functions. The volume equation can be differentiated to produce a growth function:

$$\frac{\mathrm{d}V}{\mathrm{d}t} = \beta_2(V/B)\left(\frac{\mathrm{d}B}{\mathrm{d}t}\right) - \beta_3 V/A^2$$

This formulation led to compatible equations for standing volume, basal area growth, volume growth, predicted basal area, and predicted stand volume.

This approach is heavily based on stand age as an independent variable. Therefore, it is not suitable for uneven-aged stands, where the definition of stand age is at best ambiguous. For uneven-aged stands, a formulation based on stand density (defined by basal area) was introduced. A following system of equations, also providing compatible estimates, was used:

$$\begin{aligned} V &= \beta_0 B^{\beta_1} \\ \left(\frac{\mathrm{d}V}{\mathrm{d}t}\right) &= \beta_1 V B^{-1}\left(\frac{\mathrm{d}B}{\mathrm{d}t}\right) \\ \left(\frac{\mathrm{d}B}{\mathrm{d}t}\right) &= nB^m - kB \end{aligned}$$

In this approach, the parameter estimates are inefficient in statistical respect, i.e., estimates with better statistical quality could be derived. Therefore, in later applications, simultaneous estimation methods such as two- and three-stage least-squares and seemingly unrelated regression have been used. With these methods, compatibility can be achieved between the prediction and projection models in the system of equations.

Utilizing Size Class Models

Current yield Later, the growth and yield equations were used to construct stand growth simulators for computers. After that it was possible to compute yield tables for any desired management schedules that were computable. These first stand simulators, however, could not produce enough information for modern forest management. There was a growing demand for single-tree information. For example, the timber assortments and value of the stand are difficult to predict with stand information.

Therefore, information concerning the frequencies in different diameter classes, i.e., diameter distribution, was strived for. The current yield is often predicted using probability density functions such as normal, log-normal, beta, gamma, Johnson's S_B or Weibull. For Weibull, an analytical cumulative distribution is available. It describes the probability of values smaller than x. It is of the form:

$$F(x) = 1 - \exp\left[-\left(\frac{x-a}{b}\right)^c\right]$$

The proportion of trees in any diameter class $[d_1, d_2]$ can be calculated from the distribution function F as $F(d_2) - F(d_1)$. The diameter distribution can also be formulated with respect to basal area. Then, the distribution gives the proportion of stand basal area in desired diameter classes. It is a weighted version of diameter distribution, which gives more emphasis to the most valuable trees in the stand.

For predicting the distribution, two main methods have been applied, namely the parameter prediction method (PPM) and the parameter recovery method (PRM). In PPM, the parameters of some distribution function, for example the Weibull distribution, are predicted with regression models from measured stand characteristics. In this approach, site index and age may be quite poor predictors of the parameters, but mean (or median) diameter usually gives a fairly good fit. In PRM, the parameters of the distribution function are solved from a system of equations, equating (measured or predicted) stand attributes to their analytical counterparts. The characteristics can be, for example, percentiles or moments of diameter distribution. In some cases, some of the parameters are predicted and others are solved using a parameter recovery approach.

Another possibility is to use a percentile-based diameter distribution method. In this method, a number of percentiles (of frequency or basal area) across the range of diameters are defined. Usually 12 or more percentiles are used. The distribution is obtained either by linear interpolation (i.e., assuming a uniform distribution of frequencies between adjacent percentiles) or any other monotony-preserving interpolation method. Recently, the distributions have also been predicted using nonparametric approaches. Then, the tree list is obtained as a weighted mean of tree lists from measured stands similar to a target stand.

The predicted diameter distribution is usually scaled to the measured number of stems, so the stem number obtained from the distribution corresponds to the known characteristic. Using the parameter prediction method or nonparametric approach, there is no guarantee that other stand characteristics obtained from the predicted diameter distribution correspond to the measured stand characteristics. With PRM, the compatibility of predicted and measured stand characteristics can be guaranteed for the characteristics used for solving the parameters of the diameter distribution function. Recently, calibration or adjusting techniques have been proposed for such situations.

Future yield When growth of a stand is predicted via size class models, both the current and future stand table are predicted, and the growth is calculated implicitly from the differences between the yields obtained from these tables. A simple way to accomplish such predictions is to predict the parameters of a probability distribution as a function of age and site for desired time points. Another possibility is (simultaneously) to project variables such as number of stems, basal area, and dominant height, and to predict the distribution in the future based on these variables. Then, however, the diameter distributions at different time points are not necessarily compatible.

To obtain a logical development of the distribution, the changes in the diameter distribution are directly predicted. This can be done, for example, by projecting the development of the parameters of the used probability distribution (PPM) or the development of percentiles of diameter distribution for a given time. In the latter case, the future distribution is obtained by analytically solving the parameters of the probability distribution from these percentiles (PRM) or by interpolating between the predicted percentiles (percentile-based method).

It is also possible to project the stand table directly. Then, the whole tree list is assumed to be known. The development of the list is based on an assumption that the relationship between the basal area of a tree and the average basal area follows a certain function. The stand table is constrained so that the projected number of stems and the basal area are consistent with the whole stand estimates. A mortality function is an important part of this system. Such models are already approaching modern single-tree models.

In the matrix approach, the stand is also described with the aid of size classes. These models, however, are stochastic. The model predicts the development of the stand via the probability that a tree will grow up to the next size class, die, or remain in its current class. Therefore, matrix models implicitly include models for recruitment and mortality. The probabilities are usually assumed to depend only on the current size of the trees. The results of these models are the frequencies of trees in different size classes.

The matrix models used are referred to as Usher, Lefkovitsch, or Leslie matrices depending on their characteristics: Leslie used age classes for animal populations, Lefkovitsch used development classes for insects, and Usher used diameter classes for forests. If the probabilities of movements are expressed as a matrix **M**, and the initial and final state of the stand with vectors $\mathbf{V}_0$ and $\mathbf{V}_1$, the prediction for one period is obtained as

$$\mathbf{V}_1 = \mathbf{M}\mathbf{V}_0$$

and for n periods as

$$\mathbf{V}_1 = \mathbf{M}^n\mathbf{V}_0$$

It has been argued that the maximum exploitation of the stand and the stable stand structure can be revealed from the first eigenvalue and eigenvector of matrix **M**. However, they cannot be used to evaluate the optimal density of the stand.

One obstacle in using matrix models for growth prediction is that the basic models do not allow for probabilities to change in time, e.g., as a function of stand density or structure. This problem can be avoided, however, by estimating a new matrix for each iteration using equations.

Assessing the Accuracy of Predicted Forest Development

Models need to be evaluated before they are used in real-life applications. Evaluating growth and yield models requires both qualitative and quantitative analysis. The qualitative analysis of the logics and biological consistency are as important as quantitative analysis of statistical properties. However, the models cannot be proved correct in evaluation: they can only be validated with respect to their usefulness in the applications for which they are meant.

The accuracy of different growth and yield models has been assessed with empirical validation studies. The simpler the models are, the more often they are also validated. The stand level models have generally performed better in these tests than the tree level models, due to the cumulating errors in the tree level. This concerns the short-term predictions — in the long term there are very few validation studies. Consequently, the long-term results may be much worse than expected.

The empirical accuracy assessments based on validation studies are, however, calculated for certain past time periods and for a certain area. To anticipate the precision and accuracy of future predictions, a model-based approach is required. It is possible to model directly the observed past errors of interesting variables predicted using the simulator.

There are also methods for assessing the accuracy of predictions which are not based on empirical validation studies. For instance, the precision of long-term predictions has been assessed through Monte Carlo simulation or Taylor series approximations, where the total prediction error is composed of several error sources. These methods can be applied in producing error budgets for simulators. Such budgets give the contribution of each and every error source in the results. On the other hand, it is difficult to take all sources of error into account. For example, the errors in the model structure, causing biased predictions, are difficult to incorporate into these methods. Yet, in the long term, the model misspecifications may be the most important source of error.

Data for Growth and Yield Modeling

For standwise growth and yield tables, data not identifying individual trees are sufficient. The simplest estimate for growth is the difference between the volumes from two points of time. However, accounting for mortality and recruitment requires more information. Net growth can be defined as:

$$\Delta V = V_2 - V_1 + V_c$$

where V_c is the harvested volume. Gross growth is obtained by adding mortality V_m to the net growth. The growth of the trees observed at both time points is defined as survivor growth.

Permanent, temporary, and semitemporary plots have been used for estimating yield tables and equations. The first tables were based on temporary plots, but permanent plots have later been used in most countries. The obvious explanation for this is that temporary plots do not provide a good basis for analyzing the effect of different management options. However, at the time the first permanent experiments were established, statistical principles such as replications were not known. This somewhat reduces the value of the experiments.

If a retrospective analysis of the development of the stands can be accomplished, temporary plots may, however, be a fairly good option. Temporary plots are cheap and fast to measure, in contrast to permanent plots. In temporary plots the measurement personnel, equipment, and calculation techniques do not vary in the data. Furthermore, the studied treatments are not restricted to a few possibilities, and they can be chosen to be up-to-date options. In temporary plots, natural damages do not affect the studies. Nevertheless, the treatments carried out before the measurements are difficult to define afterwards.

Semitemporary data remeasured at fixed intervals may be a suitable compromise for most occasions. However, the remeasurements should cover a sufficient period in order to include the whole range of variation due to weather conditions. It is also important to cover the extreme densities and treatments in the data. The remeasurement intervals also need to be long enough to ensure that growth can be detected from noise introduced by measurement errors.

Final Remarks

Forest simulators have been developed from simple standwise yield tables and models to increasingly complex single-tree models. The new models are more flexible and suitable for many applications, for mixed stands and even for changing management practices. The causal relationships governing the growth of forests are easier to account for in single-tree models than is a stand model. However, the accuracy of the predictions has not been improved likewise. On the contrary, the more complex a simulator is, the more uncertain the predictions may be.

All in all, it is important to study the contribution of different sources of uncertainty (i.e., to formulate error budgets) to concentrate research efforts where they are most needed. It may well be that the main source of uncertainty is not the growth simulator at all, but the quality of initial data, for example. It would also be useful to separate the inherent randomness of growth from pure ignorance.

See also: **Experimental Methods and Analysis**: Statistical Methods (Mathematics and Computers). **Inventory**: Modeling. **Mensuration**: Forest Measurements; Growth and Yield

Further Reading

Assmann E (1970) *The Principles of Forest Yield Study*. Oxford, UK: Pergamon Press.

Bailey RL and Dell TR (1973) Quantifying diameter distribution with the Weibull-function. *Forest Science* 19: 97–104.

Borders BE and Bailey RL (1986) A compatible system of growth and yield equations for slash pine fitted with restricted three-stage least squares. *Forest Science* 32: 185–201.

Borders BE and Patterson WD (1990) Projecting stand tables: a comparison of the Weibull diameter distribution method, a percentile-based projection method, and a basal area growth projection method. *Forest Science* 36: 413–424.

Buongiorno J and Mitchie BR (1980) A matrix model for uneven-aged forest management. *Forest Science* 26: 609–625.

Clutter JL (1963) Compatible growth and yield models for loblolly pine. *Forest Science* 9: 354–371.

Hyink DM and Moser JW (1983) A generalized framework for projecting forest yield and stand structure using diameter distributions. *Forest Science* 29: 85–95.

Kangas A (1999) Methods for assessing the uncertainty of growth and yield predictions. *Canadian Journal of Forest Research* 292: 1357–1364.

Maltamo M (1998) Basal area diameter distribution in estimating the quantity and structure of growing stock. DSc (Agr. and For.) thesis summary. Reports of the Faculty of Forestry 67. Joensuu, Finland: University of Joensuu.

Moser JW Jr and Hall OF (1969) Deriving growth and yield functions for uneven-aged forest stands. *Forest Science* 15: 183–188.

Pienaar LV and Turnbull KJ (1973) The Chapman–Richards generalization of von Bertalanffy's growth model for basal area growth and yield in even-aged stands. *Forest Science* 19: 2–22.

Porté A and Bartelink HH (2002) Modelling mixed forest growth: a review of models for forest management. *Ecological Modelling* 150: 141–188.

Pretzsch H (2001) Models for pure and mixed forests. In: Evans J (ed.) *The Forests Handbook*, vol. 1, pp. 210–228. London, UK: Blackwell Science.

Vanclay JK (1994) *Modelling Forest Growth and Yield: Applications to Mixed Tropical Forests*. Wallingford, UK: CAB International.

Vuokila Y (1966) Functions for variable density yield tables of pine based on temporary sample plots. *Communicationes Instituti Forestalis Fenniae* 60: 4.

Wiedemann E (1949) *Ertragstafeln der wichtigen Holzarten bei verschiedener Durchforstung sowie einiger Mischbestandsformen mit graphischen Darstellungen*. Hannover.

Tree-Ring Analysis

M Worbes, University of Göttingen, Göttingen, Germany

Introduction

Tree-ring analysis or dendrochronology is both an old and a modern science. Just counting tree rings sounds simple, but in the context of forest dynamics tree age is an important and valuable parameter. The pattern of tree-ring width, wood density, element content, and other features store information on past growth conditions. Biomonitoring is the reflection of growth factors by biological organisms and their change in time. Tree-ring analysis extends the monitoring period considerably into the past and could be considered as retrospective biomonitoring.

For a long time dendrochronology (from Greek: dendros, tree; chronos, time, and logos, science) was associated with the dating of old houses, paintings, and archaeological samples. In recent decades however it has become a science with a broad range of applications such as global climate change, canopy process decline, the carbon cycle, and many others. Due to its manifold applications for other branches of science dendrochronology is sometimes considered as just a tool for archaeology, art history, biology, climatology, forestry, glaciology, etc. The development of techniques like X-ray densitometry, isotope analysis, special statistical analysis for tree ring interpretation, etc., together with new aspects in the theory of tree-ring formation mean that tree-ring analysis should be considered as an independent branch of earth science.

History of Dendrochronology

Leonardo da Vinci, who in the sixteenth century realized the relation between climate and widths of tree rings, is considered the father of dendrochronology. The beginning of broad scientific knowledge of wood formation, tree rings and climate, however, can be dated to the middle of the nineteenth century, when Theodor Hartig and others postulated their theory of tree-ring formation as a consequence of low temperature in winter. Additional milestones reflect the progress in dendrochronology during the last 150 years.

- 1927: Ch. Coster, a Dutch forester, proved the existence of annual tree rings in the tropics for many species on Java and explained the climatic background.
- 1935: First age dating of a wood sample by cross-dating the tree ring patterns of a construction beam by A. E. Douglass (Pueblo Bonito).
- 1954: E. Schulmann found the oldest living tree in the white mountains of California (bristlecone pine (*Pinus longaeva*): 4798 years).
- 1976: Hal C. Fritts introduced statistical methods to analyze climate signals in tree ring sequences as the base for climate reconstruction using tree rings.
- 1983: Fritz H. Schweingruber established modern dendro-ecology and developed X-ray densitometry.
- 1993: B. Becker developed the longest oak chronology with 11 800 years of tree rings in southern Germany.

Wood Anatomy and the Ecological Background of Tree-Ring Analysis

It is still widely assumed that tree rings occur only in the temperate and boreal zones. The gradual deceleration of growth until cambial dormancy as a consequence of low temperature results in the formation of latewood, which differs structurally from the earlywood of the previous growing season.

In general three different types of climatic seasonality affect annual tree growth (**Figure 1**):

1. Variation of annual temperature with temperature near or below the freezing point in winter.
2. Annual flooding of the great river systems in the tropics (e.g., the River Amazon) rising up to 5 m above the forest floor for 6 or more months per year causes anoxic conditions in the soil. Root respiration and water uptake is hindered; many species shed their leaves and have a cambial dormancy. This is reflected by annual rings in the wood.
3. Variation of precipitation between rainy season and dry season. This climate type covers the major part of the tropics.

Tree rings are bound to the process of secondary radial growth of the xylem. This is the case in gymnosperms and dicotyledonous angiosperms. Woody monocotyledons never form tree rings due to the absence of secondary xylem. In general, growth zones can be classified into four basic anatomical types according to the features at the ring boundaries (**Figure 2**). Many species combine several of the four growth zone features.

Type 1

Density variations occurring in gymnosperms as a unique feature and in broadleaved trees together with one or more of the following features: cell wall thickness becomes greater and the cell lumen becomes smaller from earlywood to latewood (all coniferous species, Annonaceae, Verbenaceae, Lauraceae, and many other families).

Type 2

Marginal parenchyma bands run around the entire cross-section and consist usually of one or few cell rows (Annonaceae, Bignoniaceae, Leguminosae, Meliaceae).

Type 3

This is the tissue pattern type. The most complicated and frequently misinterpreted structure is to be found in Euphorbiaceae, Moraceae, Sapotaceae,

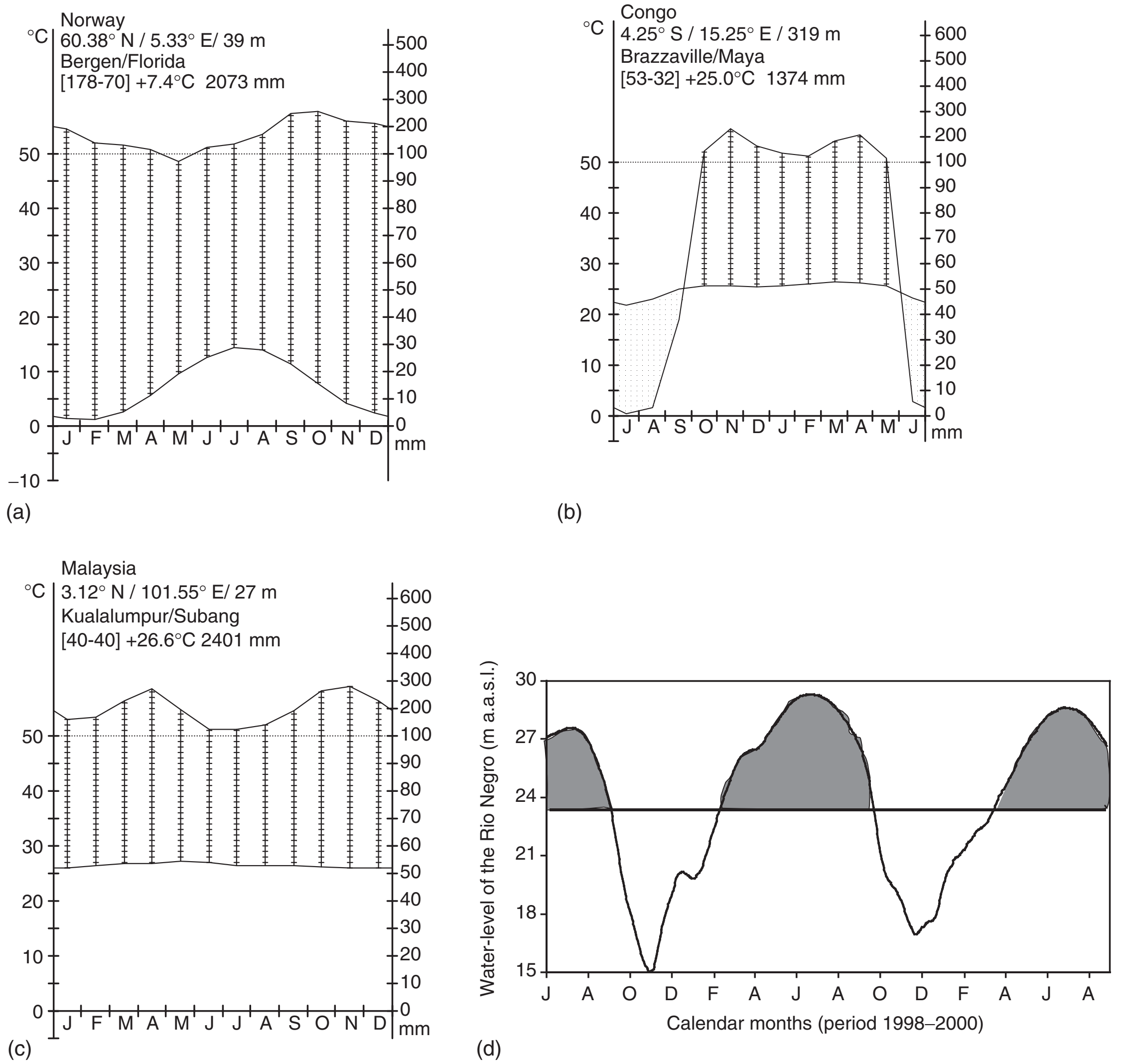


Figure 1 Typical climate diagrams from (a) the temperate zone, the tropics ((b) seasonal and (c) everwet), and (d) the flooding regime of the Amazon river. Seasonality is expressed in high latitudes through temperature variation, in low latitudes through variation in precipitation in the course of the year.

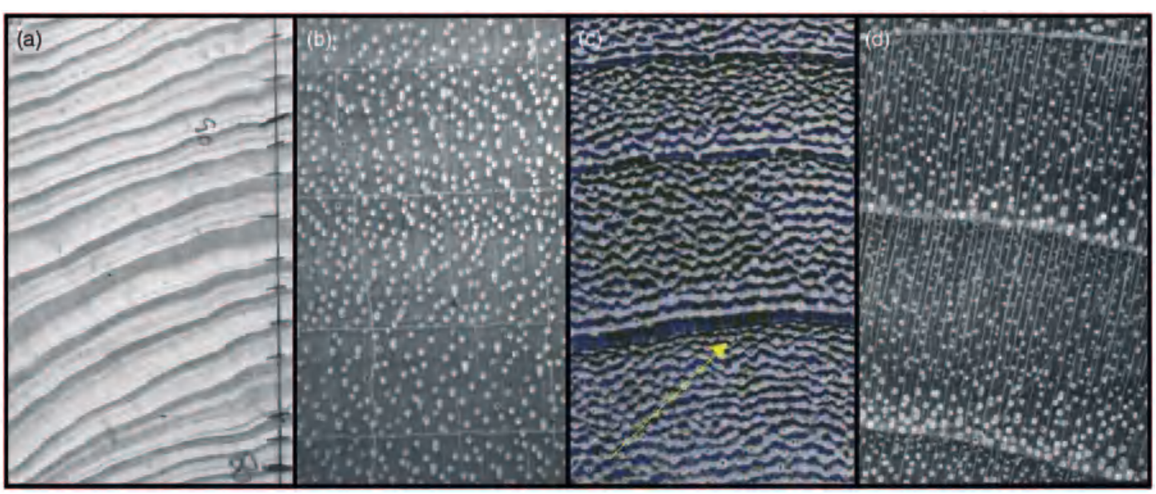


Figure 2 Wood structure of (a) *Pinus caribaea* (São Paulo, Type 1), (b) *Tetraberlinia bifoliolata* (Cameroon, Type 2), (c) *Piranhea trifoliata* (Brazil, Type 3), and (d) *Tectona grandis* (historical wood sample from India, Type 4).

Bignoniaceae, in *Ulmus* spp., *Fraxinus* spp., and many others. Rings are characterized by periodical patterns of parenchyma and fiber tissue. The bands usually become narrower towards the end of a growth zone.

Type 4

This type has vessel distribution in the growth zone. Ring porousness is widely distributed in the temperate zones (e.g., *Quercus*) but occurs in only a few examples in the tropics (e.g., *Tectona grandis*, and some Meliaceae).

Basic Principles of Dendrochronology

One of the most important dendrochronological techniques is the comparison of tree-ring time series of different trees. This is based on ecological principles.

Variation of Tree-Ring Features from Year to Year Based on the Influence of Growth Factors, Mainly on Climate Variations

This is a specification of the ecological rule of limiting factors, especially temperature, radiation, and precipitation which vary from one year to the other. This variation is the reason for the existence of unique tree-ring patterns and makes possible the identification of certain growth time periods. Site conditions influence the intensity of reaction to these factors. Sensitive species usually show great variations in ring width from one year to the other while complacent trees react little.

Since the Climate Influences All Trees on a Given Stand Equally, Tree-Ring Patterns Are Similar between Individuals of a Stand

The degree of similarity depends on the distance between growing sites, the climatic variability in a region and the ecological range of a tree species. As an example oak tree-ring chronologies from sites in the flat plains of northern Central Europe have a high degree of similarity and are even comparable with chronologies from Ireland, both being influenced by an oceanic climate type. Chronologies from spruce (*Picea* spp.), however, may differ over a short distance when the trees grow at different elevations.

Every Ring Can Be Dated to a Certain Growing Period or to a Calendar Year

Tree-ring patterns are the mirror of the growth conditions of a tree. The rings and their features represent an archive of growth conditions during a tree's life.

Methods

Sample Collection and Preparation

One advantage of dendrochronological investigations is the low impact on the living tree when samples are taken with an increment corer. For yield estimations stem disks are chosen from breast height. In dendrochronologically unknown or seldom used species it is helpful to start with the investigation of a cross-section. The structure of the growth zones and the occurrence of matching and wedging rings can be more easily identified on a stem disk than on a small core beam.

The core samples must be glued in wooden supports. Careful preparation of the sample surface is essential for a successful analysis. This can be carried out by polishing the sample with sandpaper of increasing gradation.

Data Measurements

Douglass built chronologies to date the Pueblo Bonito group by estimating and classifying the ring widths in three classes ('skeleton plots'). This method is based on the concept of 'pointer years,' which are substantially smaller or wider than the neighboring rings (**Figure 3**). This system was further developed by Schweingruber and extended to 'abrupt growth changes' (**Figure 4**). In most cases ring widths will be measured by means of a typical measuring device usually with a precision to the nearest 0.01 mm.

Besides ring width several additional features of tree rings were tested in the past for climatological or ecological signals. One of the most important is wood density. A thin sample is irradiated with X-rays, thus developing an image of its density on a film. A densitometer measures the darkness of the film indicating the variations in density (**Figure 5**). The results provide several kinds of information. It is obvious that the latewood of coniferous trees from high elevations and high latitudes carries a strong

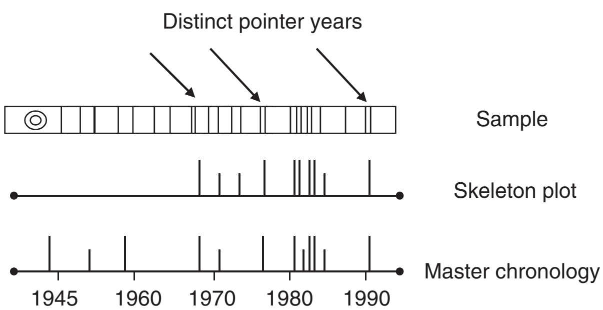


Figure 3 Translation of ring width variation into a skeleton plot and the comparison with a master chronology (below). Small rings are indicated by a bar of different length corresponding to the intensity of growth reduction.

climate signal, i.e., the temperature of the late summer. Recently image analysis has played an increasing role in dendrochronology in the search for additional relevant signals of climate. Time series of tree-ring features such as vessel size and vessel area may help to clarify the relation between tree growth and rainfall patterns (**Figure 6**).

The content of chemical elements and isotopes in tree rings has been tested in different situations. The best results can be expected from elements and isotopes which are bound to the cell wall structure. Some other elements tend to be mobile within the stem. The content of these elements can serve for the detection of environmental stress. Stable isotopes, especially those which are part of the cellulose molecule (D, ^{13}C, ^{18}O) have recently been used to test for climatological signals.

Radioactive isotopes, especially radiocarbon, play an important role in dendrochronology. The analysis of exactly dated oak and bristlecone pine wood samples have served to calibrate the radiocarbon concentration curve for the past 12 000 years. This was necessary since the concentration of CO_2 in the atmosphere has varied considerably in the past and one radiocarbon date could be linked to more than one calendar age (**Figure 7**). The calibration was the precondition for a much higher precision of radiocarbon dating of archaeological samples. Furthermore ^{14}C estimations can be used to test the existence of annual rings in tropical trees. Based on the atomic weapon effect (the ^{14}C content in the atmosphere almost doubled between 1950 and 1964 because of 404 atomic bomb explosions in the atmosphere) single isolated growth zones can be dated by comparing their radiocarbon content with that of the atmosphere (**Figure 8**).

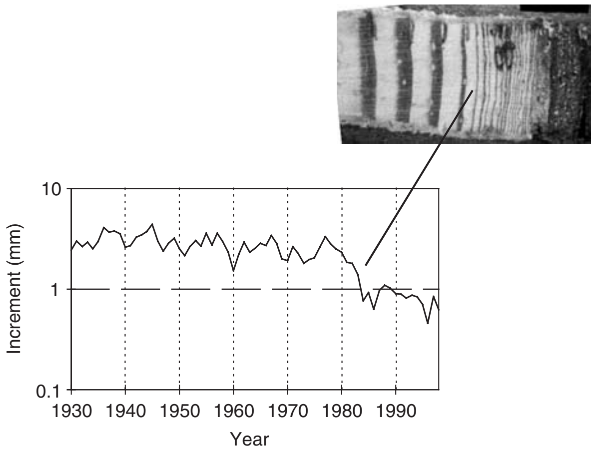


Figure 4 Example of an abrupt growth reduction in Scots pine (*Pinus sylvestris*) and the corresponding ring curve.

Cross-Dating of Ring Curves

The second principle of dendrochronology, the comparison of tree-ring patterns of different individuals, requires tools and limits for matching ring curves. Typical statistical methods are correlation, Student's *t*-test, which combines correlation and length of the compared time series, and the

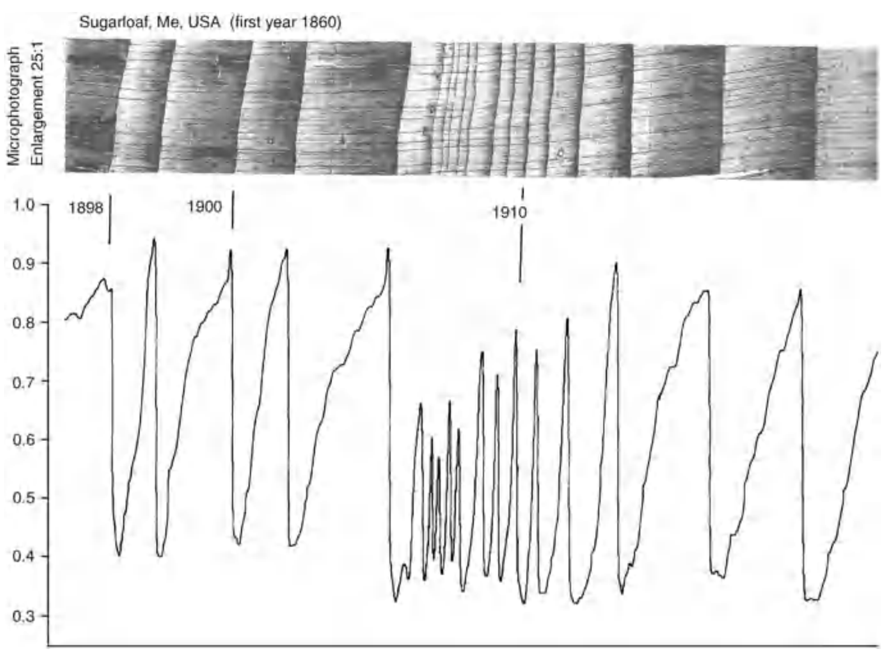


Figure 5 Microsection and corresponding densitogram of pine (*Pinus sylvestris*) derived from X-ray densitometry. Note the variation within one ring and also year by year. 1951 has a considerably lower maximum density than the previous year.

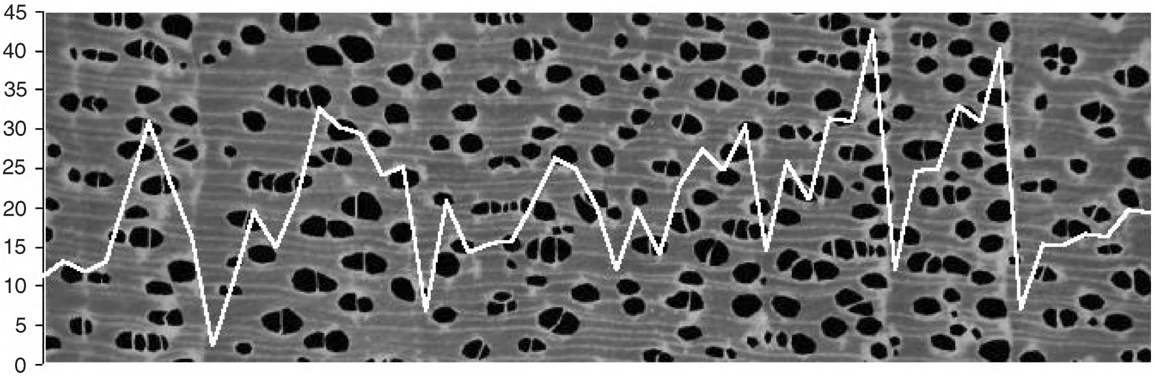


Figure 6 Image analysis of *Terminalia sericea*. In the digitized photograph different features like the vessels can be highlighted, and their dimensions will be measured automatically. The line shows the intra-annual change of vessel area as a percentage of the entire cross-section.

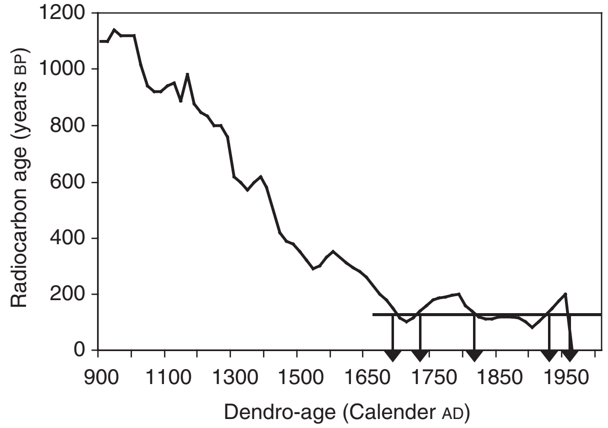


Figure 7 Calibration curve for radiocarbon values to (real) dendro-ages. The curve is derived by analysing tree rings from exactly dated bristlecone pine and European oak. It shows the fluctuation of past ^{14}C content in the atmosphere. The variations between 1650 and 1950 impede the age dating of wood samples from this period, since one radiocarbon age has several possible dendro-ages.

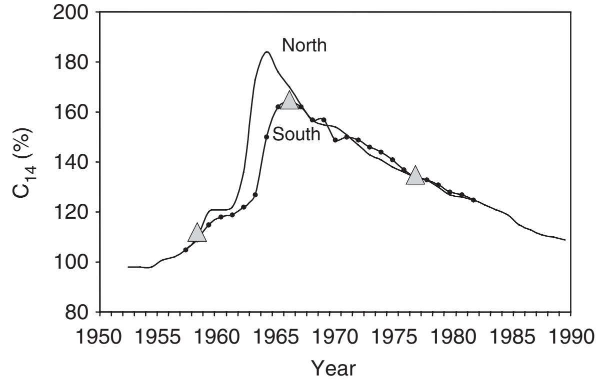


Figure 8 Radiocarbon content of the atmosphere in the northern and the southern hemispheres since 1952. In 1963 the test ban treaty stopped the majority of atmospheric atomic bomb explosions. The ^{14}C content in the atmosphere has declined continuously from that time. The variation makes possible the exact age dating of individual growth zone using two or three samples on different angles of the curve as it is indicated by the triangles.

'Gleichläufigkeit.' The latter means the percentage of parallel trend changes (**Figure 9**). Only those individual curves that match other curves can be included in the chronology.

Data Processing and Transformation

Tree-ring sequences and patterns store various information including the age of the tree, short-term climatic oscillation, and long-term trends. Year by year variation can be traced back to climate variability, but other biotic factors (e.g., pests) or abiotic factors (e.g., air pollution damage by storms, or severe floods) also may cause abrupt growth changes from one year to the next (**Figure 10**). Long-term trends in tree-ring curves can be traced back to long-term environmental changes, mainly processes

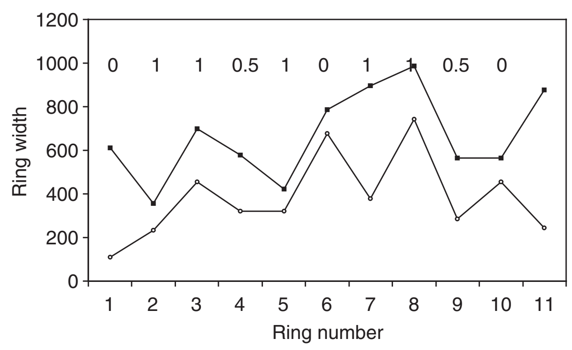


Figure 9 'Gleichläufigkeit' is an important measure for the similarity of tree-ring curves from different trees. It measures the concurring number of trend changes from one year to another. In this example every parallel trend change counts 1. When one curve does not change its direction the value 0.5 is given. The calculated Gleichläufigkeit is 60%.

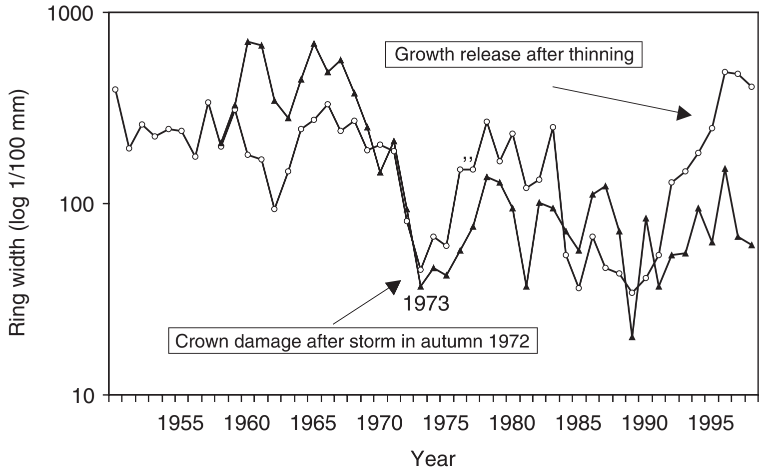


Figure 10 Tree-ring curves of trees exposed to crown damage after a catastrophic storm. One tree released after a couple of years, the other remained on a very low increment level. Note that the scale on the *y*-axis is logarithmic. This presentation points to the minima of a curve and helps to identify 'pointer years.'

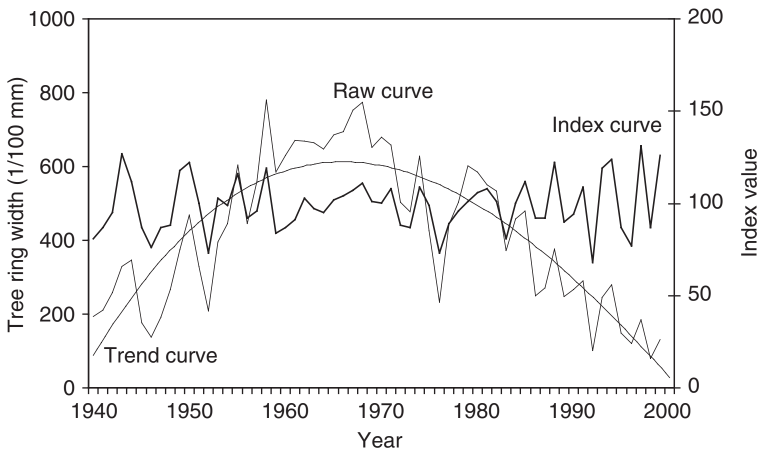


Figure 11 Detrending of an original raw ring curve. For the raw curve a trend is calculated, so that different smoothing functions are possible. The individual raw data and the related data points of the end curve were divided by each other. The resulting residuals form the detrended index curve.

such as increased competition or sudden loss of competition when gaps are opened through tree fall or human activities.

The influence of climate on tree growth can be shown by statistical analyses of tree-ring time series. After cross-dating the calculated mean curve must be detrended to differentiate between short-term oscillation and long-term trend. This procedure is called indexing and starts with the calculation of a trend curve. Various algorithms may be used such as Hugershof or moving average (**Figure 11**). The detrended curve consists of the residuals of raw curve values divided by the values of the trend curve. The residuals vary around a mean and show a normal distribution, a precondition for the calculation of a correlation with climate data.

Applications

Old Trees and Long Chronologies

The maximum age of a tree species is genetically fixed to a certain degree. The oldest living being is a bristlecone pine (*Pinus longaeva*) in the White Mountains in Arizona, USA at 4767 years. *Pinus longaeva* and *P. aristata* grow very slowly due to poor site conditions at the timberline at 3400 m with precipitation of about 100 mm per year. *Fitzroya cupressoides* (3600 years) and *Sequoia sempervirens* (2200 years) reach their ages at lower elevations and higher precipitation. All these species with a longevity over 1000 years are gymnosperms. Angiosperm trees are always much younger. The oldest dendrochronological confirmed ages are known from

Quercus spp. in North America and northern Europe (600–700 years) and for *Weinmannia trichosperma*, an emergent broadleaf tree from Chile (about 730 years). For tropical trees only a few dendrochronological confirmed ages have been published. The oldest trees are *Hymenolobium mesoamericanum* in a Costa Rican forest and *Piranhea trifoliata* from the Amazonian floodplain forests, with ages of between 550 and 600 years, respectively.

A driving force of dendrochronological progress is the construction of ever longer chronologies. Their construction starts with coring living trees to construct a first master chronology. This will be extended to the past by additional samples from already felled and old timber. This is possible when the innermost part of the recent sample shows overlapping parts with the outermost part of old samples. Both parts can be cross-dated and linked (**Figure 12**). In some cases beams of a location can not be dated immediately. Then a floating chronology will be build and dated preliminary by means of radiocarbon analysis. Later the floating and the master chronology might be connected with a 'missing link.'

The longest times series, consisting of thousands of individual samples is the 11 800 years long chronology of oak from southern Germany. A longer chronology is under construction for *Pinus sylvestris* stems, which have been found in alluvial sediments in the southern French Alps. Additional chronologies from other parts of the world are listed in **Table 1**.

Dating of Buildings, Works of Art, and Archaeological Samples

The existence of described chronologies has made possible substantial progress in many historical scientific applications, such as archaeology and the history of art and of buildings.

Many paintings in the late sixteenth and the seventeenth century were made on oak panels; these can be dated and differentiated from later copies. Expensive violins, e.g., from Stradivari, have also been tested for their originality. In some cases the wood of violins labeled from the beginning of the eighteenth century has proved to have been cut in the late nineteenth century, about 100 years after Stradivari's death (**Figure 13**).

Table 1 Chronologies with long timespans and their origin

Species	*Timespan (years BP)*	*Location*
Quercus spp. (oak)	11 800	Southern Germany
Pinus longaeva (bristlecone pine)	8 400	Arizona, USA
Pinus sylvestris (Scots pine)	7 500	Finnish Lapland
Picea, Larix spp. (spruce, larch)	6 000	Alps
Lagarostrobos franklinii (Huon pine)	4 000	Tasmania, Australia
Larix sibirica (Siberian larch)	4 000	Western Siberia
Fitzroya cupressoides (alerce)	3 600	Southern Chile
Tectona grandis (teak)	415	Java

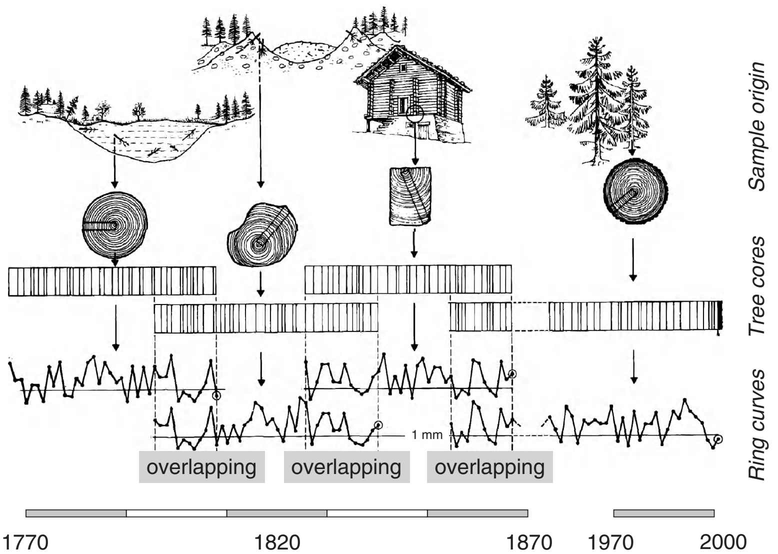


Figure 12 Scheme of the construction of a tree-ring chronology starting with samples from a living tree (right-hand side) and then including stepwise construction wood and subfossil samples. The diagram shows the ring-width patterns of the samples, their transformation into curves, and the overlapping sequences which match the individual curves together.

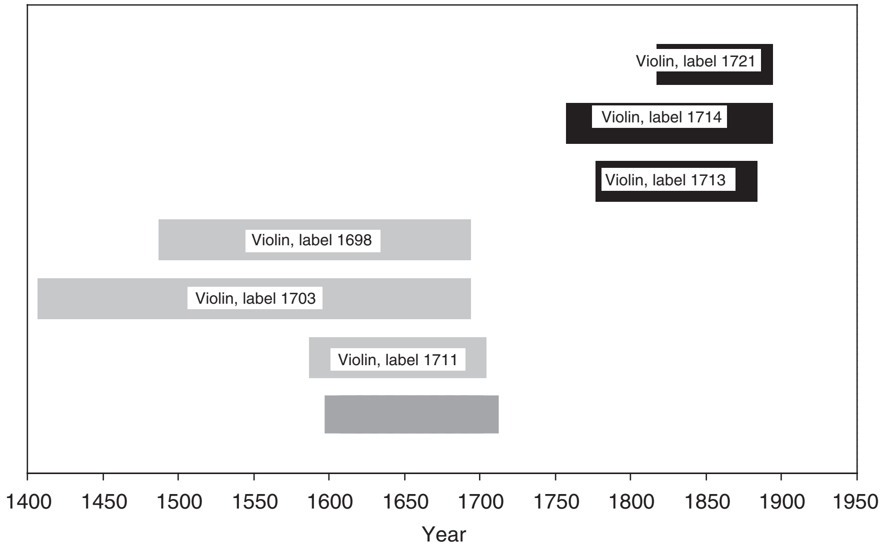


Figure 13 Tree-ring sequences of dendrochronologically dated violins which mostly were labeled as 'Stradivari.' The left-hand group probably were built by the famous master, while the wood of the right-hand group was still growing in the forest after his death.

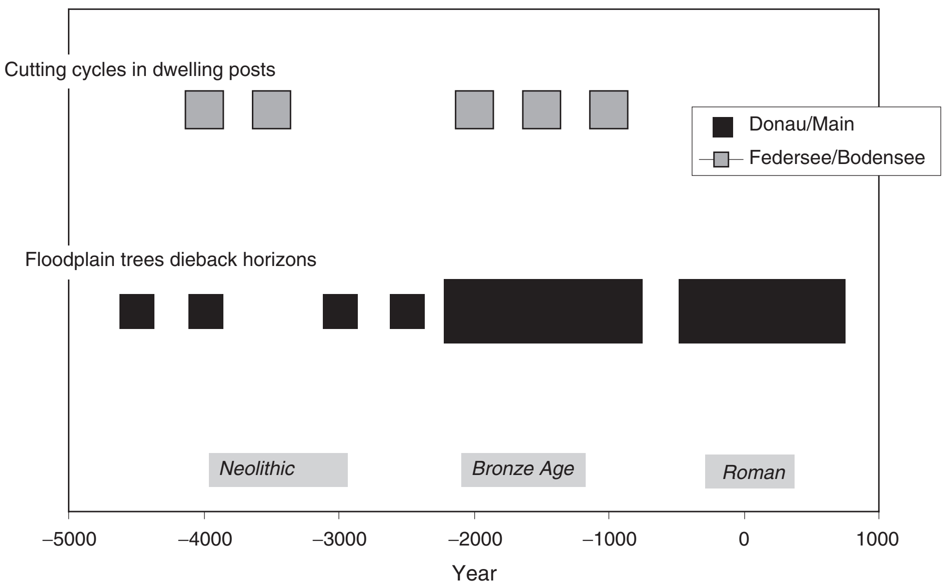


Figure 14 Dieback horizons of oak in southern German floodplain sediments and felling intensity around Bronze Age and Early Iron Age villages. Increasing clearing of the landscape and agricultural use led to an increase in erosion followed by sedimentation in river valleys. The intense dynamic probably led to the dieback of oaks in the floodplain forest.

Dendrochronology also contributed extensively to the knowledge of prehistory of human settlements. In southern Germany, the British Islands, and Switzerland, detailed information on prehistory since the Neolithic and the Bronze Age is known from excavation of dendrochronologically datable wood. During the building phases the surrounding areas of the villages were deforested for agricultural purposes, construction, and fuelwood. Since the early farmers settled on the best and deepest soils, erosion started and rivers changed their courses due to increasing sedimentation. This is visible in the ages at death of oaks excavated from alluvial soils in the floodplains. Several 'dieback horizons' are visible. The last and most distinct appeared during the Roman empire in southern Germany (**Figure 14**).

Climate Reconstruction

One of the most important applications of tree-ring analysis is the reconstruction of past climate. Most reliable climate records start in the second half of the nineteenth century. This is not long enough to judge whether the present global warming has natural correspondences in previous centuries.

As a first step it is necessary to understand the relation between climate and growth in different species. The main problem is that the two variables, temperature and precipitation, act in a complicated and often contradictory way: in the temperate zone high precipitation is related to a relatively cold summer and high temperature to a dry summer. One attempt at solving this problem is the use of samples from sites where one of the two factors is limiting such as temperature in high altitudes. In the tropics, however, the temperature is constant and only rainfall varies.

Analysis of pointer years or discontinuous time series Strong stress-related events like abnormal frosts in spring, exceptionally dry summers, prolonged flooding, insect attacks, and others are usually visible in tree-ring patterns as a 'pointer year.' One example can be traced back to the eruption of the volcano Katmai in Alaska, which occurred on 6 June 1912. The dust particles in the stratosphere then reduced solar radiation. The following August and September in some regions of the northern hemisphere were the coldest in 120 years of temperature records. Coniferous trees at higher altitudes stopped growth abruptly and could not develop typical latewood. In consequence the latewood density in 1912 is much lower than in the neighboring rings.

Analysis of tree-ring sequences or continuous time series The existence of at least two climate variables influencing tree growth requires multiple correlation analyses; the most common is the response function. **Figure 15** gives an example of the regression between ring width and climate at higher elevations. Precipitation and temperature are differentiated monthly back to June of the previous year. This is based on the assumption that climate conditions of the preceding year influence storage of carbohydrates and thereby affect the increment of the current year. Values of the previous year shift between positive and negative influence from one month to another. The results for temperature of the current year follow a clear and interpretable trend with strong positive correlation in June and July.

Reconstruction of climate The relation between late summer temperature and density of latewood allows the reconstruction of pre-instrumental climate history. Time series of density and/or ring width can be used as climate 'proxies' and show events such as the 'Little Ice Age' at the beginning of the seventeenth century and the 'Medieval Warm Period' in the northern hemisphere. One of the longest and probably most reliable climate-sensitive chronologies gives hints of an unusually cool period in the ninth century. This may be one cause of climatic catastrophes in that period and the stepwise extinction of the Maya culture in Central America (**Figure 16**).

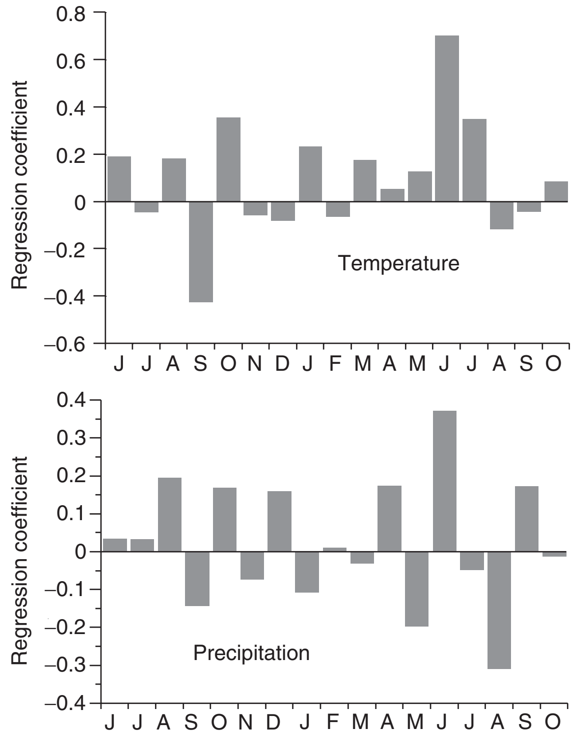


Figure 15 Multivariate analysis of the relation between tree-ring width of high-altitude (about 700 m) spruce trees (*Picea* spp.) and the climate variables precipitation and temperature. Each variable is split into monthly subvariables from June of the previous year (before formation of the tree ring) to October of the current year.

Tree-ring series in the tropics reflect variation in precipitation. One important periodical climate event in the tropical Pacific region is the Southern Oscillation-El Niño Effect. The occurrence of this weather effect was described in 1931 by analyzing a teak tree-ring chronology from Java (**Figure 17**). A recent investigation of tree rings from a floodplain tree species shows the influence of El Niño on precipitation anomalies in the Amazon basin. It seems that its strength increased and its period decreased slightly from the nineteenth to the twentieth century.

Landscape Ecology and Geomorphology

One of the simplest features of a tree-ring sequence, the age of the tree, is most valuable for the detection and interpretation of the movement of glaciers and

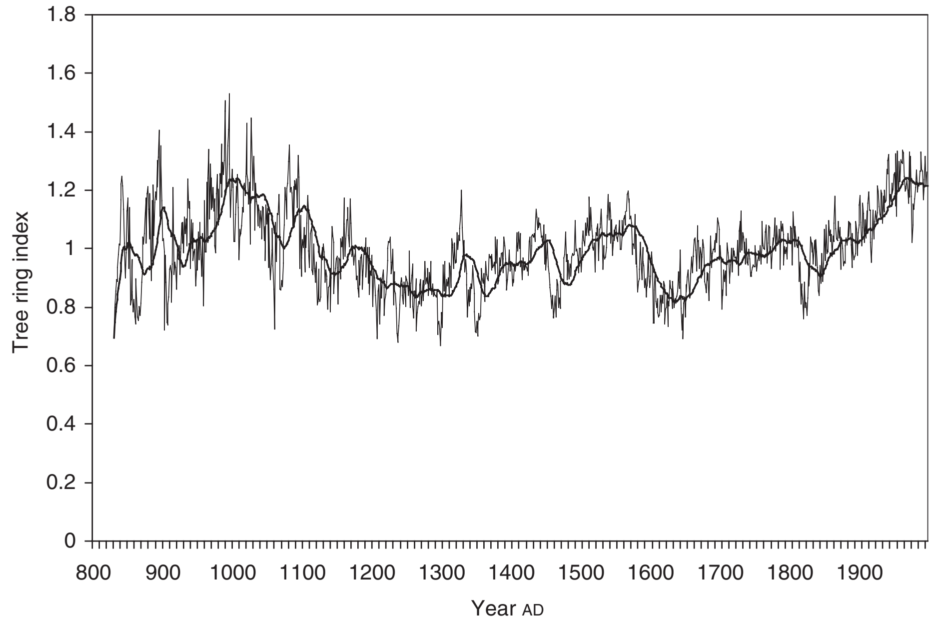


Figure 16 Temperature-sensitive chronology from the northern hemisphere. The chronology is constructed of 1205 individual tree ring series from different species (genera *Picea*, *Pinus*, *Larix*, and *Abies*). Trees origin from 14 high-elevation or high-latitude sites and from the entire Northern hemisphere. The 'Medieval Warm Period' and the 'Little Ice Age' as well as recent global warming are clearly shown.

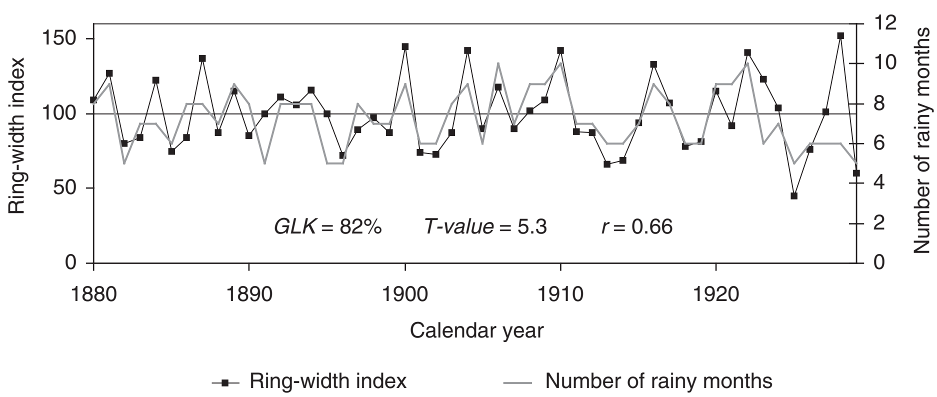


Figure 17 The Java teak (*Tectona grandis*) chronology of Berlage from 1931 shows the concurrence between tree-ring width and precipitation, which is expressed as duration of the monsoon. The tree-ring curve is detrended. The periodical pattern of recurring minima and maxima reflects the influence of the El Niño-Southern Oscillation effect. Berlage was the first to detect the influence of El Niño in tree rings. The graph only shows the latest period of the chronology, which goes back to 1514. GLK, Gleichläufigkeit.

the dynamics of rivers. In the case of glacier dynamics the age of the pioneer trees that follow its retreat can be estimated easily. Information on the course and frequency of avalanches, landslides, mudflows, and stonefalls can also be gained from trees surviving with datable damage to crowns or stems. This information provides estimates of the degree of danger for newly constructed roads and buildings in mountain areas.

Forest Dynamics, Ecology, and Management

Information on forest growth is important for sustainable forest management. Changing environmental influences such as the increasing acid emissions in the twentieth century, fertilization through increasing N deposition, temperature, and damage due to pests and storms require a tool for fast measurement of growth reactions to these factors. In the tropics the current state of knowledge on growth rates and forest dynamics is extremely poor due to the lack of reliable yield tables and the assumed absence of tree rings.

Forest dynamics European forests have been managed intensively for centuries. The network of monitoring and documentation often is dense. However yield tables are based on means and undisturbed situations. Changes of site and environmental conditions are usually not considered. Thinning and

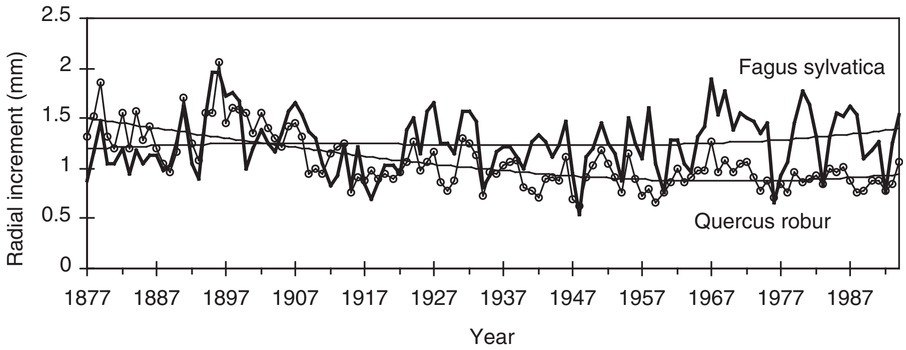


Figure 18 Ring-width curves: raw data and long-term trends of oak (*Quercus robur*) and beech (*Fagus sylvatica*) trees growing at dry sites on steep slopes and shallow soils. Beech outcompetes oak from the beginning of the 1930s. Presently their crowns are at least 3–5 m higher than oak.

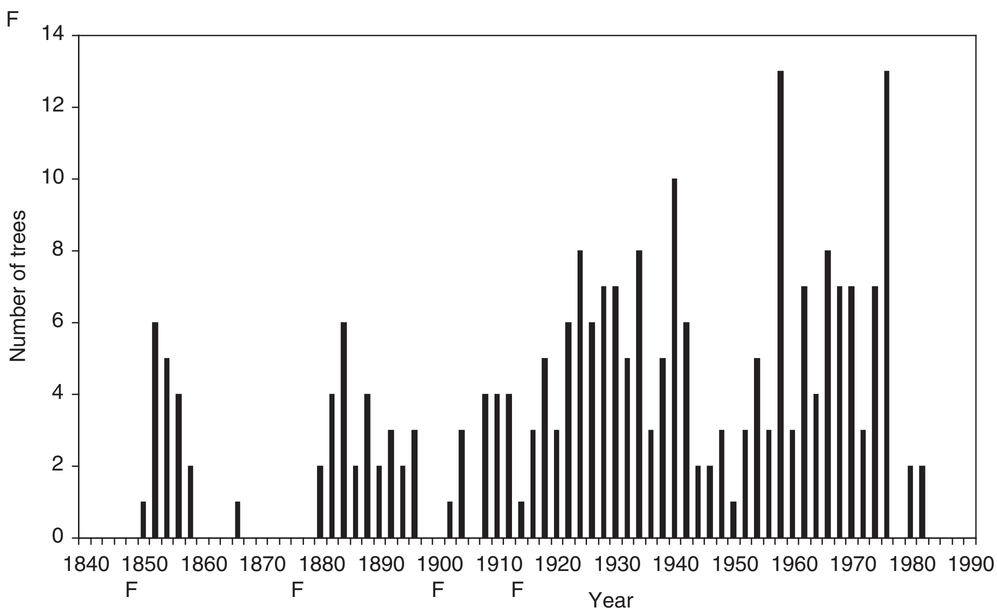


Figure 19 Age structure for *Pinus banksiana* from a boreal site in Canada affected by forest fires. The fire years are identified by age dating of fire scars and abrupt changes in radial increment.

spacing have the effect of increasing the growth of the remaining individuals, whereas growth reductions take place after storms, when trees are partially damaged but survive, and when pests like budworms effect a recurring pattern of pointer years. Competition between species can be described by interpreting long-term trend curves. The example in **Figure 18** explains the predominant growth of beech (*Fagus sylvatica*) in comparison with neighboring oaks, even on the driest sites, where recent ecological knowledge had postulated the opposite.

In certain ecosystems frequent catastrophic events trigger the regeneration of the forest. This is the case after hurricanes, after erosion and sedimentation in floodplains, and after intensive forest fires. These are necessary for regeneration in some temperate and boreal coniferous forest ecosystems. Fire scars in the wood help to identify the fire frequency (**Figure 19**).

Tree decline In the late 1970s in Europe and North America the sudden devastation of entire forest stands, mainly of coniferous tree species, forced an intensive search for its causes and for the basis of prediction of future development. It soon became clear that the deposition of acid rain on unbuffered soils was one of the major causes. In this context tree-ring analysis was the best tool for the comparison of growth trends before and after the intense influence of acid rain. Tree rings show clearly the decrease of increments in heavily polluted areas.

The percentage of trees with increment losses declined with decreasing altitude, and on calcareous

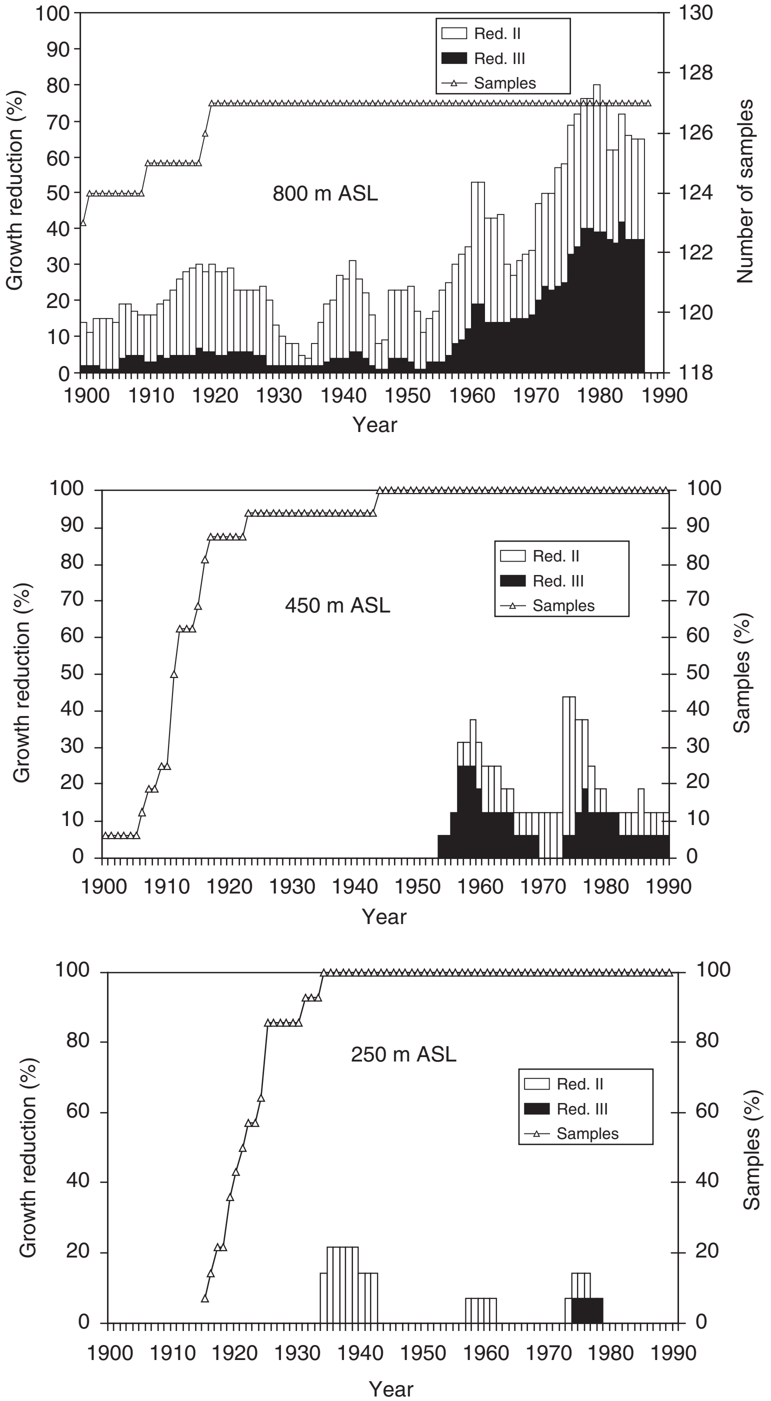


Figure 20 Number of spruce trees (*Picea* spp.) with growth reduction in relation to total sample from different elevations in Northern Germany. Trees from high elevations (ASL, above sea level) show partially letal growth decline since the beginning of the 1960s. Sites were mainly orientated on western slopes of the mountains, where emissions from the Rhine/Ruhr industries are transported on the prevailing wind.

soils in the lowlands the problem was clearly not existent (**Figure 20**). The main agent of damage was sulfur dioxide. Based on tree-ring studies Switzerland enacted new laws aimed at reducing emissions of sulfur dioxide. The reduction was followed by a slight increase of tree growth.

Sustainable forest management in the tropics Many tropical forests are managed intensively, but one way to avoid overexploitation is to support sustainable management systems. Many key factors for timber certification have been developed, but it is still unclear how fast trees grow. However, the existence

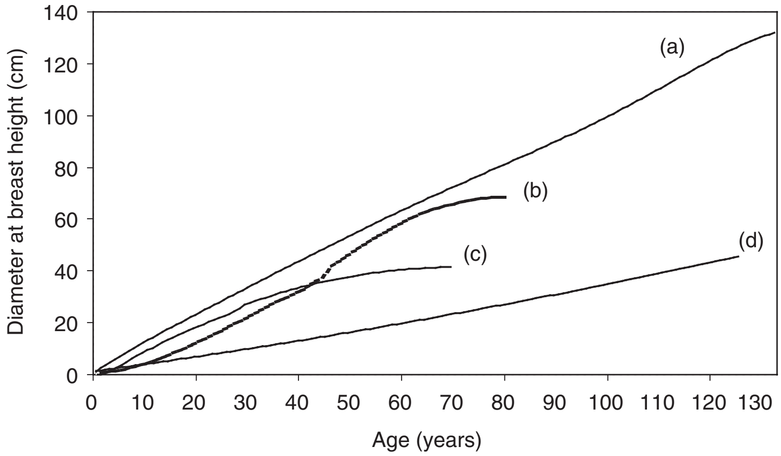


Figure 21 Mean cumulative diameter increments of the softwood species (a) *Triplochiton scleroxylon* from Cameroon and (b) *Macolobium acaciifolium* from the Amazonian floodplains. The growth of the hardwood species *Tabebuia barbata* varies according to origin: (c) from a natural secondary forest and (d) a mature forest, indicated by distinct differences in the shape of the long-term trends. Each curve is a mean curve of 5–20 individuals.

of distinctive annual rings, e.g., in the main West African timber species, has been known for more than 30 years. One of the faster-growing species there is *Triplochiton scleroxylon*, which needs 70 years to reach the minimum logging diameter. In Amazonian floodplain forests, trees of different wood densities and growing environment need different time to reach the cutting diameter (**Figure 21**). A species-specific management system would help to establish more economical use than the recent system with identical measures for all species.

Conclusions and Outlook

'For 70 years dendrochronology was a purely academic science; today certain aspects have become accepted in the sphere of applied sciences.' This statement of Fritz Schweingruber from 1986 is even truer today. Progress can be traced back to the personal dedication of some promoters of tree-ring science, writing textbooks, organizing conferences, teaching students, and running internet sites. However, the main cause of dendrochronological success is the scientific work on modern themes leading to accepted studies in most of the abovementioned fields of research.

Acknowledgment

We are indebted to Margaret Devall, Stoneville, MS, for her careful review, useful suggestions, and substantial linguistic improvement of the manuscript.

See also: **Ecology**: Natural Disturbance in Forest Environments. **Environment**: Impacts of Elevated CO_2 and Climate Change. **Tree Physiology**: Physiology and Silviculture. **Wood Formation and Properties**: Formation and Structure of Wood.

Further Reading

Fritts HC (1976) *Tree Rings and Climate*. London: Academic Press.

Schweingruber FH (1988) *Tree Rings: Basics and Applications of Dendrochronology*. Dordrecht, The Netherlands: Kluwer.

Schweingruber FH (1996) *Tree Rings and Environment: Dendroecology*. Bern, Switzerland: Paul Haupt.

Worbes M (2002) One hundred years of tree ring research in the tropics: a brief history and an outlook to future challenges. *Dendrochronologia* 20(1–2): 217–231.

N

NON-WOOD PRODUCTS

Contents

Energy from Wood

J I Zerbe, USDA Forest Products Laboratory, Madison, WI, USA

Introduction

In most developing countries wood and charcoal are the predominant fuels for preparation of food to maintain the quality of life that encompasses the majority of citizens. In many developing countries wood fuels are also important for small and medium-size industries.

Moreover, energy from wood continues to be important in industrial countries. In the USA biomass including waste wood and alcohol from corn provided about 3.3% of total energy consumption in 2000. This was more than was provided by conventional hydroelectric power and more than other forms of renewable energy. Wood energy is consumed in a variety of forms that include fireplace lengths, chunkwood, chips, sawdust and shavings, black liquor from pulp manufacture, pellets, fireplace logs, briquettes, charcoal, gasified wood fuel, and liquefied wood fuel. Wood provides warmth and comfort to homes through burning in fireplaces and automated heating systems. And even in industrial countries wood is used for cooking where it is burned in specially designed stoves for convenience or on grilles to bring out special flavors.

Wood fuel is important to commercial wood manufacturing facilities where waste wood can be disposed and used profitably for energy at the same time. In areas where wood from logging and manufacturing is abundant, other industries such as brickmaking and cement manufacture also benefit from sales of wood fuel. In some South American countries wood charcoal provides the fuel for smelters in manufacturing steel.

Some major considerations in using wood for fuel are environmental impact, economics, convenience, reliability, and simplicity. On balance, wood is an environmentally benign fuel. It tends to be more economic than some other fuels, but may be less convenient.

How Wood Is Used for Energy

Solid Wood

Fireplace lengths The most common way of using wood for fuel is to burn pieces about 40–50 cm long that are split from logs. We burn much of such wood in our fireplaces today, and, formerly, such firewood provided the main fuel source for home heating, domestic hot water, and food preparation. Wood is still used for heating some homes in industrial countries. Usually heat is not produced efficiently in fireplaces, but some fireplaces are designed to use blowers to be more effective. Stoves and furnaces burn firewood more efficiently. However, for many applications, wood is converted to other forms of fuel that are more convenient, waste less energy, and are less prone to emit undesirable particulates and other pollutants to the air.

Chunkwood A few manufacturers make machines that can produce fairly uniform particles about the size of an average fist. Such fuel is called chunkwood. Chunkwood can be readily dried since there are openings for air to circulate when it is piled for storage. Drying green wood to lower moisture contents makes it easier to burn with less smoldering and smoking and gives the wood a higher heating value. Transfer of creosote residues to chimneys is of lesser impact. Chunkwood is rarely used now, but it will probably become more popular in the future.

Chips and sawdust Chips and sawdust are more common types of particulate wood fuel. There are some special combustors that can burn green (unseasoned) sawdust, but it is usually necessary that chips and sawdust be fairly dry. Chips are dried in special dryers that may use wood or fossil fuels to generate heat. Sometimes dry sawdust and chips are available at secondary wood manufacturing plants such as furniture plants. Dry sawdust can be a very desirable fuel for use in special combustors that burn particles in suspension. In such cases grates are not necessary. Chips are advantageous for handling and storing. They can be used effectively in automated stoker applications.

Shavings Shavings are produced when lumber is planed or molded or spun off from logs that are peeled. Since shavings are usually produced in the processing of dry lumber they make good fuel. Green shavings from applications such as rounding logs for log home construction may be further processed by chipping and drying.

Pellets

Wood pellets are becoming increasingly popular. They are made by compression milling small wood particles such as sawdust. When pellets are made from clean wood with little bark, the ash content is low. Pellets are sold at retail outlets in 18 kg (40 pound) sacks. They handle and store easily. They should be kept dry to prevent disintegration, and to avoid risk of mold and decay. Sometimes pellets for cooking are made from woods with special flavors that can be used in barbecuing, directly or with charcoal or gas, for conveying this flavoring to meat or poultry.

However, the most common use of pellet fuel is for heating with modern and convenient pellet stoves. Some of these stoves burn pellets with 85% efficiency and have automatic ignition, feed, and control systems.

Manufactured Fireplace Logs and Briquettes

Manufactured fireplace logs (firelogs) are made from waste wood to provide open-hearth warmth and ambience with clean fuel. Wood briquettes are similar products of smaller length that are used as barbecue fuel or industrial stoker fuel.

There are two types of firelogs or fuel logs; one type is made with the addition of around 50% wax. The other type is all wood. In the USA wax-type logs are more popular, but the all-wood type is more popular throughout the rest of the world. Wax-type logs burn with fewer gaseous emissions to the air, but they do emit carbon compounds from nonrenewable fuel that lead to an increased greenhouse effect. All-wood logs do not emit nonrecyclable carbon.

All-wood logs are made in machines that apply pressure with screws or pistons. The heat developed in the process is sufficient to cause the lignin in the wood to flow and act as a binder for the particulate wood waste. Many machines to make fireplace logs are designed to take advantage of the heat generated by high pressure and do not use supplementary heat. Other machines have extrusion cylinders that are externally heated to temperatures between 180°C and 300°C. Electrical resistance coils provide heating, and after the manufacturing process starts a temperature control setting permits operation at an optimum temperature level. The heating process slightly carbonizes the surfaces of the logs or briquettes and gives them a dark brown color. Heating may also contribute to better particle adhesion and less friction in the extrusion process.

Briquettes are made in the same ways as all-wood logs, but the log lengths from the machines are cut into thin disks. In developing countries brickmaking presses have been adapted for briquetteing. In these cases pressures are lower and inexpensive adhesives are used as binders.

The wax-sawdust firelog manufacturing process is not used for producing briquettes, only for fireplace logs. Wax-sawdust logs are composed of about 40–60% wax with the remaining portion being sawdust. The heat content of wax-sawdust logs is higher than all-wood logs. Compared to wood, which has a high heating value of about 20 MJ kg^{-1} (8500 Btu lb^{-1}), wax-sawdust logs have a heat content of 36.4 MJ kg^{-1} (15 700 Btu lb^{-1}).

Charcoal

In industrialized countries wood charcoal is often used as a cooking fuel, particularly in barbecuing or grilling. But consumption for such use is minor. In developing countries charcoal is much more commonly used as a fuel. This is an advance from use of solid wood fuel for use in domestic or light institutional or industrial (e.g., baking) applications. Charcoal is more easily stored and transported than wood, and it is more durable in the presence of moisture.

In developing countries primitive earth or pit kilns are still used in charcoal manufacture. In industrialized countries, various types of improved kilns are used. They may be of brick, concrete or cinder block, or steel construction. Kilns are designed to char the wood without burning it. This is accomplished, after the charge of wood has been ignited and preliminarily heated, by regulating the amount of air entering the kiln so that only ‘glowing’ and not combustion takes place.

Gaseous Fuel

Charcoal is only one of several different forms of advanced products that may be obtained through pyrolyzing wood in the presence of insufficient oxygen to cause complete combustion. Depending on pyrolysis temperature there may be different proportions of char, tar, liquids, and gases. With high temperatures and proportionately low oxygenation, mostly gas is formed. Wood gasification results in gaseous products composed of mainly hydrogen and carbon monoxide and some hydrocarbons that include methane.

Wood gasifiers are of different types that include updraft, downdraft, side draft, and fluidized bed. Most experience in using wood gasifiers has been with the downdraft type. Downdraft gasifiers produce cleaner gases that have less tar. These gases may be filtered further so that they are clean enough to use as fuel in internal combustion engines without causing severe carbon deposits in the pistons and heads of the engines in short periods of time. The gasifiers and engines are most often used in combination with electrical power generators or transmission drive mechanisms for powering automobiles or other modes of transportation. Such combinations are known as gasogens. Wood gas may also be combusted directly. However, unless it is refined it has much lower heating value than natural gas.

Gasogens were used in many countries to power automotive transportation during World War II, but were abandoned after the war because of higher maintenance costs. Today there are better filters for removing tars from the gases before they enter the internal combustion engines so maintenance costs are less. Today gasogens are becoming increasingly popular for power generation, especially in locations where electrical demand is low and power from the electrical grid distribution network is not readily available.

There are also efforts to use gases generated through pyrolysis of wood with insufficient oxygen for complete combustion in turbine generators, but for use with turbines gases must be even cleaner than for use with internal combustion engines. Combustion gases have also been tried in turbines, but in this case corrosive ash that might get through to the turbine is a greater problem.

Liquid Fuels

Alcohols Previously wood distillation through heating in a retort without introducing oxygen was popular in the USA, and the process is still applied in some countries of the world today. This process can produce methanol for fuel along with other chemicals and charcoal.

However, for producing methanol from wood it is more efficient to use a synthesis process similar to that used for making methanol from natural gas. In the synthesis process wood is first gasified. Then it is compressed for removal of carbon dioxide, nitrogen, and hydrocarbons. This is followed by a shift reaction to obtain a gas with two parts hydrogen and one part carbon monoxide. This gas is subjected to high pressure and conversion to methanol results.

There is much more effort to produce ethyl alcohol or ethanol for fuel. In the process for making ethanol wood is first separated into its main constituents of cellulose (about 50%), hemicellulose (about 25%), and lignin (about 25%). The cellulose is then hydrolyzed to glucose and the glucose is fermented to ethanol. Previously this was the extent of the process. But, more recently, ways have been found to ferment xylose. Now xylose can be liberated from hemicellulose and fermented to ethanol.

Little alcohol fuel is made from wood today, but the promise for the future, with continuous development of cost-lowering technology, appears better.

Black liquor The kraft paper manufacturing process is popular throughout the world. It can produce high-quality paper with less pollution than with the sulfite process. In the kraft process recovery of papermaking chemicals is important. These chemicals are contained in the large amounts of liquid waste known as ‘black liquor’ from the process. Therefore the overall process includes a large recovery boiler that produces much energy in using the black liquor as fuel. In 1992 in the USA 32.5 million tonnes or 26.5% of the energy obtained from wood came from black liquor (**Figure 1**).

Where Wood Is Used for Energy

Home Heating

Throughout industrialized countries wood for home heating is a minor, though increasingly important, application. In developing countries wood is a major source of fuel, but there is little need for domestic heat, because of warm tropical temperatures.

Nonetheless flaming wood is appreciated as a source of warmth and center for socializing. In industrialized countries, also, wood for home heating is often used in fireplaces for the warmth and ambience of the hearth, although fireplaces are relatively inefficient means of producing heat.

But, there are also efficient ways of using wood for home heating. One traditionally effective and efficient example is the masonry stove commonly used in Europe. These unique heaters are sometimes known as Russian stoves, German tiled stoves, Finnish masonry stoves, or Finnish contraflow fireplaces. Such stoves may be constructed in place by masons, but there are also fully fabricated wood-fired masonry heaters that may be purchased for simpler installation.

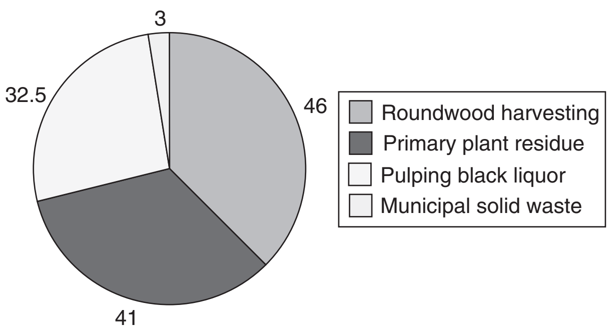


Figure 1 Source of fuels derived from wood in the USA in 1992 (in million tonnes).

Other improved stoves and furnaces for handling wood or wood-derived fuels supplement traditional firewood stoves and furnaces. The more recent technologically advanced stoves and combustors operate with wood chips and pellets.

In the USA wood was an important fuel from the beginning of European settlement. First wood was used mainly for domestic heating, but charcoal fired furnaces for making iron became important during the eighteenth century, and by 1870 when consumption of wood fuel reached a maximum, use in steam engines such as in locomotives and for riverboat propulsion was significant (**Figure 2**).

Industrial Plants

Industrial use of wood fuels today is a typical practice in primary and secondary forest products manufacturing plants. Unseasoned wood and bark fuel is typically used in sawmills and plywood and particleboard manufacturing plants. Pulp and paper mills burn green manufacturing waste, and, sometimes, forest harvesting waste. The black liquor that pulp mills use is a high percentage of total overall wood fuel usage. Furniture plants often have premium dry wood fuels available.

Outside the forest industry, wood fuels are often used in brickmaking, lime kilns, and cement manufacture throughout the world. In countries including Brazil and Argentina wood charcoal is used extensively in the manufacture of steel.

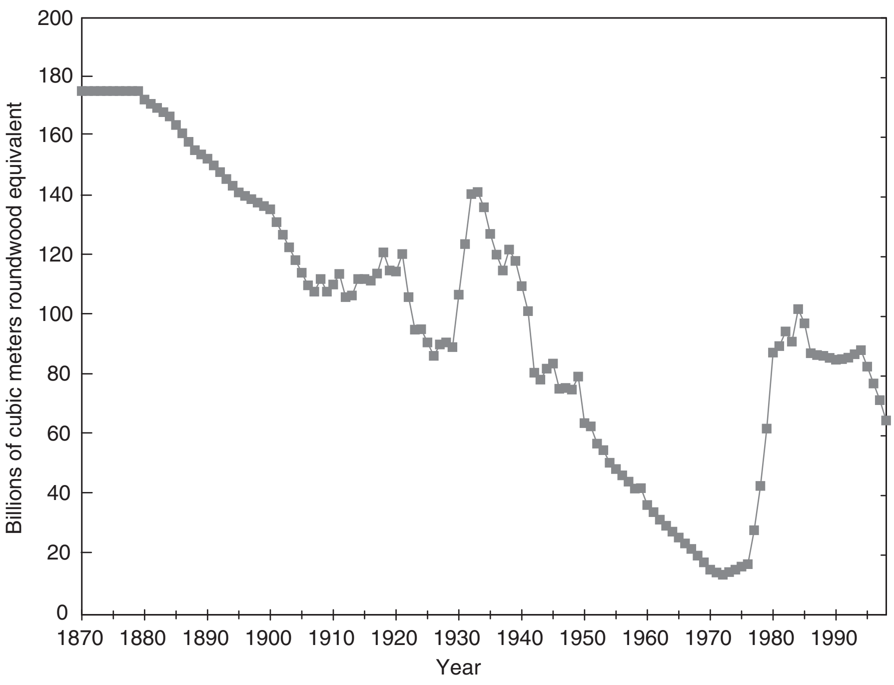


Figure 2 Trend line for wood fuel consumption in the USA from 1870 to 1998.

Institutional Wood Fuel Usage

In the US Midwest and New England and in Canada wood fuel is an important base for providing heat for schools during moderately severe winters. On several campuses district heating is employed. Many other schools have individual heating units in separate buildings. Other wood fuel applications provide heat for hospitals, prisons, government administrative offices, and small businesses. In another application wood is used to provide fuel for both heating and air conditioning in a large Midwest US conference center.

Power Plants

Electricity generation in wood-fueled power plants in the USA became significant with the passage, in 1978, of legislation favorable to small producers who would generate less than 80 MW of electricity. More recently competition for smaller generating plants has become more critical, and some plants have shut down. However, besides the stand-alone generating plants, the majority of the existing capacity is operated in combined heat and power (CHP) facilities in the industrial sector, primarily in pulp and paper mills and paperboard plants. Other countries that have wood-fueled generating plants include Sweden, Finland, and Brazil.

In addition to larger power plants to provide electricity to a distribution grid, there are opportunities to generate electricity at smaller capacities at locations away from grid supply, or at locations where electricity from the grid is very high cost. Often such locations are dependent on diesel engine generators for electricity. Wood gas fueled generators may be competitive in these cases. Examples are a coconut plantation in the Philippines and an Indian reservation in the USA.

Importance of Wood Fuel in Developing Countries

Energy use in developing countries is much more dependent on wood than in industrial countries. As a typical example in 1992 nearly 70% of the final energy consumption in the Southern African Development community countries was derived from wood biomass. In the household sector, wood fuel accounted for 97% of the energy consumed. This consumes significant amounts of wood from developing country forests, but use of wood in more refined form, mainly charcoal, causes an even greater demand.

In many cities in developing countries charcoal is the major cooking fuel. For example, in Abidjan, Côte d'Ivoire, to satisfy the household supply of charcoal the annual demand is about 300 000 tonnes, produced from 5 million tonnes of wood.

Besides household use the demand of wood fuel and charcoal for industry use is also great. Fuelwood is the dominant source of energy for many rural industries in Malaysia. In 2000 almost 85% of the energy source for numerous medium-scale industries such as smoking of rubbersheets, curing of tobacco leaves, firing of bricks, and the drying of foodstuffs came from fuelwood.

Figures 3 and **4** show charts of the sharp difference between the developing world and the industrialized world in relative use of wood for fuel and for roundwood. In the developing world the relative use of wood for fuel is much higher.

Vehicles

Since automotive vehicles consume such a large portion of the world petroleum resources, they present a market opportunity for wood-derived fuels. Today small quantities of ethanol derived from wood are used, but the potential for greater future use of wood converted to liquid fuel is good.

Co-Firing Wood with Other Fuels

Coal

Wood fuel is fired together with coal in some power plants where the primary coal fuel has high sulfur content. Wood is low in sulfur so that the mixture of coal and wood facilitates meeting sulfur emission requirements.

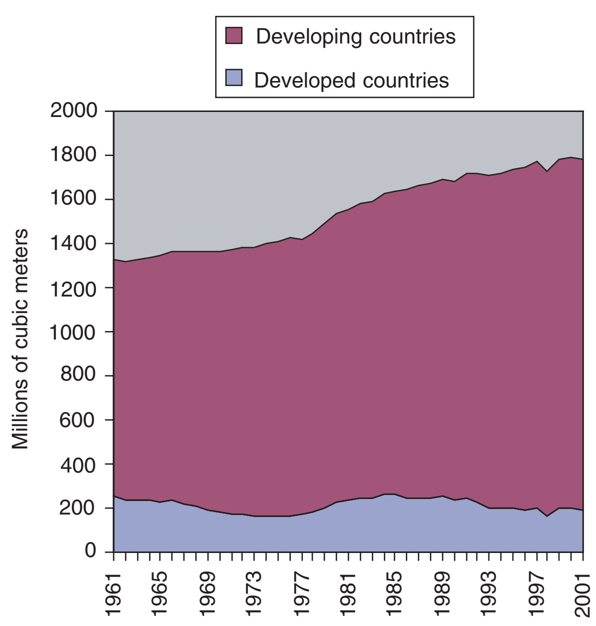


Figure 3 Annual fuelwood consumption in millions of cubic meters for developing and developed countries. Estimated data from Food and Agriculture Organization.

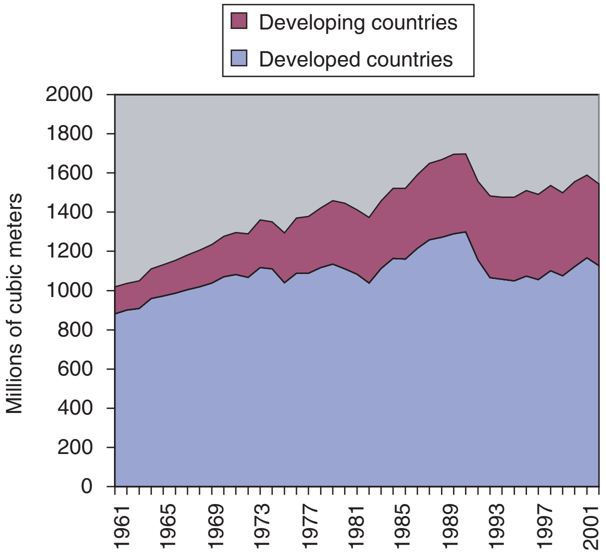


Figure 4 Annual roundwood production in millions of cubic meters for developing and developed countries. Data from Food and Agriculture Organization.

Gas

Gas is co-fired with wood to overcome difficulties when wood is at a higher moisture content than that at which it can readily be combusted. With co-firing gas it is fired through one or more burners mounted above wood fuel feeders. The gas burners can also be fired to maintain up to 100% of the heat delivery load for start-up and as a back-up during fuel supply shortages.

Wood Energy and the Environment

Carbon Dioxide

The increasing accumulation of carbon dioxide and other greenhouse gases in the atmosphere is generally considered to be a threat to future stability of the earth's climate, and, though there are disagreements, climate change could be unsettling to our modus operandi and quality of life. There can be no doubt that our vast use of fossil fuels is the major contributor to increased atmospheric carbon. The renewability of wood and other biomass fuels makes them a desirable alternative to fossil fuels to prevent or retard increasing retention of carbon dioxide emissions. In wood fuels when new trees are grown to replace the wood that was the source of the fuel, carbon is constantly used and regenerated in the growth cycle. The carbon that is emitted to the atmosphere is absorbed by photosynthesis in new growth.

Sulfur

Sulfur emissions to the atmosphere are undesirable because they can precipitate and cause harmful acidic conditions in soil and water. Wood contains little sulfur, but some coal and some oil contain substantially more. Therefore sulfur emissions from wood are more easily controlled than those from their fossil fuel counterparts.

Oxides of Nitrogen

Oxides of nitrogen emissions tend to be lower with wood fuel than with fossil fuels. On the other hand, a major source of nitrous oxide, a greenhouse gas, in the atmosphere is forest fires. Higher oxides of nitrogen emissions usually accompany combustions at higher temperatures. New technology stoves designed to be more efficient have higher oxides of nitrogen emissions than conventional stoves.

Particulates

Emission of particulates is the most common cause for concern in meeting environmental requirements with the burning of wood fuel. In the USA in some municipalities and under some atmospheric conditions, particularly air inversions, there are periods when wood burning in fireplaces and stoves is not permitted. Catalytic stoves can help in attaining lower emission rates.

See also: **Non-wood Products**: Chemicals from Wood.

Further Reading

Ayensu ES, Bene JG, Bethel JS, *et al*. (1980) *Firewood Crops, Shrub and Tree Species for Energy Production*. Report of an ad hoc panel of the Advisory Committee on Technology Innovation. Washington, DC: National Academy of Sciences.

Clark W (1974) *Energy for Survival: The Alternative to Extinction*. Garden City, NY: Anchor Books.

Deudney D and Flavin C (1983) *Renewable Energy: The Power to Choose*. New York: WW Norton.

Hall CW (1981) *Biomass as an Alternative Fuel*. Rockville, MD: Government Institutes, Inc.

IUFRO (2000) *Forests and Society: The Role of Research*, vols. 2 and 3. Vienna: International Union of Forestry Research Organizations.

Johnson JE, Pope PE, Mroz GD, and Payne NF (undated) *Environmental Impacts of Harvesting Wood for Energy*. Chicago, IL: Great Lakes Regional Biomass Energy Program.

Morris G (1999) *The Value of the Benefits of U.S. Biomass Power*. NREL/SR-570-27541. Golden, CO: National Renewable Energy Laboratory.

Skog KE and Watterson IA (1986) *Residential Fuelwood Use in the United States: 1980–1981*. Resource Bulletin no. WO-3. Washington, DC: US Department of Agriculture Forest Service.

Stanford G (1977) Short-rotation forestry as a solar energy transducer and storage system. In: Lockeretz W (ed.)

Agriculture and Energy, pp. 535–557. New York: Academic Press.
Stout BA, Myers CA, Hurand A, and Faidley LW (1979) *Energy for World Agriculture*. FAO Agriculture Series no. 7. Rome: Food and Agriculture Organization.
US Department of Agriculture (1980) *Cutting Energy Costs: The 1980 Yearbook of Agriculture*. Washington, DC: US Government Printing Office.

Chemicals from Wood

T Elder, USDA – Forest Service, Pineville, LA, USA

Introduction

A wide array of both commodity and specialty chemicals can be derived from wood, either as a primary product or by-product of another process. The technologies in which chemicals are the primary products include thermal degradation, hydrolysis/fermentation, direct collection, and extraction methods. Chemicals collected as by-products generally come from fiber-producing processes, including pulp and paper and steam explosion. While cellulose, lignin, and derivatives thereof could be classified as chemicals derived from wood, the current review will be limited to low-molecular-weight chemicals from wood. The synthesis and utilization of various chemicals from renewable resources have received considerable recent attention through research efforts in green chemistry.

Extractives

Perhaps the oldest of the chemicals produced from wood are those derived from the extractives. The term 'naval stores' provides a clue to the waterproofing applications for which these chemicals were originally used. The extractives can broadly be divided into terpenes, resin acids, and fatty acids.

Terpenes

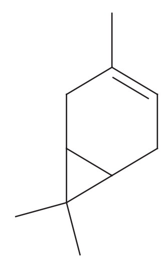
Terpenes are relatively volatile hydrocarbons based on isoprene (2-methyl-butadiene) units, and are the major components of turpentine. Turpentine was once produced largely by tapping trees and collecting the exudates, which after processing are called 'wood naval stores.' Currently, most turpentine comes from the sulfate pulping process, in which the volatile materials are removed by the action of heat and pressure in the digestion step. The volatiles consist mainly of the monoterpenes, α-pinene, β-pinene, and Δ^3-carene, depending on the wood species (**Figure 1**). While turpentine was once used extensively as an industrial solvent, the monoterpenes are now modified into much more valuable products, used in perfumery, flavorings, and to some extent insecticides and disinfectants. Although most terpenes are now produced as a by-product of the pulping industry, the exception to this generalization is natural rubber production. Natural rubber (*cis*-1,4-polyisoprene) comes from *Hevea brasiliensis*, and is still collected by tapping living trees and collecting the latex sap.

Resin Acids

The resin acids, the main components of rosin, are diterpenoids such as abietic acid, neoabietic acid, palustric acid, pimaric acid, and isopimaric acid (**Figure 2**). Rosins can be isolated from directly collected oleoresins, but are now more commonly separated from tall oil as a by-product of the kraft, black liquor recovery process. Metallic salts and esters of resin acids are used as additives to printing inks to improve gloss, mechanical stability and resistance to chemicals. Rosins are also extensively used in paper sizing and in rubber manufacture as emulsifiers and tackifiers.

Fatty Acids

In addition to the resin acids, tall oil also contains fatty acids. Given the acidic character of both of these components and the very high pH in kraft black liquor, during the recovery process, the acids are converted to insoluble salts, referred to as soaps, that are skimmed from the concentrated black liquor. The skimmings are acidified to release the acids resulting in crude tall oil (CTO). Resin acids, fatty acids, and any unsaponifiable neutral compounds are separated by vacuum distillation. Among the fatty acids are oleic and linoleic acid. The fatty acids find applications in ore separation, metal working, rubber, as detergents, and as drying agents in finishes.



α-pinene β-pinene Δ^3-carene

Figure 1 Monoterpenes.

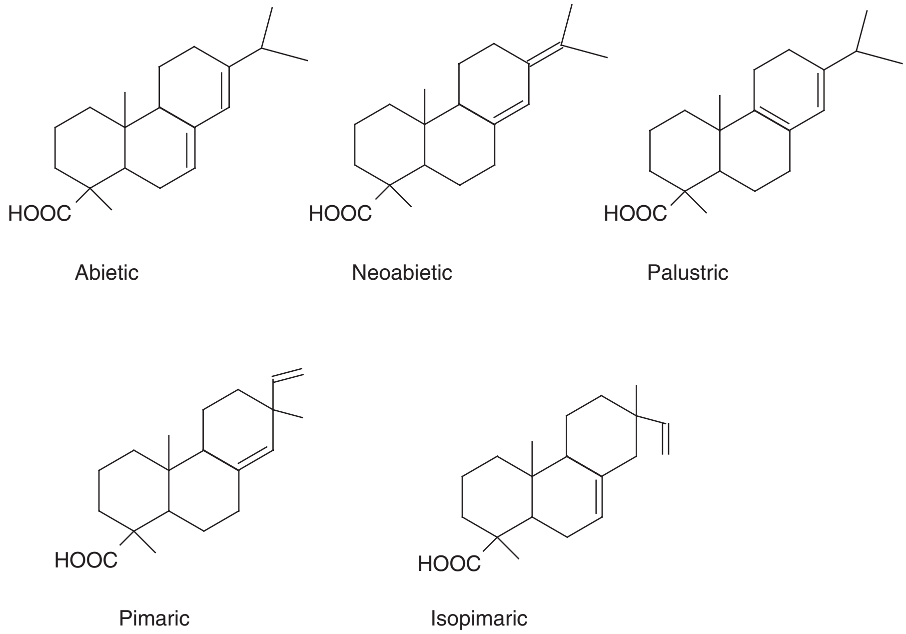


Figure 2 Resin acids.

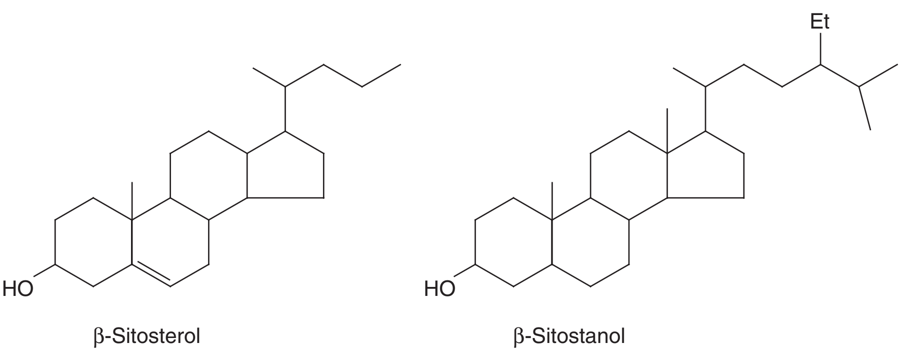


Figure 3 Triterpenes.

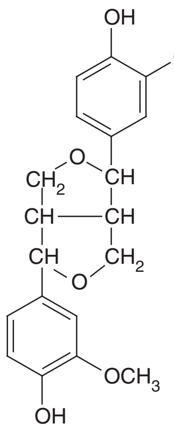
The neutral fraction of the tall oil is made up of triterpenoid β-sitosterol, β-sitostanol, and lignoceryl acohol (**Figure 3**). Given the structure of the former compounds, these have been of interest in the synthesis of other steroids that may have biological applications. The butter/margarine substitute Benecol that reduces low-density lipoprotein cholesterol contains sitostanol.

Phenolics

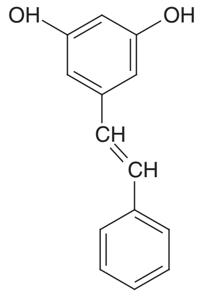
Among the other extractives that are present in wood are a number of phenolics (**Figure 4**). These include the lignans that occur through coupling of C_6C_3 groups, and the stilbenes, made up of 1,2 diphenyl ethylenes. In addition are the flavonoids, and their derivatives, with $C_6C_3C_6$ skeletons. These may be antifungal, can repel insects, act as antioxidants, and are responsible for the colors in flowers. Tannins, originally used as leather tanning agents, due to their ability to bind to proteins, are represented by the condensed tannins, which are oligomeric flavonoids, and the hydrolyzable tannins that are polymers attached to sugars through ester linkages, which yield gallic and ellagic acid upon hydrolysis. More current applications of the tannins have been as adhesives, antioxidants, and viscosity control agents.

Pharmaceuticals

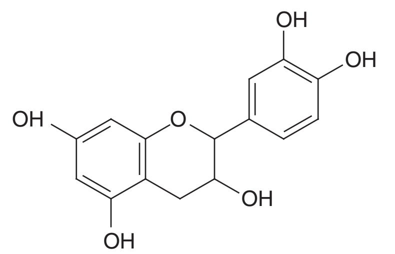
The extractives from wood and bark have had both a long history and recent success with respect to the isolation of important drugs (**Figure 5**). Perhaps the oldest and best known of these applications is the alkaloid quinine, present in the bark of *Cinchona calisaya*, *C. cussiruba*, *C. legeriana*, and *C. officinalis*.



Pinoresinol
(a lignan)

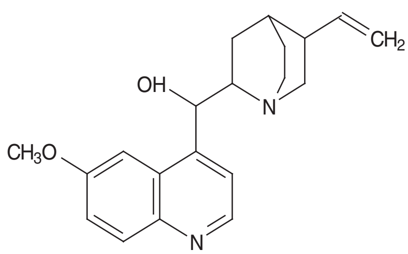


Pinosylvin
(a stilbene)

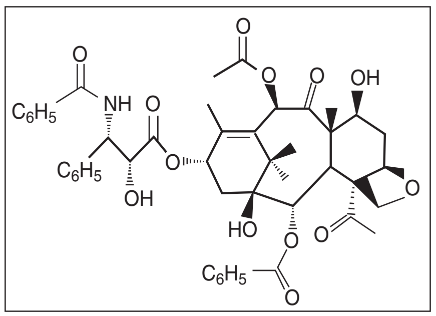


Catechin
(a flavonoid)

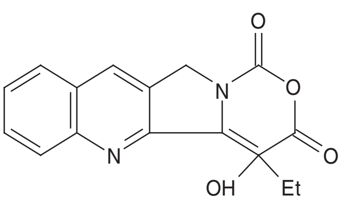
Figure 4 Other extractives.



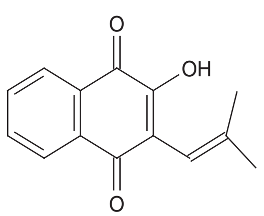
Quinine



Taxol



Camptothecin



Lapachol

Figure 5 Biologically active extractives from wood and bark.

These trees are native to the Andes and the bark may contain up to 15% quinine. Natives of South America used the bark as medicinal, but it appears that Jesuit missionaries first found that the powdered bark had antimalarial properties. The bark from both the tree and branches is used in a powdered form, and usually taken as an infusion.

A more recent development, of course, is the case of taxol, a diterpene originally isolated from the bark of *Taxus brevifolia*. An extract of pacific yew bark was first found to be effective against rodent cancers in 1962, in 1966 taxol was identified as the active compound, and in 1971 the structure was published. Taxol is active against leukemias, breast, ovarian, brain, and lung cancers. Limitations in its use have been encountered due to the slow growth, environmental restrictions, and low concentrations of taxol in the bark of Pacific yew. It has been reported that six 100 year-old trees would be required to treat one patient. Recently, several semisynthetic analogs of taxol have been produced from other species of yew.

Camptothecin, an alkaloid isolated from *Camptotheca acuminata* and its analogs topotecan and irinotecan, has been used in the treatment of ovarian and colorectal cancers. Topotecan has been found to be as effective or more so than taxol in such applications. The tree *C. acuminata*, a member of the Nyssaceae, is native to China and Tibet, where it is known as xi shu ('happy tree'). Harvesting for medicinal purposes caused a rapid decline in the availability, leading to restrictions of cutting and seed exportation. Prior to the exportation bans, plantings were established in the USA, but yields of camptothecin were low. In the meantime, another species, *C. lowreyana*, which is a shrub, has been planted with some degree of success.

Several species of *Tabebuia* (Pau d'Arco), from the rainforests of Central and South America, have been examined as a source of the compound lapachol that has been reported to be effective against some tumor cells. Severe toxicity problems have been reported, however, and to date this compound is not used in cancer therapies.

Polysaccharides

In addition to extractives, polysaccharides have been examined as possible therapeutic agents. A 4-O-methylglucuronoxylan has been isolated from *Fagus crenata* and tested in mice. Cancers in the peritoneal cavity were suppressed, as were the growth rates of tumors. Arabinogalactan, a highly branched, water-soluble hemicellulose with very high molecular weights, that can be isolated from larch heartwood and echinacea, has also received attention from the health care community. This polysaccharide has found use as dietary fiber, for which it is approved, and may have efficacy in immune system responses and as a supplement in cancer treatments. As a dietary supplement, the polysaccharide is rapidly fermented in the intestine, producing short-chain fatty acids that are used by cells in the colon as an energy source. These fatty acids also protect the intestine from diseases and carcinogens. In animal studies, arabinogalactan has been reported to reduce the colonization of the liver by tumor cells.

Lignin

Other by-products from pulping processes are the lignin that is removed during sulfite or sulfate pulping. While most of the sulfate (or kraft) lignin is burned for energy, and as an integral part of the recovery process, the sulfur-containing fractions can be utilized to produce dimethyl sulfoxide (DMSO), dimethyl sulfide, and methyl mercaptan. Methyl mercapatan and dimethyl sulfide are used as odorants in natural gas, while DMSO, due to its solvation properties, is used as a carrier for drugs and agricultural chemicals. Sulfite lignin, or lignosulfonates, have also been used in chemical applications. Under alkaline hydrolysis or oxidation conditions lignosulfonates will produce vanillin. Vanillin is used as a flavoring agent, upon derivatization can be used in sunscreens and fibers, and is an intermediate in the synthesis of the antiparkinson's drug L-dopamine. Lignosulfonates are also used as viscosity control agents in oil well drilling muds, dust suppressants in paving materials, dispersants, and adhesives.

Hydrolysis and Fermentation

The saccharification of wood for the production of monomeric sugars can be accomplished by several methods, including concentrated acid hydrolysis, dilute acid hydrolysis, and enzymatic hydrolysis. Concentrated acid hydrolysis employs mineral acids (mainly hydrochloric or sulfuric acid) at percentages as high as 80%, such that relatively low reaction temperatures (20–25°C) can be used. The drawbacks to this process involve corrosion of equipment due to the acidic environment, neutralization of the product stream, and recovery of the acid. In the dilute acid process, a two-step reaction is used to maximize the sugar recovery from both cellulose and the hemicelluloses. In the first step, a dilute acid pretreatment is performed (0.7% sulfuric acid, 190°C, 3 min), followed by a hydrolysis step at 0.4% sulfuric acid, 215°C for 3 min. The disadvantage of this method lies in the dilute nature of the product. In order to overcome this limitation, a great deal of engineering work has been reported on varying reactor designs. Enzymatic hydrolysis originally used cellulase enzymes as a substitute for the mineral acid, converting the polysaccharides to simple sugars that would be fermented in a separate step. Subsequently, simultaneous saccharification and fermentation (SSF) methods were developed, in which the cellulase and fermenting microorganisms are combined. The enzymes used in both of these processes have largely been isolated from *Trichoderma reesei*, and can be subdivided into endoglucanases that react randomly along the cellulose chain, exoglucanases that react endwise to produce glucose and cellobiose (a glucose dimer), and β-glucosidases that convert cellobiose to glucose.

Upon hydrolysis, the monosaccharides can be converted to a large number of chemicals via either fermentations or chemical processes. The most familiar of the fermentation methods is the conversion of glucose to ethanol by the action of *Saccharomyces cerevisiae*. More recently pentose sugars, which had been problematic in this regard, have been fermented to ethanol by recombinant strains of *Zygomonas mobilis*, *Escherichia coli* and *S. cerevisiae*. Acetic acid can be produced by fermentation with *Acetobacter*, or *Clostridium thermoaceticum*, while lactic acid is fermented from glucose by *Lactobacillus*. An acetone–butanol–ethanol blend can be made with an anaerobic *Clostridium*. Acetaldehye can be produced as a secondary product of ethanol by *Candida utilis* or *Pichia pastoris*, but can also be a direct fermentation product from glucose by either *Z. mobilis* or *S. cerevisiae*. While hydrocarbons are industrially produced from petrochemical sources, it has been found that ethylene, propane, and propylene can all be fermented from sugars by microorganisms. Succinic acid is an important intermediate in the synthesis of butane-diol, tetrahydrofuran, and adipic acid, all of which can also be used in subsequent syntheses. Succinic acid has been successfully produced by the direct conversion of sugars by recombinant *E. coli*.

Another product of fermentation processes is single-cell protein, derived from the dried cells of microorganisms. These may include bacteria, fungi, yeasts, or algae, that produce protein to be used by humans or animals. Sugars in the form of molasses were used as the carbon source for Torula yeast (*Candida utilis*) in Germany during World Wars I and II to extend meat supplies. Lignosulfonates, from sulfite pulping, have also been used as the substrate, and lignocellulosic material, upon either enzymatic or acid hydrolysis, has been used to produce simple sugars, used by a number of fungi and yeasts.

The monosaccharides that arise from the acid hydrolysis of cellulose and hemicelluloses can undergo dehydration reactions upon continued exposure to acidic conditions. The products of these reactions are furfural from the pentoses, hydroxymethyl furfural from the hexoses, and levulinic acid (**Figure 6**). Levulinic acid has recently received considerable attention due to the wide range of potential products that can be derived therefrom. These include ethyl levulinate used as a component in biodiesel fuels, delta-amino levulinic acid (DALA), a biodegradable herbicide, and 1-4 butanediol for use in polyesters. Hydroxymethyl furfural may be used as an intermediate for plastics, resins, and nylon manufacture. Furfural is used as an industrial solvent and in resin production.

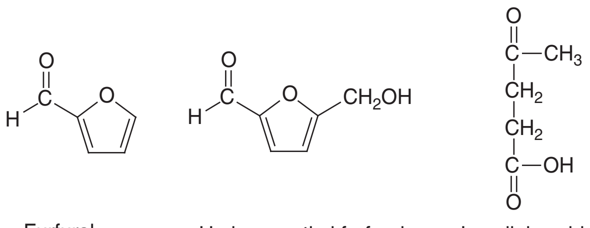


Figure 6 Dehydration products from acid hydrolysis.

The monosaccharides can also be converted to their corresponding alcohols (alditols) by chemical reduction. Xylitol, mannitol, and sorbitol are used as sweeteners, and sorbitol can be used in the synthesis of ascorbic acid.

The hydrolysis process, in addition to the monosaccharides, produces a lignin residue. While this material can obviously be burned as a fuel, ongoing research is examining its reformation into additives for gasoline. The lignin is initially depolymerized under alkaline conditions and is then subjected to deoxygenation and hydrocracking. These steps convert the lignin polymer into a mixture of hydrocarbons that are proposed as octane enhancers for gasoline.

Thermal Degradation

The production of chemicals from wood by the action of heat includes a broad continuum of processes, varying with respect to conditions and products. In general, these methods are done in the absence of air or other oxidizing agents, such that the substrate is thermally degraded, rather than combusted. The general terms used to describe this process include pyrolysis, liquefaction, and gasification, the latter two selectively producing liquid and gas, respectively, while pyrolysis results in a mixture of all three, the relative amounts of which are a function of the conditions.

Pyrolysis can broadly be divided into conventional pyrolysis and fast pyrolysis. The former encompasses techniques such as carbonization or destructive distillation, while the latter includes flash pyrolysis, rapid pyrolysis, and ultrapyrolysis. In any of these, the process variables are the residence time, temperature, and heating rate.

Probably the oldest of the thermal processes is destructive distillation, occurring under long residence times, on the order of hours to days, slow heating rates, and moderate temperatures (300–500°C). The main product is charcoal, with the liquid phase producing turpentine, pine oil, methanol, acetic acid, and a tar fraction that was originally used in sealing and waterproofing wooden ships. The technology used for this process ranges from a simple pit kiln, in which wood is stacked in a hole in the ground, ignited and covered to limit the amount of air, to industrial-scale furnaces. The charcoal that is produced may be used as either a fuel or a source for activated carbon, that can be applied to filtration and purification processes.

Under shorter residence times, higher levels of the more volatile liquid phase can be collected. The liquid consists of a water-soluble fraction containing methanol, acetic acid, acetone, and relatively low-molecular-weight terpenoids. A heavy insoluble pyrolysis oil or tar is also produced. This is an extremely complex mixture of hundreds of chemical compounds, any one of which is present in limited concentration. The cellulose present will preferentially produce levoglucosan, the hemicelluloses are degraded to furans, while the lignin is represented by a large number of phenolic compounds. These phenolics have been exploited in the proposed utilization of pyrolysis oils in adhesive applications. The gas from conventional pyrolysis is relatively low-energy (1–3 $MJ\,kg^{-1}$) and mainly consists of carbon monoxide and carbon dioxide, with small amounts of hydrogen, methane, and ethane.

Fast pyrolysis is characterized by very short residence times, and very high heating rates, with thermal flux values as high as 3000 $cal\,cm^{-2}\,s^{-1}$. These conditions quench the reactions, preventing the formation of secondary products. While all three phases can be produced, as a function of process conditions, at the very highest heating rates gaseous products are preferred, with the major component being acetylene. The heating methods by which fast pyrolysis is performed have been varied and novel, including microwave, radiofrequency, and focused solar radiation.

Liquefaction of wood involves treatment at elevated temperatures in the presence of various liquids and catalysts. At relatively high temperatures (300–425°C) and in the presence of an aqueous solution of sodium carbonate, wood is liquefied at yields as high as 80%. The liquid, which is a complex mixture, can nevertheless be largely composed of phenolic compounds. Alternatively, wood can be liquefied under less severe conditions (temperatures 80–150°C) in the presence of acid catalysts such as hydroiodic, sulfuric, hydrochloric, or phosphoric acids, or simply with solvents, such as phenols, ketones, alcohols, or glycols, at somewhat higher temperatures (240–270°C). These conditions will convert the wood into a liquid product with a paste-like consistency that has been used in adhesive applications, foams, and molded products.

Gasification, as the name implies, is the generation of a gas, with low- to medium-energy contents, and a composition that can be used in subsequent synthetic processes. Gasification can be broadly divided into pyrolysis, partial oxidation, and reforming processes. Under very high pyrolytic temperatures the solid and liquids phases will be suppressed, such that the gas is the main product. Partial oxidation uses less than the stoichiometric amounts of oxygen that would be needed to support combustion. This results in a partially oxidized product. Reforming in this context refers to gasification that is done in the presence of additional reactants, such as steam, steam–oxygen, or steam–air. The products of all of these processes are similar, with carbon monoxide and hydrogen being the main components of the gas. The energy content can range from 100–300 Btu/SCF (standard cubic foot) in processes that utilize direct contact of the wood with air (due to dilution), 300–700 Btu/SCF when oxygen is used, and 700–1000 Btu/SCF when conditions favor the formation of light hydrocarbons such as methane (which is responsible for a large proportion of the energy).

See also: **Medicinal, Food and Aromatic Plants**: Forest Biodiversity Prospecting; Medicinal and Aromatic Plants: Ethnobotany and Conservation Status; Medicinal Plants and Human Health. **Non-wood Products**: Resins, Latex and Palm Oil. **Sustainable Forest Management**: Definitions, Good Practices and Certification. **Wood Formation and Properties**: Chemical Properties of Wood. **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

Danner H and Braun R (1999) Biotechnology for the production of commodity chemicals from biomass. *Chemical Society Reviews* 28(6): 395–405.

Elder T (1991) Pyrolysis of wood. In: Hon DN-S (ed.) *Wood and Cellulosic Chemistry*, pp. 665–699. New York: Marcel Dekker.

Fengel D and Wegener G (1983) *Wood: Chemistry, Ultrastructure, Reactions*. Berlin: Walter de Gruyter.

Goheen D (1971) Low molecular weight chemicals. In: Sarkanen KV and Ludwig CH (eds) *Lignins: Occurrence, Formation, Structure and Reactions*, pp. 797–831. New York: Wiley-Interscience.

Goldberg I (1985) *Single Cell Protein*. Berlin: Springer-Verlag.

Klass DL (1998) *Biomass for Renewable Energy, Fuels, and Chemicals*. San Diego, CA: Academic Press.

Koch P (1972) *Utilization of the Southern Pines*. Agriculture Handbook no. 420. Washington, DC: US Department of Agriculture.

Sjöstrom E (1993) *Wood Chemistry: Fundamentals and Applications*, 2nd edn. San Diego, CA: Academic Press.

Yoshioka M, Yao Y, and Shiraishi N (1996) Liquefaction of wood. In: Hon DN-S (ed.) *Chemical Modification of Lignocellulosic Materials*, pp. 185–196. New York: Marcel Dekker.

Zinkel DF (1981) Turpentine, rosin, and fatty acids from conifers. In: Goldstein I (ed.) *Organic Chemicals from Biomass*, pp. 163–187. Boca Raton, FL: CRC Press.

Cork Oak

H Pereira and M Tomé, Instituto Superior de Agronomia, Lisbon, Portugal

Introduction

The cork oak (*Quercus suber*) is an evergreen oak that spreads in the countries of the western Mediterranean basin, over a total area of 2 million ha. It extends in the western coastal Mediterranean and adjoining Atlantic areas between 34° and 45° N latitude.

The species has a particular characteristic that sets it apart from other evergreen oaks: its ability to produce a thick bark with a continuous layer of cork tissue on the outside, with a thickness and properties that make it a valuable raw material for industry. Whenever the outer cork bark is removed, the tree has the capacity to form a new cork bark by adding new layers of cork every year, and this may be repeated throughout the tree's lifetime.

Cork oak forests nowadays cover considerable areas in Portugal (*c.* 725 000 ha) and Spain (*c.* 475 000 ha), and also in Algeria, France, Italy, Morocco, and Tunisia. The annual world production of cork totals about 370 000 tonnes, mostly from the cork oaks of Portugal and Spain, which produce respectively 51% and 23% of the total.

The Cork Oak Tree

Cork oaks are low spreading trees with a short stem and thick branches (**Figure 1**). The trees do not attain heights greater than 14–16 m but open-grown trees may have very large crown dimensions, e.g., 500 m^2 of crown projection in some mature trees 150–200 years old. The circumference at breast height of these 'monument' trees can be as large as 9 m. When growing in dense stands, the shape of the tree is strongly influenced by competition, giving rise to trees with narrower crowns and higher stems.

Figure 1 Cork oak trees under cork production.

The root system is characterized by a strong and long taproot with thick lateral ramifications that in open-grown trees may show a large horizontal expansion with many superficial roots. The association of the root system with different micorrhyzae is quite frequent.

Cork oak is a monoic species with flowers emerging between April and June; the flowering period may sometimes be longer, with flowers emerging in autumn. Due to the long flowering period, the acorns do not ripen at the same time. The amount of acorns varies widely from year to year, with 2–3 years of high fruit production out of 10 years. Flowering and fructification begin at around 15–20 years of age.

Tree diameter and cork growth are concentrated in spring and the beginning of the summer and are highly controlled by annual weather variations, namely by the precipitation in the previous winter and spring.

The cork oak is a semitolerant species, well adapted to mild climates, like Mediterranean climates with Atlantic influence, with mild winters but hot and dry summers. It grows well with mean annual precipitation of 600–800 mm, even surviving with 400 mm of precipitation. The optimum mean annual temperature is in the range 13–16°C but it survives up to 19°C. Mean temperature of the coldest month should not be below 4–5°C and the absolute minimum survival temperature is −12°C. The optimum growth occurs at 300–600 m of altitude, although the species can be found at higher altitudes (up to 1300 m).

The species prefers deep and well-drained soils, however, it is very soil tolerant and will grow on poor and shallow soil sites. It grows poorly on calcareous or excessively sandy soils.

Cork Biology

Cork Formation

In the cork oak the phellogen is formed as a continuous layer surrounding the stem and branches and producing an external layer of cork cells with an appreciable thickness. Unlike most species, where the phellogen only lives for some years, in the cork oak it may be active as long as the tree.

The phellogen differentiates in the young plants during the first year of growth in the cell layer immediately under the epidermis after the formation of the vascular cambium and the initiation of its activity. Several layers of suberized phellem (cork) cells are produced to the outside by the meristematic division of the phellogen mother-cells during each growth season (**Figure 2**). In the very young stages, the phellem cells are tannin-filled and tangentially stretched due to growth stress, but after approximately 7 years they acquire the characteristics of adult cork cells with empty lumina, thin suberized walls, and a regular arrangement.

Cork Structure and Composition

Cork is a cellular material made up of a regular structure of closed, thin-walled, hollow cells. The cells may be described as hexagonal prisms, packed base-to-base in columns oriented parallel to the tree radial direction. There are no cell-to-cell communication channels (i.e., pits) nor intercellular voids, with the exception of the natural occurrence of lenticular channels.

The structure of cork is anisotropic. In the tangential section (perpendicular to the radial direction), cork cells have a honeycomb-type arrangement and are seen as polygons, mostly with five to seven faces and with areas of $4–6 \times 10^{-6}\,\text{cm}^2$. The radial and transverse sections (perpendicular, respectively, to the tangential and axial directions) are similar and show a brick-layered-type arrangement with the cells aligned in radial oriented rows and with a rectangular form of 30–40 μm length.

Corrugation of cork cells is an important characteristic of their prism lateral faces. Late cork cells show little or no wall corrugation, in contrast to the first spring early cells that are often heavily corrugated due to radial compression resulting from growth stresses.

One conspicuous macroscopic feature of cork is the presence of lenticular channels that cross the planks radially from the external surface to the phellogen; these are usually referred to as cork pores. In a tangential section the lenticular channels appear in cross-section with a more or less circular form, mostly elongated in the tree's vertical direction. There is a very large variation on the number and dimensions of lenticular channels, probably related to tree genetics. The porosity of cork is directly in relation to cork quality. In a good-quality cork, the porosity represents in general less than 4% of the area.

The chemical structure of cork cells is dominated by the presence of suberin as the main component (around 40%). Suberin is an insoluble tridimensional cell-wall polymer with an ester-linked glyceridic framework of long-chain fatty acids and alcohols. The supramolecular structure of this component is still a matter of investigation, regarding its connection to other cell-wall components. Cork cells also contain lignin to a considerable extent, as well as extraneous compounds such as fats and waxes and phenolics. Cellulose and hemicelluloses are also present but their role is much less important when compared to wood cells.

The summative chemical composition of cork is, on average: ash $<1\%$, extractives 14%, suberin 40%, lignin 23%, cellulose 9%, hemicelluloses 11%. Variability of chemical composition has been found between corks of different trees.

Silviculture

Cork oaks can be managed according to two different silvicultural systems:

1. In most cases, cork oak stands have a relatively small number of trees per hectare (sparse forest) and are associated with agricultural crops or pasture for cattle grazing (**Figure 3**); this system is called montado in Portugal and dehesa in Spain.

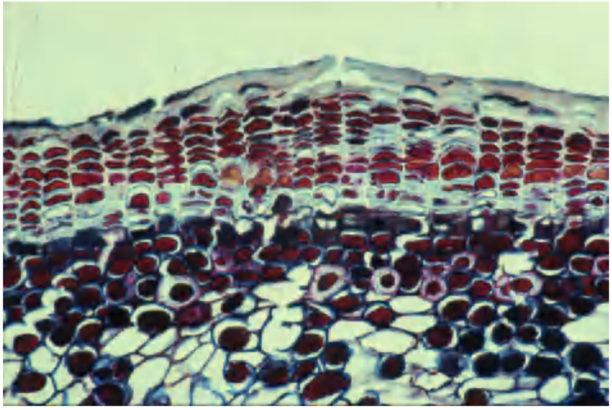


Figure 2 Phellem (cork) cells produced by the tree phellogen during its first year.

Figure 3 A montado in Portugal.

2. In some cases, in mountainous regions, cork oaks are grown in denser stands which do not permit the practice of agriculture underneath the trees.

Both systems are frequently associated with hunting, mushroom picking, and bee-keeping.

Most of the present mature cork oak stands resulted from the management of naturally regenerated stands by generations of landowners or, in some cases, through artificial seeding complemented by natural regeneration. As a result, a large percentage of the stands is characterized by a heterogeneous spatial distribution, and some can be classified as uneven-aged.

Harvesting of cork oaks usually occurs only for sanitary purposes and the present mature stands include a large percentage of old trees. The decision on the best management option or silvicultural system towards the rejuvenation and maintenance of these stands may consider:

- clearcutting the stand (as a whole or in small plots), followed by natural or artificial establishment of a new stand (even-aged silviculture)
- the gradual transformation of the stand towards continuous-cover forestry (continuous-cover silviculture)
- the use of successive regeneration fellings.

In several countries of the Mediterranean region, afforestation with cork oak has been emphasized in the last two decades and even-aged silviculture has been the option for these new stands.

Even-Aged Silviculture of Cork Oak Stands

Stand regeneration Artificial regeneration of cork oak stands is relatively recent but was greatly increased as a consequence of EU policy for the afforestation of agricultural lands. Either plantation or direct seeding by placement of two to three acorns in small holes is used. Acorns are very attractive to small rodents, and the use of repellents is recommended.

In both cases, correct site preparation is essential for the success of the new stand. This includes weeding, usually by disk-harrowing, and the improvement of soil characteristics for the development of the root system. Soil preparation depends on soil type and slope: it may include ripping or subsoiling to 60–80 cm depth, especially in soils overlying hard rock, or plowing and mounding along the contours followed by deep plowing and/or disk harrowing. Site preparation may cover the whole area or be concentrated on the planting line. Starter NPK fertilization is usually applied at 40–100 g per plant.

Plantation and/or seeding can occur either in spring or autumn. The number of trees per hectare at planting is not as high as in other species planted for wood production, and common spacings range from 4×4 m (625 trees ha^{-1}) to 8×4 m (312 trees ha^{-1}).

Operations in the regeneration stage The success of plantations with cork oaks is not guaranteed and mortality during the first years may be very high. The operation of beating-up is very common. The protection of young seedlings with individual tree shelters is considered to be beneficial against browsing and for stimulating initial height growth. However, in regions with high temperatures, this technique has caused higher mortality rates. Whenever spring and summer precipitation is too low, irrigation should be applied two to three times during periods of higher stress. During the first years after planting, weeding is highly recommended around each seedling or on the whole area. Suppression of cattle grazing during the regeneration stage is a precondition for the success of the plantation.

Operations in the juvenile stand The juvenile phase of a cork oak stand refers to the period until the beginning of cork extraction. Young cork oak trees show abundant ramifications without a leading shoot and pruning is therefore an important operation to obtain trees with a clear stem height of at least 2.5–3 m. Depending on site productivity, the first pruning occurs between 3 and 6 years of age and eliminates all the branches in the first two-thirds of the tree. A second pruning is made between the ages of 12 and 15 years. Depending on stand density at planting, this operation may be complemented by a first thinning to reduce stand density to 400–600 trees ha^{-1}. The last pruning is usually made immediately after first debarking. The first debarking for cork extraction is regulated in most countries by legislation. In Portugal only trees with a circumference at breast height ≥ 70 cm can be debarked. Depending on site productivity and stand density at planting, this operation is possible between 25 and 40 years of age.

During the juvenile stage of a cork oak stand, weeding may be undertaken. If the landowner aims at grazing underneath the future stand, the establishment of pasture may occur from the age of 10–15 years.

Operations in mature stands The most important silvicultural operations in mature stands are thinning and, naturally, cork debarking. Some managers sometimes consider applying fertilizers and tree pruning. Weed control, depending on the type of cultivation underneath, may also be needed. It is highly recommended that the method used to control weeds – usually mechanical weeding – does not damage the superficial root system.

Stand density after the first debarking is usually controlled according to a preselected spacing factor. The spacing factor is defined as the quotient between mean distance between trees and mean tree crown diameter:

$$\text{Spacing factor} = \frac{\text{mean tree distance}}{\text{mean crown diameter}}$$

It is usually assumed, even if there is not enough experimental data to confirm this empirical rule, that cork production is affected when intertree competition is too high. The use of a spacing factor that gives each tree enough space to develop its crown without substantial restrictions is recommended. The space between trees should be at least half of its mean crown radius. This rule is equivalent to the maintenance of a spacing factor of around 1.2.

After the first cork debarking, the rotation of cork extractions is also regulated in most countries. In Portugal and Spain, the minimum period allowed between successive extractions is 9 years. The cork extraction of a stand may be done either simultaneously in all the trees – even-aged cork – or in only a selection of the trees, therefore cork age is not the same for trees in the same stand – uneven-aged cork. In uneven-aged cork stands two cork-debarking rotations should be defined: (1) tree cork-debarking rotation, which is usually 9 years; (2) stand cork debarking, depending on how many different cork ages are present in the stand.

In an even-aged cork stand, thinning should occur after cork debarking, so that the landowner can profit from the cork income from the trees that will be thinned and also be able to use cork quality as an additional criterion to select trees to be thinned.

One important parameter of cork debarking is the so-called debarking coefficient, which defines the height in the stem to which cork can be stripped off (debarking height). The debarking coefficient is defined as the quotient between the debarking height and the perimeter at breast height over cork (pbh_{overcork}):

$$\text{Debarking coefficient} = \frac{\text{debarking height}}{pbh_{\text{overcork}}}$$

In some countries the debarking coefficient is also regulated by legislation. For instance, in Portugal, maximum legal debarking coefficient depends on the stage of development of the tree: 2.0 for the first cork debarking, 2.5 for the second cork debarking, and 3.0 for subsequent debarkings.

The application of fertilizers during the period between cork extractions is often made by landowners to improve cork quality. However, the few experimental results available do not show its effect on cork growth and quality.

The acorns of cork oaks were an economically important product in past years and the trees were pruned to increase fruit yield. This practice is still used by some farmers who associate pruning with tree vigor and cork yield, a fact that has never been experimentally proved.

Rotation period Cork oak trees may attain 250–350 years of age. The trees maintain their ability to produce cork but cork thickness decreases as trees age and 150–200 years seem to be the limit for an industrially useful cork production. Rotation periods between 100 and 150 years are usually assumed in most management plans.

Continuous-Cover Silviculture

Continuous-cover silviculture is a very interesting alternative to even-aged silviculture for the management of the existing mature stands, even if at present there are no examples of the use of continuous-cover silviculture in cork oak stands. Some tentative studies using growth and yield models have compared cork yield under this type of silviculture. The main conclusion is that the total production of cork in a continuous-cover silviculture strongly depends on the selected target diameter distribution. It is possible to find options that in the long term will originate cork yields comparable to those obtained with even-aged silviculture.

Three main consequences of using continuous cover forestry are: (1) the proportion of virgin cork – of low commercial value – is higher than in even-aged silviculture due to the continuous maintenance of a large number of young trees in the stand; (2) cork yield is highly dependent on one or two large trees, and if one of these dies, there is a strong negative impact on cork yield during the next period; (3) it is difficult to make this silvicultural system compatible with underneath grazing or game browsing.

Cork Extraction

The first cork taken from the tree is called virgin cork (**Figure 4**). It has deep fractures due to tissue failure upon the tangential stresses of tree radial growth and is of low commercial value. The second cork obtained in the following extraction is more homogeneous in

Figure 4 A young cork oak tree with virgin cork and second cork, respectively, in the upper and lower part of the stem.

thickness but still has numerous longitudinal running cracks (**Figure 4**). It is only from the third extraction that the cork planks show a continuous and uniform thickness that will allow their full utilization by the industry. The cork layer is removed from the tree as large planks by manually cutting with an ax along vertical and horizontal lines on the stem and thick branches and subsequent stripping-off (**Figure 5**). This operation is made in spring and early summer when the tree is physiologically active and allows easy separation of the outer bark.

The raw cork planks have variable dimensions, depending on the tree size and operational conditions at the tree debarking. They are rectangular with dimensions usually falling in the range of 1–1.8 m height and 0.4–0.8 m width. The cork planks are piled up in the field while waiting for transport to the industrial premises (**Figure 6**).

A distinctive feature of cork planks is the presence of a thin layer of lignous materials to the outside of the cork tissues, named the 'back' of the cork planks. The trees under cork production show on the stem and branches the characteristic dark grayish-brown color due to weathering of the back of cork planks and numerous fissures resulting from the radial tree growth. The inside surface of the cork planks corresponding to the tree inner side is industrially named the 'belly.'

Figure 5 Cork extraction from cork oak trees.

Figure 6 Field storage of raw cork planks.

Growth and Yield

Tree Growth

Cork oak is a slow-growing species. The SUBER model, the only published growth and yield model for the species based on data from Portugal, expresses site productivity as the number of years that dominant trees take to attain diameter at breast height (dbh) level. In this model this index is assumed to vary in the range 5–9.

Figure 7 shows the dbh growth of individual trees obtained in tree disks collected at dbh-level as well as the corresponding growth curves used in the SUBER model. As can be seen, dbh growth is very slow but trees can attain very large dimensions as a consequence of the large rotation period.

Cork Growth

The production of new cork is more intense in the years immediately after debarking and decreases from then on. Cork thickness after 4 years is around 75% of the thickness at 9 years of age. When analyzing cork growth, which can be done after cork harvest by measuring cork growth rings, one can show that the first cork growth ring, located adjacent to the cork back, is usually smaller than the subsequent rings. This ring corresponds to the growth of cork in the growing season during which cork was extracted, after debarking. Therefore it is not a complete growth ring and is usually called the first half-ring. Similarly, the last cork growth ring also corresponds to a partial growing period and is called the last half-ring. Cork growth capacity of a tree can be expressed by the accumulated thickness of the first 8 complete years. This index, the cork growth index (CGI), is used in the SUBER model.

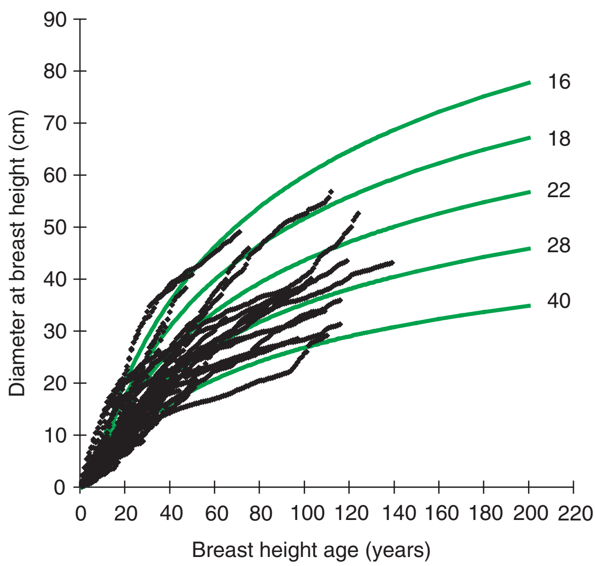


Figure 7 Diameter at breast height (dbh) growth obtained from stem disks at dbh-level as well as simulated dbh growth curves used in the SUBER model.

Stand Development

Stand development depends on site characteristics and on forest management. **Table 1** gives an example of the predicted development of a cork oak stand in a site of mean productivity, managed as an even-aged cork stand, maintaining a spacing factor close to 1.2, and following the maximum legal debarking coefficients. As can be seen, number of trees per hectare, in comparison with other species that are planted for wood production, is quite low, leading to low values of stand basal area. **Figure 8** shows cork yield and stand characteristics in four different stands with a percent crown cover of approximately 58%.

Cork Processing and Products

Cork is a light material, with a density ranging from 0.2 to 0.3. It is rather impermeable to water and other liquids. It is a very durable material, being stable as regards weathering and biotic attacks. On compression, cork behaves as a viscoelastic material, allowing large deformations without fracture and appreciable dimensional recovery. It is an insulation material, with low conductivity. Cork is also a sound and vibrational insulator.

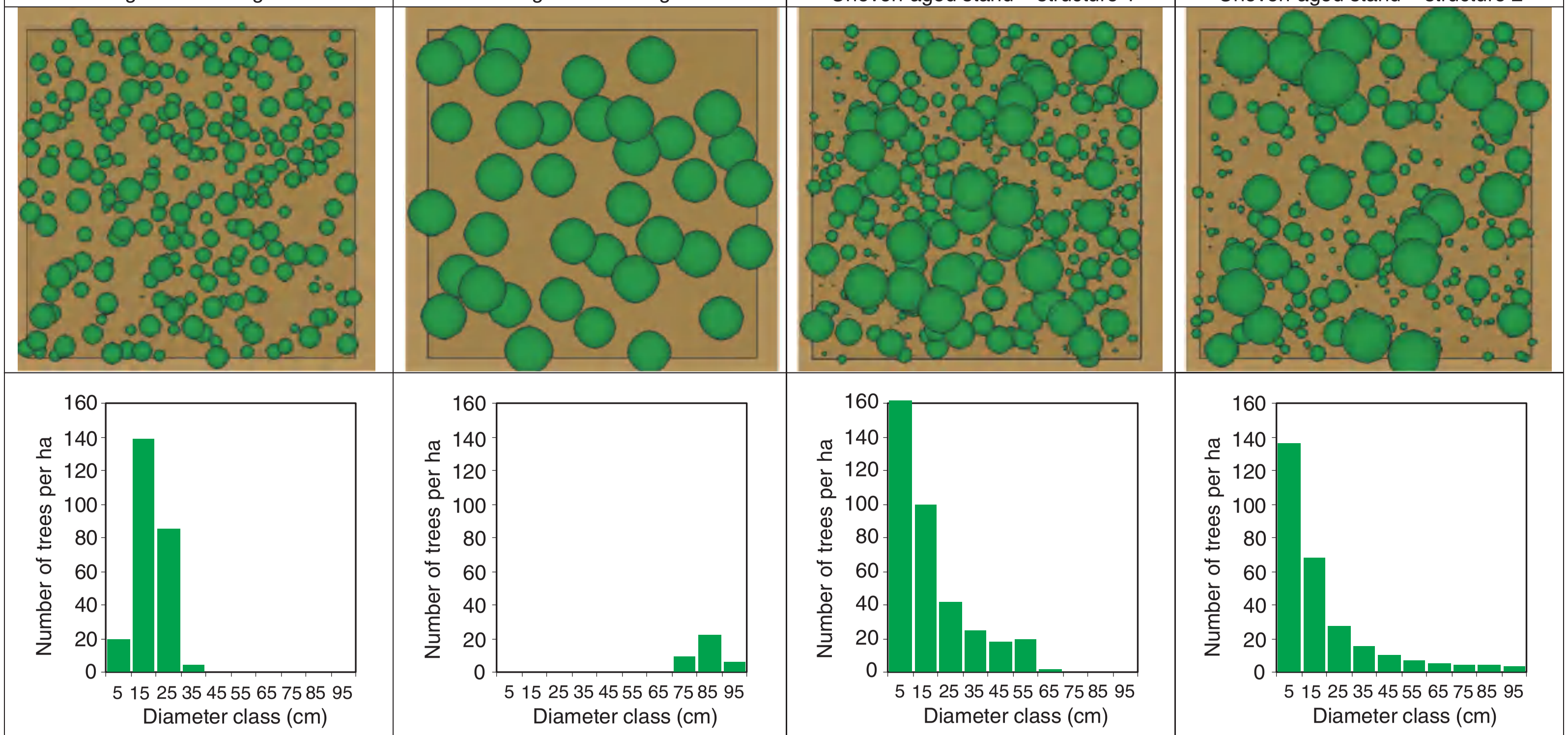
These properties led to cork being used for several purposes, some ancient, others more recent: buoys and floating material, sealants of liquid recipients (i.e., wine bottles), insulation of buildings and industrial equipment, surfacing of walking areas, surface joint sealant in engines, and antivibrational joints in structures (i.e., antiseismic construction).

At present, the cork industry produces different products with variable incorporation of cork and technological transformation. However the economic viability of the whole sector is determined by the production of stoppers of natural cork for use in the bottling of wine. Nowadays it is the suitability of the cork raw material for this production that establishes its commercial quality and the objectives for the forest manager.

Table 1 Yield table for an even-aged stand of mean site productivity managed to maintain a spacing factor of 1.2 and using the legal debarking coefficients

Age (years)	*Stand characteristics after thinning*					*Cork weight (kg ha^{-1})*	
	N *(ha^{-1})*	G *(m^2 ha^{-1})*	d_g *(cm)*	d_{crown} *(m)*	*Crown cover (%)*	*Virgin cork*	*Mature cork*
27	250	7.1	19.0	5.0	49.4	833.0	1153.1
45	114	12.0	36.7	7.8	54.4	639.1	3833.9
63	76	14.6	49.5	9.5	54.2	23.7	4656.3
81	59	16.3	59.4	10.8	53.8	42.8	4853.3
99	50	17.8	67.3	11.7	53.9	60.2	4993.7
117	44	19.0	74.1	12.5	54.0	63.1	5171.2
135	40	19.9	79.6	13.1	53.9	40.9	5293.9
153	37	20.5	84.0	13.6	53.5	38.5	5393.6

N, number of trees per ha; *G*, basal area; d_g, quadratic mean diameter; d_{crown}, crown diameter.



Even-aged stand – age 27	Even-aged stand – age 153	Uneven-aged stand – structure 1	Uneven-aged stand – structure 2
Crown cover = 49%	Crown cover = 54%	Crown cover = 58%	Crown cover = 58%
Stand density = 250 trees ha^{-1}	Stand density = 37 trees ha^{-1}	Stand density = 181 trees ha^{-1}	Stand density = 143 trees ha^{-1}
Basal area = 7 m^2 ha^{-1}	Basal area = 20 m^2 ha^{-1}	Basal area = 12.5 m^2 ha^{-1}	Basal area = 15.0 m^2 ha^{-1}
Mean quadratic dbh = 19 cm	Mean quadratic dbh = 83 cm	Mean quadratic dbh = 30 cm	Mean quadratic dbh = 36 cm
Mean crown diameter = 5 m	Mean crown diameter = 14 m	Mean crown diameter = 6 m	Mean crown diameter = 7 m
Virgin cork weight = 833 kg ha^{-1} Mature cork weight = 1153 kg ha^{-1}	Virgin cork weight = 40 kg ha^{-1} Mature cork weight = 5394 kg ha^{-1}	Virgin cork weight = 342 kg ha^{-1} Mature cork weight = 3076 kg ha^{-1}	Virgin cork weight = 274 kg ha^{-1} Mature cork weight = 3760 kg ha^{-1}

Figure 8 Cork yield and stand characteristics in four different stands with a percentage crown cover of ≅58% (stands simulated with the SUBER model): 1, even-aged young stand; 2, even-aged stand close to rotation age; 3, uneven-aged stand with maximum diameter at breast height (dbh) in the class [62.5; 67.5]; 4, uneven-aged stand with maximum dbh in the class [92.5; 97.5]. dbh, diameter at breast height.

Figure 9 Cork planks after the water-boiling operation.

Figure 10 Boring of stoppers from a cork strip in the industry.

The processing of cork depends on the type of cork: virgin and second cork are directed for trituration to produce cork granules that will be used for cork agglomerates; the reproduction cork planks (from the third extraction on) are used to produce stoppers.

The cork planks undergo postharvest preparation for further industrial processing consisting of immersion in water at approximately boiling point for 1 h. The objective of this operation is to flatten the stem-curved raw planks and to soften the cork tissue for easier subsequent cutting (**Figure 9**). In boiling water the cork expands and the most important practical consequence is that the raw cork planks increase in thickness, on average by 12%. There is a high variation in thickness increase with water boiling between different cork planks, with values ranging from almost nil increase to more than one-third of the initial dimension.

Cork planks that have a thickness over 27 mm are directed for production of stoppers. For this they are cut into strips and the stoppers are bored with a hollow cutting cylinder with an inner diameter equal to the desired stopper diameter (**Figure 10**). The stoppers are dimensionally rectified, washed, bleached, dried, and classified into commercial quality classes according to the extent of the porosity shown on their surface, as given by the lenticular channels. In the stoppers the lenticular channels run parallel to the top and bottom faces.

The cork planks that have a thickness below 27 mm are directed for the production of disks. The planks are cut into bands, and laminated tangentially in the cork into 2–5-mm-thick cork sheets from which the disks will be punched out. The disks will be used glued on bodies of agglomerated cork, i.e., for champagne and sparkling wine.

The residues from the boring of stoppers and of disks (amounting to more than 75% of the initial cork plank) are triturated and agglomerated. Cork agglomerates are used to produce agglomerated stoppers and for cork boards and sheets used in various surfacing situations, i.e., flooring, paneling, joints. In a mixture with rubber, a composite material is produced for industrial and construction vibrational absorption.

A special insulation material called expanded cork agglomerate is made by high-temperature (*c*. 300°C) expansion and self-agglomeration of cork granules in autoclaves with superheated steam. The agglomerate has a dark brown color and is used for heat and sound insulation.

See also: **Temperate Ecosystems**: Fagaceae.

Resins, Latex and Palm Oil

P P Bhojvaid and D C Chaudhari, Forest Research Institute, Dehradun, Uttaranchal, India

Introduction

Besides timber and fuelwood, many commercial products of biological origin are sourced from forests all over the world. These comprise medicinal herbs, edible plants and plant parts, aromatic oils, gums, resins, latex, fibers, flosses, and a variety of other products commonly referred to as non-wood forest products. Resins, latex, and palm oil are one such category of product which have found place in industrial, commercial, and subsistence use with humans. While resins and latex are exudations which are secreted in response to natural and induced injuries to plants, palm oils are extracted from the fruits and seeds of certain tree species. The purpose of this article is to provide basic information on important resins, latex, and palm oil-producing forest plants with special reference to plant sources and description, uses, collection, primary processing, and value-added processing.

Resins

Definition and History

The term oleoresin is used to distinguish the fresh liquid exudation from trees having a high content of volatile oil. These are amorphous (noncrystalline) substances with a complex mixture of organic compounds called terpenes, which are insoluble in water but soluble in certain organic solvents. These yield on distillation two important commercial products, turpentine oil and nonvolatile solid rosin, which is also known as calophony.

Use of pine resins dates back to the period when wood was used for shipbuilding. The pitch obtained from pine trees for caulking the seams of wooden ships and preserving their ropes and rigging was the initial phase of the resin production industry. Consequently, the term naval stores industry denotes the industrial production of oleoresin or resin, used for waterproofing wood ships.

Resin Canals

Resin is produced in two types of resin canals, which are distributed in the tree stem. The large longitudinal ducts have an irregular distribution in the middle and outer portion of tree stem and the smaller horizontal canals are restricted to the outer part of the stem bark. These canals are formed by secondary division of growth cells (cambium), and are lined with a thin-layered wall of secretory epithelium enclosing a central hollow portion. The canals are interconnected to form a continuous network of resiniferous canals in the tree stem. Consequently, when one of these canals is cut at the stem surface, the resin flows to the openings from the inner portions of the stem.

Tapping Process

Resin is a secondary product which is produced by normal metabolic processes in trees; however, it exudes only in response to natural or induced injury to tree stems. Consequently secretion of resin is a defense mechanism in response to wounds and injuries and acts as a disinfectant against microbes and prevents the ingress of borer insects.

In normal resin tapping, a small superficial incision results in resin flow from horizontal canals, which in turn stimulate flow from longitudinal canals located deep in the stem. Trees above 30 cm diameter at breast height (1.37 m above ground level) are suitable for economical tapping. The best time for tapping is March to October; however, maximum resin yield is obtained in the months of May to July and September to October. In light-intensity tapping, superficial blazes result in minor injuries, which are healed in one to two growing seasons. However, unscientific blazing can cause irreversible damage and make trees prone to fire due to the inflammable nature of resin and pine-wood. Consequently, the classical method of tapping with the use of random blazes, which are frequently repeated, leading to large scars on tree stems, has been replaced by the environmentally friendly and ecologically sound rill method. In this method, only tree bark is chipped and small surface incisions are made in a definite geometric pattern using a sharp knife. The resin flow is enhanced with the use of dilute acid, 2-4-D, or other chemical stimulants, thereby increasing resin yield (**Figure 1**).

Processing of Resin

Processing of resin is essentially a technique to separate its main constituents, rosin and turpentine oil. Two different methods in vogue are direct heating and steam heating. The former involves heating resin in vats covered by light lids with the intermittent addition of water in small quantities. The resultant steam from the vat runs through a spiral pipe passing through cold water. This condensation process results in separation of turpentine, which is collected in a vessel at the end of a pipe. The rosin left in the vats is filtered before filling in packing vessels. This method, however, does not yield superior-quality rosin.

In steam heating, vats with a V-shaped bottom are provided with steam jackets for heating resin. Some quantity of inferior turpentine oil is added to the crude resin and the vat is covered with an airtight lid. The mixture is then heated by steam jackets and stirred by a helical belt mixer provided in the vessel. Subsequent cooling facilitates heavy impurities settling at bottom, while the lighter fraction accumulates at the surface and is removed by a ladle. The resin is then allowed to flow into a tank, leaving the sludge in the welter. Subsequently, resin is pumped for distillation in a still heated by a steam jacket. The lighter oil comes first, followed by heavier fractions during distillation. The steam injection is stopped and rosin is allowed to cool

Figure 1 Recurrent incisions on stem surface in the lip and cup method of resin tapping result in injuries (a) leading to fires and subsequent tree mortality (b). In the rill method of tapping (c), the application of chemical stimulants facilitates higher yields and the small superficial incisions are quickly healed by the natural process of bark growth (d).

for complete dehydration and evaporation of remaining traces of turpentine oil. The pine rosin obtained in this process is of much higher value than that obtained by direct heating.

Classification of Resins

The classification of resin is very complex. The resins occur in a pure to nearly pure state or as a mixture with essential oils and gums. Furthermore, resins are produced from several plant species. Consequently satisfactory classification and grouping of resins or of the resin-yielding plants become difficult. However, a simplistic classification can be into three broad categories: (1) hard resins; (2) oleoresin; and (3) gum resins, as shown in **Table 1**.

Hard resins These are usually solid, more or less transparent, colorless, odorless, brittle substances with a little amount of essential oils and are the best source of raw material for varnishes. The most important commercial resins in this category are copals, dammars, mastic, and dragon's blood.

Copal Copal is characterized by its hardness and high melting point. Copal is soluble in alcohol and oils; the oil-soluble forms were also used in the manufacture of linoleum. Commercial copal is obtained from *Agathis*, a tree species of Southeast Asia, found in Malay, Indonesian archipelagos, and the Philippines.

Damar (dammar) Damars are solid resins, less hard but more durable than copal, and white to yellow in color. Damars are soluble in hydrocarbon solvents and drying oils. Damar for international commerce is obtained from dipterocarp trees in Southeast Asia. The sal (*Shorea robusta*) tree is tapped in India to obtain damar. Its main use is in the manufacture of paper, wood varnishes and lacquers, and paints. Minor uses include manufacture of inks, polishes, and water-resistant coatings. In India, sal dammar is widely used as incense and in the indigenous system of medicine.

Mastic Mastic is obtained from *Pistacia lentiscus*, a small tree of the Mediterranean region. Bombay mastic is obtained from *P. cabulica*, occurring in Afghanistan, Baluchistan, and Gilgit (Kashmir). Mastic is produced in the form of small tears, pale yellow in color, clear and glassy in nature, and is liable to fracture. Its age-long use in Arab countries has been for chewing as a mouth freshener and to help preserve the teeth and gums. Its aromatic properties also make it suitable as a flavoring agent for alcoholic beverages. In the past, it was also used in the manufacture of high-grade varnishes for paintings, and for medicinal purposes.

Dragon's blood The plant sources of dragon's blood are *Daemonorops* spp. (Southeast Asian rattan), *Dracaena* spp., and *Croton* spp. *Daemonorops didymophylla* bears bunches of scaly fruits, which are covered with red resin. The major production of this resin comes from the islands of Sumatra and Borneo and some parts of peninsular Malaysia. The resin of commerce is in the form of powder, granules, sticks, or friable lumps with a deep dull red color and its use is largely confined to very specialized markets, such as violin varnish.

Oleoresins Oleoresins contain a considerable amount of essential oil in addition to resinous materials and have a distinct aroma and flavor. Among the oleoresins used in commerce, turpentine, balsam, copaiba, and elemis are prominent. The distinction between these groups is very slight and often confusing.

Turpentines Turpentines are oleoresins obtained almost exclusively from coniferous trees. For commercial purposes, crude turpentine is obtained by tapping trees of *Pinus* spp. On distillation, oleoresins

Table 1 Resin types, resin-producing species, and main resin-producing regions

Resin type	*Main genera*	*Plant family*	*Main producing region*
Hard resins			
Copal	*Agathis*	Araucariaceae	Southeast Asia
Dammar	*Shorea, Hopea, Vatica, Vateria*	Dipterocarpaceae	Southeast Asia
Mastic	*Pistacia*	Anacardiaceae	Mediterranean
Dragon's blood	*Daemonorops*	Palmaceae	Southeast Asia
Oleoresins			
Turpentine	*Pinus*	Pinaceae	Southeast Asia, Europe, USA
Benzoin	*Styrax*	Styracacae	Southeast Asia
Styrax	*Liquidambar*	Hamamelidaceae	Asia Minor, Central America
Peru/tolu balsams	*Myroxylon*	Leguminosae	Central and South America
Copaiba	*Copaifera*	Leguminosae	South America
Elemi	*Canarium*	Burseraceae	Southeast Asia
Gum resins			
Asafoetida/galbanum	*Ferula*	Umbelliferaceae	Asia Minor
Gambose	*Garcenia*	Sapotaceae	Siam, Indochina, India, Ethiopia
Myrrh	*Commiphora*	Burseraceae	Somalia, Arabia
Frankincense	*Boswellia*	Burseraceae	Southern coast of Arabia, Northeast Africa

yield the essential oil or spirits of turpentine and the solid residue is called rosin. Turpentine and rosin are one of the major forest-based industries in the world. Rosin has a variety of uses in industry, in the paper industry (paper sizing), printing-ink industry, paint and varnish industry, leather industry, soap industry, and in the production of batteries, synthetic rubbers, perfumes, joysticks, fireworks, and adhesives. Turpentine oil is one of the basic raw materials for chemicals for a wide range of industries such as paints and varnishes, polishes, aromatic chemicals and pharmaceuticals, soap, and perfumery. Its products are also used in the manufacture of synthetic rubber, waxes, insecticides, and germicides.

Principal sources of oleoresin Out of 100 species of pines, only a few dozen are being tapped commercially as a source of crude oleoresin for rosin and turpentine production. In others, the poor yield or quality of resin makes tapping uneconomic. More than three-quarters of pine oleoresin is obtained from *P. palustris, P. elliottii* (USA), *P. sylvestris* (Russia and Northern Europe), and *P. pinaster* (France, Italy, Portugal, and Spain). The principal sources for commercial production of oleoresin are listed in **Table 2**.

Benzoin Benzoin is obtained from trees of the *Styrax* species native to Southeast Asia. There are two types of benzoin of commerce: Siam benzoin is obtained from *Styrax tonkinensis* and Sumatra benzoin from *S. benzoin* and *S. paralleloneurus*. Fresh Siam benzoin is semisolid but soon hardens to form brittle drops, often translucent, and yellowish-red to brown in color. Sumatra benzoin also hardens to form solid drops. Both are traded as solid blocks and are used in aromatic chemical industries such as expensive delicate perfumes. Sumatra benzoin is widely used in pharmaceutical preparations, as inhalations for the treatment of catarrh and as antiseptics. In China, it is also used in traditional Chinese medicine.

Table 2 The principal sources for commercial production of oleoresin

Species	*Resin-producing countries*
Pinus elliotii	Brazil, Argentina, South Africa, USA, Kenya
P. massoniana	People's Republic of China
P. kesiya	People's Republic of China
P. pinaster	Portugal
P. merkusii	Indonesia, Vietnam
P. roxburghii	India, Pakistan
P. oocarpa	Honduras, Mexico
P. caribaea	Kenya, South Africa, Venezuela
P. sylvestris	Russia
P. halepensis	Greece
P. radiata	Kenya

Styrax Styrax or storax is a balsamic oleoresin extracted from the genus *Liquidambar*. Asian styrax is obtained from *L. orientalis* of Asia Minor and American styrax from *L. styraciflua* of Mexico and Central America. Asian styrax is a semisolid, sticky brown substance. American styrax is usually darker but cleaner than Asian styrax. Both contain cinnamic acid or derivatives of cinnamic acid, whereas American styrax has a typical balsamic odor masked by a styrene-like odor. On distillation, both types of styrax yield an essential oil which is widely used in perfumery. Styrax is also used in pharmaceutical preparations, particularly in bronchial medicine.

Peru and tolu balsams Peru and tolu balsams are oleoresins, obtained as exudates from the *Myroxylon* tree, which is native to Central America and northern parts of South America. Balsam of Peru is obtained from *Myroxylon balsamum* var. *pereiraie* (syn. *M. pereirae*), a tree of Central America. Balsams contain benzoic or cinnamic acid and are highly aromatic. True balsam contains much less oil than turpentine. Balsam yields essential oils on distillation, which is used in perfumes as a fixative and in medicine as a mild antiseptic for treating cutaneous disorders and in the preparation of expectorants.

Copaiba Copaiba is obtained from certain Amazonian species of *Copaifera*. This resin yields copaiba oil on distillation. Crude copaiba balsam is a clear, pale yellow in liquid form. It darkens and becomes less fluid on prolonged storage or exposure to air. It is employed in pharmaceutical preparations, mainly as an antiseptic and anti-inflammatory agent. Copaiba oil is one of the ingredients used in shampoos, soaps, and cosmetics. While *C. guianensis*, *C. multijuga*, and *C. reticulata* are the principal sources of copaiba in Brazil, the major production in Colombia, Venezuela, and Guiyana is from *C. officinalis*.

Elemi Elemi is a resinous product obtained from *Canarium* species in the Philippines and Manila. Manila elemi is soft and fragrant and is obtained from the trunk of *C. luzonicum*. Fresh elemi is oily and pale yellow or greenish in color, but becomes hard on exposure to air. It has a balsamic odor and a spicy, rather bitter taste. Distilled oil from elemi is used in the perfume industry. It is also one of the ingredients in the preparation of lacquers and varnishes.

Gum resins These are mixtures of gums and resins and exhibit the characteristics of both. Gum resins also contain a small amount of essential oils and are usually produced by plants of dry arid regions. The important gum resins are gambose, asafoetida, myrrh, and frankincense.

Asafoetida This plant exudate is obtained from *Ferula asafoetida* species, which occur in Afghanistan, Iran and Turkey. The product is obtained by cutting the stem of the shrubby plant close to the ground (prior to the flowering stage) to expose the taproot. A small quantity of latex exudes and this is collected every few days. Sometimes the root is sliced every few days to produce more exudate. Asafoetida has a strong odor and a bitter acrid taste due to the sulfur compounds present in the essential oil. It is used throughout Asia in spice blends and as a flavoring agent for meat sauces, pickles, curry and other food products, and as a medicine. Since it is so strong in taste and odor, asafoetida is often blended with diluents such as starch and flour and is sold in compounded form.

Galbanum Galbanum is obtained from *Ferula galbaniflua*. The natural distribution of this species is in Iran and northwest India. The oleoresin is obtained by making an incision or cuts on the stem and the resultant exudate is an orange-yellow gummy fluid, which hardens on exposure to air. Like asafoetida, it is also often mixed with extraneous matter. It has a tenacious and powerful aromatic odor. The essential oil contains a number of sulfur compounds. It is used in medicine as well as to a limited extent as a perfume fixative.

Gambose This is a hard, brittle, yellow gum resin produced by several species of *Garcinia,* specially *G. hanburyi* of Siam and Indochina and *G. morella* of India. It is used to color golden lacquers, as a watercolor pigment, and in medicine.

Myrrh This is the myrrh of antiquity, used in incense, perfume, and in embalming. One of the oldest and the most valuable gum resins, it occurs in two forms. The first type is derived from *Commiphora myrrha*, a large shrub or a small tree of Ethiopia, Somalia, and Arabia. The second type is sourced from *C. erythraea*, an Arabian species of similar appearance.

Frankincense or olibanum A fragrant gum resin obtained from the stems of *Boswellia* species, specially *B. carterii*, native to northeastern Africa and the southern coast of Arabia, its principal use is as incense in Roman Catholic and Greek churches.

Latex

Natural latex is a hydrocarbon polymer obtained from the sap of a number of plants. It is usually white, but rarely buff-yellow to grayish in color. Latex contains 30–40% rubber and the rest are nonrubber constituents such as proteins, amino acids, starches, sugars, organic acids, resins, gums, tannins, pectin, and minerals. Nonrubber constituents stabilize the rubber particles, which are otherwise in a state of continuous motion known as Brownian movement. Further details on the history and production of latex are given elsewhere (*see* **Papermaking**: Paper Raw Materials and Technology).

Palm Oil

History

The history of palm oil can be traced back to the days of the Egyptian pharaohs 5000 years BC. It has been used for a very long time for food, medicine, and industrial purposes. The palm oil of commerce is obtained from fruits of the tree *Elaeis guineensis*. This species is a native of West Africa and was introduced to Malaysia in the beginning of the twentieth century. Most of the introduced plants in Malaysia were obtained in 1884 from four palm trees growing at the botanical gardens in Bogor. Commercial production started in 1917 in Malaysia. Indonesia and the Philippines have also started massive palm oil plantation programs.

Next to soybean, palm oil is the most important vegetable oil in world vegetable oil trade. Tree species such as *Cocos nucifera* (coconut) and *Elaeis guineensis* (African palm oil) are major species, which are commercially cultivated throughout tropical regions for palm oil production. Two types of oil are obtained from the palm fruit: mesocarp oil and endocarp (kernel) oil. African palm oil is a source of both types of oils, the mesocarp and the kernel each containing about 50% oil. Palm oil is also obtained from the following tree species:

- *Jessenia bataua* occurs in North and South America, including Panama and Trinidad. Its fruit is a source of oil. The composition of its oil is similar to that of olive oil.
- *Bactris gasipaes* (Pejibaye palm) has great potential as a crop in humid neotropics for starch, protein, oil, and carotene. Its mesocarp yields 40–60% oil on a dry-weight basis.
- *Attalea colenda* is a native of the coastal plains of western Ecuador. The oil content of the seed is 56.9% on a dry-weight basis. This palm oil has a high concentration of lauric acid. Its kernel is similar to coconut oil and kernel oil of African palm oil.
- *Phytelephas aequatorialis* (Tagua palm) the interior mesocarp has 22% fat, and is rich in linoleic acid (21%).

Uses

Palm oil is used in food, chemical, cosmetics, and pharmaceutical industries. It is considered best for manufacturing solid-fat products. Palm oil olein and stearin are used worldwide in making margarine, shortening, and confectionery, and in frying snack foods. It is a cost-effective option as it does not require an expensive hydrogenation process for solidification. Palm oil has a high content of natural antioxidants and its stability at high temperatures makes it excellent as a deep-frying medium. It also gives fried products a longer shelf-life, while its bland taste brings out the natural flavors of food.

Palm oil is also used in the manufacture of soaps, detergents, and other surfactants. It is a good raw material for producing oleochemicals, fatty acids, fatty alcohols, glycerols, and derivatives for the manufacture of cosmetics, pharmaceuticals, household, and industrial products. Oleochemicals manufactured from palm oil and palm kernel oil are now popular for the manufacture of environmentally friendly detergents as they are readily biodegradable.

Nutritional Value

Nutritional scientists have established that palm oil is cholesterol-free and does not require hydrogenation. Red and golden palm oil are the richest natural sources of carotenoids, including β-carotene, a potent antioxidant and precursor of vitamin A. Palm oils are natural sources of the antioxidant vitamin E constituents such as tocopherols and tocotrienols, which play a protective role in cellular aging, arteriosclerosis, and cancer. Further, palm oil contains linoleic acid, an essential fatty acid, which facilitates absorption and availability for use in the body.

Palm oil production

Each tree is capable of bearing about 10–12 bunches of fruit per year. The number of fruits per bunch varies from 1000 to 3000 in mature trees. The average weight of each bunch varies from 20 to 30 kg. The fruit-producing life of the palm is around 20–30 years. The average yield of palm oil is more than 3700 $kg\,ha^{-1}\,year^{-1}$ compared to 857 $kg\,ha^{-1}\,year^{-1}$ for peanut and 389 $kg\,ha^{-1}\,year^{-1}$ for soybean oil. World production of palm oil is 25.66 million tonnes. Malaysia and Indonesia palm oil production accounts for 20% of all world vegetable oil production. Some basic data on production, consumption, and world trade of palm oils are given in **Table 3**.

Table 3 World trends in plantation area, production, export, and import of coconut and palm oils

Parameter	*Palm oil*	*Coconut oil*
Area planted (million ha)	6.5	11.9
Production (million tonnes)	25.66	10.0
Export (million tonnes)	14.2[a]	1.16[c]
Import (million tonnes)	8.89[b]	1.3[d]

[a] Indonesia and Malaysia.
[b] Europe, Middle East, China, India, and Pakistan.
[c] Philippines.
[d] Europe and USA.

Future Directions

There has been a general decline in the use of latex and resins in the world in the last century. This is due to the preference of industry for raw materials which are of consistent, predictable quality and are not subjected to the vagaries of weather, insect pest, disease, and political stability in producing countries, and which are available at an attractive price. In many cases the synthetic alternatives meet these needs and are also technically superior to the natural products they replace. However, certain gums, resins, and latex are still being used, either due to their functional properties, which synthetics cannot meet, or due to their lower price compared to synthetics. These observations are, however, limited to the larger consumer markets at a global level and essentially the natural products described in this article do contribute enormously to local, regional, and national economies. Consequently, this group of non-wood forest products has great potential in alleviating poverty and in the sustainable management of natural forests in developing countries. Therefore, there is a need to maintain quality and improve it in order to retain and increase the markets of these natural products. This will require focused efforts to improve, standardize, and catalog the collection, harvesting, and postharvesting techniques. This will facilitate increased yields and minimum damage to forests, thereby adding incentives to collectors in terms of green and sustainable marketing. In conclusion, there are good grounds for optimism that, despite recent changes in global markets, there will continue to be a demand for these natural products. There are opportunities in the producing countries, provided due attention is given to aspects such as quality control of the product, equitable utilization, and sustainable management of the resource.

See also: **Medicinal, Food and Aromatic Plants**: Forest Biodiversity Prospecting. **Papermaking**: Paper Raw Materials and Technology. **Silviculture**: Managing for Tropical Non-timber Forest Products. **Sustainable**

Forest Management: Definitions, Good Practices and Certification.

Further Reading

Anonymous (1950) The Wealth of India- Industrial Series, Publication and Information Directorate, pp. 242–271. New Delhi, India: CSIR.

Anonymous (1972) *Indian Forest Utilization*. Dehradun, India: Forest Research Institutes and Colleges.

Anonymous (1973) *Processing of Natural Rubber*. FAO Agricultural Services Bulletin, no. 20 Rome: Food and Agriculture Organization.

Balick MJ (ed.) (1988) The palm–tree of life: biology, utilization and conservation. *Advances in Economic Botany* 6: 1–282.

Balick MJ and Beck HT (eds) (1990) Useful Palms of the World: *A Synoptic Bibliography*. New York: Columbia University Press.

Basu SK and Chakraverty RK (1994) *A Manual of Cultivated Palms in India*. Calcutta, India: Botanical Survey of India.

Chaudhari DC (1995) *Manual of Rill Method of Resin Tapping from Pines*. Dehradun, India: Indian Council of Forestry Research and Education.

Coppen JJW (1995) *Gums, Resins and Latexes of Plant Origin*. Rome: Food and Agriculture Organization.

Corner EJH (1966) *The Natural History of Palms*. Berkeley, CA: University of California Press.

Data on Agriculture/Agricultural Production–Primary Crops/Natural Rubber. FAOSTAT- FAO statistical databases. Available online at: http://apps.fao.org.

Hillis WE (1987) *Heartwood and Tree Exudates*. Berlin: Springer-Verlag.

Howes FN (1949) *Vegetable Gums and Resins*. Waltham, MA: Chronica Botanica.

Johnson DV (1998) *Tropical Palms*. Rome: Food and Agriculture Organization.

Jones DL (1995) *Palms Throughout the World*. Washington, DC: Smithsonian Institution Press.

Mantell CL (1950) The natural hard resins: their botany, sources and utilization. *Economic Botany* 4: 203–242.

Rubber Trees

P W Allen, Harpenden, UK

Introduction

The forest tree *Hevea brasiliensis*, native to the Amazonian rainforest, has been grown in Asia and Africa for over a century to produce natural rubber, a raw material used for the manufacture of a range of products, especially tires. Production and export of natural rubber has played a major role in the socioeconomic development of the producing countries. Until the start of World War II natural rubber was the sole supply of an elastic material. Since the 1950s it has had to compete with a variety of oil-derived synthetic rubbers; nevertheless natural rubber has managed to establish good markets in products that require natural rubber's specific properties. The obvious environmental advantages which natural rubber possesses over the synthetic rubbers have never translated into financial advantage: both kinds have for decades suffered, like most industrial raw materials and agricultural commodities, from poor prices. Despite this, producing natural rubber remains the main and often the sole source of family income for millions of small farmers around the world.

History

Natural rubber is found in the form of latex in at least 2000 species of plants: these include *Hevea* spp., *Manihot*, and *Castilloa* from tropical America; *Landolphia* and *Funtumia* from Africa; and *Guayule* from Russia. There is only one rubber-bearing species of commercial significance – *Hevea brasiliensis* – a native of the Amazonian (mainly Brazilian) rainforest.

Hevea is widely distributed in the rainforest, a few trees per hectare, and rubber had been extracted by forest-dwellers from these trees for centuries for the manufacture of playballs and religious artefacts. During the eighteenth century several European explorers noted the existence of the tree and its product. In England, the eminent chemist Joseph Priestley observed the ability of the product to erase pencil marks and gave it the name 'rubber.' It is odd that this name has persisted in the English language for it relates to a property of the material that is of little use. The name in most other languages (e.g., caoutchouc, Kautschuk) is more apt, stemming from the Tropical American Indian *cachuchu*: 'weeping wood.' The older English name 'india rubber' represents a misunderstanding of rubber geography.

With the development in the mid-nineteenth century, mainly in Britain and the USA, of technologies (shaping, vulcanization) for converting the raw material into useful products, the demand for natural rubber started to grow so fast that the supply from Brazil was proving inadequate, despite savageries inflicted on forest rubber-gatherers, and the price was rising excessively. During the 1860s Sir Clement Markham of the India Office (UK), who had been responsible for transferring the quinine-bearing plant *Cinchona* from tropical America to organized plantings (plantations) in India, had the inspiration of doing similarly with *Hevea*. He commissioned two English botanists to collect specimens of *Hevea* spp. for study at Kew Gardens: they identified *Hevea brasiliensis* as the most promising. After several failed attempts to collect and ship seeds from Brazil, the British government commissioned Henry Wickham to make another attempt: he succeeded and brought some 70 000 seeds to Kew Gardens. Just over 2000 seeds germinated; some were sent to Ceylon (Sri Lanka), some to Malaya (Malaysia).

By 1890 *Hevea* seedlings were widely distributed, forming the basis of a major new industry, first in Asia, subsequently in West Africa. Production grew fast, stimulated by the invention of the pneumatic tire by John Dunlop in 1888 and arrival of the motor car.

Brazil has long ceased to be a major producer of natural rubber for a number of reasons, especially that attempts to establish plantations of *Hevea* have been largely vitiated by South American leaf blight, an untreatable fungal disease which has providentially not arrived in the main rubber-growing countries.

Producing and exporting natural rubber has played a major role in the socioeconomic development of the producing countries (**Figure 1**), providing much employment, inward investment, and importation of hard foreign currency.

Until the entry of the USA into World War II in 1942 natural rubber had no serious competitors. There had been some modest development of synthetic rubbers in the USA and Germany but these were expensive compared with natural rubber. Following the Japanese occupation of the rubber-growing areas in Asia, the USA embarked on a massive program (in size, second to the atom bomb project) to devise a major synthetic rubber (styrene/butadiene copolymer). During the next two decades, a number of synthetic rubbers, of different properties and prices, were developed and commercialized in many countries. Thus, from the 1960s natural rubber was faced with serious competition. Today (2002) natural rubber accounts for some 40% of the world market for rubber, having climbed back from a low of 30% two decades ago.

The Tree

In the wild the rubber tree can grow to over 40 m with a lifespan over 100 years. Because the economic life in plantations is 25–30 years, the final tree height is some 20 m. From planting, it requires some 5–7 years before a tree yields a useful amount of rubber and the yield of rubber will steadily rise to a maximum after about 15 years, and thereafter decline. Good practice is to replant after about 30 years.

The rubber tree is relatively robust, a reason for its suitability for small farmers. It does suffer from a number of diseases (mainly fungi), e.g., varieties of *Phytophora* attacking leaves and bark, and some root diseases, especially *Rigidoporus*. These are all treatable, albeit sometimes with difficulty and

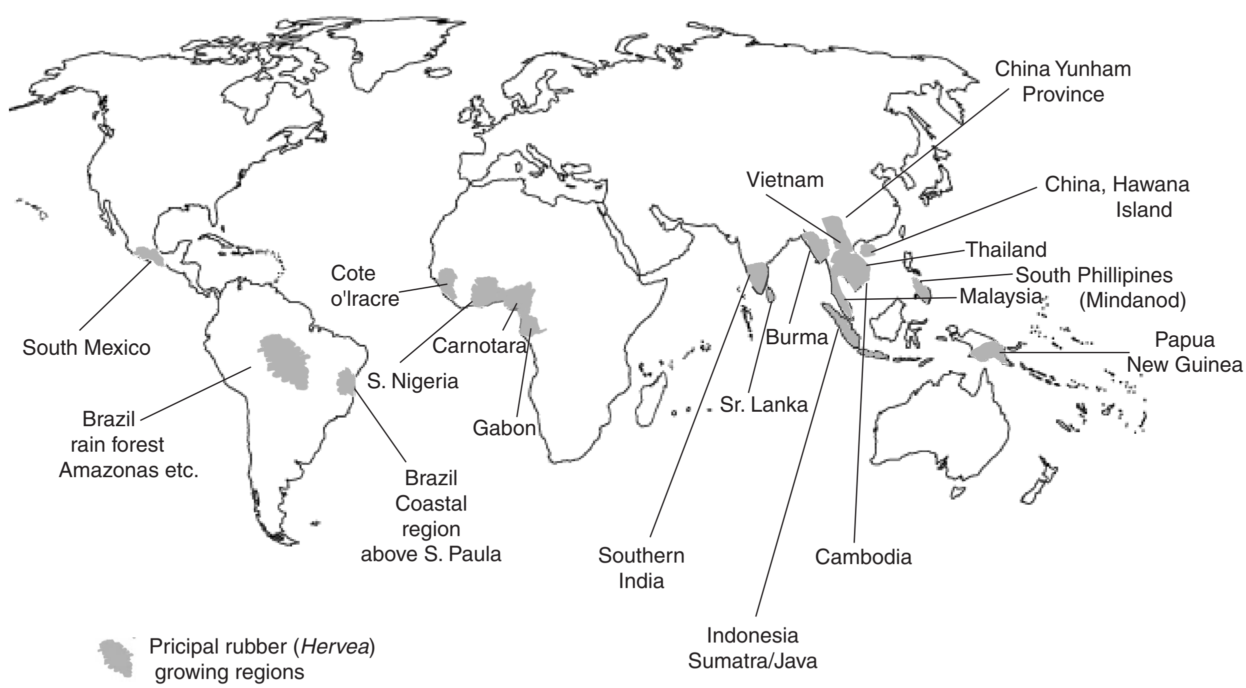


Figure 1 Principal rubber (*Hevea*) growing regions.

expense. Reference has been made to South American leaf blight (*Dothidella ulei*) for which no effective treatments have yet been found and has not yet appeared in the main rubber-growing areas.

The reason why *Hevea* and other rubber-bearing trees and shrubs produce rubber remains a mystery: various theories (e.g., wound healing) have been advanced but do not stand up to scrutiny.

The biochemical processes whereby the tree converts carbon dioxide and water into rubber have been fairly extensively studied, a number of intermediates (e.g., isopentenyl pyrophosphate) have been identified, and the basic pathway is more or less understood. It must be said that such work, though academically interesting, has not yet contributed to the well-being of the industry.

Breeding to Enhance Yield

As regards yield, the original importations into Asia yielded no more than about 500 kg ha^{-1}. There is a long history of work to enhance yields by breeding. In the early days of rubber growing in Asia, trees were replicated by growing from unselected seedlings; later, use was made of selected seedlings. Subsequently, from about 1920, largely from work by the Dutch in the former Netherlands East Indies, vegetative propagation from proven high-yielding trees by bud grafting became the standard practice resulting in the establishment of a number of well-characterized clones. The choice of a clone for a particular situation is a matter of judgment: some are very high yielders but oversusceptible to specific diseases or wind damage, etc., others yield less rubber but are more robust. Today, yields of around 3000 kg ha^{-1} are achievable under favorable circumstances, an almost 10-fold increase on nature.

The Producers

Traditionally, shortly after the original importations of *Hevea* into Asia, the normal way of growing and selling natural rubber was by establishment of large (>1000 ha) estates, owned by commercial enterprises, many of which were London-quoted companies especially in Malaya. Indeed, the impetus to establish such estates, from the early 1900s, was that it was a very profitable operation for the owners. During the past few decades growing and selling natural rubber became distinctly uninteresting compared with other investments: alternative crops (e.g., oil palm) gave better returns, so also did selling the land for industrial development or housing. Over the years virtually all the Western-owned estates have gradually withered away.

Parallel with establishment of estates, many small farmers (smallholders) in Asia and subsequently in Africa started to grow rubber on holdings of a few hectares; in some countries, notably Thailand, estates have never been a significant feature. It must be said that until the 1960s most observers of the industry disregarded the increasing dominance of the smallholder sector. Today, over 80% of natural rubber comes from smallholdings, a significant feature of the socioeconomic development of the industry. Rubber is in fact a very suitable crop for smallholders: it is very robust, will withstand much abuse and neglect, and is able to provide a modest family income.

As regards geography, in theory *Hevea* can be cultivated wherever conditions are similar to those in the Amazonian rainforest: high humidity, temperatures in the range 25–35°C, and rainfall not less than 5000 mm year^{-1}. The actual distribution is a matter of history, especially the former existence of British, Dutch, and French colonies in the tropics. Britain naturally sent the first *Hevea* seedlings to its then colonies in Southeast Asia; the Dutch to Netherlands East Indies; the French to Indochina.

Some 85% of production remains within Asia, especially in Southeast Asia where Malaysia, Indonesia, and Thailand have long been dominant: in recent decades China has become a significant producer. In Africa, Côte d'Ivoire, Nigeria, and Cameroon produce modest quantities; production in tropical America has been low and static for decades.

Production

Natural rubber exists in the tree as latex, a colloidal dispersion of rubber particles in an aqueous serum, contained in an interconnecting system of tubular vessels in the inner bark. It is extracted by 'tapping,' a semiskilled procedure involving paring away with a special knife a sliver of bark about 1 mm thick to a depth that just stops short of cutting the cambium layer. The first tapping opens up a 'tapping panel' which is developed by further tappings, working down the tree (**Figure 2**). Bark is renewed below the descending cuts. After some 5 years a new tapping panel is started, leaving the first panel to regenerate. There is a variety of tapping regimes such as 'half spiral, alternate daily' and there are other methods such as 'puncture tapping' involving making holes in the bark. Each has its adherents and critics. Whichever method is chosen, tapping is always carried out at dawn, when latex flow is fastest (**Figure 3**). The latex is collected in cups and then amalgamated into buckets to be taken to the collection center. Yields can be enhanced by use of ethylene-generating yield

Figure 2 Close-up of tapping panel and collecting cup. Photograph courtesy of Tun Abdul Razak Research Centre.

Figure 3 Rubber tapper at work. Photograph courtesy of Tun Abdul Razak Research Centre.

stimulants applied to the tapping panel. This technique, devised in the 1970s, is now widely used.

Production of natural rubber by tapping *Hevea* is inevitably very labor intensive. In Western eyes this might seem a grave disadvantage but employment opportunities in most producing countries are often somewhat limited. Against this, in some producing countries the recent growth of new industries has started to encourage people, especially young people, to move from the growing areas into the cities. In Malaysia, for example, it has become increasingly difficult to maintain production on small farms. Nevertheless, over the decades growing and exploiting *Hevea* has been a major engine of growth in the producing countries.

Processing

One may distinguish between primary processing which produces 'raw rubber' for conversion into rubber products such as tires, and those processes that convert raw rubber into products. The former is undertaken close to the trees; the latter may be within a rubber-producing country or other countries which have imported raw rubber. Most raw natural rubber is exported.

Primary Processing

The latex from the tree contains about 30% rubber. Some 90% of production is converted into 'dry rubber' by coagulating the latex with formic or acetic acid. Until the 1960s most coagulated rubber was dried in smokehouses to produce 'ribbed smoked sheet' which was sold in various qualities dependent on appearance. This procedure, which seems quaint today, has been gradually superseded by the introduction by Malaysia in 1965 of technical specifications (Standard Malaysian Rubber), stimulated by competition from synthetic rubbers. At the same time, new processing techniques were introduced whereby the coagulated rubber is granulated, dried, and compressed into bales. The Malaysian initiative was rapidly followed by most other producing countries.

Natural rubber is also marketed in another form: latex concentrate, produced by centrifuging latex to increase the rubber content to about 60% so as to minimize the cost of shipping rubber in liquid form. This material is used to manufacture items such as gloves and condoms.

Conversion into Products

'Raw rubber' whether natural or synthetic is a soft rather weak material of little use until it has been 'vulcanized,' a process that introduces crosslinks between the very long molecules of which all rubbers are composed. The crosslinks comprise sulfur atoms: vulcanization involves mixing raw rubber with sulfur and various other chemicals (vulcanization agents, anti-aging chemicals, etc.) plus, usually, carbon black to impart extra strength. The resultant mix is shaped, for example in a mold or by extrusion and simultaneously heated to about 150°C for a period of time sufficient to achieve vulcanization.

Products made directly from latex concentrate, such as gloves, are made by dipping porcelain formers into the latex with its mix of added chemicals, drying and simultaneously vulcanizing, and then stripping off the product.

Figure 4 Manufacturing a radial-ply tire. Photograph courtesy of Tun Abdul Razak Research Centre.

Markets and Competition

The term 'rubber' does not denote a unique chemical composition as does, for example, 'water.' Rubbers are a group of materials distinguished by elasticity – the ability to be stretched many-fold and to return more or less to the original size on removal of the stretching force.

In fact, natural rubber and the majority of synthetic rubbers do have much in common. All are long-chain high polymers with molecular masses around 1 million. Most are related to (but not synthesized from) butadiene, an unsaturated molecule with four carbon atoms. Replacing, hypothetically, one hydrogen atom in butadiene with a methyl group (CH_3) gives isoprene and natural rubber is a polymer of isoprene: *cis* 1.4 polyisoprene. Replacing a hydrogen atom with a chlorine atom gives the synthetic rubber polychloroprene. Some synthetic rubbers are copolymers: the most important synthetic rubber, in terms of tonnage, is a copolymer of styrene and butadiene. There is a synthetic replica of natural rubber. This has not proved to be a threat to natural rubber's markets, despite earlier fears: it is expensive to produce and its properties do not quite match those of natural rubber.

Competition

From the above it will be understood that there is a range of synthetic rubbers. Some are relatively inexpensive general-purpose rubbers; others are very expensive speciality rubbers used when their unique qualities, such as ability to resist very high temperatures as in, for example, gaskets in aero engines. The former group compete with natural rubber; the latter do not.

To give one example, the most important synthetic rubber – styrene/butadiene copolymer – has properties very suited to use in the treads of car tires, imparting good skid resistance. This synthetic rubber has entirely supplanted natural rubber in this application. Before the arrival of radial-ply tires, natural rubber had virtually ceased to be used in car tires. In radial-ply tires, the technical demands on sidewalls require use of natural rubber (**Figure 4**).

There has thus developed during the last few decades a reasonably clear view as to what rubber to use in a particular application: there have been winners and losers.

There was a time, around the 1960s, when some supposed that natural rubber would cease to be of any significance, that it would wither away. This has not happened, partly because of intelligent reactions by the main producing countries but – more importantly – because natural rubber has been endowed by nature with some unique qualities. It has very high resilience, indicating low heat build-up in tire carcasses; it has excellent strength at high temperatures which is why it is the material of choice for aircraft tires; it has excellent fatigue resistance. It is especially suitable for high-performance applications, and a number of new markets have been opened up from this, such as natural rubber/steel laminates used to isolate buildings from vibrations, including the protection of buildings against earthquake damage. Also, as noted natural rubber retains a good foothold in the tire market, to the extent that over 70% of natural rubber goes into the manufacture of tires.

Prices

Bearing in mind that several million small rubber farmers rely on selling their output to provide an income for their families, the price they receive is obviously of prime importance; sadly, the price history of natural rubber has been dismal for the past several decades. The same is more or less true for other agricultural commodities.

Natural rubber, like all agricultural commodities (and oil), is sold on the open market, receiving whatever price is, more or less, determined by supply and demand or, to be more precise, by buyers' and sellers' expectations as to future trends. The main markets are Singapore, Kuala Lumpur, London, and New York. As with stock markets, short-term price movements are essentially irrational, affected by rumors rather than by facts. This makes life hard for small farmers because they face fluctuating incomes.

Several attempts have been made to stabilize and if possible enhance prices. The Stevenson Scheme (1922) planned to restrict output but, since it was a British government initiative, its effect was limited to Malaya and Ceylon: it did succeed in raising the price but engendered fury among major consumers, especially in the USA. The Rubber Regulation Scheme of the 1930s, involving quotas for production, worked to an extent but was terminated by World War II. A much more ambitious scheme, launched under UN auspices from the 1970s but now terminated, was based on the creation of a buffer stock whereby rubber would be bought or sold from the buffer stock with the intention of stabilizing the price: this did not achieve what was expected by the progenitors.

Measures to Combat Low Prices

The natural rubber producers – and their countries – have realistically come to understand that there are no simple formulas for stabilizing and enhancing prices; that they must take actions on their own.

The obvious routes to helping the producers to derive a decent income are (1) to minimize production costs, for example by encouraging use of high-yielding clones, and (2) to establish new applications for natural rubber. In some but not all producing countries the first approach has been moderately successful: a small farmer with a reasonable area of rubber (around 10 ha) can make a reasonable living, whereas with a smaller area and low-yielding trees the income will be very poor. Use of intercropping also helps; growing other crops or even keeping animals such as goats between the trees can help to support the small farmer.

Much effort over many decades has gone into attempts to establish major new uses. Some – for example the use of rubber in road surfacing materials – turned out to be overly ambitious and unsuccessful, from which the lesson was learnt that it is better to establish a number of low-tonnage new applications that require natural rubber's unique properties. A number have been successfully developed.

The general strategy adopted by the major rubber-producing countries has comprised (1) to aim to enhance the incomes of the rubber farmers by various means, and (2) to improve the contribution of the overall rubber industry (the raw material and products therefrom) to national economies, recognizing that this strategy will not directly nor immediately benefit the farmers.

A relatively recent development is 'downstream manufacturing': establishment of rubber products factories in the producing countries, thus adding value to the raw material, creating new, skilled jobs, and enhancing national incomes. Malaysia has been especially active in this area, and to a lesser extent so also has Thailand. Rubber products, many of high technical content, are now being exported around the world.

Rubber Wood

Until the 1980s it was normal practice to get rid of rubber trees at the end of their economic life by using them as fuel, either domestically or for burning in smokehouses. It then became recognized that wood from *Hevea* had value in its own right as a medium-grade hardwood suitable for use in, for example, inexpensive furniture. Trade in rubber wood has become an important way of generating additional income for the producers.

Research

Since the 1920s most natural rubber-producing countries have established public sector research institutes whose activities range from agronomics, including extension services for small farmers, to product development work. These institutes are linked together by the International Rubber Research and Development Board, thus enabling effective communication between researchers in the producing countries. In addition to coordinating research programs, the Board has successfully raised large sums of money to operate international research and development programs ranging from agronomy to product design and development.

Final Comment

Professor Richard Shultes, the distinguished Harvard Professor of Botany and leading authority on tropical plants of economic value once wrote:

> No single of species of plant has, in the short span of 100 years, so utterly altered life styles around the globe as *Hevea brasiliensis*.

See also: **Silviculture**: Managing for Tropical Non-timber Forest Products.

Further Reading

Allen PW (1972) *Natural Rubber and the Synthetics*. London: Crosby Lockwood.

Anonymous (1981a) Rubber: the Plantation. In: *The International Book of the Forest*, p. 198. London: Mitchell Beazley.

Anonymous (1981b) Rubber products. In: *The International Book of the Forest*, p. 200. London: Mitchell Beazley.

Barlow C (1978) *The Natural Rubber Industry: Its Development, Technology and Economy in Malaysia*. Kuala Lumpur, Malaysia: Oxford University Press.

Roberts AD (1988) *Natural Rubber Science and Technology*. Oxford, UK: Oxford University Press.

Sethuraj MR and Mathew NM (1992) *Natural Rubber: Biology, Cultivation and Technology*. Amsterdam, The Netherlands: Elsevier.

Seasonal Greenery

A L Hammett and M A Murphy, Virginia State University and Technical Institute, Blacksburg, VA, USA

Introduction

For generations, a multitude of non-wood forest products have been extracted from forests to supplement incomes and diet sources. Here we define non-wood forest products (NWFPs) as biological produce found in forests such as edible plants, medicinal and dietary supplements, decorative or floral products, and specialty wood products. Commonly collected edible forest products include mushrooms, herbs, and spices. Several plants are processed into medicines for household and local consumption and, more importantly for international markets. Decorative NWFPs include vines, ferns, and other plant products used for floral arrangements, dried decorations, and ceremonial or religious ornaments (**Figure 1**). Specialty wood products include handicrafts, carvings, turnings, utensils, containers, and crafts. For many landowners and forest dependent communities NWFP options diversify and complement traditionally timber-based forestry operations (**Figure 2**).

Figure 1 Examples of wreaths, boughs, and trees displayed for sale.

Figure 2 Example of a typical North American Christmas tree plantation.

In the USA, Canada, and several European countries, the Christmas tree trade flourishes during the months leading up to the holiday season. Several countries have an emerging Christmas tree trade including Japan, Ecuador, and Mexico. Closely tied to this trade is the cutting and sale of seasonal greenery. Often the greenery is produced from branches or branch tips which are the by-products of pruning necessary to shape trees so they are ready for market. In many instances, greenery is collected by cutting tips of branches in natural or planted

Figure 3 Tree farmer trimming branches and shaping a Christmas tree.

Figure 4 Floral wreaths and boughs displayed for sale.

forests (**Figure 3**). These tips are fashioned into wreaths for hanging on doors or walls, tied in roping sometimes 20 m long to drape over doorways or along railings, and tied into short 60–120 cm swags to decorate rooms or lamp posts during the winter season. In North America and Europe, local and regional markets are well developed, readily accessible to local producers, and offer opportunities for adding value to forest resources (**Figure 4**). However, recently the South America and Asia regions have emerged as greenery producers and markets for Christmas trees and greenery products. Increased markets for greenery products warrant further examination for impacts on forest management and the potential for economic development.

History of Greenery Use

Since the use of seasonal greenery is tied to the tradition of the Christmas tree it is important to review its history. The tradition of decorating a holiday tree began with Northern European tribes in traditional festivals and religious rituals to induce the return of the sun. The oldest record of Christmas tree use came from the early to late sixteenth century. A 1605 diary found in Strasbourg, France mentions a decorated tree, while in 1531 also in Alsace, there was mention of Christmas trees being sold in local markets and set up in homes. Several sources credit Martin Luther as being the first to decorate an indoor tree. He mentioned that after a walk through a forest of evergreens with shining stars overhead, he tried to describe the experience to his family and showed them by bringing a tree into their home and decorating it with candles. First evidence of a lighted tree appeared more than a century after Martin Luther's death in 1546.

Using greenery for holiday decorations is closely tied to the traditional Christmas tree. Greenery was brought into homes and places of worship as part of these ceremonies during the sixteenth century. Evergreens were the symbol of life because they do not die back over the winter – a feeling still commonly shared. Perhaps the first use of greenery documented was in Austria and Germany during the seventeenth and eighteenth centuries, where the tops of evergreens were cut, hung upside down, and decorated. The first holiday greenery use in the USA was in the German Moravian Church's settlement in Bethlehem, Pennsylvania during 1747. Wooden pyramids covered with evergreen branches were decorated with candles. The public display of decorated trees and seasonal greenery is now commonplace in several countries outside North America and Europe.

The Greenery Trade

Christmas trees are sold primarily in domestic markets as the trees are large, and difficult to keep fresh when shipping to distant markets in time for the Christmas holiday. The focus here is on greenery and greenery products, an NWFP that seems more suitable for more diverse and distant markets (**Figure 5**).

Holiday greenery products include wreaths, roping, door swags, and boughs or other hangings produced from evergreen or holly (*Ilex*) species. Some of these products are accented with dried flowers or cones, ribbons, or other decorative treatments. Since the whole tree is not harvested, greenery provides a seasonal source of income, while assuring the sustainable management of forest resources. Specialized greenery grown and harvested under forest cover in subtropical areas supports a large industry supplying accent material for floral

Figure 5 Example of decorated wreath and bough.

arrangements. For this article, we will concentrate on products that are produced from tips and branches of conifer trees – such as pine boughs – and assembled for Christmas and winter decorations.

Finding Greenery Markets

Greenery operations seem appropriate for small enterprises as the level of processing and marketing needs are low. Before starting a greenery enterprise one should first consider the size and location of markets. Visits to tree farms where raw materials may be gathered, trips to observe nearby and regional markets, and meetings with buyers of decorative products are important. It is important to note prices, sizes, how greenery products are assembled, appropriate decorative accents (ribbon, dried cones, etc.) that may be added to suit customer desires. The internet is increasingly a reliable source of information on products and competitors. Many small producers serve distant customers through website sales.

Planning for shipping is very important as greenery is perishable and needs to be delivered fresh. Producers need to harvest, stock, and transport their products in a timely fashion. Customers seek fresh (no needle drop) full-shaped greenery products in dark green colors. Labeling with species, care, and source information helps customers understand the product is high quality and fresh.

Once the holiday marketing season is over, leftover greenery stock often cannot be sold. To ensure extra greenery is not harvested some producers take advanced orders for club or civic organizations' fund-raising projects, and mail out brochures with order blanks or use a website to assure sales in advance. To help preserve freshness greenery products are often packed and shipped by express or overnight services. One small producer in the Appalachian Mountains sends much of his production several hundred miles to the New York City market.

There are two common ways to sell seasonal greenery – direct to the customer or through wholesale channels to greenery-product producers. For producers willing to invest time to cut and make greenery products themselves, direct sales through mail or visits to Christmas tree farms are common. Direct sales are effective in helping to learn customers' needs and how to increase markets. Taking orders from customers in advance helps producers plan for labor, raw materials, and shipping arrangements, and customers can be assured of fresh, high-quality products on a promised date. Recently, agrotourism or other promotional programs have drawn urban customers to visit farms where they learn about forestry, cut their own Christmas tree or greenery, and see first-hand how greenery products are made.

Selling greenery in large quantities to wholesale buyers as a raw material is a viable alternative. For instance, several large wreath manufacturers buy in bulk from landowners, or will send a crew to cut greenery under harvest contracts. However, such production of large volumes takes careful planning considering tips should be kept cool and moist until used to make wreaths and other products. It is preferred to have a contract to protect the producer and the landowner.

Cultivating an evergreen plantation with the goal of harvesting seasonal greenery can be very productive, environmentally sound, and economically beneficial. These plantings may help reclaim fallow land, prevent soil erosion, provide buffer zones to agricultural and other land uses, and serve as excellent cover for wildlife. Greenery plantations often require only small initial investments for planting, annual care, and harvesting, and their management involves few tools and equipment common to agricultural enterprises. Clearly harvesting greenery for making wreaths, boughs, sprays, roping, and other decorative purposes is a viable, often profitable, forest-based enterprise.

Species Used for Seasonal Greenery

Cut greens constitute a large share of the decorative floriculture market. In the USA alone, yearly sales of cut greens are estimated at US$2–3 billion. However, there are several countries that produce Christmas trees and seasonal greenery. The US-based National Christmas Tree Association has members from both Canada and Mexico as well as from Germany, the UK, and Australia. Production in Germany, Denmark, and Mexico serves as an example of an ever-broadening forest products sector. A study by the Food and Agriculture Organization of the United Nations (FAO) of conifer-based non-wood forest products reviewed greenery production in these and other countries. In Germany, boughs are produced from noble fir (*Abies procera*) and white pine (*Pinus strobus*) in forests managed to produce both timber and Christmas boughs. Douglas-fir (*Pseudotsuga menziesii*) and Norway spruce (*Picea abies*) are planted with beech (*Fagus sylvatica*) in mixed plantations.

In Denmark, greenery is produced from Nordmann fir (*Abies nordmanniana*) and noble fir – both cultivated for ornamental foliage. According to the FAO, Denmark is the largest European producer, with an annual yield of 27 000 tonnes of ornamental foliage, exporting most of these products to Germany, Austria, Sweden, and the Netherlands.

Mexico has an important seasonal greenery market. The sacred fir (*Abies religiosa*), known to the people of Mexico as *oyamel*, *abeto*, or *arbolito de Natividad*, grows in forests at elevations between 2700 and 3400 m. Both the scientific name and the common name of this tree originated from a tradition of the Mexican people gathering the branches of this tree to decorate churches and homes during religious festivals. The greenery laden forests in the state of Michoacan are the over wintering site for the migrating monarch butterfly (*Danaus plexippus*).

The US greenery industry utilizes several evergreen species, each desirable and successfully marketed for different purposes. Depending on the location, growers may have a choice of species, producing a variety of products. Species most commonly harvested for greenery include long-needled pines Austrian pine (*Pinus nigra*), red pine (*P. resinosa*), Scotch pine (*P. sylvestris*), Virginia pine (*P. virginiana*), and white pine (*P. strobus*). In the central and northern Appalachian regions, white pine is desirable due to its vivid green color and ability to stay fresh for longer periods than other species. In addition to harvesting pine and spruce species for holiday greenery, northern white cedar (*Arbor vitae*), pond cypress (*Taxodium ascendens*), dwarf juniper (*Juniperus communis*), holly (*Ilex opaca*), dwarf mistletoe (*Arceuthobium pusillum*), and laurel (*Kalmia latifolia*) are also popular.

Pines are popular because they grow quickly, in a wide range of climates and on most soils, and they are more drought resistant than many other greenery species. Firs, as well as spruces, grow well further to the north in the boreal zones of the USA and southern Canada. They have shallow roots and like the coolness and moisture content of north-facing slopes. However, several species that have early spring growth are vulnerable to late frosts.

Greenery production techniques are covered in more detail in several of the publications listed in the Further Reading section.

Opportunities for Income from Greenery

Greenery harvests provide interim income during the period between timber crops. Landowners can benefit from incorporating greenery production into existing activities. Greenery provides additional income from Christmas tree production, as pruning during shaping provides raw material for products such as fragrant Christmas and holiday wreaths, sprays, roping, and decorative centerpieces. As with other non-wood forest products, landowners may profit more from managing for greens and greenery products than from growing only Christmas trees. In addition, several other raw materials can be incorporated into greenery products. For instance, value can be added to corsages of evergreen when they are accented with a dried cone or berries, and then easily shipped to distant markets.

In Denmark, Christmas trees and greenery production are valued at US$38 million year. Because of the wildlife habitat created in the plantations, hunting values are also enhanced. In one study, forest landowners' greenery production combined with hunting revenue produced more income than from timber harvested.

Value added opportunities abound. Small, plastic bags of evergreen tips can be sold to decorators. Some enterprising growers market do-it-yourself wreath kits. Each kit will include fresh greens, a metal ring, metal wire, a length of ribbon to add color, and a few pine cones with instructions to build a wreath.

In the past few decades, wholesale prices have risen in the US market for both decorated and undecorated wreaths. Decorated items with artistic detail demand higher prices. Hand-produced items would seem ideal products for developing countries to market to local tourist and export markets. Landowners in boreal and temperate zones could develop new products simply by adding plantations of greenery species.

Additional by-products from greenery production offer year-round income opportunities. Scented pillows and air freshener products are made with dried greenery such as very aromatic balsam fir (*Abies balsamea*). Some firms produce greenery extracts for medicinal and cleaning products.

Opportunities for Increased Greenery Production

A greenery plantation may not be limited to a rural setting. Some urban renewal programs are encouraging Christmas tree plots and income generation projects in large urban areas in the USA such as Detroit and Baltimore.

Those who do not own land may also participate in this potentially lucrative enterprise. Forest lands may be leased for cutting greenery, and cultivation of greenery species.

Greenery raw material may also be close at hand and readily available in unique ways. Some producers collect tips and branches from forest stands prior to a scheduled timber harvest. This raw material would be destroyed and wasted as a result of timber harvest operations.

Agroforestry operations should lend themselves very well to greenery production. Planting desirable greenery producing species with other timber species and agricultural crops may offer additional income sources and product diversity. Establishing a buying cooperative will help with initial raw material consolidation and quality control, and will facilitate economies of scale for processing. Pooling resources of small greenery producers may help them access remote markets.

For example, Christmas tree production and sales in Ecuador have grown recently. Greenery would be a natural complement to this industry and to the country's huge cut-flower export trade. Ecuador has increased its production for cut flowers that are exported to regional and distant markets. It seems that countries such as Ecuador could well benefit from complementary products such as greenery sold to the same markets.

Emerging Issues

For those countries with coniferous forests, harvesting greenery and other related NWFPs could prove very lucrative. For those areas where previous forest cover is degraded or removed, planting evergreen plantations with their potential benefits should be considered.

However, greenery production should not be considered by many landowners and communities. One emerging issue for greenery producers is fire safety. After natural greenery becomes dry and brittle, it is more flammable and the risk of fire increases. With adequate product labeling and chemical treatment during processing, this danger can be greatly diminished.

Partly as a result of the perceived fire risk, natural greenery now has competition from substitute material. Some customers feel that the safety risk is enough to warrant purchasing flame-retardant greenery made of vinyl, metal, or other artificial materials. These materials can resist ignition and flame spread, perhaps have a 15–20-year lifespan, some are claimed to be made from recycled materials, and may be stored from year to year. However, their purchase price is higher, and they lack the natural aroma and ambiance so popular with natural greenery. There are now techniques that can preserve seasonal greenery extending its market potential.

Another problem is that the greenery business is labor intensive and sometimes not perceived to be equitable or fair. Many migrant workers move to high-production areas to make holiday garlands and wreaths, between mid-October and early December. During this heavy workload season, cutters climb trees and cut pine branches, which ropers feed into sewing machine devices that rope the branches together. Most laborers work for contractors who pay them piece rate wages, for each pound of pine branch limbs handled. In some cases it is alleged that operators do not pay adequate wages and hence can afford to undercut their competitors' prices.

See also: **Plantation Silviculture**: Multiple-use Silviculture in Temperate Plantation Forestry. **Temperate Ecosystems**: Pines; Spruces, Firs and Larches.

Further Reading

Cercone M and Lilley WD (1998) *Making Wreaths for Profit*. Christmas Tree Notes, Fact Sheet no. 3, Bulletin no. 7013. Orono, ME: University of Maine Cooperative Extension.

Chamberlain J, Bush R, and Hammett AL (1998) Non-timber forest products: the other forest products. *Forest Products Journal* 48(10): 10–19.

FAO (2003) *Non-Wood Forest Products from Conifers*. Rome: Food and Agriculture Organization.

Hammett AL (2002) Non-timber options: white pine holiday greenery. In: *Wealth in Woodlands 2002: Sustainable Micro-Business Options for the Forest Landowner*, pp. 66–73. Charleston, WV: Center for Economic Options.

Hauslohner AW (1999) Cash bough: money grows on white pine trees. *Virginia Forests* Fall: 10–11.

Hill L (1989) *Christmas Trees: Growing and Selling Trees, Wreaths, and Greens*. Pownal, VT: Storey Communications.

Lilley WD and Holmes VJ (1991) *Growing a Continuous Supply of Balsam Fir Tip Brush*. Christmas Tree Notes, Fact Sheet no. 4, Bulletin no. 7089. Orono, ME: University of Maine Cooperative Extension.

Mater C (1994) *Minnesota Special Forest Products*, revd edn. St Paul, MN: Department of Natural Resources, Division of Forestry.

McConnon JC and Lilley WD (1999) *Marketing Maine Christmas Wreaths*. Bulletin no. 3019. Orono, ME: University of Maine Cooperative Extension.

Plum P (1998) Denmark: non-wood forestry in a densely populated temperate country. In: Lund G, Pajari B, and Korhonen M (eds.) *Sustainable Development of Non-Wood Goods and Benefits from Boreal and Cold Temperate Forests*, pp. 125–130. European Forest Institute Proceedings no. 23, Joensuu, Finland.

University of Illinois at Urbana (2003) *History of Christmas Greenery Use*. Available online at http://www.urbanext.uiuc.edu/trees/traditions.html

Virginia Department of Forestry (1999) Forest products for the holidays: the roping industry. *Virginia Forests* Fall: 7–9.

Western Maryland Research and Educational Center (2003) *Holiday Greenery*. Natural Resource Income Opportunity Series. SFP-1. Keedysville, MD. Available online at http://www.naturalresources.umd.edu/fsgreenery/greeneryspf1.html

O

OPERATIONS

Contents

Ergonomics

E Apud and F Meyer, University of Concepción, Chile

Introduction

Ergonomics is mainly oriented to the adaptation of work to the human being in order to obtain an adequate balance between workers' well-being and productivity. In forestry, there are two important aspects in which ergonomics can make useful contributions. One is the adaptation of heavy manual work. In this kind of job, a man using simple manual tools supplies most of the energy required to carry out his work. The opposite side is represented by mechanized work where human energy is replaced by machines. The workers become progressively more sedentary limiting their activities to perceiving and interpreting information and then executing their decisions with light muscular actions, usually highly monotonous and repetitive.

One aspect that is important to highlight is that forest work has evolved in a different way in developing and industrialized countries. In most developing nations, a high proportion of forest work is done using labor-intensive methods, while in most industrialized countries forest work is carried out using advanced mechanization. In the two types of work, ergonomics has a different approach, but based on a common root which is illustrated in **Figure 1**. This figure shows for two very different activities, such as barking logs manually and sorting logs with a forwarder, that in both cases workers perceive information from the surrounding environment, make decisions, and execute them through mechanical actions. Although the basic scheme is the same, the demands of the work are completely different; the decisions of the manual worker are simple but the physiological demands are high, while the operator of the forwarder makes a minimal physical effort but the complexity of his decisions are significantly higher. In both cases, independent of the kind of work, the workers are in a continuous feedback loop with their jobs, perceiving information, interpreting, deciding, and acting through mechanical actions to let the process flow. Ergonomic design should allow them to fulfill each stage of their job safely and efficiently, no matter whether the activity is manual or mechanized.

The previous description corresponds to the interaction of the man with his tool or machine. However, forest work is carried out in a physical environment where workers can be exposed to heat, cold, noise, and mechanical vibrations. These agents, when they exceed certain limits, may alter physical

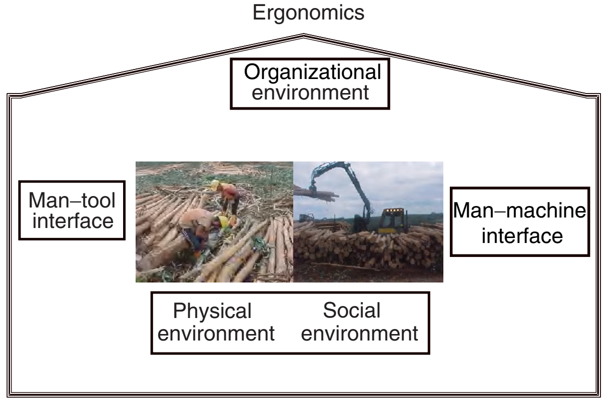


Figure 1 The ergonomic approach to manual and mechanized work.

and mental health and well-being. Some of them originate in the tools and machines, like for example noise and vibrations, while others, such as heat and cold, may have their origin in the environment. Although these agents may be present at levels that do not produce any disease, they may be the cause of occupational stress leading to psychological and physiological strain.

From the ergonomic point of view, there are other factors that are not related to the work station or the physical environment, but to the organization of the system in which each forest task is situated. Therefore, the modern concept of ergonomics considers the activities of a worker as part of a system which, as a whole, has to be efficiently designed. Work processes have an entrance and an exit, passing through a variable number of intermediary stages, where human beings interact with tools and machines to achieve their goals. This way of approaching forest work may be highly efficient, as human adaptation is suited to a multidisciplinary approach, with the participation of the workers and the managers who have the responsibility for planning and optimizing forest work.

One further aspect that cannot be ignored within the framework of ergonomics in forestry, particularly in developing countries, is the social environment. Forest work is usually carried out in isolation far from urban areas. Often, the workers have to remain in forest camps, not by choice. In such cases, forest camps become their temporary homes where they have to stay for different periods of time without the opportunity to choose their own options for food, recreation, or even sleep. Hygiene, privacy, and tranquility are basic requirements for these workers' well-being.

This is a brief synthesis of the purpose of ergonomics. As a summary it can be said that ergonomics provides integrative criteria for the solution of the problems of forest workers, both in manual and mechanized work.

Labor-Intensive Methods

Fundamentals for the Study of Heavy Manual Work

Most manual operations in forestry work are heavy. This statement is supported by a number of publications in which energy expenditure and work load have been reported for forestry tasks. However, a high energy expenditure does not necessarily mean that every worker within a crew will be strained when performing a similar task. To support this argument, it is necessary to answer at least two questions: (1) What is heavy manual work? (2) How can we fix limits of work load for sustained work? The answers are not easy to find because there are many factors determining the heaviness of a job, partly depending on the difficulty of the task and partly on the physical fitness of the workers. In other words, to define the limit of work that can be sustained during a shift, the relationship between the energetic demands imposed by muscular work and the physical working capacity of the laborers has to be established.

Human energetic processes are classified as aerobic and anaerobic. In mild or moderate exercise, oxygen supplied to the muscles is sufficient to oxidize food and thus to provide all energy aerobically. However, if work becomes more demanding available oxygen may not be enough and part of the energy has to be released by means of anaerobic processes. It is known that anaerobic work leads to the accumulation of lactic acid and this is related to muscular fatigue. For this reason, most human physiologists nowadays accept that work should be considered heavy when anaerobic metabolism starts contributing significantly to the total energy release. The higher the participation of the anaerobic processes, the more exhausting the activity is and shorter is the time that the job can be performed without a rest pause. Afterwards, when resting, the aerobic metabolism remains elevated because a major portion of lactic acid is oxidized. This is the reason why, when carrying out anaerobic work, an 'oxygen debt' is contracted which has to be repaid during recovery. As energy metabolism depends on the utilization of oxygen, the measurement of oxygen uptake is a practical method to estimate energy expenditure. It is known that 1 liter of oxygen consumed is equivalent to an energy expenditure of approximately 20.3 kJ (4.85 kcal).

To define whether a job is heavy or not it is not only necessary to determine the intensity of the activity, but also to understand the concept of physical working capacity. From all the factors influencing the aptitude for manual work, nowadays the maximal capacity of the aerobic processes, also known as aerobic capacity or aerobic power, is accepted as an international standard of reference for studying the fitness of world populations. The aerobic capacity can be assessed by measuring or estimating the maximal oxygen uptake, which reflects the combined capacity of the cardiovascular and respiratory systems to obtain, transport, and deliver oxygen to the working muscles, as well as the efficiency of this tissue to metabolize oxygen.

Although the transition from aerobic to a combination of aerobic and anaerobic effort is not clear-cut, in most people doing dynamic work, lactic acid will accumulate at loads calling for an expenditure of no more than 40–60% of the aerobic capacity. The intensity of effort at which anaerobic work starts can be measured with different methods and nowadays is called anaerobic threshold or lactic acid threshold. Based on these findings it is accepted that a laborer, during an 8-h shift, should not be loaded on average at over 40% of his aerobic capacity. This will ensure that the work is carried out under aerobic condition or, more precisely, that the sum of heavy and light operations, after the complete shift, will not exceed this limit. This means that the rest pauses after heavy operations are sufficient to recover and that lactate will not accumulate. It has to be considered that manual labor, carried out for 8 h, varies in energy requirements and, therefore, the limit of 40% of the aerobic capacity is meant to be the average value obtained from heavy and light operations and rest pauses.

In studies of heavy manual forest work, measurements of energy expenditure and cardiac frequency are the most useful for field surveys. Common methods for measuring energy expenditure demand the isolation of all the operations carried out by a worker and the measurement of the time employed in each of them. Afterwards, oxygen uptake can be measured to estimate energy expenditure in each representative activity. It is not easy to obtain reliable information because it is difficult for the forest workers to accept repetitive measurements of oxygen uptake, specially if they are carried out for more than a few minutes in each activity. For that reason, when the purpose is to evaluate the work load it is preferable to measure cardiac frequency since it reflects the demands imposed by work on the cardiovascular system. It may be argued that cardiac frequency also increases when the subject is exposed to other agents, e.g., environmental heat, but in such cases, it is a better indicator of strain than energy expenditure. Cardiac frequency can be registered, during a whole shift, with simple noninvasive methods that do not interfere with the activity of the subject. Nowadays it is accepted that, as an average for an 8-h shift, the cardiovascular load should not exceed 40%. This is because, if the work is carried out in a temperate environment, there is a good relationship between cardiac frequency and energy expenditure, so one can assume that workers will perform as average under their anaerobic threshold. In cases where the work is done in a hot environment, this limit seems also a reasonable load for the cardiovascular system, in spite of the fact that the work is performed at a lower pace due to the heat.

On the basis of the criteria already discussed, systematic studies of workers' physiological responses have proven to be a powerful ergonomic tool in assisting work organization. A number of examples will be given to illustrate this statement.

Selection of Tools and Techniques: Medial Pruning as an Example

Pruning is becoming more and more important in commercial forests to obtain wood of high quality. This activity has the purpose of eliminating branches, cones, and epicornics in order to obtain wood free of knots. To make this job efficient, the worker must have a good technique. If a branch is not properly cut, occlusion will be delayed and the amount of clearwood will decrease.

Until a few years ago a common tool for pruning was a hook which for medial pruning, at heights from 4 to 6 m above ground, was supported by a pole 6 m long. The working posture was very poor and the neck of the worker was kept in a very uncomfortable position. His arms, supporting the tool, were kept high and he had to move them rhythmically to operate the sawing hook at the other end of the pole. All in all, this was a very fatiguing job. The workers complained of pains in the neck, shoulders, arms, and lower back. On the other hand, it is an ergonomic rule that the longer the distance from the work object, the greater is the risk of doing a job of bad quality. Therefore, pruning at a 6 m distance from the ground produced wounds or other defects in the cortex of the tree which delayed occlusion.

An alternative method is to use ladders which the workers fix to the trunk of the tree. Afterwards they climb and when they are close to the branches they proceed to saw them. The advantage of that method is that the worker can do his job close to the work object, which facilitates a better cut. Furthermore, the job is not as uncomfortable for the neck, arms, and shoulders which are kept in a more natural position. The main disadvantage of this technique is that the workers have to climb up and down the ladders, but when they are properly fixed, the risks of accidents are minimal.

Table 1 shows the results of the evaluations carried out to compare both techniques. The workers using ladders to prune could trim an average of 125 trees per working day, whereas the workers on the ground covered only 96 trees per working day. Very important, cardiac frequency was not significantly higher with the more productive method, even though tree trimmers had to climb up and down the ladder. This was because pruning from the ground required constant movement to maneuver into a position where the branches could be seen. Pruning from a ladder also produced a much better quality cut. The

Table 1 Mean values and standard deviations for cardiac frequency and output when pruning was carried out with the laborers standing on the ground using a long pole hook (Method A) and when the job was done with the workers climbing up a ladder cutting the branches close to the work object with a saw (Method B)

Variable	*Method A (n = 10)*		*Method B (n = 10)*	
	Mean	*Standard deviation*	*Mean*	*Standard deviation*
Cardiac frequency (beats per minute)	98	11.3	102	11.8
Output (trees per shift)	96	18.8	125	22.0

workers mentioned that they did not experience arm or leg fatigue, while neck and shoulder complaints were fewer. As can be seen the incorporation of a physiological variable to work studies may help to select productive alternatives less dangerous for the workers.

Scheduled Rest Pauses

When rest pauses are not properly scheduled, the trend is toward diminished output and, in some cases, to an increase in the physiological work load because of insufficient recovery. The following example is based on a study of pruning. In **Figure 2**, a follow-up of trees pruned per hour and cardiovascular load for the equivalent period is shown. As can be seen, work in the first hour of the morning starts with a high level of production and a relatively intense work load. As time goes by, the number of trees pruned per hour tends to decrease but the work load is maintained. In the last hour of the morning, the cardiovascular load increases significantly but the output of the workers decreases. In general terms, an increment of cardiac frequency with a reduction in the level of performance is a signal of fatigue due to the shortness of rest. A very common error is not to schedule the rest in such a way that the workers can take at least 15 min after 2 hours' work. Depending on the type of work sometimes it is even convenient to give 10 minutes of rest per hour. As a general rule, short and frequent breaks are more effective than long and spaced pauses. Of course, the decision has to be evaluated in the field.

To show an example of the positive effect of rest pauses, a study conducted in a group of workers delimbing trees with axes will be described. The workers cut branches without any rest during the whole morning. To evaluate the effect of rest pauses, breaks of 15 min duration were introduced at mid morning and mid afternoon. As can be seen in **Figure 3**, the output of those workers increased 16%, from 2.6 to 3.2 $m^3 h^{-1}$, while the cardiovascular load diminished from 35% to 33%. In other words, the good recovery allowed the workers to do more work with a slightly lower physical work load.

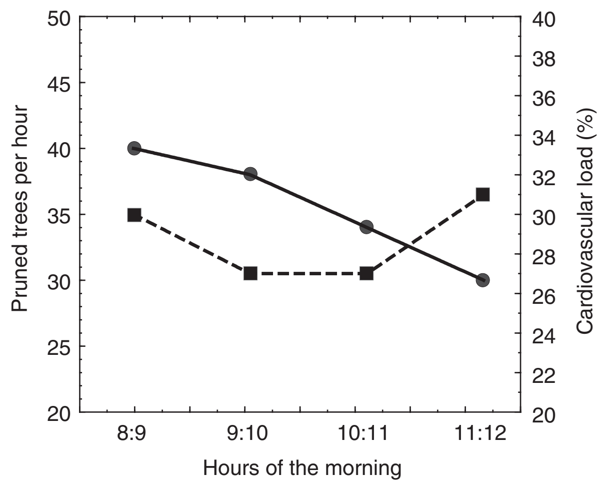


Figure 2 Average number of trees pruned per hour (solid line) and percent cardiovascular load (dashed line) as average of 10 workers controlled during the first 4 hours in the morning.

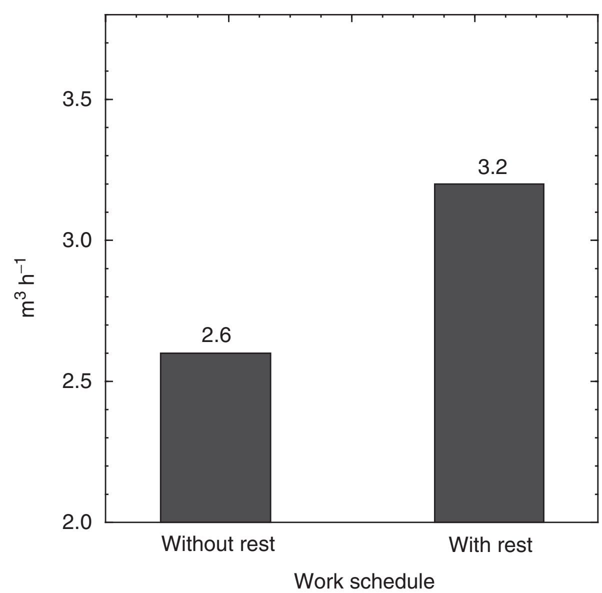


Figure 3 Average output ($m^3 h^{-1}$) and cardiovascular load (%) in a group of ax workers debranching with and without scheduled rest pauses.

Job Rotation

Another aspect which has been demonstrated to be very useful, when working conditions allow it, is to

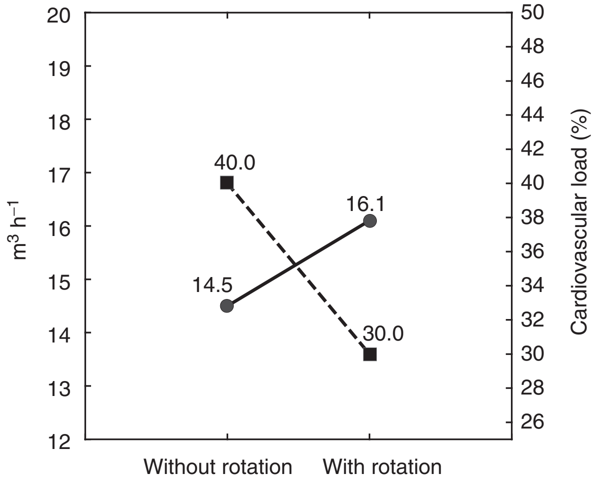


Figure 4 Average output ($m^3 h^{-1}$) (solid line) and percent cardiovascular load (dashed line) for a group of power-saw operators felling trees during the whole shift and rotating job with the power-saw operators who were doing cross-cutting in a log-yard. Rotation was done three times per shift (10 a.m., midday, and 3 p.m.).

introduce job rotation. Changing activities may reduce the work load for those doing the heavier part of the job.

A clear example is the work of power-saw operators felling trees in the forest compared to that of workers cross-cutting in log-yards. The first activity is far heavier than the second. Therefore, these are the sort of jobs that can be rotated. A good example is a study in which the chainsaw operators started working at 8 a.m. and rotated after 10 min rest at 10 a.m. Then they had 1 hour for lunch at 12 when they changed again and finally after another 10 min rest they rotated at mid afternoon. **Figure 4** shows that, with rotation between felling and cross-cutting, the physical work load was lower than when the workers were only felling trees, and their output was 11% higher.

Number of Workers per Activity

Different studies have shown the importance of the balance within working groups. Although harvesting can be fully mechanized (*see* **Operations**: Forest Operations Management), in many countries it is still carried out with manual tools. In some cases power saws are used for both felling and debranching while in others, axes are used to remove the branches. In this last case, it has been demonstrated that when power-saw operators work with only three ax workers, the work load for the latter can be extremely high, so the recommendation is to organize the work with four persons cutting branches with axes for each power-saw worker felling the trees. It has been shown that power-saw operators can increase their level of productivity, within reasonable levels of work load, if the crews are organized with the correct number of workers. For example, in the study illustrated in **Figure 5**, power-saw operators increased their productivity by 36% (from 11.1 to 15.1 $m^3 h^{-1}$) when they worked with four instead of three ax workers.

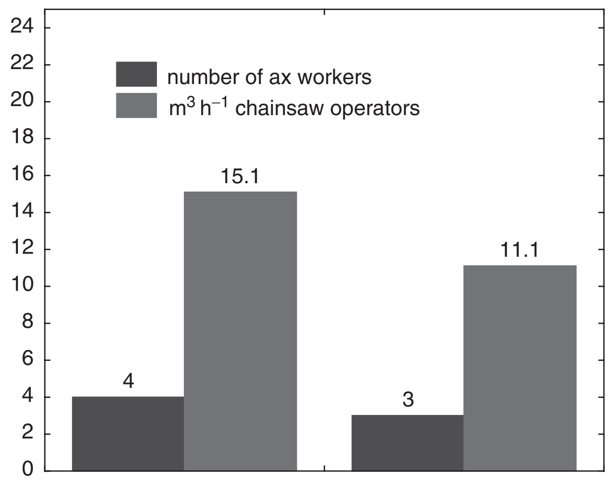


Figure 5 Performance of a power-saw operator felling trees when working with three or four ax workers debranching.

Standard Performance as a Basis for the Calculation of Salaries and Incentives

On many occasions it has been confirmed that forest work is a heavy task. However, the question is: How much is too much? To answer this question it has to be considered that output depends on the physical workload that a worker can reach in a sustainable way during his working life without fatigue or other risks and on the difficulties he encounters in carrying out his job, mainly related to type of trees, climate, and ground. In other words, in forestry it is not possible to demand of a worker that he always performs the same amount of work. This makes it difficult to calculate incentives and salaries, specially when workers are paid by piece rate. In the literature several functions for calculating output of different forest activities have been proposed, based on studies in which performance has been measured as well as physical workload and characteristics of the forests, ground, and climate. A brief example will be given from a study of power-saw operators cross-cutting in a log-yard. After a detailed statistical analysis it was found that around 75% of the variation in output of those power-saw operators could be explained by the average volume (AV) of the trees they cross-cut, the time devoted to the principal activities (PT), and the effort they did as judged by the cardiovascular load (%CL), according to the following formulae:

$$\text{OUTPUT}(\text{m}^3\,\text{h}^{-1}) = -7.5 + 0.16 * \text{CL} + 0.23 * \text{PT} + 8.1 * \text{AV}$$

Using the formula, **Table 2** was calculated to show the estimated variation in performance, for two levels of cardiovascular load, for 70% and 80% dedication to principal activities, and for trees of different average volume.

The idea of such tables is to show the companies and contractors that when salaries are paid according to the amount of work that the workers can do, they should consider carefully how much work they can really expect to be done. In a practical sense, with these tables a company engaging the services of a contractor and the contractor himself can plan his job considering part of the difficulties that the worker will find in the field. These tables can also be used to calculate basic salaries and incentives. For example, if a previous sampling of the forest shows that the average volume of the trees is $0.9\,\text{m}^3$, an average worker with a cardiovascular load of 30%, devoting 70% of the time to principal activities, should produce around $20\,\text{m}^3\,\text{h}^{-1}$. To reach this production a fair salary should be paid allowing the worker to fulfill his and his family's needs. Of course, a motivated laborer can still do more work without risk. **Table 2** shows that for the same forest with average $0.9\,\text{m}^3$ per tree, if the laborer devotes 80% of time to the principal activities and makes a higher effort at the limit of 40% cardiovascular load he may produce $24.2\,\text{m}^3\,\text{h}^{-1}$, which is nearly 20% more. So, to stimulate the laborer, incentives should be paid. Although to work at that level is still safe, we are talking of the higher limits of physical performance and that is not possible to obtain if the worker does not feel that his effort is recognized. It has to be warned that incentives should be discontinued over the higher levels given in the table since there are serious risks of fatigue, accidents, and work of poor quality when these limits are exceeded. On the other hand, the main limitation of the system is that we are talking of an average worker and not every human being is alike, so the tables cannot be used in a rigid way; they are more useful in calculating group incentives.

Table 2 Expected output for power-saw operators cross-cutting in a log-yard

AV (m^3)	*CL30%*		*CL40%*	
	PT		*PT*	
	70%	*80%*	*70%*	*80%*
0.3	15.5	17.8	17.1	19.3
0.5	17.1	19.4	18.7	21.0
0.7	18.7	21.0	20.3	22.6
0.9	20.3	22.6	21.9	24.2
1.1	22.0	24.2	23.5	25.8
1.3	23.6	25.9	25.2	27.4
1.5	25.2	27.5	26.8	29.1

AV, average volume; CL, cardiovascular load; PT, time devoted to principal activity.

Mechanized Work

Mechanization in forestry is increasing. The part of the work usually done with great human muscular effort is being replaced by machines. Although mechanized work is physically lighter it involves other risks for the machine operators, e.g., those derived from the working posture, the noise and vibrations produced by the machines, and also a noticeable increment of the mental work load. For this reason, job rotation and scheduled rest pauses are also very important for the machine operator.

The 'man–machine interface' is an imaginary plane across which information is exchanged between man and machine. Man receives information from the displays of the machines. In the use of forest machines the information that the operator obtains from the surrounding environment is also important. The signals received by the worker have to be interpreted based on knowledge which has to be acquired through previous training. In consequence, the laborer takes decisions which usually means decisions to operate the controls of the machine. In simple words, the operators are in a constant feedback with the machine 'perceiving–deciding–acting.' What is important is that at any stage there might be problems leading to errors which may result in accidents, health impairment, and inefficiency. Therefore, well-designed machines should allow the worker to see and perceive what is needed and they should also have well-designed controls so the worker can make fast and precise responses from a comfortable position. It is equally important that the worker should be trained for the correct interpretation of the information received.

We have illustrated very simply some of the facts that may impair the processes of perception, decision, and action in machine work. However, these are not the only problems faced by machine operators. In forest work, machines are used in the open air, where often the workers have additional stresses because of the climate and the terrain. Furthermore, machines produce noise and vibrations.

All the agents previously described can be quantified. However, the main problem is that when machines are not correctly built, it is easy to detect what is wrong, but is extremely difficult to modify the design, mainly because most of the modifications are very expensive and also because some of the required adaptations may produce other problems, leading to a vicious circle. In such cases 'remedy can be worse than disease.'

Foresters, administrators, and in general all those who plan technological innovation should consider not only cost and output but should also add basic concepts of the adaptation of the workers. However, this is easy to write but difficult to put into practice. At present there are ergonomic checklists for machines which allow the evaluation and selection of forest machinery. By definition they contain an ordered list of questions on different aspects to be checked when evaluating a machine. In current literature, several checklists are described for different purposes. Some of them are brief and concise and others are very detailed. Experts state that check lists do not substitute for knowledge; however, they may provide help which will be the more effective the more knowledgeable the user is.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Forest Operations under Mountainous Conditions; Wood Delivery. **Operations**: Forest Operations Management.

Further Reading

Apud E and Valdés S (1993) Ergonomics in Chilean forestry. *Unasylva* 44: 31–37.

Apud E and Valdés S (1994) Physical work load and output on grounds with different slopes. In Sessions J (ed.) *Proceedings of the International IUFRO/NEFU/FAO Seminar on Forest Operations under Mountainous Conditions*, 24–27 July, 1994, Harbin, pp. 181–190.

Apud E and Valdés S (1995) *Ergonomics in Forestry: The Chilean Case*. Geneva, Switzerland: International Labour Organization.

Apud E and Valdés S (2000) Ergonomic research in developing countries as a contribution to increase productivity and social development. In: Krishnapillay B and Soepadmo E (eds.) *Forest and Society: The Role of Research*, vol. 2, pp. 617–627. Kuala Lumpur, Malaysia: Proceedings of the XXI IUFRO World Congress.

Apud E, Bostrand L, Mobbs ID, and Strehlke B (1989) *Guidelines on Ergonomic Study in Forestry*. Geneva, Switzerland: International Labour Organization.

Apud E, Gutiérrez M, Lagos S, *et al*. (1999) *Manual de Ergonomía Forestal*. Available online at http://www.udec.cl/ergo-conce/.

Apud E, Meyer F, and Maureira F (2002) *Ergonomía en el Combate de Incendios Forestales*. Concepción, Chile: Valverde.

Apud E, Gutierrez M, Maureira F, *et al*. (2003) *Guía para la Evaluación de Trabajos Pesados*. Concepción, Chile: Trama.

Bostrand L (1992) *Introduction to Ergonomics in Forestry in Developing Countries*. FAO Forestry Paper no. 100. Rome: Food and Agriculture Organization.

Gellerstedt S, Alnqvist R, Attebrant M, Olov Wikstrom B, and Winkel J (1999) *Ergonomic Guidelines for Forest Machines*. Uppsala: Skogforsk.

ILO (1992) *Fitting the Job to the Forest Worker: An Illustrated Training Manual on Ergonomics*. Geneva, Switzerland: International Labour Organization Sectoral Activities Programme.

Johansson K and Strehlke B (1996) *Improving Working Conditions and Increasing Profits in Forestry*. Geneva, Switzerland: International Labour Organization Sectoral Activities Programme.

Wilson J and Corlett N (eds) (1992) *Evaluation of Human Work: A Practical Ergonomics Methodology*. London: Taylor & Francis.

Logistics in Forest Operations

B Dahlin, Swedish University of Agricultural Sciences, Alnarp, Sweden
D Fjeld, Swedish University of Agricultural Sciences, Umeå, Sweden

Introduction

Logistics concerns the organization of business operations in order to maximize the total benefit. Besides the flow of material (in forestry mainly wood), personnel, machinery, capital, and information are important factors. Different strategies may be chosen for the supply chain depending on the overall conditions. Harvesting operations in most of the industrialized world have changed from a seasonal activity to a round-the-year occupation. Due to uncertainty in the planning process a buffer in the wood supply needs to be met. This can be done by storing wood, but also by having an overcapacity in the harvesting organization. A supply chain management perspective is important not to suboptimize a system. Transport planning is the final subprocess in the wood supply chain from forest to mill. The high number of possible transport methods, combinations, and the restrictions applied to transport planning make it difficult to achieve economically optimal transportation without the help of computerized planning functions. This article explains the basic content of and requirements for planning functions for truck transport. The implementation of these functions relies upon an advanced information and communication (ICT) infrastructure. Mobile data systems (MDS), consisting of vehicle PCs linked on-line to a central company server, represent one such configuration of an ICT infrastructure. This article explains how transport planning is implemented and the role of such an ICT infrastructure in efficient implementation.

General Logistics

Logistics may be defined simply as methods for planning, execution, and control of operations governing the flow of material, machinery, personnel, and information. The role of logistics in forest operations is to coordinate roundwood supply with mill demand. This is in the context of demands for high capacity utilization and low levels of roundwood storage, in a geographically dispersed supply chain subject to numerous climatic disturbances.

Logistics in forest operations can be based on two different supply chain strategies efficiency and flexibility. With lower degrees of customer orientation (harvest-to-stock) it is primarily efficiency of forest operations which is in focus. With an increasing degree of customer orientation (harvest-to-plan for pulpwood or harvest-to-order for saw-logs) increasing flexibility and control is demanded (**Figure 1**).

Figure 1 Logistics in forest operations. The supply chain strategies (below the line) corresponding to different degrees of customer orientation (above the line).

The whole wood supply process can generally be divided into five subprocesses; prognosis planning (yearly horizon), demand and supply planning (rolling 3-month horizons), delivery planning (confirmed harvesting teams production aimed for specific mills on a monthly horizon), and finally harvest planning and transport planning (on weekly horizons). The supply chain from forest to mill can be described in terms of three nodes (forest harvesting, roadside inventory, and mill inventory) and two connecting links (extraction and transport). Each link with its connecting nodes is the basis of planning of delivery, execution of supply, and control of flow for harvesting and transport.

These two planning, execution, and control (PEC) cycles are used to adjust the rates of flow from both forest to roadside and from roadside to mill to meet varying mill demand under varying conditions (**Figure 2**).

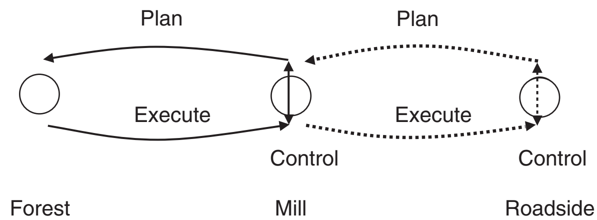


Figure 2 Planning, execution, and control (PEC) cycles for harvesting and extraction (forest–roadside) and transport (roadside–mill) operations.

Harvesting

In many parts of the world forest operations used to be a seasonal activity. Winter was in many places preferred for harvesting, the increased flooding in spring was used for river driving and silvicultural operations were conducted during the growing season. Changes in technology, employment law, and costs for inventories have altered the wood procurement process as well. Today, all year round harvesting and wood delivery are most common. But this also put new demands on the logistics of the operations.

Normally, the prognosis planning (yearly horizon) is based on the predicted harvesting, estimated by known factors if the forest is in control by the organization or experience if the harvesting is done for other landowners. In the latter case, the identity of harvesting objects may only be known at very short notice, depending on the type of agreement made by the seller of the harvesting and the buyer. The task of prognosis planning is to allocate known and anticipated harvestings in time and space to match the requirements from industry, the machinery and personnel available, and probable seasonal variation in harvesting conditions. If conditions change during the period, e.g., the demands of industry or weather, plans must change as well. The very nature of forestry makes it susceptible to climatic uncertainty. Heavy rain may cause terrain and roads to be inaccessible and harvesting plans must be changed accordingly. The role of harvesting planning is to make as good decisions as possible with the information available. The closer a specific harvesting is in time, the more accurate information is at hand and the more precise the planning can be made. However, harvesting planners must act with a great deal of flexibility.

One feature of forestry that makes it somewhat different from many other businesses is that it has a divergent flow of materials. Different assortments, based on use and tree species, cause one harvesting to produce material for many industries. Saw timber, pulpwood, wood for board mills, and wood for energy are examples of such assortments, and most often the industries are tree-species specific. This complicates the planning further. As an example, if there is an increased demand for pulp from hardwoods, as these trees very often grow in mixed stands other tree species will be in the harvested volume as well, and so will hardwood saw timber.

To achieve the flexibility in meeting fluctuations different strategies can be chosen. One way is to have large inventories. Inventories buffer the harvestings from changes, allowing a longer time to respond. However, inventories cost money in terms of capital and degrading quality. Another way is to have a very flexible harvesting organization that can adapt very fast to changes. Good planning routines can achieve some of this flexibility, but some overcapacity in the organization is required. This also costs money. A balance between those strategies must be found, and logistics theory emphasizes the importance of looking at the cost and benefits for the whole supply chain. Otherwise, suboptimizing is a big risk. Forest operations may solve a problem in a way that is very efficient for the harvesting, but which introduces costs into other parts of the supply chain that may well exceed those benefits. Hence, the growing interest in supply chain management which is based on a holistic perspective of the problem. This also points in a direction where harvest planning is much more integrated with the other parts of the supply chain: transport, industry, and customers. Without doubt, this is a development that is only just beginning.

Transport

Transport work from forest to mill has undergone considerable changes during the last 50 years. Structural changes in the forest products industries have led to a reduction in the number of roundwood destinations with a corresponding increase in average transport distances from forest to mill. At the same time road standards and transport capacity has increased.

Transport planning is the final subprocess of five in wood supply and is therefore subject to the greatest number of planning constraints. The high number of possible transport methods, their combinations, and the restrictions applied to transport planning make it difficult to achieve an economically optimal transport organization without the help of computerized decision-support tools. The most common transport method for short distances (<100 km) is truck transport. Rail and boat transport dominate on longer distances.

There are two general classes of trucks: self-loading trucks that work alone and trucks that work in groups and require a separate loader. For truck transport there are two general classes of planning functions: roundwood destination and vehicle routing. Destination aims to minimize the loaded transport distance between all forest supply nodes (active landings) and demand nodes (mills). This is done within the supply and demand restrictions imposed by the supply and demand planning process. Vehicle routing aims to maximize capacity utilization of the transport fleet within the constraints imposed by destination. Different goals may be used and minimizing the unloaded distance from mill back to forest by locating backhauls is one of the most common. Typical planning horizons are less than a month for destination and less than a week for routing.

Destination Functions

The destination function in transport planning can be studied from different perspectives. The first is that of the large forest companies with long-term wood supply responsibilities to major mills. The second is that of forest owners' associations or wood procurement groups who act as independent traders purchasing roundwood and selling to mills on short-term contracts on an open market.

Destination of roundwood may be optimally solved as a network model with the application of the classic transport algorithm and linear programming to minimize the loaded transport distance. This formulation may be well suited for large forest companies with long-term wood supply responsibilities to their own mills. There are important differences in the model formulation between the independent trader perspective and the forest company case. Independent trade aims to maximize the net revenue between price paid to the forest owner and the price received from the customers. Since contract prices for wood received may be at forest roadside or at the customer's location, this must be included in the model. This ensures that when the price is based on delivery at the roadside, the transport costs for wood transported from forest owner to customer is not taken into account. When the prices are based on delivery at mill site the transportation costs are included in maximization of net revenue. Often the prices paid to forest owners are also reduced with increasing transport distance to the nearest mill according to an agreed norm. Prices paid by the pulp mill, on the other hand, are determined through negotiations for each delivery contract specifying the prices for roundwood, and the delivery location.

There are also differences between assortments of roundwood which are important in the rigidity of restrictions of delivery. With the cut-to-length system it is more difficult to change the destination of wood which is already cross-cut for specific sawmills. Pulpwood, however, is often a by-product which it is possible to deliver to a number of different customers. Deviations from the delivery plans may therefore be compensated for by purchase from other suppliers. In this case it is therefore possible to relax the constraints of delivery precision.

Vehicle Routing Functions

Routing of timber trucks demands the comparison of a great number of possible driving patterns and combinations. For this reason mathematical techniques creating smaller subproblems involving the use of heuristics have been common for optimal routing. These subproblems are then easier to formulate and solve by a simpler algorithm such as the 'traveling salesman' algorithm. More exact methods such as tree-searching or 'column generation' (where each possible route represents a column) followed by tree-searching are efficient methods for solving more complex problems. While general vehicle routing problems have been in use for many years, roundwood transport represents a special case where the number of restrictions are especially large. This includes, for example, factors such as the geographic movement of supply nodes (active landings) and the specificity of certain landings for certain truck types. The influence of climate on infrastructure standards and the effects of roundwood freshness (time from harvest to use) for mill processes and product quality are also critical restrictions. Examples of successful implementation are to be found in ASICAM in Chile, EPO in Finland, and SMART in Sweden.

The probability of successful implementation increases with the stability of operational conditions and the simplicity of the planning function. Under stable conditions relatively advanced tools will function well. While under changing conditions, the number of restrictions increases, leading to the need for real-time operational data. Destination is the simplest of decision-support tools. Requirements concerning both computational capacity and operational data are limited.

Transport Administration Systems

A wood supply system which gives complete control should include the following modules:

- communication with both external and internal networks
- delivery follow-up in real time
- transport infrastructure databases
- decision support for optimizing transport plans
- mobile data systems.

Implementation decision support for optimizing transport planning requires an advanced information and communication technology (ICT) infrastructure. Mobile data systems (MDS), consisting of vehicle PCs linked on-line to a central company server, represent one such configuration of an ICT infrastructure. MDS consists of hardware and software with the following functions:

- distribution of transport orders and plans
- monitor with navigation aid to forest site (global positioning systems (GPS)/geographical information systems (GIS))
- reporting of transport volumes.

MDS support is a necessary element for future wood supply where structural changes create larger procurement areas which grow beyond each truck operators' area of local knowledge.

In transport planning there are two key interfaces where complexity management is important: (1) an external interface between the transport environment and the transport organization, and (2) an internal interface in the organization between its operating system (trucks, operators) and its management system (planners). Because of the complexity of the system as a whole, most of the organization's management capacity is aimed at handling the complexity of its operating system. The remaining capacity can be focused on handling the complexity of the environment (a multitude of roads, roadside inventories, and disturbances in operating conditions or supply).

In the absence of computerized decision-support systems and ICT infrastructure, the most common response to the complexity of transport planning is to reduce larger routing systems to a number of smaller subsystems through decentralized transport planning. Responsibility for operative planning is then moved from the company or regional level to the district level, reducing the number of possible transport combinations to a number readily solved with local knowledge and routines. This leads to each district's roundwood flow being executed independently of transportation in neighboring districts or companies, with drawbacks including difficult coordination and reduced backhauling. Reducing uncertainty of the transport system by real-time access to current information (e.g., road conditions and inventory volumes) is important to meet disturbances within these complex systems. The most advanced transport planning solutions with optimized functions, however, offer direct countermeasures to system disturbances.

See also: **Harvesting**: Roading and Transport Operations; Wood Delivery. **Operations**: Forest Operations Management.

Further Reading

Bowersox D and Closs D (1996) *Logistical Management: The Integrated Supply Chain Process*. New York: McGraw-Hill.

Harstela P (1993) Forest work science and technology, part 1. *Silva Carelica* 25: 51–93.

Harstela P (1996) Forest work science and technology, part 2. *Silva Carelica* 31: 125–136.

Karanta I, Jokinen O, Mikkola T, Savola J, and Bounsaythip C (2000) Requirements for a vehicle routing and scheduling system in timber transport. In: Sjöström K (ed.) *Logistics in the Forest Sector*, pp. 235–251. Helsinki: Timber Logistics Club.

Linnainainma S, Savola J, and Jokinen O (1994) EPO: A knowledge based system for wood procurement management. In: *7th Annual Conference on Artificial Intelligence*, Montreal, pp. 107–113.

Winston WL (1997) *Operations Research: Applications and Algorithms*, 3rd edn. Belmont, CA: Duxbury Press.

Nursery Operations

K McNabb, Auburn University, Auburn, AL, USA

Introduction

Forest regeneration is the very foundation of sustainable forestry. While many forests are regenerated using natural techniques, increasing annual wood harvests will depend upon plantation forestry. Moreover, planting is necessary for afforestation on degraded lands, abandoned agricultural lands, or anywhere that trees are to be reintroduced without a natural seed source. According to the most recent Food and Agricultural Organization (FAO) Forest Resource Assessment, there are close to 4.5 million ha planted each year. If one assumes that planting area is also a reflection of nursery production and using an estimated average spacing of 3×2 m (1666 trees ha^{-1}), this is an annual nursery production of 7.5 billion seedlings. Asia has the largest planting area with 62% of the world total, followed by Europe with 17%. Pines occupy 20% of all plantations worldwide, other conifers 11%, and eucalyptus 10%. The stock used for planting these areas almost invariably come from forest tree nurseries. Nursery managers are responsible for producing a seedling of suitable quality in a reasonable amount of time at a reasonable cost, which can withstand the rigors of processing, storage, transportation, planting, and what is more likely as not, harsh environmental conditions. If the stock does not survive, more is lost than just the cost of the planting stock. Also forfeited may be the cost of preparing the site, growth forfeited until the next planting date, and the expenses incurred if additional weed control, fertilization, or other cultural practices must be conducted. These costs may be, and usually are, substantially greater than the cost of planting stock. It is no wonder that organizations dependent upon successful plantation management consider nursery operations to be the heart of their regeneration program.

As a general rule, there are two types of planting stock – bareroot and container. The decision to rely on bareroot or container technology depends upon many factors. Certainly the physiological requirements of the species is tantamount in importance. Certain genera, such as *Eucalyptus*, are invariably grown in containers and survive poorly when planted bareroot. Other genera, such as the pines, are commonly produced bareroot. Even so, certain pine species, particularly those in the tropics (e.g., *Pinus caribaea)* require containerization. Boreal species may be containerized to shorten their time in the nursery. Whereas producing plantable bareroot stock may take 2–3 years for some boreal species, the environment of container production can produce smaller planting stock in far less time. The ability to control the growing environment is also important when producing vegetatively propagated material which is high in value and/or may require more exacting conditions to root and/or develop. Finally, planting adverse (droughty) sites may require the use of containerized stock. A possible disadvantage to containerization is a substantial increase in cost. In the southeastern United States, for example, the price of container grown stock is generally four to five times higher than the same species grown bareroot. Container stock is also more expensive to transport.

Bareroot Production

Site and Facilities Requirements

The selection of a good site is of paramount importance to the efficiency of a bareroot nursery. The most important characteristics are soil texture and water quality. Only a few decades ago, a medium textured soil was generally considered a requirement for a good bareroot nursery site. Older nurseries tend to be found on loams and silt loams. These soils, however, are not always conducive to using machinery during the wet season which is also frequently the planting season when seedling harvesting must take place. Sandy soils are preferred for bareroot nurseries as for the most part they can be better worked during wet seasons without damage to soil integrity, machine use is more efficient, and equipment may re-enter a field sooner after a rain. Slope to insure efficient yet low energy water flow is a requirement. Slopes of around 0.5% (50 cm over 100 m) are generally considered ideal. When constructing a bareroot nursery, topsoil is usually removed from the site, and the site leveled using modern techniques. The topsoil is then redistributed over the site for a final grading.

Water availability, both in terms of quality and quantity, is essential to bareroot nursery management. There is little a manager can do if the water supply, be it underground or surface, is only seasonally available or of insufficient quantities. Perhaps the most commonly overlooked of these two factors is that of water quality. Managers tend to look for the quantity of water and often forget to check the quality. Extremes of pH, particularly alkaline water with high salt contents, will greatly increase the difficulty of producing quality bareroot seedlings. A simple chemical test will determine if there are hidden problems in the water supply.

The physical facilities normally required for a bareroot nursery are: office and managerial space including a space for nursery workers to meet and eat, an area for seedling processing, a seedling cold storage facility including a truck loading area, sheds for equipment and machine storage, equipment maintenance shop, pesticide storage and mixing facility, irrigation pumping station, and a seed storage unit, with the size of each of these components depending upon seedling production goals. Seedling cold-storage units are typically built to store millions of seedlings with easy loader access and maneuverability. Although this is expensive space, larger seedling storage units allow the nursery manager more flexibility in the harvesting process. As long as seedlings can be stored, the manager can make use of good weather and labor availability by lifting seedlings. Another facility that deserves considerable thought is the pesticide storage and mixing facility. These are specialized structures that may have special legal requirements regarding their construction. Specific airflow volumes, shelf spacing, spill containment, backflow prevention, and other safety specifics should be considered.

Soil Preparation and Sowing

A typical sequence of ground preparation for bareroot production is; subsoiling, plowing and/or harrowing, and bed shaping (**Figure 1**). Subsoiling is usually done with a 3 to 5 shank agricultural

Figure 1 *Pinus radiata* in a bareroot nursery in Chile. Bareroot stock is typically produced on a large scale in raised beds with several rows per bed. In this particular case, the plants originated from cuttings planted directly in the bed. Most bareroot stock, however, is produced by sowing seed.

implement to a depth of 40–60 cm. Many nursery managers will subsoil in perpendicular directions across their fields. Depending upon soil type and previous crop, the site should be turned with a plow or simply harrowed to incorporate and chop plant materials, aerate the soil, and break up soil clods. The bedding plow is then used to shape and level a bed, usually 120 cm in width and approximately 20 cm deep. Alleys between beds are typically the width of one tractor tire, around 40 cm. The number of beds per irrigation unit varies but is selected in function of the irrigation system. The life blood of the nursery is water, with the irrigation system consisting of a network of pumps, pipes, controls, and sprinklers. Most modern bareroot nursery irrigation systems are removable to facilitate soil preparation. Field pipes may be laid out and connected anytime after subsoiling, to facilitate bed layout.

Sowing in bareroot nurseries may be done using machines, or by hand, with species usually the determining factor. Fairly sophisticated tree seed sowers have been developed. Commercially available vacuum sowers are adjustable to seed size and spacing. Such sowers usually provide more control of within-row seed placement and theoretically result in a more uniform spacing for individual seedlings, producing a more uniform crop. Other common sowers dribble the seed along a furrow in the bed in a semicontrolled rate. In either case, the seed are pressed into the soil by a roller following seed placement. In many cases, however, particularly for very large seed or very small seed, hand-sowing is still the typical sowing method. After sowing, bareroot seedbeds are mulched to protect the soil surface from rain impact and maintain bed integrity. Although chemical soil adhesives are used with common success, many nursery managers prefer organic materials such as bark or other by-products from fiber processing that have the other advantages of helping maintain seedbed moisture and contributing to soil organic matter content.

Controlling Morphological Development

Seedling spacing has a tremendous impact on individual seedling development. Larger seedlings survive and grow better after outplanting and are more expensive to grow, but might reduce overall reforestation costs. Seedbed spacing, therefore, is a compromise between production costs and seedling size/quality. Spacing is also species dependent, although as a general rule pine are sown with a seedbed density target of around 150 to 300 seedlings m^{-2}. Hardwood spacings generally require more bed space for production, but again this is species specific. Seedbed density targets may typically vary from 50 to 150 m^{-2}.

Application of the major fertilizer elements of nitrogen, phosphorus, and potassium is almost always necessary to produce seedlings of suitable size within a reasonable time-frame. Fertilizer applications should be based on a soil chemical analysis and professional recommendations supported by empirical observations. Phosphorus and potassium may both be applied to the soil at the time of harrowing. Nitrogen is generally applied over the top of seedlings, either in liquid or granular form, beginning 1 to 2 months after germination. Most species respond well to nitrogen and fairly significant amounts of this element (100–200 kg ha^{-1}) may be applied to nursery beds. Because large amounts of nitrogen are used in bareroot production and because nursery soils are often well drained, nitrogen use efficiency and loss through leaching may be a concern to nursery managers. Micronutrients can be important in specific cases depending upon local soil conditions. Micronutrients are typically applied in a liquid spray. Soil organic matter maintenance is a variable that profoundly affects soil quality and nutrition management. Other than organic matter additions and seedbed mulching, nursery managers typically follow a rotation of 1 or 2 years of seedling crops with 1 or 2 years of cover crops in order to increase or maintain soil organic matter levels as well as a possible reduction in soilborne disease populations.

Top-pruning and root pruning may be used to manipulate morphological development of planting stock. Top-pruning involves the removal of the top of the seedling using a rotary or shearing blade. The primary objective of this treatment is usually to slow the growth rate of the crop. An anticipated secondary benefit is increased crop uniformity resulting from allowing smaller (unpruned) seedlings more of an opportunity to catch up to the larger (pruned) seedlings. An even more severe reduction in seedling growth rate can be achieved by undercutting or wrenching seedling root systems. Another important objective of root pruning may be to provide for a more fibrous root system (expanded water absorbing surfaces) and a better root to shoot ratio. Both shoot and root pruning are species dependent and may not be employed in all cases. Transplanting in the nursery, for example, may be a better method to promote a more desirable root to shoot ratio (**Figure 2**).

Pest Control

Weed, insect, and disease pests are serious threats to the production of quality planting stock. Many pests can be controlled through the use of modern

Figure 2 Transplanting Sitka spruce (*Picea sitchensis*) in a nursery in Scotland. Boreal species and temperate conifers are often transplanted in the nursery to improve seedling quality. A 3-year-old tree having been grown for 1 year in a seedbed and 2 years in a transplant bed is known as 1 + 2 stock. Subtropical and tropical species are rarely transplanted in the nursery and are usually outplanted to the field as 1 + 0 stock.

pesticides. Even so, constant vigilance is necessary on the part of the nursery manager as significant losses to pests can occur in a relatively short time. Nursery herbicides include oxyfluorfen, napropamide, glyphosate, and sethoxidim, to name a few. Both oxyfluorfen and napropamide are pre-emergence compounds, while glyphosate is a postemergence compound used as a directed spray. Sethoxidim is active against grass species only and with appropriate caution may be used over the top of most species. Cost-effective herbicides tremendously impact seedling cost and quality. An integrated pest management program should be employed for insect and disease pest control. Careful almost daily monitoring of pest levels is necessary in nursery operations, with insect and disease pests easily controlled if identified early enough. On the other hand, many nursery managers use prophylactic pesticide applications for soilborne diseases such as damping-off. Soil fumigation prior to seedbed preparation is a common approach in this case. All pesticide use requires a knowledge of the compound, how it works, and any potential environmental impact. It is the ultimate responsibility of the nursery manager to see these compounds are used appropriately.

Seedling Processing

Bareroot seedlings may be harvested by hand or machine. Machine lifting is much more efficient, enabling nursery workers to lift 600–800 thousand pine seedlings per day (spacing $200\,\mathrm{m}^{-2}$) with a crew of fewer than 12 people (**Figure 3**). There are questions, however, as to whether machines may damage the stems and roots of seedlings and therefore decrease seedling quality. After lifting seedlings may be 'graded' (separated into morphologically based classes) or 'culled' (removal of 'nonplantable' seedlings). The decision to grade or cull seedlings has significant influence on the cost of processing. The definition of a 'quality' seedling (i.e., the 'target') is species dependent, and affected by many factors including acceptable seedling cost, environmental conditions at the planting site, and planting method. This is a broad and often debated topic that must be considered by each nursery operation. Upon grading, bareroot seedlings are packaged in one of three ways: boxes, bales, or bags. Both boxes and bags provide a nearly complete seal for seedling storage, while bales protect only the roots and may need watering if stored for several weeks. Water or water-absorbent gels may be sprayed on the roots prior to storage. Cold storage of bareroot seedlings helps reduce the heat of respiration and slows metabolic rate. Storage temperature varies by species with some, particularly boreal species, stored at below freezing temperature, while others are stored at 2–5°C. Storage time before seedling quality is compromised is species dependent and may vary from 1 week to several months.

Figure 3 Mechanical lifting of slash pine (*P. elliottii* Engl.) in the southeastern United States. This nursery produces 1 + 0 bareroot stock that is sown in April (spring) and is lifted 8–10 months later during winter. The machine lifts the entire seedbed in one pass. In this example, packing in bags is done in the field as opposed to transporting to a central processing area.

Container-Grown Stock

Site and Facilities Requirements

There is a great deal more flexibility when selecting a site for a container nursery. Because soil quality has been removed from consideration, a container nursery can be placed at nearly any location where power, roads, labor, and water are available. Many container operations require a reliable semiskilled workforce and labor availability is an important consideration. Water quality, however, is of paramount importance. There is little buffering capacity in the small cells of container-grown plants. Water quality problems may appear and become significant in a relatively short time-frame. In addition, because nursery operations invariably use fertilizers and pesticides, proximity to habitation, streams, or environmentally sensitive areas should be considered.

About the only buildings that are universal to container nurseries are those related to personnel requirements (e.g., administrative, meeting, eating, and restroom locations). Other common structures are a medium preparation and container filling facility and their associated storage spaces for media and containers. The types and requirements of other structures are highly dependent upon the propagation techniques used. Most operations require a seed germination or misting chamber for rooting cuttings. In this case, tight control of water amount, spray droplet size, humidity, and temperature are important (**Figure 4**). Some facilities have heated pads to increase the temperature of the root environment. After the initial seed germination or rooting phase, plants are typically transported to protected plant development areas. These areas may be entirely closed systems, or may be outdoors. Finally, upon reaching a suitable size, the stock is transported or exposed to ambient conditions so they may begin the process of physiological acclimation to planting conditions. Each of these phases may require a specific facility.

Container and Medium

Forest tree seedlings are grown in a variety of containers. In nurseries in many developing nations, small plastic bags filled with subsoil are common. However, most containers used today in modern nurseries are small polyethylene (hard plastic) tubes or styrofoam blocks with cavities. In both situations, the container is reused after cleaning and disinfection. The small tube-type container may be hung in wire or plastic racks at waist height, while styroblocks are typically placed on benches. Both systems should allow roots to air-prune on the bottom. The size of the cavity varies widely but those used for pines and *Eucalyptus* are commonly about 2–4 cm in diameter at the top and 12–18 cm deep, narrowing to a smaller drainage hole at the bottom and ribbed along the length of the cavity to prevent root

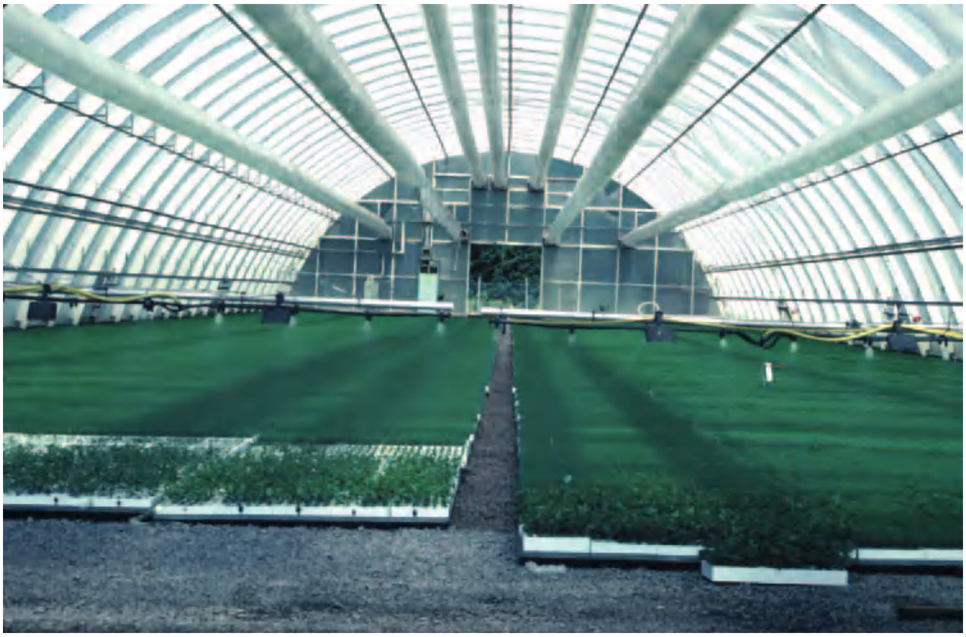


Figure 4 A single indoor unit of a container nursery in Sweden. Temperature, humidity, irrigation, and, to some extent, light can be managed in such structures. This speeds up the morphological and physiological development of the plants. Fertilization and pest control is typically done through the irrigation system, which in this case is an overhead traveling boom sprayer.

spiraling. Other than water quality, the container medium is the most important factor contributing to successful container growing. While media are often available commercially, many growers create their own mixtures. Normally, the medium is based on a locally available and abundant organic compost (e.g., pine bark, rice hulls, or other processing residues) that is used alone or mixed with vermiculite, soil, or other materials. These mixtures attempt to provide a well aerated, well drained, disease-free medium, with good water-holding capacity. The correct mixture promotes root growth throughout the medium. Commercially available and 'homemade' machines are used to fill containers.

Starting the Crop

Container stock may originate from seed, germinants, cuttings, and plantlets. Seed may be hand- or machine-sown. Automatic sowers are commonly used for pine and *Eucalyptus*. Whether or not to sow more than one seed per cell depends upon germination percentage, value of the seed, and the availability of labor to thin and transplant. Transplanting may well result in uneven growth between seedlings and the need to segregate later by size. After sowing, seed may or may not be covered depending upon the species and sowing technique. Germinants are produced by germinating seed in special flats or beds and transplanting the young plants (usually with the cotyledons still attached) into the containers. A number of species may be transplanted from specialized seedbeds to containers including species of both the genera *Pinus* and *Eucalyptus*. Usually transplants are shaded and maintained in high humidity conditions until well rooted.

Vegetative propagation through the use of cuttings is increasingly common for initiating container-grown planting stock, particularly for the genus *Eucalyptus* (**Figure 5**). To be successful, such a program depends upon an intensive clonal selection effort which includes research regarding the age, size, location, and season for taking woody plant cuttings for cost effective success. There may be physiological conditioning of the cutting source, the use of rooting hormones, and the posttransplanting environment may require exacting conditions. Large-scale production nurseries must have adequate rooting success if this technology is to be cost effective. Cutting based programs usually manage 'clone banks' or 'clone gardens' as a ready source of superior genotypes used as a source of material.

Container-grown planting stock may also originate from plantlets which are small plants or cuttings produced *in vitro* using various tissue culture methods. Individual clones may be 'stored' in jars in the laboratory and then 'bulked up' according to the requirements of the planting sites. Although not as common as using traditional vegetative propagation

Figure 5 A container nursery in southern Brazil. The majority of these plants are *Eucalyptus* spp. originating from cuttings. After rooting the cuttings in indoor facilities with humidity and temperature controls, the stock is moved outdoors to acclimate to planting conditions. The different colors seen in the photograph are different clones.

techniques based on cuttings, the use of plantlets will undoubtedly become more frequent as biotechnology programs are further developed.

Morphological Development and Pest Control

Fertilization of container-grown stock is done both by adding nutrients to the container medium prior to filling the containers, and as supplemental foliar sprays. Fertigation is particularly appropriate for container-grown technologies, requiring the use of specialized injectors and fertilizer holding tanks. It is imperative that irrigation systems provide even distribution of water over the growing area. In addition, slow-release fertilizers may be effectively added to the container medium, insuring nutrient availability over an extended period of time. A factor of increasing importance relative to container stock fertilization is the ultimate fate of fertilizers (and pesticides) used in the production process. Container operations usually have fast and efficient drainage away from the site. Also, unlike bareroot operations there is no soil medium to hold, transform, or otherwise process fertilizer elements. The result is an increased possibility of chemical movement from the production site. Many container operations now ‘close the system,’ by collecting and reusing water that drains from the seedling racks.

Container-grown stock needs to be segregated by size. For whatever reason, growing medium, seed vigor, transplant shock, or fertilizer distribution, container stock frequently shows remarkable variation in morphological development. Larger plants may be the first sent to the field for transplanting or segregated so that their growth may be slowed through irrigation reduction. Smaller plants may receive additional fertilizer to accelerate their development in order to reach plantable size. Sorting by size is a labor-intensive operation and adds considerably to planting stock cost.

Because container-grown stock is generally produced in soilless media, pest problems tend to be less frequent. Weed control, for example, is greatly reduced and occasional hand-weeding often suffices. Likewise, the protected environment of the greenhouse limits insect pests. The most serious pest problem for container stock is normally disease, particularly those associated with damping-off, although leaf molds such as *Botrytis* and *Cylindrocladium* may quickly become destructive without quick resolution. The high humidity and temperatures often associated with the early stages of container production are ideal for fungal development.

Storage and Shipment

The existence of a functioning soil/root interface provides a great deal of flexibility in the storage of container-grown plants. With protection from desiccation provided by the medium plug and occasional

Figure 6 A truck used for transporting seedlings from the nursery to the field. Note these seedlings are in containers and resting on a stack of specially developed platforms for placement on to the truck.

watering, plants may be stored just about anywhere, including the planting site, for an indefinite period of time. What is gained in storage flexibility, however, is lost in transportation cost, as the amount of space and energy needed for container plant transportation is considerably higher than for bareroot planting stock (**Figure 6**). In addition, because container stock cannot be vertically stacked, specialized transportation structures are required.

Final Considerations

Clonal Technology

The increased used of clonal technology has impacted seedling production in many areas of the globe. Although the decision to use container techniques for planting stock production has generally been mandated by biological and environmental factors in the past, this is changing with the increasing importance of clonal propagation to maximize the benefits of genotypic selections. Whether through tissue culture techniques such as somatic embryogenesis or cutting propagation from clone banks, the production of forestry planting stock is becoming more associated with the 'bulking up' of highly productive genotypes derived from intensive programs of selection and testing. Some genera, *Eucalyptus* for example, easily lend themselves to vegetative techniques necessary for clonal production (**Figure 7**). Others, such as the pines, require a higher economic threshold as they are so cheaply produced in bareroot systems. The continual progress in the science of biotechnology, however, may profoundly influence the economics of planting stock production. If lignin content, disease resistance, or drought tolerance can be introduced into cell lines through such technology, the economics of bareroot versus container grown stock will have to be rethought.

An Integrated Approach

In the past, individuals working in nursery science did not regularly interact with those working in site preparation or weed control. Each was typically viewed as an independent topic. Forestry enterprises, whether investigatory or managerial, were typically organized along these different areas and acted independently of each other. Forest regeneration managers are coming to view plantation establishment as an integrated process. That is, none of the parts in the process is wholly independent of the others. This is important because seedling quality is now mandated by considerations broader than just a 'survivable' seedling. Larger seedlings may compensate for chemical weed control, for example, or planting may take place year-round through the use of irrigation so that nursery and planting operations are seamless and independent of season. Nursery operations directly affect seedling quality, both morphologically and physiologically. Nursery managers can manipulate their product through cultural techniques such as spacing, fertilization, and pruning.

Figure 7 Multiple shoot tips of a *Eucalyptus grandis* and *E. urophylla* hybrid (known as urograndis) produced through tissue culture techniques. Individual clones can be kept in this form and then bulked up to produce indoor 'clonal gardens' which in turn are used to produce planting stock based on cutting technology. Such systems may become much more common with the development of biotechnology science.

It is becoming more recognized that seedling quality interacts with silvicultural techniques used in site preparation and weed control and therefore seedling cost should be evaluated as related to the entire regeneration process. As the forestry research community further investigates this important topic, we may find that nursery techniques are more important to plantation establishment and growth than has been believed in the past.

See also: **Afforestation**: Ground Preparation; Species Choice. **Genetics and Genetic Resources**: Propagation Technology for Forest Trees. **Operations**: Forest Operations Management. **Plantation Silviculture**: Forest Plantations; Tending. **Tree Breeding, Practices**: Genetic Improvement of Eucalypts.

Further Reading

Aldhous JR and Mason WL (1994) *Forest Nursery Practice*, Forestry Commission Bulletin no. 111. London: HMSO.

Chavasse CGR (ed.) (1981) *Forest Nursery and Establishment Practice in New Zealand*. New Zealand Forest Service, Forest Research Institute.

Colombo SJ, Menzies MI, and O'Reilly C (2001) Influence of nursery cultural practices on cold hardiness of coniferous forest tree seedlings. In: Bigras FJ and Colombo SJ (eds) *Conifer Cold Hardiness*, pp. 223–252. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Duryea ML and Dougherty PM (eds) (1991) *Forest Regeneration Manual*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Duryea ML and Landis TD (eds) (1984) *Forest Nursery Manual: Production of Bareroot Seedlings*. The Hague: Martiinus Nijhoff/Dr W. Junk.

Gonçalves JLM and Benedetti V (eds) (2000) *Nutrição e Fertilização Florestal*. Piracicaba, Brazil: Instituto de Pesquisas e Estudos Florestais.

Landis TD, Tinus RW, McDonald SE, and Barnett JP (1998) *The Container Tree Nursery Manual*, vol. 1–6, Agriculture Handbook no. 674. Washington, DC: US Department of Agriculture Forest Service.

McNabb KL (ed.) (2001) The interaction between nursery management and silvicultural operations. *New Forests* 22(1–2): 1–158.

Rose R, Haase DL, and Boyer D (1995) *Organic Matter Management in Forest Nurseries: Theory and Practice*. Corvallis, OR: Nursery Technology Cooperative, Oregon State University.

South DB (1993) Rationale for growing southern pine seedlings at low seedbed densities. *New Forests* 7: 63–92.

Williams RD and Hanks SH (1994) *Hardwood Nursery Guide*, Agriculture Handbook no. 473. Washington, DC: US Department of Agriculture Forest Service.

Forest Operations Management

E Mikkonen, University of Helsinki, Helsinki, Finland

Introduction

Modern information and communication technology (ICT) is widely used in forest operations management nowadays. In particular large forest industry companies operating globally have developed sophisticated systems to manage their forest operations. Many of the smaller companies are introducing these systems as well. The necessary condition for the use of these systems is a well-developed communications infrastructure in the country concerned. Similar systems are applied elsewhere, too, but maybe not as sophisticated as these.

The basic data on forests are continuously gathered and monitored through inventories at all levels: national, provincial, company, and private woodlot owner. The data are available in digital form which allows use of modern geographic information systems (GIS). The data are based on satellite and aerial images as well as field surveys, i.e., multisource data. This is important for managing companies' own forests and national forests.

Modern tools are used at every level of management and planning, i.e., strategic, tactical, and operative.

Operational harvesting plans are based on these basic data. Maps and other relevant marked information on the stand are shown on the screen of an on-board computer of a harvesting machine. The harvester optimizes the utilization of the tree stems according to a bucking-to-order scheme radioed to the machine. Environmental aspects are monitored through on-line follow-up of the location of the machine warning the operator of the hazards of exceeding the cutting area borders, protection zones, etc. Forwarding follows immediately after the logging, and the location information of the log piles is sent to the database. The performance record of the machine is stored in the memory automatically.

After logging the information is sent to the company's district office, which organizes optimal long-distance transportation schedules given by the optimization routines. The truck fleet can be monitored on-line with global positioning systems (GPS) and rescheduled easily. There are several vendors for these systems on the market.

These systems have intensified wood procurement and cut the costs of operations considerably. Another advantage is that the environmental risks of traditional harvesting can be minimized, thus increasing the acceptability of direct commercial use of forests.

Forest Operations Today

Activities of the woodland division of a forest industry company or an independent wood procurement organization may consist of many tasks that have an effect directly or indirectly on the outcome of the operations and thus need to be taken into consideration when managing these activities.

In the following presentation 'forest operations' are understood as 'technical activities to deliver wooden raw material from the forest to the place of utilization continuously and the supporting tasks to maintain this flow.' A supporting task could be forest road construction, for instance. The term 'wood procurement' is used often as a synonym for 'forest operations' although its meaning is more restricted. Another quite frequently used expression is 'supply chain.' A supply chain does not include similar supporting activities, as forest operations does.

Forest operations management is an activity to steer the outcome of forest operation towards a desired goal. In modern wood procurement information and communication technology plays an essential role. The tools provided by the ICT are GIS, GPS, the World Wide Web, mobile phones or cellular phone networks such as NMT, GSM, and UMTS, to mention a few.

Wood procurement is basically a logistic process that can be managed with the above mentioned tools. Proper management requires measurement of the efficiency of the organization. This means that planning of activities as well as monitoring is needed at every level of management. Planning can be strategic, tactical, or operative. The management structure can be a hierarchical, functional, matrix or teamwork type organization. The modern solution seems to be in most cases a functional, teamwork-based organization. When dealing with its interest groups different levels of partnership may be applied by the companies. This varies from purely owned operations to complete outsourcing.

In the following account, forest operations are dealt without the supporting activities, i.e., as wood procurement activity. This excludes public organizations working, say, on afforestation or road construction as falling outside the scope of this article.

Wood Supply

The wood supply chain is shown in **Figure 1**. It forms the framework for forest operations management.

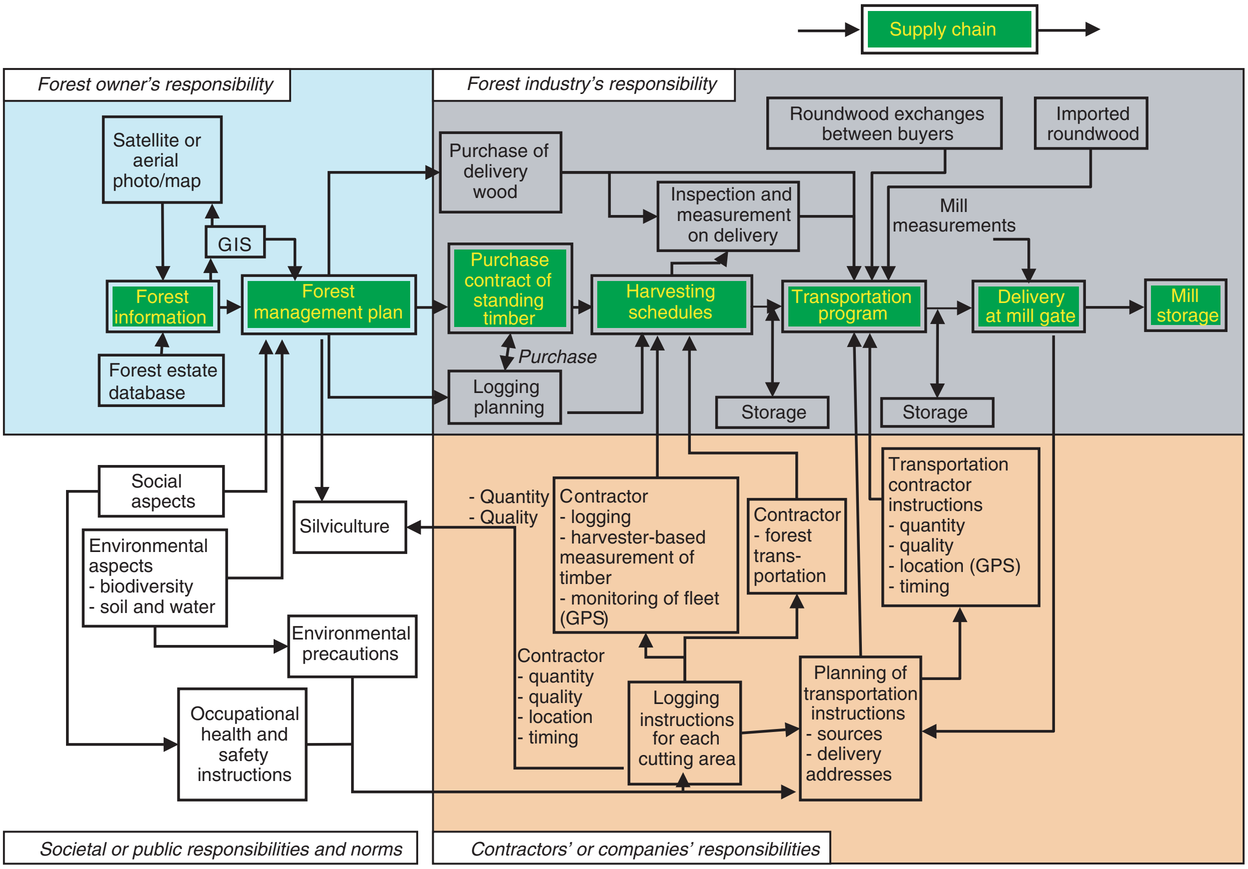


Figure 1 Framework of forest operations management.

The arrows in the figure show the relations between the activities and auxiliary activities. Auxiliary activities are needed to help carry out the actual forest operations more cost efficiently. Such an activity is wood measurement, for instance.

There are basically four independent actors in the wood supply activity. They are forest owners, forest industry, contractors, and public authorities as well as organizations of citizens (these four are shown in **Figure 1** as differently colored blocks).

Harvesting in these examples is supposed to be carried out using shortwood or cut-to-length (CTL) systems which is typical in the Nordic countries. Of course, similar types of structure can be found in any wood supply system.

Forest operations management starts with an annual strategic wood procurement plan based on pre-orders of the mills drawn from market development estimates for products. From that information a tentative wood purchase plan as well as a preliminary transportation plan can be developed. These plans allocate the volumes of different assortments needed to the procurement districts, and calculate the other resources required to carry out the task. At this stage just a small portion of the stands to be cut is known, most likely only the geographic area where they are supposed to come from. This is due to the fact that the raw material needs to be bought from the free timber market in the form of premarked stands. Only a small portion comes from the company's own forests.

In countries where the state owns the forests and sells harvesting concessions the approach might be different as regards planning.

These provisional plans are revised quarterly to become the tactical plans. At this stage the stands have been bought and full information on them is available. In the sales contract the forest owner and wood buyer agree upon the length of the time period during which the harvesting must be completed.

In the next step monthly and weekly operative plans are developed including the harvesting and transportation schedules for the stands to be harvested.

Wood Purchase

Procurement

Buying of timber on the free market is the most important activity in conditions where the public supply of timber is insignificant. In a team-based organization this activity is carried out by a specialist who knows the local conditions very well. In the wood procurement team there is also a substitute who can do the task if the specialist is not available at that moment. The information on the stand characteristics from the sales contract is transferred into the information system of the company for further planning activities.

The reliability of this information is crucial, because all the following management measures are based on this. Forest owners' forest management plans are a very important source of information for this purpose. However, they are confidential and controlled by the forest owner.

Forest Ownership

Own forests are a minor source of wood for Nordic companies but worldwide this is rather common. However, companies have long-term forest management plans for their own forests. Nowadays these utilize modern planning tools such as GIS. From these data the actual harvesting schedules can be defined and carried out. Companies tend to use their own forest resource to balance the timber flow. One typical trend today is to outsource the forest property and forestry to separate companies due to the low return on investment expected from traditional forestry. Owning the forests would decrease the return on investment figures of the actual forest industry business.

Silviculture

Silviculture operations must be carried out due to strict forestry laws and environmental aspects. This guarantees the new growth and sustainability of forestry after harvesting.

Planning and Management of Operations

As was presented in **Figure 1**, the raw material flows from the forest to the mills and management information basically flows in the reverse direction. In **Figure 2** the planning levels for forest operations management are presented. (More detailed descriptions are presented in **Figures 3**, **4**, and **5**.)

Strategic Planning

Strategic planning is carried out both at company's woodland division and district levels.

Tactical Planning

Tactical planning concerns basically logistics, i.e., how to get the raw material most efficiently to the mills. These plans are made at district level except for imported wood which is handled at woodland department level. These plans are updated quarterly.

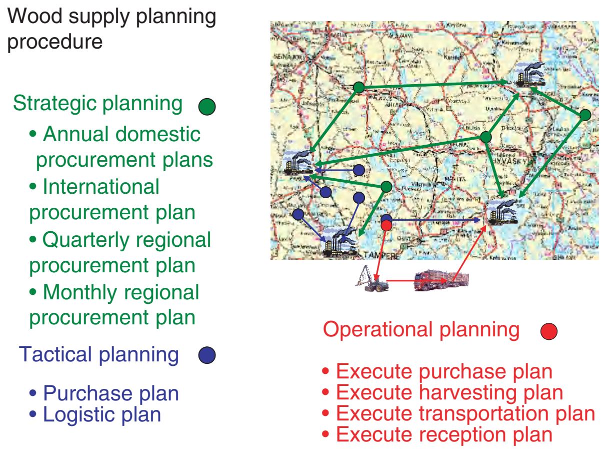


Figure 2 Typical tasks in wood supply planning.

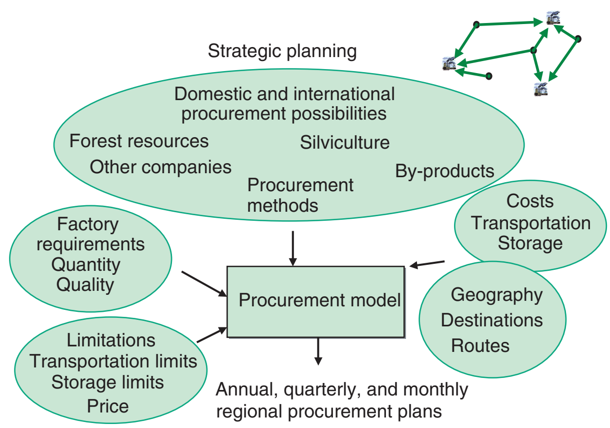


Figure 3 Concepts in strategic planning for managements of operations.

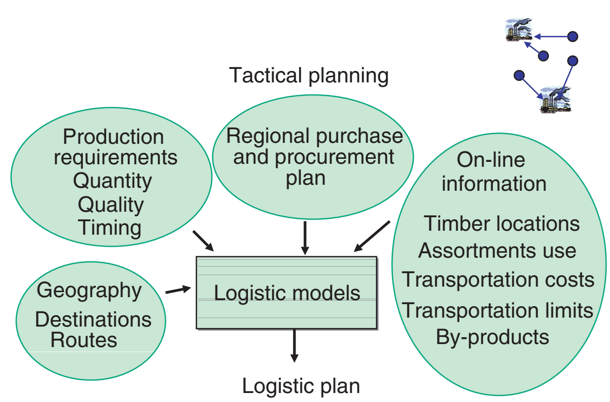


Figure 4 Concepts in tactical planning for managements of operations.

Operational Planning

Operational plans consist of the actual instructions by whom, how, and when the operations must be completed.

Once the company has obtained the authority to cut the stand owing to sales contract and the information is passed to the planning system, the operations management, i.e., harvesting and transportation plans are prepared. These include the selection to be made, the destinations for each type, schedules of the actions and other necessary plans such as precautions for environmental risks. These are then adjusted to the other stands information purchased from the same area to optimize the use of resources available. The plans are then converted to day-to-day instructions for the contractors available for the task. The companies have outsourced their forest operations to contractors almost to 100%.

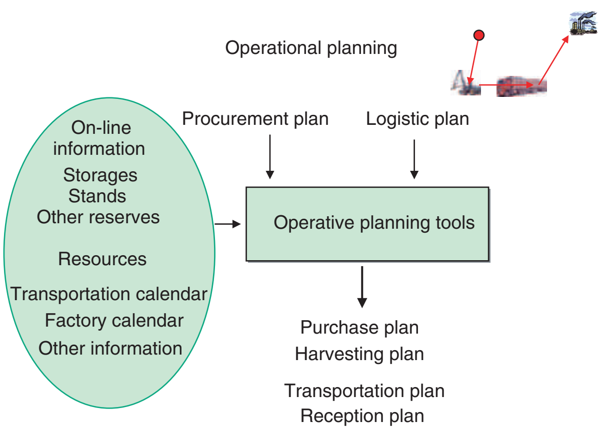


Figure 5 Concepts in operational planning for managements of forestry operations.

Monitoring Monitoring of the operations produces daily and weekly reports of the progress of operations. If something goes wrong, the team can quickly intervene in the situation by smoothly adjusting instructions.

Harvesting Harvesting of the stands includes logging and hauling. Logging is almost completely mechanized with harvesters in company operations in the Nordic countries. To some extent chainsaws are used, especially in thinnings and special wood logging, as well as in small-scale forest owners' logging. Regardless of the level of mechanization, the shortwood system is applied.

Transportation Off-road transportation is carried out by forwarders, which carry the load to the roadside. Skidding is a very exceptional operation in the Nordic countries. Long-distance transportation is carried out mainly by full trailer trucks.

Role of ICT

Modern wood procurement relies heavily on quick and reliable transfer of information. Tools are GIS, GPS, mobile phones, text messages, and wireless communication (**Figure 6**). There is a lot of information technology in a modern harvesting machine. They are equipped with an on-board computer that in addition to wood measurement functions also monitors the state of the machine operation itself.

From the operations management point of view the correct wood measurement and cross-cutting instructions are essential. At this point a wrong decision might destroy the value of the timber. This is

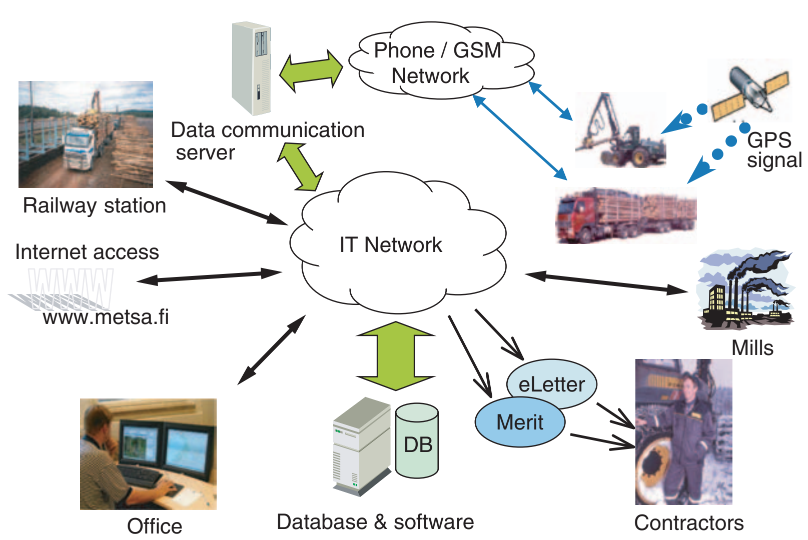


Figure 6 Data collection for operations management. Courtesy of the Finnish Forest Service (Metsähallitus).

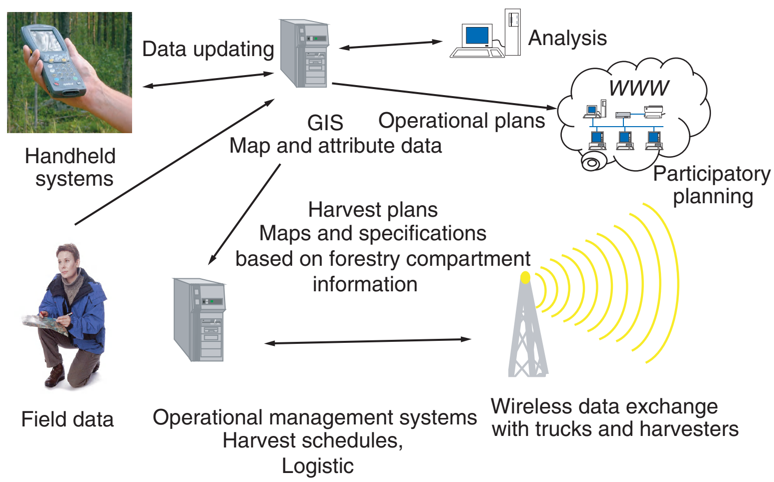


Figure 7 An example of information and communication technology application for forest operations management. Courtesy of the Finnish Forest Service (Metsähallitus).

because a customer-oriented approach is used. Bucking instructions for individual trees are defined by the bucking-to-value tables or bucking-to-order tables from the sawmill or plywood mill using the logs. These tables are transferred to harvesting machines wirelessly almost daily, according to the needs of the customer. Because of the variety of wood types and sometimes the requirement for a large quantity of special wood, a group control system for the management of a fleet of harvesters has been developed.

Productivity

Production and productivity figures can be followed continuously as well as the location of any machine through GPS. Once the location of the next harvesting site and the stand characteristics in addition to the selections to be made are known, the contractors can work independently. They only report daily to the team's office the state of the work and the finishing of the site. This information is used to define the readiness for transportation of the harvested wood. Coordinates of the log piles are also available for the route optimization routines of transport scheduling programs.

A well-functioning mobile communication network is a must for efficient data transfer between the harvesting equipment and supervision of the work (**Figure** 7).

Development of the Work Organization

The forest companies seem to pursue an ideal of having their own organization as light as possible. This has brought outsourcing into the management of operations. If someone can offer a better cost efficiency than the company's own operations would provide, they are willing to change. For instance, the measurement of wood at the mill is outsourced to specialized companies; only the information is transferred to the end users.

As mentioned earlier, modern organization for forest operations management is based on teams that cover a certain geographic area. Otherwise teams are quite independent; they report their performance to the district office and select the means to reach the goals set by the next organization level.

The supply chain for industrial wood has become faster and shorter, such that already at the stump the destination of the harvested wood is known. Delivery is as quick as possible and the running capital is kept as low as possible.

We will see even better management in the future once automation advance. This will allow even higher productivity, remote monitoring of the operations, and better utilization of raw material, and at the same time will protect the valuable production environment, nature itself.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Roading and Transport Operations; Wood Delivery. **Operations**: Ergonomics; Logistics in Forest Operations.

Further Reading

Högnäs T (2000) *Towards Supplier Partnerships in Timber Harvesting and Transportation*. Forestry Publications of Metsähallitus no. 37. Helsinki, Finland: Metsähallitus.

Anon (1999) *The Green Kingdom: Finland's Forest Cluster*. Keuruu, Finland: Metsämiesten säätiö.

Kumpula J and Leskinen J (2002) *Forest Operational Planning and Supply Chain Management in Metsähallitus*. Helsinki, Finland: Forest IT 2002.

Mikkonen E (1999) *Puunhankinnan Organisointi*. METLA Report no. 720/99. Helsinki, Finland: Metsäntutkimuslaitos.

Mikkonen E (2002) Recent developments and research needs in forest operations management and modeling. *Proceedings International Seminar on New Roles of Plantation Forestry Requiring Appropriate Tending and Harvesting Operations*, pp. 42–45. Tokyo, Japan: IUFRO.

Pekka M, Arto R, Jukka A, (1997) *Puunhankinnan organisointitavat*. METLA Report no. 647. Helsinki, Finland: Metsäntutkimuslaitos.

Small-scale Forestry

P Hyttinen, Regional Council of North Karelia, Joensuu, Finland

Introduction

This article reviews various aspects of small-scale forestry in the world, with an emphasis on industrialized countries. Definitions and demographic information on small-scale forestry are discussed. Aspects of administrative structures and policy instruments for small-scale forestry are presented. In particular, the importance of forestry to social welfare is noted, and the role of small-scale forests in conducting environmentally and socioeconomically sustainable forest management is discussed.

Small-Scale Forestry in the Center of Interest

Forestry has traditionally been conducted in most countries mainly by the public sector on public land or by industrial companies on large-scale natural forest areas or plantations. On the other hand, private nonindustrial and small-scale management of forests has been dominant in Western Europe and Japan, where forests may remain in the ownership of the same family for centuries. In recent years, there has been a trend to move gradually away from large-scale forestry towards landholder-based small-scale forest management. This trend is especially clear in developing countries in Africa and in Asia, as well as in the former socialist countries of Eastern Europe.

Small-scale forestry has been recognized as a promising tool in achieving the multiple forest-related objectives of society, as well as in addressing the various global environmental issues of today. Regardless of the fact that the demand for forest industry products is continuously growing, environmental considerations and recreation have become increasingly important, often competing with financial considerations and wood production. Around the world, loss of biodiversity has become a major concern in the management of forest lands. Substantial deforestation has taken place in many developing countries. The wide range of social, economic, and ecological objectives of forest management are seen to be better met by small-scale forestry rather than by large-scale forest management.

What is Small-Scale Forestry?

It is apparent that small-scale forestry means different things in different parts of the world. There is no simple or consistent definition of what constitutes small-scale forestry. A farmer operating with a woodlot of 5 ha would certainly be a small-scale forest owner, whereas an industrial company with thousands of hectares would be large. But in between these examples there exists a wide variety of sizes that can be considered either small or large depending on the viewpoint taken.

There is no comparable or consistent statistical information about the amount of small-scale forests in different countries and continents. According to the latest United Nations Economic Commission for Europe/Food and Agriculture Organization statistics, private forest ownership plays a significant role in Japan (59%), Europe (55%), North America (37%), and New Zealand (31%). However, it is important to make a difference between small-scale forestry and private forestry, as private does not always mean small.

The terms 'small-scale forestry,' 'nonindustrial private forestry,' 'family forestry,' and 'farm forestry' are parallel and they are used rather synonymously to separate this type of forestry from industrial or public large-scale forestry. Small-scale forestry differs in many ways from large-scale forestry, for example, in aspects such as motivations for the establishment and management of forests, social and economic objectives of forestry, and the likely markets for wood and non-wood forest products.

Appearance of Small-Scale Forestry in Selected Countries

In the USA, the term adopted for small-scale forests is nonindustrial private forests (NIPFs) referring to forestlands owned by farmers, other individuals, and corporations that do not operate wood-processing plants. NIPFs account for 59% of total timberland in the USA, and contribute nearly half of US timber production. In total, there are about 7 million NIPF landowners. Only about 600 000 holdings are larger than 40 ha, yet they contribute 80% of the NIPF harvest.

In Canada, private land ownership is unusually low in comparison with other developed countries. Only 6% of forest land is privately owned, whereas some 70% is provincially owned, with an additional 23% being owned federally by the national government.

In Japan, family-owned small-scale forestry is present in an extreme form: of the 2.5 million forest households, 1.5 million hold less than 1 ha. Nearly 90% of forest holdings are less than 2 ha. The national average for a forest holding is 2.7 ha. Private small-scale forests make up 59% of all forested area, providing almost 75% of the timber harvested. In recent years, these small-scale forests have become increasingly important because of drastically decreased timber production in national forests. No large forest land-holding companies are currently active in Japan.

In Australia, the term 'farm forestry,' or 'agroforestry,' is widely used due to the fact that forestry is often integrated into the farm business, generating revenue and environmental services to complement other enterprises on the farm. Unlike many European countries and Japan, farm forestry is a relatively new phenomenon in Australia, with the majority of farm forests being early in their first rotation. This is due to the fact that forestry activities were traditionally based on the exploitation of the extensive eucalypt forests that existed at the time of European settlement. However, nowadays significant areas of native forest have been withdrawn from timber production and placed within conservation reserves. As this trend is likely to continue, the role of plantation forests is becoming increasingly important. These plantations are mainly established by large-scale industrial companies, but plantations among small-scale farmers are also increasing.

In Europe, there is no commonly adopted term for small-scale forestry, though 'family forestry,' launched by the Nordic countries, has recently gained ground in Central Europe where the term 'farm forestry' has traditionally been used most often. Forest land ownership in Europe is approximately equally distributed between public and private owners. However, in Western Europe two-thirds of forest land is privately owned, whereas in Eastern Europe forests are mainly public domain, although this is now changing rapidly with privatization in the formerly socialist countries.

Most European countries have large numbers of smallholdings. In the 15 member countries of the European Union, there are approximately 12 million private individuals who can be classified as forest owners. In France and Belgium, more than 90% of the holdings are under 5 ha. This is in contrast with Sweden and Finland, where 25% and 14% of holdings respectively are larger than 50 ha. Private forests contribute most of the industrial timber as well as other wood and non-wood products. Due to the significance of private ownership, small-scale landowners are an integral part of forest policies, forest management planning, and forest extension in Europe.

Administrative Aspects of Small-Scale Forestry

In most countries small-scale forest owners have established voluntary national organizations, associations or other such establishments, to promote sustainable forest management, to serve as a link between forest owners, and to represent them in forest policy-making. In many countries these organizations, varying with legal bases and organizational arrangements, also provide help in timber sales and silvicultural operations.

A number of international organizations for forest owners also exist. For example, the Confederation of European Forest Owners (CEPF) was established in the 1990s to form an umbrella organization of the national forest owner organizations in Europe. The most recent establishment is the International Family Forestry Alliance (IFFA), representing some 30 million family forest owners in Europe and North America.

In the governmental systems of most countries, small-scale forestry has traditionally been under agricultural administration, due to close linkages between forestry and farming. Only in some countries, e.g., Finland, has the role of forestry been emphasized by naming the ministry as Ministry of Agriculture and Forestry. A few countries, including Portugal, have a separate Directorate General for forestry administration.

The practical implementation of public forest policies on private lands typically falls under the responsibility of governmental field organizations at the regional and district level. Recently, there has been an international trend towards lighter public administration. Therefore, forestry administrations throughout the world have also faced budget reductions. In addition, along with the increasing number of nonfarmers as forest owners, the link between forestry and agriculture has gradually weakened. There has been some consideration about whether forestry administration should be made more independent of agriculture; whether there should be a common administration for all natural resources; or whether forestry should be merged with the environment (as in Denmark), industry, or trade portfolios (as in Sweden).

Small-Scale Forestry in Resolving Global Issues

In the past, the main emphasis of forest policies on small-scale forestry was to ensure a constant flow of timber to the processing industries. In recent decades, growing environmental consciousness has raised the ecological perspective to a more central position. Countries around the world have been active in taking on commitments concerning the protection, development, and sustainable management of forests.

A crucial step in this direction was the United Nations Conference on Environment and Development (UNCED) held in Rio de Janeiro in 1992. The UNCED has given forests an increasingly important role in the context of sustainable development and environmental conservation. The concept of sustainable forest management has been recognized as a fundamental guiding principle by all participating countries.

As many as 149 countries, representing 85% of the world's forests, are engaged in efforts to identify criteria and indicators of sustainable forest management, and to collect information on the indicators. Over the last 10 years, a number of private initiative certification systems have evolved based on these criteria and indicators. There seems to be no 'one-fits-all' solution when it comes to certification of sustainable forest management, but one has to support bottom-up approaches within the different regions and countries.

During the international follow-up processes of Rio, small-scale forest owners have been seen as key partners for the implementation of sustainable forest management. In the first phase, the emphasis was on ecological aspects of sustainability. The contribution that forests can make to the environment in such diverse areas as water catchment protection, habitat creation and conservation, and recreation is now widely recognized. Increasingly, forest owners are either required by statute or influenced by financial incentives to alter their management practices to increase these environmental benefits, or to decrease environmental costs.

Recently, socioeconomic aspects of small-scale forestry have gained increasing attention. For example, in the resolutions of the European Ministerial Conference in Lisbon in 1998, socioeconomic sustainability was given the main emphasis. Probably the most important socioeconomic aspect related to small-scale forestry is the income from forests, which can play an important role in maintaining a sound social structure, and thus, forestry can contribute to the overall economy of rural areas.

Generally, farm forests are concentrated in rural and mountainous areas, which are economically disadvantaged compared with industrialized areas, and undergoing depopulation. Therefore, farm forestry has a key socioeconomic role relevant to policies at regional, national, and international levels. Attention is paid not only to traditional questions such as the continuing viability of individual farms, to which the production of timber and other products can contribute, but also to more recent questions such as the contribution that the landscape value of attractive woodlands can make to the rural economy through tourism.

In the ongoing debate on forest policies, the role of forests in implementing the 1997 Kyoto Protocol to the Framework Convention on Climate Change has also raised much discussion. Developments towards a market for carbon emissions by governments and industries preparing for national reductions of greenhouse gas emissions have stimulated interest in the carbon sequestration values of forests. Forest owners could have the opportunity to manage their forests for carbon, along with other wood and non-wood products. Emissions trading could provide positive cash flows earlier than usually available from wood production, thus improving profitability. For the moment, however, the forest policy implications and practical consequences of the Kyoto Protocol remain unclear.

The most recent milestone in the international debate on the various aspects of sustainable development was the World Summit on Sustainable Development, held in Johannesburg in 2002.

Forest Policy Instruments for Small-Scale Forestry

Considerable differences exist in forest policy instruments between countries. In most countries the full range of policy means – normative, financial, material, and informative – has been adopted. However, the policy instruments are modified by so many conditions and variations that it is not possible to draw simple comparisons.

A fundamental review and reappraisal of forestry legislation has recently been or is currently being undertaken in many countries, in the light of the new priorities identified during the widespread debate on sustainable forest management.

Taxation and subsidies strongly influence the economic performance of small-scale forests. Differences can be observed in the balance between property taxation and income taxation, as well as indirect taxes such as value-added and fuel taxes. In this connection, special mandatory fees connected to timber sales have to be mentioned, as well as the general tax load on income, including social security fees which influence labor costs.

In general, financial support for forestry measures is at a rather low level, and normally only part of the costs of forestry measures can be covered by public support. Partial public support is typically available in many countries for measures such as regeneration of harvested areas, noncommercial thinning of young stands, forestry road building and maintenance, and forest fire protection.

The economic performance of small-scale forests is of importance for various policy objectives, but the availability and comparability of the information required to assess economic performance are not sufficient. Hence, evaluation of the efficiency of the policy tools is difficult. Indeed, the recent economic and political developments suggest a need for a more comprehensive information base and analysis on the socioeconomic situation of small-scale forestry.

Due to agricultural overproduction, one of the major concerns in industrialized countries has recently been the extent to which agricultural land can and should be converted to forestry or woodland, and the policy measures which would achieve this. For example, in almost all European countries there are policies to support farmers who convert their agricultural land to forestry.

Extension services, information distribution, and education are increasingly important forest policy tools. They activate forest owners to own contributions, and thus compensate for the reduced direct financial support for forestry measures. Indirect subsidies can be found in various forms, the most common example being the provision of management consulting services to small-scale private landowners by members of the forest service or foresters employed by semigovernmental institutions. Systematic forest management planning is seen as being one of the most important and efficient tools in many countries in this respect.

There appears an international trend to increase public participation in forest-related policy-making and decision-making. One sign of this is that national forest programs have become an important tool in the preparation of the future strategies for forestry. Evidently, small-scale owners play an essential role in these strategies. Especially in countries where small-scale forestry is dominating, only the strategies that are accepted by small-scale owners can be successful.

Final Remark

An important aspect to be noted here is that the land ownership structure and management goals for forestry around the world are heterogeneous and becoming even more so. One indicator of relative importance of forests for society is the share of forest area per capita. Even within Europe the extremes are from 0.2 ha in the Netherlands to 4.0 ha in Finland. It is self-evident that the owner's expectations as well as public values related to forests cannot be the same in these two countries. Indeed, the significance of forest resources for owners, as well as for the public, varies tremendously between countries and continents. This, on the other hand, guarantees the diversity of forest uses and management practices in the world.

See also: **Plantation Silviculture**: Multiple-use Silviculture in Temperate Plantation Forestry. **Tree Physiology**: Forests, Tree Physiology and Climate.

Further Reading

Blyth J, Evans J, Mutch WES, and Sidwell C (1991) *Farm Woodland Management*, 2nd edn. Ipswich, UK: Farming Press.

Evans J (2002) *What Happened to Our Wood*. Alton, UK: Patula Books.

Evans J (2003) *A Wood of Our Own*. East Meon, UK: Permaculture.

FAO (2002) *Temperate and Boreal Forest Resource Assessment 2000*. Rome: Food and Agriculture Organization of the United Nations.

Harrison S, Herbohn J, and Herbohn K (2000) *Sustainable Small-Scale Forestry: Socio-Economic Analysis and Policy*. Northampton, MA: Edward Elgar.

Harrison S, Herbohn J, and Niskanen A (2002) *Non-industrial, Smallholder, Small-Scale and Family Forestry: What's in a Name? Small-Scale Forest Economics, Management and Policy*, vol. 1, no. 1, pp. 1–11. Gatton, Australia: University of Queensland.

Hyttinen P, Ottitsch A, and Niskanen A (2000) New challenges for the forest sector to contribute rural development in Europe. *Land Use Policy* 17: 221–232.

Hyttinen P, Niskanen A, Ottitsch A, Tykkyläinen M, and Väyrynen J (2002) *Forest Related Perspectives for Regional Development in Europe*. EFI Research Report 13. Joensuu, Finland: European Forest Institute.

Niskanen A and Väyrynen J (2001) *Economic Sustainability of Small-Scale Forestry*. EFI Proceedings no. 36. Joensuu, Finland: European Forest Institute.

P

PACKAGING, RECYCLING AND PRINTING

Contents

Paper Recycling Science and Technology

M R Doshi, Progress in Paper Recycling, Appleton, WI, USA
J M Dyer, Weyanwega, WI, USA

Introduction

The principal raw material used in making paper, cellulose fiber, is derived chiefly from the wood of trees, although other plant residues such as rice straw, kenaf, and bagasse are also potential sources of fiber. Several pulping processes ranging from mechanical, chemimechanical, to chemical, are used to separate fibers in wood to produce virgin pulp (*see* **Pulping**: Chemical Pulping; Mechanical Pulping). Important hardwood species include aspen, oak, maple, and eucalyptus, while softwood types include species of pine, spruce, fir, and larch. If the fiber is not severely contaminated or has not deteriorated during its use in the paper or board product, it can be reused again as secondary or recycled fiber.

During the paper-recycling process, cellulose fibers are separated from recovered (waste) papers and reused to manufacture new products. In 2001, the US supply (= production + import − export) of pulp and paper was estimated to be 98 million tons, of which 47 million tons, or 48% of the total, was recovered (**Table 1**). The amount of paper land-filled decreased from 40.6 million tons in 2000 to 36 million tons in 2001. As shown in **Table 2**, the world production of paper and paperboard decreased from about 324 million tons in 2000 to 318 million tons in 2001, whereas paper recovery increased from 45.3% in 2000 to 45.9% in 2001. (Note that **Table 1** includes paper and board recovered for paper-making as well as for other uses, while **Table 2** includes paper recovered primarily for paper-making.)

Paper mills have many choices for the selection of raw material. Virgin sources include many species of softwoods and hardwoods while secondary sources include various grades of recovered papers. There are more than 50 grades of recovered papers. Four widely used recovered paper grades are described in the next section. The choice of raw material, virgin and/or secondary, will depend on many factors, such as geographic location of the mill, product manufactured, and economics.

Once the right paper grade has been selected, the next task of the mill is to separate fibers and contaminants like paper clips, staples, inks, and

Table 1 Paper and paperboard recovery in the USA

Year	*Supply (000 tons)*	*Recovered (000 tons)*	*Recovery rate (%)*
1990	86 796	29 112	33.5
1991	85 071	31 201	36.7
1992	88 273	33 954	38.5
1993	91 538	35 460	38.7
1994	95 718	39 691	41.5
1995	96 036	42 189	43.9
1996	94 495	43 076	45.6
1997	99 542	43 989	44.2
1998	101 139	45 076	44.6
1999	105 557	46 818	44.4
2000	103 192	47 311	45.8
2001	97 911	47 252	48.3

'Supply' includes consumption of all paper, corrugated and paperboard, including construction paper and board.
Supply = production + import − export.
'Recovery rate' is the ratio of total paper, corrugated and paperboard recovered (for paper-making and other uses) to supply.
Reproduced with permission from American Forest & Paper Association (AF&PA) (2002) *Recovered Paper Statistical Highlights*. Washington, DC: AF&PA. Available online at: www.afandpa.org.

Table 2 World paper and paperboard production and recovery (all figures (except percentages) in thousand tons)

	Total production		*Paper recovered*		*Paper recovered (%)*	
	2000	*2001*	*2000*	*2001*	*2000*	*2001*
Europe	100 066	98 255	44 775	45 434	44.7	46.2
Asia	95 797	97 661	45 706	44 998	47.7	46.1
Australasia	3526	3494	1807	1981	51.2	56.7
North America	106 603	100 433	46 702	45 589	43.8	45.4
Latin America	14 789	14 855	6558	6625	44.3	44.6
Africa	3200	3449	1238	1289	38.7	37.4
Total	323 981	318 147	146 786	145 916	45.3	45.9

Reproduced with permission from *Pulp and Paper International* (2002) 44(7): 6.

adhesives. Unit processes like pulping, screening, cleaning, flotation, and washing are used to remove contaminants from the pulp. One of the contaminants that poses a serious challenge to paper recycling arises from adhesives, glues, and binders used in inks and coatings. Strategies to handle stickies are presented, followed by a brief presentation of the changes in paper properties due to recycling.

Paper Grades

The Paper Stock Institute of the Institute of Scrap Recycling Industries (ISRI) publishes a list of more than 50 recovered paper grades. Each grade has its own characteristics related to fiber species, the original pulping process, brightness, contaminant content, and degree of converting. In general these grades can be segregated into four main categories:

1. Corrugated or boxboard.
2. Newspapers.
3. High grades.
4. Mixed papers.

The recycling process changes the properties of the fiber so that it performs differently compared to virgin fiber. Additives, coatings, and inks used to increase the value and performance of the paper or board product can cause problems during the recycling process and must be removed during the recycling operations. The value of the recovered paper or board is a function of how difficult it will be to defiber, the degree of contamination, and the requirements to restore the fiber characteristics necessary to produce paper meeting the required specifications.

Corrugated Containers

Approximately one-half of the paper recovered in the USA in 2001 was old corrugated container (OCC). Corrugated includes corrugated boxes, kraft grocery bags, multiwall shipping sacks, and similar unbleached containers. The American Forest and Paper Association has estimated that, in 2001, 75% of the OCC was recovered in the USA. The chief source of OCC is from grocery stores and retail businesses, with an increasing quantity coming from individual households and small businesses. Most of the OCC is recycled into linerboard, corrugating medium, and containerboard. A typical OCC system is shown in **Figure 1**. Some of the unit processes shown in **Figure 1** are described in the next section.

OCC quality varies depending on the source. In the USA, a large percentage of corrugated containers have virgin fiber, usually unbleached softwood kraft, in the liner. Softwood kraft fibers are desirable due to their strength properties. In the USA, liner containing up to 20% recycled fiber is still classified as virgin. When a high proportion of recycled fiber is used, the liner may be termed test, jute, or bogus liner. The use of recycled fibers in the production of liner grades does not permit the stringent control of the fiber types as in the virgin grade. Since there are differences in the distribution of long and short fibers in recycled grades, the characteristics such as strength properties seldom match those of the virgin grade.

A requirement of fibers used in corrugating medium is stiffness, which gives the medium its crush resistance. Virgin medium is usually produced from hardwood fibers pulped by one of several processes, including neutral sulfite semichemical and alkali carbonate process (*see* **Pulping**: Chemical Pulping). Recycled medium may contain OCC, old magazines, and mixed papers.

Recovered OCC is used in the manufacture of solid folding boxboard. The application of fractionating permits the separation of the recycled pulp into a long and a short fiber fraction, each of which can be directed to the desired end use. Short fibers, which tend to be stiffer, are used in the top ply to provide good printing characteristics. The longer fibers, which provide better strength and runnability, may be used in the filler plies.

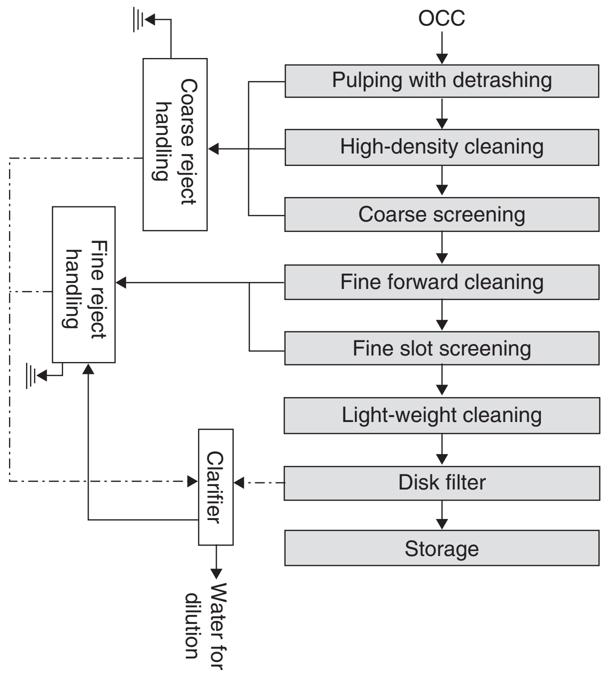


Figure 1 Recycling system for old corrugated container (OCC) to linerboard.
Notes

1. High-density cleaning corresponds to cleaning in large-diameter (30–75 cm) hydrocyclones, usually at consistency of 3–4%.
2. Cleaning in hydrocyclone to remove contaminants with density greater than that of water is termed heavy-weight cleaning or forward cleaning.
3. Cleaning in hydrocyclone to remove contaminants with density less than that of water is termed light-weight cleaning.
4. Disk filter is used as a thickening device.
5. Dissolved-air flotation (DAF) is generally used here for water clarification.

Reproduced with permission from Spielbauer JL (1998) Recycling systems overview. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge*, vol. III, *Process Technology*. Appleton, WI: Doshi & Associates, Inc.

Other uses for OCC include use in absorbent grades such as industrial toweling and in packaging papers such as grocery bags and industrial wrappers.

Newspapers

This category includes old newspapers (ONP) collected from residences, offices, and other sources. In the USA, approximately 78% of the newspapers printed are now being recovered. In 2001, 9 million tonnes of ONP were recovered, or nearly twice the recovery rate in 1989. About 60% of all ONP recovered is recycled domestically to manufacture newsprint or recycled paperboard. In paperboard, ONP serves as filler.

ONP has a high percentage of mechanical fiber, which includes groundwood and thermomechanical pulp. Chemical fiber such as kraft may comprise up to 30% by weight and is added to improve the strength properties of the paper. Other constituents may include additives such as starch, inorganic fillers, and dyes for color control. Inorganic filler content (ash) may range from 3 to 12% by weight. Newspapers are printed by letterpress, offset, and flexographic processes. Ink content in printed newspapers comprises 1–2% by weight.

When recycled to produce newsprint, ONP is processed through a sequence of deinking steps. While there are several variations in the deinking process, the common unit processes consist of:

- pulping (and detrashing)
- washing (and thickening)
- screening
- dispersion
- cleaning
- bleaching
- flotation deinking
- water clarification.

A typical deinking system is shown in **Figure 2**.

Deinking technology for recycling ONP is well established; however, there have been distinct differences in the approaches developed in Europe and Asia compared to North America. Dispersed-air flotation deinking was traditionally applied in Europe and Asia, whereas in North America washing was the primary deinking process. In recent years, flotation deinking has gained acceptance in North America, where it is commonly used in combination with washing.

In mills deinking with flotation, ONP is commonly blended in a 70 : 30 ratio with old magazines (OMG). The presence of OMG in the furnish aids in flotation due to the high filler content (clay and/or calcium carbonate) which may stabilize the foam. OMG also enhances product brightness and strength due to the presence of bleached chemical fibers. Deinking chemicals such as fatty acid soap, sodium silicate, chelants, and caustic are added to the pulp to aid in ink detergency. Soap promotes ink particle attachment to air bubbles by making the ink more hydrophobic and it promotes a stable foam, allowing the flotated ink to be removed from the process before the bubble breaks.

High Grades

These grades are usually processed by a deinking operation. High grades are primarily printed and unprinted white papers collected from converting

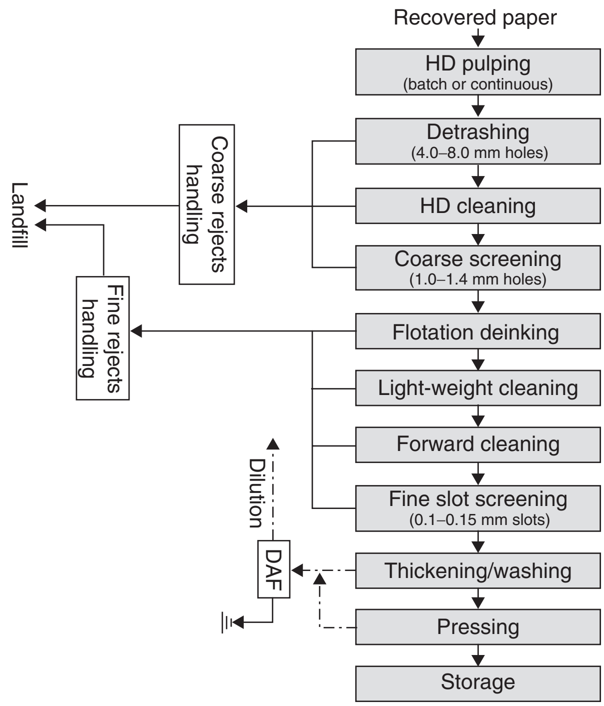


Figure 2 Flow diagram for old newspaper deinking system. *Notes*:

1. HD (high-density) pulping stands for pulping at solids concentration (consistency) of 12–18%.
2. HD cleaning corresponds to cleaning in large-diameter (30–75 cm) hydrocyclones, usually at a consistency of 3–4%.
3. Cleaning in hydrocyclone to remove contaminants with density less than that of water is termed light-weight cleaning.
4. Cleaning in hydrocyclone to remove contaminants with density greater than that of water is termed heavy-weight cleaning or forward cleaning.
5. DFA stands for dissolved-air flotation. DAF is used here for water clarification.

Reproduced with permission from Spielbauer JL (1998) Recycling systems overview. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge*, vol. III, *Process Technology*. Appleton, WI: Doshi & Associates, Inc.

operations, printing plants, and offices. These grades are versatile raw materials and have been recycled to make a range of products, from tissue to recycled paperboard to printing and writing papers. Demand for some grades is high, for example pulp substitutes; however, the potential for growth of some high grades is limited since virtually all sources have been exploited. Additional supplies of mixed and sorted office papers will be generated through expanded office paper recovery programs.

Mixed Papers

Unlike the preceding categories, mixed paper grades are not segregated. The category mixed papers is comprised of several types of papers commingled together. As a result, the fiber is more heterogeneous, filler content is variable, and contamination levels are higher. However, demand for mixed papers is increasing as the more valuable grades reach the limit of recovery, and as recycling technology advances. Mixed papers are generally substituted for other grades such as ONP and OCC in containerboard. Mixed papers are generally collected from homes and offices.

Recycling Unit Processes

The recycling of recovered paper involves several unit processes that separate the paper-making fibers from contaminants which may detract from the appearance or strength properties of the final product. Contaminants include sand, staples, wood, inks, plastics, adhesives, coatings, and inorganic fillers. The number and sophistication of the unit processes increase as the requirements for cleanliness and brightness in the final product increase.

Pulping

The primary purpose of pulping is to defiber the paper into its constituent fibers without significantly degrading contaminants. Important parameters in pulping include stock consistency, temperature, pulping intensity, pH, and pulper configuration. Progress has been made in understanding and modeling pulping and ink detachment.

Pulping is accomplished through three basic mechanisms:

1. Wetting the paper to the desired consistency.
2. Circulation either to return the material to a high shear zone or to promote fiber-to-fiber friction.
3. Attrition, by which flakes are torn apart in a high shear zone.

Pulpers are characterized by their operating mode, whether batch or continuous, geometry, rotor type, operating consistency, and accessories. They can be broadly classified as either vat-type or drum-type. A typical vat-type pulper is shown in **Figure 3a**. This pulper consists of a vat or tub in which the stock is mixed by a rotor positioned at the bottom or side of the tub. The type of rotor used is dependent upon the consistency requirements, operating mode, and fiber type. Helical rotors, which resemble a large screw (**Figure 3b**), operate at high consistency and promote fiber-to-fiber friction through radial motion. Attrition rotors, used in low-consistency pulpers, have blades that maximize turbulence and shear.

The drum-type pulper consists of a rotating vessel through which the recovered paper tumbles and is

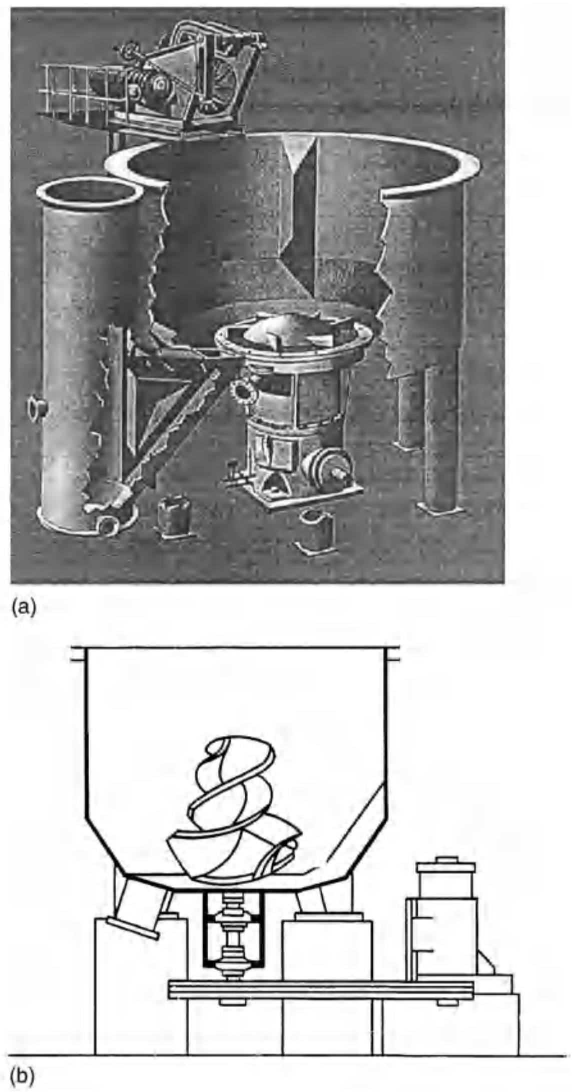


Figure 3 (a) Side cut-away of a vertical pulper. (b) Helical rotor pulper. Reproduced with permission from Silveri L and Wagner MM (1998) The pulper/detrasher module in the recycle system. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge*, vol. III, *Process Technology*. Appleton, WI: Doshi & Associates, Inc.

defibered as it is transported along the length of the drum. Drum pulpers operate at high consistency (15–20%) and are used for treating low-strength materials such as newspapers which defiber easily. A schematic of a drum pulper is shown in **Figure 4**. Recently, variations in the design of drum pulper have been introduced. Applications of drum pulpers have been extended to other paper grades such as office papers and OCC.

Many modern pulpers are fitted with ancillary equipment that removes trash and contaminants before they are broken down into small pieces. This equipment includes the ragger to remove wires and rope-like contaminants, junk tower, for larger trash, and the secondary pulper. The secondary pulper, or detrasher, which receives a small side stream from the main pulper, consists of a dual-chamber device in which the rejects chamber and the accepts chamber are separated by an extraction grate, a perforated plate. The rotor wipes the extraction plate to keep it free of contaminant build-up during the passage of accepted fiber.

Pulpers are operated in one of two modes: batch or continuous. In batch pulping, paper stock, water, steam, and chemicals, if necessary, are charged to the pulper and the entire mixture is processed for a set amount of time before it is dumped to a receiving chest. Batch pulping is more commonly used in deinking where high consistency is desired and when the residence time in the pulper must be controlled to ensure sufficient detachment of ink from the fibers.

Continuous pulpers are fed with recovered paper and water on a continuous basis while defibered materials pass out of the pulper through an extraction plate. The residence time of the material in the pulper is a function of the feed rate, size of the pulper tub, and the opening size of the holes in the extraction plate. Generally operating at 4–8% consistency, this mode of pulping is used where high production is desired and is commonly used in OCC processing systems.

Screening

Screens are able to separate a multicomponent flow into two fractions on the basis of differences in morphology or shape. Screening is the most common separation process used in recycled fiber systems. While screening is most commonly associated with the separation of contaminants from fiber, several applications are based on screening or barrier separation technology:

1. Contaminant screening.
2. Fractionation.
3. Washing.
4. Dewatering.

Contaminant screening The object of contaminant screening is to remove nonfibrous contaminants while minimizing the loss of fiber. Pressure screens are the most commonly used devices for this purpose, although some gravity screens are operating in tailing systems. The pressure screen consists of a cylinder with either perforated holes or fine slots: it is attended by a rotating hydrofoil or other rotating element providing alternating pressure or vacuum pulses to the screening surface to keep it from plugging or blinding with debris or fiber. The materials that pass through the screen openings, considered accepts, are sent forward in the system,

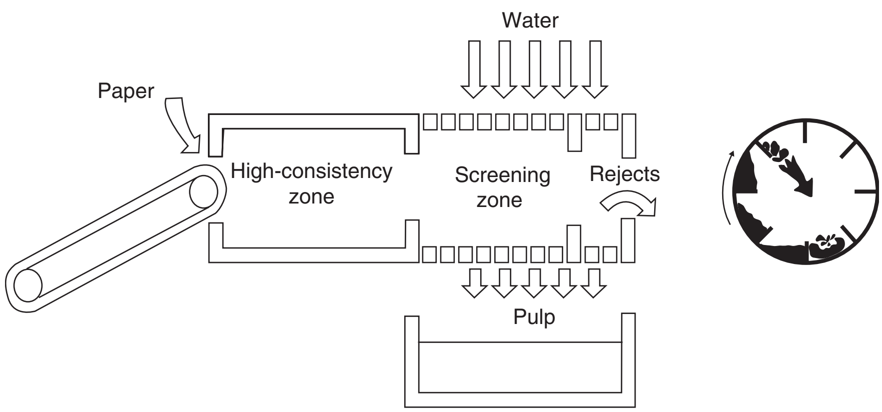


Figure 4 Drum pulper. Reproduced with permission from Silveri L and Wagner MM (1998) The pulper/detrasher module in the recycle system. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge*, vol. III, *Process Technology*. Appleton, WI: Doshi & Associates, Inc.

while the materials that are blocked at the openings are rejected and are either reprocessed in another area of the system or discarded. Coarse screens, generally positioned early in the system, process relatively contaminated stock and have perforated cylinders. Perforations are usually 1.38 mm (0.055 in.) or larger. Fine screens, with slotted cylinders, are positioned after coarse screens where they are more effective in removing small contaminants. The slot opening width of fine screens ranges from 0.10 to 0.60 mm (0.004–0.024 in.).

Fractionation Fractionating screens separate the stock into a long fiber fraction and a short fiber fraction. These devices normally use holes in the range 1.3–2.0 mm and operate in the consistency range 2–4%.

Washing When used for washing pulp, a fabric is used to retain fibers while allowing the fines, fillers, and ink to pass with water through the fabric. Traditionally, sidehill screens and deckers were used. During the last 15 years more aggressive washers, which minimize the formation of a mat on the fabric, have been developed.

Dewatering The function of dewatering screens is to maximize the removal of water from stock while minimizing the loss of solids. Disk filters are used for low-consistency applications, while belt presses, screw presses, and twin wire presses are used at high consistency.

Cleaning

Cleaners or hydrocyclones remove contaminants from pulp based on the density difference between the contaminant and water. These devices consist of a conical or cylindrical–conical pressure vessel into which pulp is fed tangentially at the large-diameter end (**Figure 5**). During passage through the cleaner the pulp develops a vortex flow pattern, similar to that of a cyclone. The flow rotates around the central axis as it passes away from the inlet and toward the apex, or underflow opening, along the inside of the cleaner wall. The rotational flow velocity accelerates as the diameter of the cone decreases. Near the apex end the small-diameter opening prevents the discharge of most of the flow which instead rotates in an inner vortex at the core of the cleaner. The flow at the inner core flows away from the apex opening until it discharges through the vortex finder, located at the large-diameter end in the center of the cleaner. The higher-density material, having been concentrated at the wall of the cleaner due to centrifugal force, is discharged at the apex of the cone.

Cleaners are classified as high-, medium-, or low-density depending upon the density and size of the contaminants being removed. A high-density cleaner, with diameter ranging from 15 to 50 cm (6–20 in.) is used to remove tramp metal, paper clips, and staples and is usually positioned immediately following the pulper. As the cleaner diameter decreases, its efficiency in removing small-sized contaminants increases. For practical and economic reasons, the 75-mm (3-in.) diameter cyclone is generally the smallest cleaner used in the paper industry.

Reverse cleaners and throughflow cleaners are designed to remove light-weight contaminants such as wax, polystyrene, and stickies. Reverse cleaners are so named because the accepts stream is collected at the cleaner apex while the rejects exit at the overflow. In the throughflow cleaner, accepts and rejects exit at the same end of the cleaner, with accepts near the cleaner wall separated from the rejects by a central tube near the core of the cleaner.

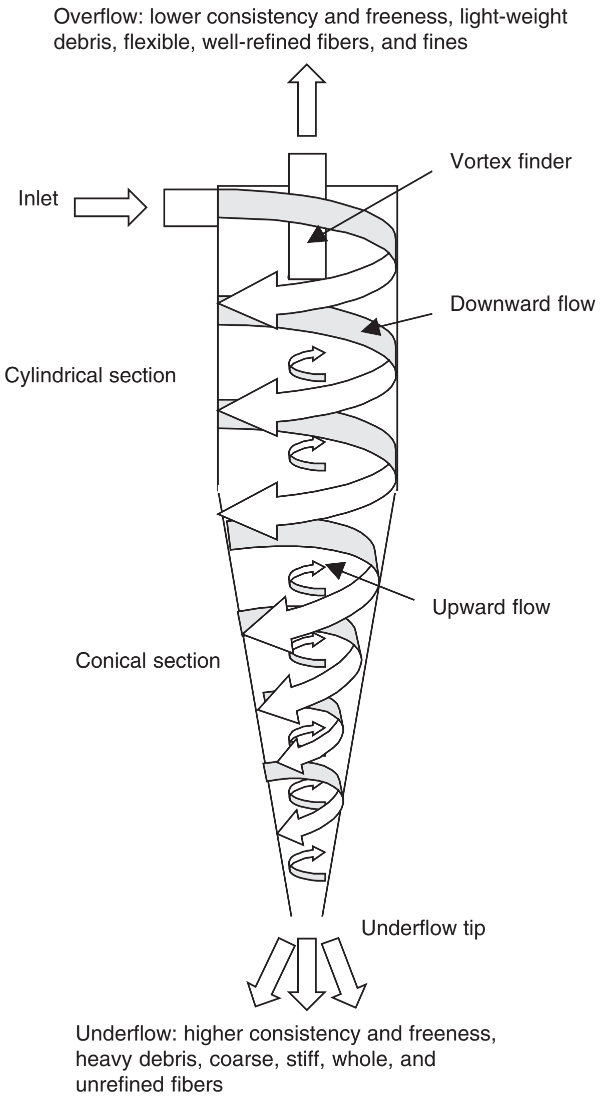


Figure 5 Parts of a hydrocyclone, major flow patterns, and separation trends.

Continuous centrifuges used in the 1920s and 1930s to remove sand from pulp were discontinued after the development of hydrocyclones. A recently designed cleaner, the Gyroclean, developed by Centre Technique du Papier, Grenoble, France, consists of a cylinder that rotates at 1200–1500 rpm. The combination of relatively long residence time and high centrifugal force allows light-weight contaminants sufficient time to migrate to the core of the cleaner where they are rejected through the center vortex discharge.

Deinking

In grades that are destined to be recycled into printing and writing grades, tissue, etc., deinking is applied to remove ink from the pulp. The deinking process begins in the pulper where fiber-to-fiber rubbing and added chemicals for detergency detach ink from the fiber surface. Processes present in the system for removing ink from pulp include cleaners, washers, froth flotation, and, to a certain extent, screens. Kneaders and dispersers are used to disintegrate residual ink into smaller particles too small to be seen by the naked eye. Kneaders and dispersers also assist in the detachment of inks and other contaminants from fibers.

Deinking chemistry The goal of deinking is to provide the conditions in the pulper that will advance the detachment of ink from fiber, and then, in subsequent equipment, separate the detached ink from the pulp. Chemicals are commonly used to enhance deinking. Sodium hydroxide is used to adjust pH. Surfactants affect detergency and dispersed ink particle size, critical for effective ink removal in the processes following pulping. In the pulper, the mechanisms of ink detachment include:

- surfactant-promoted solubilization of ink into the aqueous pulping medium
- surfactant-promoted wettability alteration of cellulose surfaces promoting ink detachment and emulsification
- cellulose fiber swelling, promoted by high pH, to enhance ink detachment from fiber
- fiber-to-fiber rubbing promoted by mechanical agitation.

Inks differ in surface chemistry and composition. As a consequence, the selection of chemistry and removal processes must focus on the type of ink that is encountered in the particular recovered paper grade. The role of the surfactant used for wash deinking is to create hydrophilic, dispersed ink particles. Flotation deinking surfactant must make the detached ink particles more hydrophobic so that they attach to air bubbles, and the surfactant must produce sufficient air bubble stability so that the froth can be removed from the pulp. Sometimes a dispersant like sodium silicate may be necessary to stabilize detached ink particles and avoid redeposition back on to fibers.

Washing Washing is effective for removing dispersed ink, fines, and filler particles of less than 15 μm. Washing devices function in a manner similar to a laundry process whereby finely dispersed particles are transported away from the pulp with the filtrate as the pulp thickens on a mesh or wire. The formation of a fiber mat during washing can reduce the removal efficiency of fine particles, therefore highly turbulent washers tend to be more efficient, but at the sacrifice of lower yields, i.e., greater fines and/or fiber losses.

Dispersed-air flotation Originating in the mining industry for enrichment of ores, the flotation process developed in Europe for deinking has gained importance in North America. In this process, hydrophobic particles such as ink and small contaminants attach to air bubbles injected into the pulp and get carried upward to the froth while fibers remain in the bulk. The particles are separated from the pulp by removing the froth from the surface of the pulp. Surfactants are commonly used to enhance the hydrophobicity of the particles and to improve the stability of the froth. The optimum consistency range of froth flotation is 0.6–1.0%, and particles in the size range 25–300 μm can be removed by the process. Several factors influence the effectiveness of flotation units in removing ink particles from pulp. These include water hardness, temperature, ink particle size, ink particle chemistry, air bubble diameter, hydraulic flow patterns, air-to-stock ratio, and the froth removal system.

Kneading and dispersion Kneading and dispersion devices mechanically treat the pulp to reduce visible particles such as ink to subvisible sizes. In disk dispersion, pulp at high consistency is forced between two parallel disks, one stationary, and one rotating at 1200–1800 rpm. The disks are separated by an adjustable, narrow gap. Under the conditions of high shear and friction within the zone between the disks, ink and contaminant particles are reduced in size.

Kneading, also referred to as low speed dispersion, imparts relatively longer mechanical treatment to the pulp with a moderate shearing effect. In principle, the kneader consists of a shaft, to which are affixed several rows of fingers, slowly turning within a stator wall on which other fingers are attached. Pulp is fed by a screw conveyor into the narrow passage between the rotating shaft and stator where it is subjected to rubbing action. A discharge door controls the pressure on the pulp and the volume of pulp in the device. Double-shaft kneaders have two counterrotating shafts, turning at different rates.

Dispersers have been used to mix bleaching chemicals into the pulp. Located near the end of the process, dispersers can disintegrate the remaining contaminants which are then removed from the pulp by a postdispersion screening, cleaning, flotation, and/or washing steps.

Bleaching

The reasons for bleaching recycled fibers include color stripping, delignification, and brightening of fibers. In oxidative bleaching, agents such as hypochlorite, hydrogen peroxide, oxygen, and ozone are used. Reductive bleaching compounds include sodium hydrosulfite and formamidine sulfinic acid (FAS). Recovered paper pulps may contain chemical pulp, mechanical pulp, and dyes, each of which requires a specific bleaching approach for maximum effectiveness.

Bleaching mechanisms The bleaching agents can be categorized as nondegrading reagents and degrading agents. The nondegrading reagents such as hydrogen peroxide reduce color bodies (chromophores) in pulp by oxidizing carbonyl groups, while FAS and hydrosulfite reduce the quinone structures. These chemicals are useful in bleaching wood-containing grades since they do not react with lignin.

The degrading agents, which include oxygen, ozone, and the chlorine-containing compounds such as hypochlorite, are used primarily for bleaching chemical pulps and act by destroying the phenolic groups and the carbon–carbon double bonds. In recycled pulps containing higher amounts of mechanical fibers, the degrading agents tend to reduce the yield and yellow the pulp due to the fragmentation and/or modification of the lignin.

Dyes pose a special problem since, with the exception of ozone, no single bleaching agent is effective in destroying the broad range of dyes found in recovered papers. In general, direct dyes that contain conjugated nitrogen–nitrogen double bonds are readily decolorized by hydrogen peroxide and the reducing agents. Basic dyes, which contain conjugated carbon–carbon double bonds in aromatic compounds, are more prone to degradation by strong oxidizing agents. High temperature (above 100°C) peroxide bleaching seems to be effective in bleaching office papers.

Microbial enzymes such as xylanases and ligninases can improve lignin and chromophore removal, thereby facilitating bleaching in subsequent processes. When followed by peroxide bleaching, enzyme-pretreated pulps show a higher level of brightness and cleanliness than conventionally deinked pulps.

Bleach application methods Three main application points for bleaching agents include the pulper, bleach tower, and disperger/kneader. Hydrogen peroxide is commonly used with chelants and/or sodium silicate directly in the pulper to increase the brightness of mechanical grades such as ONP/OMG. In bleach towers, bleaching chemicals are mixed with pulp and the mixture is allowed to remain for an extended time period, usually 0.5–1.5 h. This longer residence time permits the completion of the bleaching reaction. Dispersers and kneaders are used in bleaching since they commonly operate at elevated temperatures which drive the bleaching reaction, and they promote excellent mixing of the chemical with the pulp. Following the disperser or kneader there may be a chest in which the bleaching reaction is allowed to proceed.

Commonly, bleaching sequences comprised of two or more bleach stages, each using a different bleaching reagent, may be used to maximize the brightness increase and color removal from the recovered fiber. For example, an oxidative stage using hydrogen peroxide bleaching may be followed by a reductive stage using sodium hydrosulfite.

Water Clarification

Considerable quantities of water are used for dilution, conveying, and washing during the processing of recovered fiber. Processes that enable the reuse of water are important from an environmental and financial standpoint. Water clarification is the unit operation which removes the bulk of suspended solids and the small amount of dissolved solids from the water, thus making it possible to reuse it in the system. By reusing clarified process water both the volume of effluent discharged to the wastewater treatment plant and the amount of incoming fresh water that must be treated are reduced. For example, a deinking stock preparation system will require 11–30 m^3 (3000–8000 gallons) of water per ton of production.

Clarification processes are usually attended by a chemical conditioning program. Flocculation and/or coagulation chemicals and polymers are used to aggregate solids in water, thus making the particle size larger.

Several techniques for clarifying process water are practiced. Some of these include sedimentation, dissolved-air flotation (DAF), and filtration. In the sedimentation process, process water is held in a clarifier tank at quiescent conditions for an extended time period. Solids separate from the liquid due to differences in density, interfacial tension, degree of hydrophobicity, or a combination of these factors. The net result is for the solids either to sink to the bottom or float to the top of the clarifier where they are removed.

In the DAF process, very fine air bubbles are introduced into the clarifier to provide buoyancy to the solids. Prior to introduction into the clarifier, a small portion of clarified water is pressurized and semisaturated with air. When this water is released into the clarifier, the dissolved air leaves solution and forms very small bubbles (0.01–0.1 mm diameter) which attach to the flocculated solids. The solids containing air bubbles become buoyant and are carried to the surface of the clarifier where they are skimmed from the tank. In a subsequent process, the solids, or sludge, is dewatered for disposal. DAF has the advantage of requiring low residence time (3–8 min) compared to sedimentation clarifier and it is able to separate solids with a fairly broad range of specific gravities.

Filtration technology includes drum filters, which remove larger suspended solids such as fibers and fiber fines, and membrane filtration, including reverse osmosis, nanofiltration, and ultrafiltration. Ultrafiltration, effective on particles down to 0.005–0.13 μm diameter, is being considered for the removal of flexographic inks from ONP deinking process water. Due to high energy, maintenance, and capital costs, ultrafiltration is not widely used in the paper industry at this time.

Stickies

Contamination from adhesives, called stickies by paper-makers because they adhere to paper machine felts and wires and cause operating problems and product quality defects, are a major problem during both the processing of recovered paper and paper-making operations. Stickies are the undesirable recovered paper components that originate from pitch, ink, plastic films, converting aids, coatings, and adhesives. Adhesives are either hot melts, commonly used in book-binding and case sealing, or pressure sensitives, used in labels and tapes.

Stickies have been classified based on their behavior and size. The reason for categorizing stickies is because methods for removing the different types are different, and the strategies for minimizing their impact on paper-making are different. The size-based classification divides stickies into the two groups macro and micro. Macro stickies are those which are separated when pulp is processed through a laboratory slotted screen (>100 μm), while micro stickies are those which are able to pass through the slots of the screen (<100 μm). Based on behavioral characteristics, stickies are divided into two classes, primary and secondary. Primary stickies result from the disintegration of adhesives during pulping and subsequent stock preparation. Secondary stickies are derived via a two-step sequence: (1) formation of soluble and/or colloidal materials during pulping, and (2) destabilization of the pulp suspension either by the addition of cationic polyelectrolytes, pH, and/or temperature shock, or other means which decrease solubility, causing soluble or colloid substances to precipitate.

Strategies to control stickies during the recycling process include: (1) selecting recovered paper with lower concentrations of stickies and monitoring quality; (2) keeping pulping conditions mild in order to minimize degradation of adhesives; and (3) use of slotted screens, flotation cells, and reverse cleaners to remove macro stickies. Methods used to control dispersed and colloidal stickies include pacification by the addition of talc, cationic polymers, enzymes, and dispersants. These substances affect the surface of stickies by binding to them or modifying the tackiness. Dispersed stickies may be removed from pulp during washing; however, effective clarification of washer filtrate is essential to prevent the build-up of stickies in the process water system.

US Postal Service initiated a project at Forest Products Laboratory, Madison, Wisconsin, with the goal of implementing recycled compatible pressure-sensitive adhesives to postage stamps. Many articles resulting from this project were presented at the TAPPI Recycling Symposium in 2002.

The Effect of Recycling on Paper Properties

The suitability of fibers for recycling is a function of the origins and past treatments to which the paper product has been subjected. The manner in which the wood was pulped, the paper-making process, the printing and converting method, the consumption and collection history, and the manner in which the paper will be recycled all affect the quality of the recycled fiber.

Refined chemical pulps behave differently from mechanical pulps upon recycling. When pressed and dried, the lumen and fibrils of chemical pulps collapse. During the rewetting in recycling, the degree of fiber swelling and fibrillation decreases due to a phenomenon referred to as hornification. Because the recycled chemical fibers are less flexible, physical properties that rely on bonding such as tensile, burst, and density decrease while tear and stiffness increase (**Figure 6**). The opposite effect is seen for recycled mechanical fibers which, due to the presence of lignin that minimizes the hornification in the fiber wall, become more flexible and may show small increases in tensile strength and density.

Several strategies are available for increasing the potential of recycled fibers for paper-making. Refining can be applied to improve fiber bonding through the reswelling of the fiber wall. However, refining recycled fibers tends to shorten the fiber length and produces fines that decrease the pulp's drainage rate. Cationic starch is added at the wet end of the paper machine to improve the bonding strength. Sodium hydroxide is used during repulping to promote fiber swelling which helps to reverse hornification. Through fractionating screens, two fiber fractions, one longer fiber and one shorter, are used in separate grades or in different plies of the same paper.

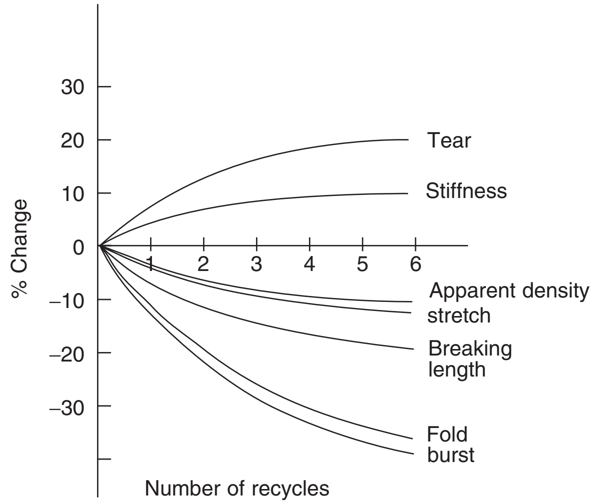


Figure 6 The general effect of recycling on the properties of paper made from refined chemical pulps. Reproduced with permission from McKee RC (1971) *Paper Trade Journal* 155(21): 34.

Summary

During the recycling process, fibers are separated from recovered paper and reused in the manufacture of new products. The practice of recycling paper is expected to grow as the worldwide demand for fiber increases. The percentage of recovered paper used worldwide in the production of paper and paperboard increased from 45.3% in 2000 to 45.9% in 2001.

Recycled fiber processing begins with pulping, during which the recovered paper is defibered. In subsequent steps, which include cleaning and screening, contaminants are removed. Depending upon the final product requirements, flotation and washing may be used to remove ink from the pulp. Bleaching is applied to remove color and increase the brightness of the fibers.

The use of recycled fibers in making paper and board poses an interesting challenge from the perspective of overall economics, removal of contaminants, and strength properties of the recycled product.

Acknowledgment

This chapter is an updated version of an original article published in *Encyclopedia of Materials:*

Science and Technology, vol. 7, 2001, pp. 6711–6720, 'Paper: Recycling and Recycled Materials,' Copyright (2001). Reprinted with permission from Elsevier Science.

See also: **Papermaking**: Overview; Paper Raw Materials and Technology; The History of Paper and Papermaking; World Paper Industry Overview. **Pulping**: Bleaching of Pulp; Chemical Pulping; Environmental Control; Mechanical Pulping.

Further Reading

Ala-Jaaski T and Kotila P (1998) Concept for gentle removal of impurities. In: *Proceedings of the TAPPI Recycling Symposium*, pp. 87–96. Atlanta, GA: TAPPI Press.

American Forest & Paper Association (AF&PA) (2002) *Recovered Paper Statistical Highlights*. Washington, DC: AF&PA.

Bennington CPJ (1998) Understanding defibering and ink detachment during repulping. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge vol. III Process Technology*, pp. 262–282. Appleton, WI: Doshi.

Biermann CJ and Kronis JD (1997) Bleaching chemistry: oxidation potentials of bleaching agents. *Progress in Paper Recycling* 6(3): 65–70.

Blanco A, Negro C, Monte C, Fuente H, and Tijero J (2002) Overview of two major deposit problems in recycling. In: Doshi MR (ed.) *Recent Developments in Paper Recycling – Stickies*, pp. 149–172. Appleton, WI: Doshi.

Bliss T (1994) Centrifugal cleaning in the stock preparation system. *Notes TAPPI Stock Preparation Short Course*, pp. 161–175. Atlanta, GA: TAPPI Press.

Bliss T (1997) *Stock Cleaning Technology.* Leatherhead, UK: Pira International.

Borchardt JK (1997) An introduction to deinking chemistry. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. II, Deinking and Bleaching*, pp. 18–30. Appleton, WI: Doshi.

Borchardt JK and Ferguson L (1998) Deinking chemistry. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 71–82. Appleton, WI: Doshi.

Brouillette F, Daneault C, and Dorris G (2001) Effect of initial repulping pH on the deflaking rate of recovered papers. *Proceedings of the PAPTAC 6th Research Forum on Recycling*, pp. 29–36. Montreal, Canada: PAPTAC.

Carré B, Brun J, and Galland G (1995) The incidence of the destabilisation of the pulp suspension on the deposition of secondary stickies. *Proceedings of CPPA 3rd Research Forum on Recycling*, pp. 187–197. Vancouver, Canada: Technical Section CPPA.

Cochaux A, Carré B, Vernac Y, and Galland G (1997) What is the difference between dispersion and kneading? In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. II, Deinking and Bleaching*, pp. 109–121. Appleton, WI: Doshi.

Doshi MR (1992) Maintaining quality while increasing the use of secondary fibers. *Progress in Paper Recycling* 1(2): 61–64.

Doshi MR (1997) What is the difference between primary and secondary stickies? *Progress in Paper Recycling* 7(1): 84–85.

Doshi MR (1998) Overview. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 1–16. Appleton, WI: Doshi.

Doshi MR and Dyer JM (2002) Overview. In: Doshi MR (ed.) *Recent Developments in Paper Recycling – Stickies*, pp. 1–54. Appleton, WI: Doshi.

Dyer JM (1998) Mill processes. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 189–194. Appleton, WI: Doshi.

Editorial (2002) *Pulp and Paper International* 44(7): 6.

Eriksson TP and McCool MA (1997) A review of flotation deinking cell technology. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. II, Deinking and Bleaching*, pp. 69–84. Appleton, WI: Doshi.

Fabry B, Carre B, and Cremon P (2001) Pulping optimisation: effect of pulping parameters on defibering, ink detachment and ink removal. In: *Proceedings of PAPTAC 6th Research Forum on Recycling*, pp. 37–44. Montreal, Canada: PAPTAC.

Fischer PC and Shaw G (2002) Operating results of a new Twindrum^{TM} pulping concept at SP Newsprint Co., Newberg, Oregon. In: *Proceedings of TAPPI Fall Technical Conference*. paper no. 23-1. Atlanta, GA: TAPPI Press.

Fitzhenry JW (2002) The critical nature of macrostickies quantification and the use of enzymes for control. In: Doshi MR (ed.) *Recent Developments in Paper Recycling – Stickies*, pp. 178–181. Appleton, WI: Doshi.

Galland G, Carre B, Cochaux A, Vernac Y, and Julien Saint Amand F (1998) Dispersion and kneading. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 131–149. Appleton, WI: Doshi.

Gilkey M (1998) Washing of secondary fibers. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 115–130. Appleton, WI: Doshi.

Hanchett GD (1994) Bleaching and color-stripping recycled fibers: an overview. *Progress in Paper Recycling* 3(2): 24–31.

Howard RC (1995) The effects of recycling on pulp quality. In: McKinney RW (ed.) *Technology of Paper Recycling*, pp. 180–203. Glasgow, UK: Chapman & Hall.

Hsu N and Pandolfo J (1998) Process water clarification. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 166–271. Appleton, WI: Doshi.

Julien Saint Amand F (1998) Principles and technology of cleaning. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 42–70. Appleton, WI: Doshi.

Julien Saint Amand F (2002) Optimization of stickies removal in screens and cleaners. In: Doshi MR (ed.)

Recent Developments in Paper Recycling – Stickies, pp. 78–125. Appleton, WI: Doshi.
Kankaanpaa V (2002) Fundamental pulping research with pilot drum pulper. In: *Proceedings of TAPPI Fall Technical Conference*, paper no. 23-3. Atlanta, GA: TAPPI Press.
Klungness JH, Sykes MS, Abubakr S, and Tan F (1996) Upgrading recovered paper with enzyme pretreatment and pressurized peroxide bleaching. *Progress in Paper Recycling* 5(4): 39–45.
Kotila PS and Estes TK (1994) Closed mill systems and implications for process water reuse. *Progress in Paper Recycling* 3(4): 42–46.
Lachenal D (1994) Bleaching of secondary fibers – basic principles. *Progress in Paper Recycling* 4(1): 37–43.
Lunabba P, Granfeldt T, Grundstrom P, and Lary E (1997) Top quality deinked pulp from mixed office waste by high temperature peroxide bleaching. *Proceedings of CPPA 4th Research Forum on Recycling*, pp. 207–213. Montreal, Canada: PAPTAC.
McCool MA and Rosier MA (1998) Screening technology in recycled fiber systems. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 29–41. Appleton, WI: Doshi.
McKinney RW (1995) Manufacture of packaging grades from wastepaper. In: McKinney RW (ed.) *Technology of Paper Recycling*. Glasgow, UK: Chapman & Hall.
McKinney RW (1998) Flotation deinking review. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge,* vol. III, *Process Technology.* Appleton, WI: Doshi.
Meltzer F (1998) Fractionation: basics, development and application. *Progress in Paper Recycling* 7(3): 60–66.
Rangamannar G and Sharpe PE (1998) Recycled fiber bleaching processes overview. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge,* vol. II, *Deinking and Bleaching*. Appleton, WI: Doshi.
Ruzinsky F and Bennington CPJ (2001) The attachment force of ink to paper in paper recycling operations. *Proceedings of PAPTAC 6th Research Forum on Recycling*, pp. 19–27. Montreal, Canada: PAPTAC.
Scholz B (1994) Pressure sensitive adhesives. *Progress in Paper Recycling* 4(1): 71–73.
Silveri L and Wagner MM (1998) The pulper/detrasher module in the recycle system. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 17–28. Appleton, WI: Doshi.
Spielbauer JL (1998) Recycling systems overview. In: Doshi MR and Dyer JM (eds) *Paper Recycling Challenge, vol. III, Process Technology*, pp. 180–188. Appleton, WI: Doshi.
TAPPI (2000) *Proceedings of Recycling Symposium*. Atlanta, GA: TAPPI Press.
Upton BH, Krishnagopalan GA, and Abubakr S (1997) Deinking flexographic newsprint: using ultrafiltration to close the water loop. *Tappi Journal* 80(2): 155–164.
Weinstock IA (1993) Use of the term “bleaching” in the context of virgin and secondary fibers: a clarification. *Progress in Paper Recycling* 3(1): 89–91.
Woodward T (1996) The behavior of recycled pulps during papermaking. In: *Proceedings of Wastepaper VII Conference*, paper 45. San Francisco, CA: Miller Freeman.
Yordan JL, Biza P, and Williams G (2002) Talc for contaminant control in recycled fiber. In: Doshi MR (ed.) *Recent Developments in Paper Recycling – Stickies*, pp. 173–177. Appleton, WI: Doshi.

Related Literature

Abubakr S (ed.) (1997) *Recycling: Anthology of Published Papers*. Atlanta, GA: TAPPI Press.
Doshi MR (ed.) (1994) *Recycled Paper Technology: An Anthology of Published Papers*. Atlanta, GA: TAPPI Press.
Doshi MR (ed.) (2002) *Recent Developments in Paper Recycling – Stickies*. Appleton, WI: Doshi.
Doshi MR and Dyer JM (eds) (1997) *Paper Recycling Challenge,* vol. I, *Stickies*. Appleton, WI: Doshi.
Doshi MR and Dyer JM (eds) (1997) *Paper Recycling Challenge,* vol. II, *Deinking and Bleaching*. Appleton, WI: Doshi.
Doshi MR and Dyer JM (eds) (1998) *Paper Recycling Challenge,* vol. III, *Process Technology.* Appleton, WI: Doshi.
Doshi MR and Dyer JM (eds) (1999) *Paper Recycling Challenge,* vol. IV, *Process Control and Mensuration.* Appleton, WI: Doshi.
Seifert P and Gilkey M (1996) *Deinking*. Leatherhead, UK: Pira International.
Spangenberg RA (ed.) (1993) *Secondary Fiber Processing.* Atlanta GA: TAPPI Press.

Printing

P D Fleming, III, Western Michigan University, Kalamazoo, MI, USA

Introduction

Printing has been called the single most significant technical development of human history. Prior to the invention of printing, virtually all communication was verbal. It was difficult to communicate to a large number of people. Printing provided the ability to record ideas in a manner that can be passed through generations. Paper is still the most utilized substrate for printing.

As early as 35 000 BC, people were drawing messages on cave walls. Pictographs were used to represent real objects. Pictographs evolved to ideographs, which were developed by the Phoenicians. By 900 BC, the Phoenicians had also assigned sounds to the symbols.

The Greeks adopted and expanded the Phonetic system. The Romans borrowed 13 Greek letters, revised eight, and added two more in order to write in Latin. Three additional letters were added later for a total of 26, as we know the Roman alphabet today.

Printing Processes

All printing processes produce lines and/or dots to form an image. Printing has made possible the production of multiple copies of graphic images. There are five types of processes, which can be used for graphic reproduction. They are all used to print on paper as well as other substrates. These processes are:

1. Relief printing
2. Intaglio printing
3. Screen printing
4. Lithographic printing
5. Nonimpact printing

Relief Printing

Relief printing was the basis for the original printing press, as invented by Johann Gutenberg. This is based on raised letter type (**Figure 1**). Gutenberg's characters were molded out of lead, a metal, which was used until only recently. This process came to be known as Letterpress and was the basis for all newspaper printing until only recently.

The letterpress process is still used today for die cutting, numbering, perforation, scoring, hot-foil stamping, and embossing. Letterpress inks are relatively high in viscosity to assure its even distribution as it passes through the multiple rolls (**Figure 2**) of the inking system. To distribute the ink better, some or all of the rolls oscillate.

Letterpress has evolved into flexography (flexo), which uses a flexible plate, which contains a raised image area of a cured photopolymer. The plate is wrapped around a cylinder and is used to put ink on the substrate. A typical flexo print station is illustrated in **Figure 3**.

Flexo is the fastest-growing conventional printing process, especially in packaging, such as corrugated containers and flexible films. It has also made significant advances in publication printing, particularly newspapers. Because the quality of flexo printing has improved so much, it is now used extensively for process color printing, as well as spot color, on a wide variety of substrates. It is used extensively for printing tags and labels, many in full process color.

Flexography was originally called 'aniline' printing because of the aniline dye inks originally used in the process. These were made from coal tar and were banned from food packaging by the Food and Drug

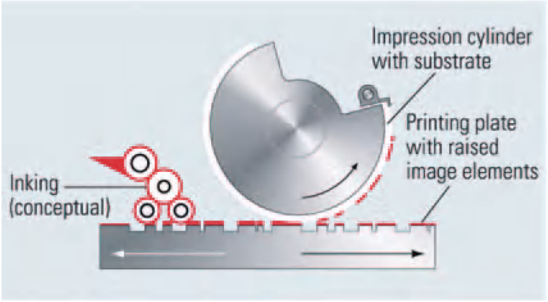


Figure 1 Illustration of raised image as used in relief printing. Source: © H. Kipphan, *Handbook of Print Media*, Springer 2001.

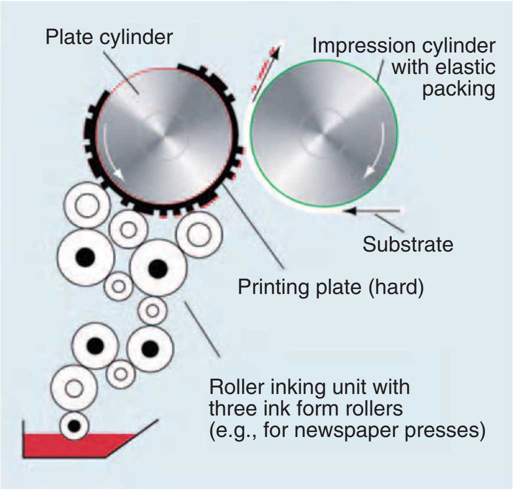


Figure 2 Illustration of multiple rollers used for letterpress printing. Source: © H. Kipphan, *Handbook of Print Media*, Springer 2001.

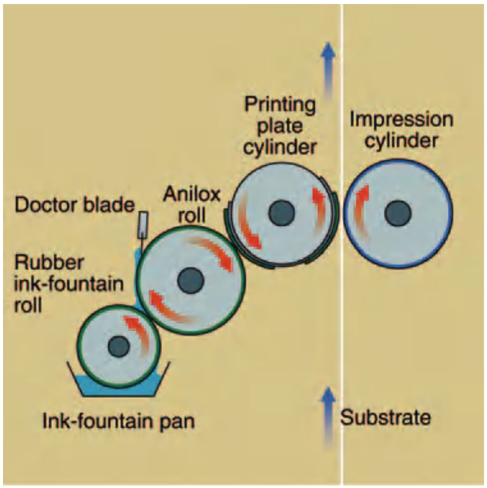


Figure 3 Typical arrangement of rollers for flexographic printing. Courtesy of the Flexographic Technical Association.

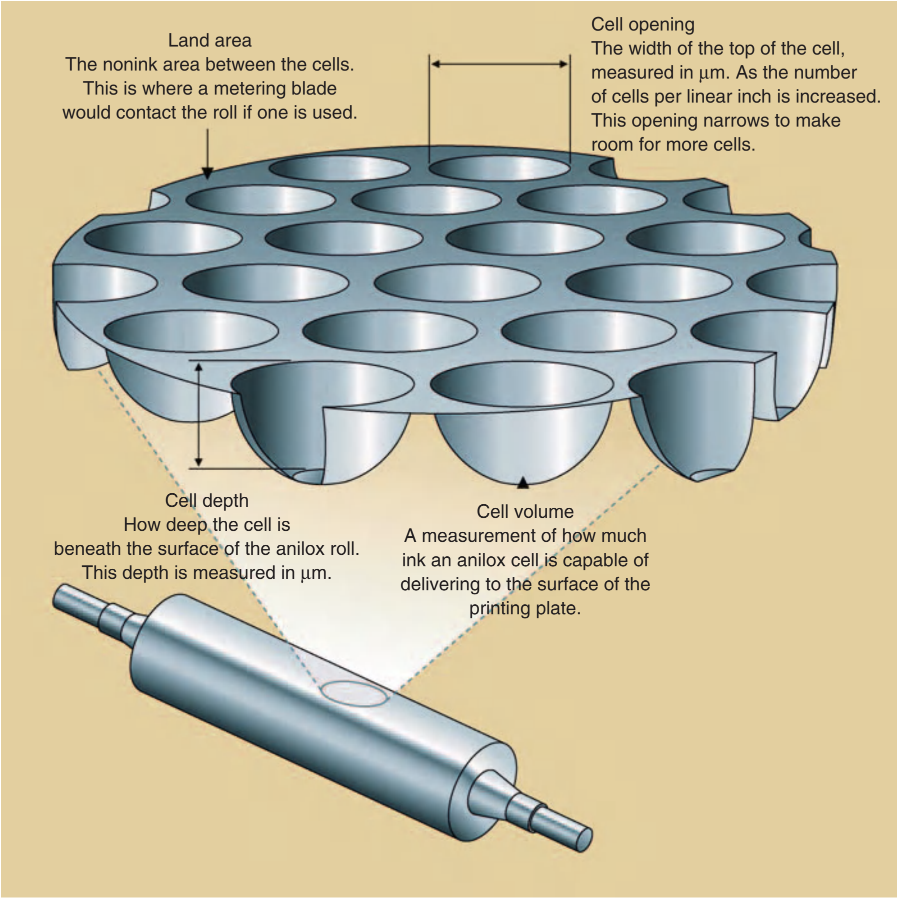


Figure 4 Cells in anilox roll. Courtesy of the Flexographic Technical Association.

Administration because of their toxicity. Other coloring agents were developed that were safer, but the name aniline printing persisted. Because the name carried bad connotations, the name was changed to flexography in 1951.

Flexo plates are flexible and imaged in relief, a natural outgrowth of letterpress printing. The origin of these plates was in rubber stamps, which were formed in Bakelite molds that had been pressed with lead type. Thus, the original plates for aniline printing were made of molded rubber.

The first aniline press was built in 1890 by Bibby, Baron and Sons in Liverpool, UK. It used water-based dye inks, which were not chemically bleed-proof. In 1905 C.A. Holweg built an aniline press as a tail-end unit on a bag machine and patented it in 1908. The ink metering on these presses was crude until 1938, when the anilox roll was introduced. This employed a mechanically engraved copper-coated roll with controlled cell sizes (**Figure 4**). The idea grew out of gravure printers laying down coating from a uniform cell-engraved roll. The anilox uses this process to coat the raised surfaces on the plate.

Anilox rolls are coated with chrome to prevent corrosion and wear. The original aniline inks gave way to ones based on polyamide resins. These stable, fast-drying inks enabled web speeds to increase from 45–230 $\mathrm{m\,min^{-1}}$.

The 1980 Clean Air Act led to more extensive use of water-based inks in flexo. Water-based inks are now used extensively for printing on paper-based substrates. The quality is now approaching that of lithography and is even impinging on gravure.

Intaglio Printing

Intaglio (engraved or cut in) printing is the reverse of relief printing. As used in commercial printing, it is called gravure or rotogravure. The process utilizes an engraved image consisting of a series of recessed cells, which hold a liquid ink. The ink is transferred to the substrate from these cells with an image based on the cell pattern. A gravure press generally employs a rotating metal cylinder consisting of these cells, and hence the roto in rotogravure. A typical gravure print station is illustrated in **Figure 5**.

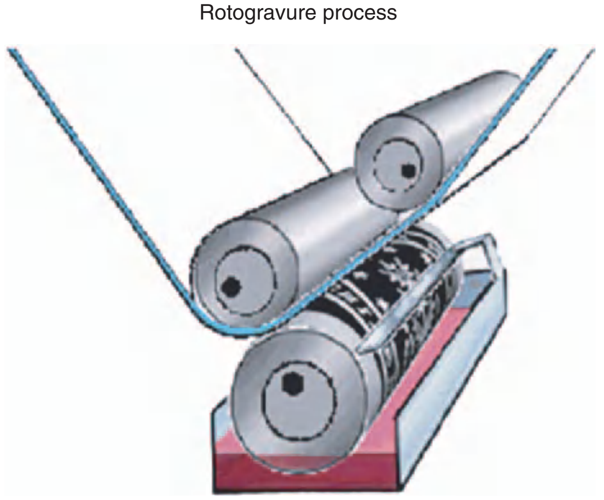


Figure 5 A rotogravure printing unit.

Rotogravure printing has a significant advantage relative to other printing processes for medium to long runs. Gravure can produce very-high-quality multicolor printing on a variety of substrates. Its success results from the simplicity of the process. Having fewer variables to control ensures consistent print quality throughout a run. Each print unit has four basic components: an engraved cylinder, the ink fountain, the doctor blade, and the impression roller.

The origins of gravure printing were with the creative artists of the Italian Renaissance in the 1300s. Fine engravings and etchings were cut by hand into soft copper.

Considerable force or pressure is needed to press the entire surface of paper against an image carrier evenly. Early presses were made entirely of wood. Thus, it was possible to print only small images without cracking. The first metal intaglio plate was used for printing in Germany in 1446, about the same time as Gutenberg. Unfortunately, the intaglio process was not compatible with Gutenberg's letterpress, so it was not adopted by early printers. The first metal printing press was built in 1550. This allowed larger sheets, but was still difficult to operate.

The modern gravure printing press resulted from the invention of photography and the adoption of rotary printing from cylinders. Auguste Godchaux received a patent for a reel-fed rotary gravure perfector press in 1860. This press was still in use in 1940! The process was refined by the German Karl Klic (Klietsch) and Samuel Fawcett. They did not have patents on their process, so they tried to keep the process secret. They sold prints from their press as 'heliogravure' prints, even though they were really rotogravure, as we know it today. Their process remained a trade secret, until an employee emigrated to the USA and made it public.

The process continued to improve and gravure presses were used to print Jell-O cartons, starting in 1938. Engraving continued to improve with electromechanical engravers being introduced in 1968, with digital controls added in 1983.

Screen Printing

This process transfers an image by allowing ink to pass through openings in a stencil that has been applied to a screen mesh. The process is often called silk screen printing, because silk was originally used to make the screens. Silk is not used industrially any more. Screen printing is commonly used to print on textiles.

Screen printing has two characteristics that make it distinctive from other forms of printing.

1. Versatility – screen printing can be adapted to print on almost any shape or object. It has been called 'the print-anything' process.
2. Variable ink thickness – screen printing can vary the ink film deposit from 25 to 130 μm.

This is the widest range of ink deposit of all the forms of printing.

The origins of screen printing are unknown. Evidence dates the process back to the Orient with links to China and to ancient Egypt. They used a simple open-stencil process. The stencil was pressed against the substrate surface. To hold the stencil in place, they brushed or painted the natural pigmented color on to the object.

Using this simple open-stencil process the Japanese devised a way to hold small stencil areas in place. A long piece of hair or silk thread was used to 'glue' an open spot on the stencil. This stencil process was also used to adorn fine silk fabric. Hence, the term 'silk screen' came into use.

In the 1830s silk was woven into a mesh and used for sifting purposes in the flour-milling industry. It was not until about 1870 that silk was used for 'silk screen' printing in Germany, France, and England. In 1907, John Pilsworth, an American, started using the screen method to make banners and short-run signs.

The basic concept of screen printing is based on a stencil. A stencil must be open or permeable in the image area and impermeable in the nonimage area. It is well suited for low-cost production of high-quality, short-run printed materials. It is versatile, capable of printing on nearly any surface, texture, or shape. The process is limited only by the size of the screen frame. Very high ink densities can be obtained.

Lithography

This process is based on a process discovered by Alois Senfelder in 1789. It literally means 'stone writing,' because it was originally based on images created on limestone plates. The plates are neither raised nor recessed and the process is often referred to as planographic.

Lithographic printing is based on wettability of different areas of the plate. The image area is oil (ink)-wet and the nonimage area is water-wet. The process makes use of the nonmixing of the oily ink and water (actually aqueous fountain solution). Lithography is the most chemical of the printing processes and Senfelder preferred the designation 'chemical printing.'

Because the transfer was made directly to the substrate, it was necessary to generate a mirror image on the plate. This was changed by the invention of the offset press, attributed to Ira Rubel in 1904. In this process, a set of three rotating cylinders is used and the image is first transferred from the plate (on a plate cylinder) to a rubber blanket (on a blanket cylinder) from which it transfers (offsets) to the substrate. A schematic of the cylinder arrangement of an offset press is shown in **Figure 6**.

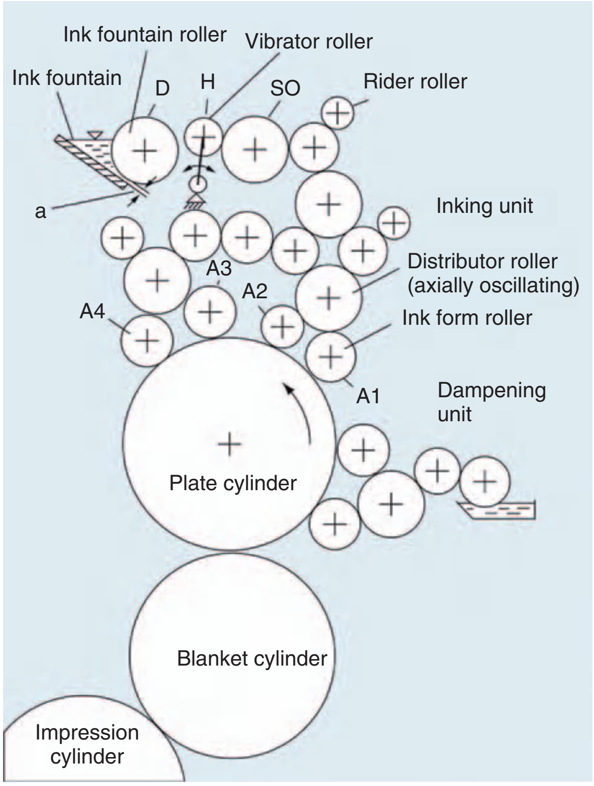


Figure 6 Complicated roller arrangement of an offset lithographic press.

On this we see the master, or plate, cylinder, the blanket cylinder, and the impression cylinder. The substrate passes between the blanket cylinder and the impression cylinder. The other rollers are part of the inking and dampening systems.

The advent of the offset press did not change the basic printing process; the image area needs to be oleophilic (oil-liking) or hydrophobic (water-hating), while the nonimage area must be hydrophilic (water-liking) or oleophobic (oil-hating).

Originally, when stone lithography was employed, letterpress was good for text, but poor for images, while lithography was good for images but poor for text. Books were often printed by a combination of the methods.

Stone lithography was primarily a picture-printing process. This changed and the printing industry was revolutionized by the advent of photography. It created demand for a totally new kind of printed picture. It became possible to combine pictures, including photographs, with text, on a single printing plate.

The relationship between lithography and photography was very strong from the beginning. Joseph Nicephore Niepce, a pioneer in photography, experimented with lithography. Lithography was the first printing process to make its whole plate, graphics and text together, photographically and photomechanically.

Nonimpact Printing

All of the conventional printing processes are impact methods. The plate and/or image carrier comes in direct contact with the substrate. Nonimpact printing refers to series of computer-driven devices that have evolved in a revolutionary fashion over the past 15–20 years. The developments in these devices have followed the dramatic improvement price and performance in desktop computers and the rapid reduction in cost of microelectronic devices. Because of the association with digital computers, nonimpact printing is often referred to as digital printing. These printing devices include laser printers, ink-jet printers, dye sublimation printers, thermal transfer printers, and others.

Because all these devices print directly from digital files, it is just as easy to print a single copy as many. This has made possible on-demand and variable data printing. Some concepts of on-demand ('I want it now') printing can be applied to conventional printing, but they are most appropriate for digital printing. A more rigorous difference between nonimpact printing devices and conventional presses is that nonimpact devices do not have 'permanent image carriers' (e.g., plates). On-demand printing provides many opportunities for printers and publishers to expand their capabilities.

On-demand printing is defined as short-notice, quick turnaround of short, economical print runs. When used efficiently, this can result in lower inventory costs, less risk of obsolescence, lower production costs, and reduced distribution costs.

This definition is not satisfied by traditional printing, where 31% of output is discarded before obsolescence. This includes 11% of all publications, 41% of promotional literature, and 35% of other material. Approximately one-third of magazines displayed on a newsstand are discarded.

Digital printing is defined as any printing completed via digital files. This includes all types of devices, from desktop printers to wide-format printers and digital 'presses.' These generally employ nonimpact printing processes as opposed to conventional impact printing. Digital printing also includes some of the devices used to make plates for conventional printing.

Variable printing is printing capable of incorporating data from a database to generate a short- to medium-length run of different but related pages. A traditional press may perform on-demand printing, but not variable printing.

Shorter runs comprise an increasing share of the total printing market. Short runs are usually defined as less than 5000 copies. Fifty-six percent of commercial, book, and office printing is between 500 and 5000 copies.

Digital color printing is the fastest-growing sector of printing, because of its suitability for short-run and variable printing. Unlike conventional printing devices, digital printers are falling in price and improving in performance.

Digital color printing currently supports the following:

1. Just-in-time production – printed items often have an unpredictable demand. With shorter runs, a purchaser can buy smaller lots more frequently.
2. Individual or variable output – it is just as easy to print every copy differently as the same. An advertiser can tailor a communication to different readers.
3. In-house production – simple color document production can be accomplished through in-house reprographics, as devices get cheaper and better.
4. Distributed information – reference items such as encyclopedias, manuals, and catalogs are now distributed more efficiently in electronic forms. High-quality digital printers at business locations allow use of the distribute-and-print model, rather than the traditional print-and-distribute model that has been in use since Gutenberg.
5. Visualization and prototyping – it is easy to produce single copies or short runs to test and approve visual concepts. The customer can view a printed copy on a local printer or soft-proof it on a monitor.
6. Compilation and offprints – if journal or magazine articles are stored in a digital database, then individual articles (or even bound custom collections) can be printed and distributed (or distributed and printed) easily.
7. Short-run printing – reports, manuals, posters, and specialty books can be produced with on-demand digital printing.

All digital printing systems have three basic components:

1. raster image processor (RIP) – converts image into device-specific bitmap.
2. A buffer to store rasterized data for printing.
3. A marking engine, which forms the image on the substrate.

Some of the marking engines are reviewed here.

Laser (or electrophotographic) printers use the same imaging method as office copiers. Indeed, modern color copiers have a direct computer and/or network interface, so they can be printed using the appropriate printer driver. A color copier is really a color laser printer with a built-in scanner. These devices can be versatile and may sustain high throughputs. The printing process is also known as xerography (literally, 'dry' writing) and has formed the basis for the success of the Xerox Company.

Electrophotographic printing also includes high-speed digital presses from Xeikon (now Punch) and Indigo (now Hewlett Packard). The Xeikon uses fixed light-emitting diodes (LEDs) instead of lasers, while the Indigo uses liquid toners. The process is illustrated in **Figure 7**, where a charged photoconducting drum is selectively discharged by the laser or LED. The drum is toned by charged pigment particles and the image is transferred and fused to the substrate with heat and pressure.

Inkjet printers use tiny nozzles to spray ink precisely on to the substrate. There are two broad classes of inkjet printers: continuous and drop-on-demand.

For continuous ink-jet printing, a thin stream of liquid is ejected from a container through a tiny orifice and is broken up into a steady stream of uniform droplets when subjected to a high-frequency vibration. After being electrically charged, the drops

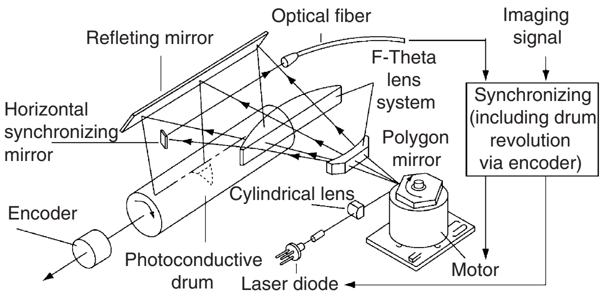


Figure 7 Mechanism of a laser or electrophotographic printer.

can be placed by an electrostatic deflector. Undeflected drops are recirculated. The Scitex 3600 digital press can print at 305 m min^{-1} in monochrome.

For drop-on-demand ink-jet printing, ink droplets are expelled from tiny orifices and directed immediately to the substrate. Most commonly, these devices use heat to vaporize a small amount of water-based ink in a chamber to form a gas bubble (bubble-jet). An illustration of the bubble jet process is shown in **Figure 8**.

The piezo drop-on-demand printer uses pressure pulses instead of heat to expel ink drops. The pressure pulses are generated by precisely charging a piezoelectric crystal. These are offered for desktop applications by Epson. An illustration of the piezo drop-on-demand process is shown in **Figure 9**.

Drop-on-demand inkjets are available in multiple formats, from letter size to 1.83 m-wide web. The wide-format versions can be used to proof imposition.

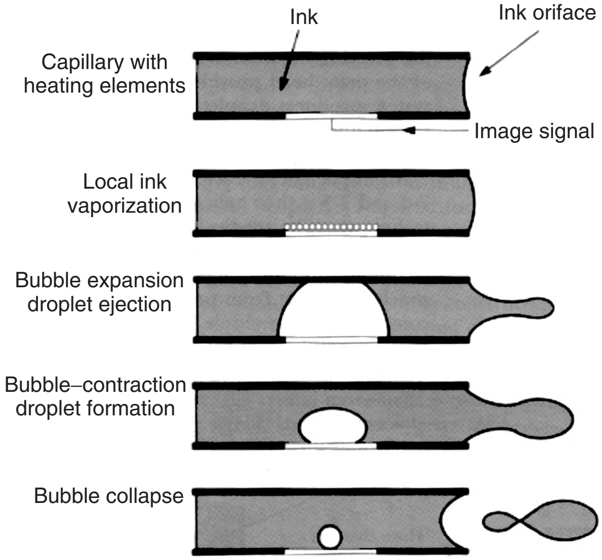


Figure 8 Illustration of thermal ink jet process.

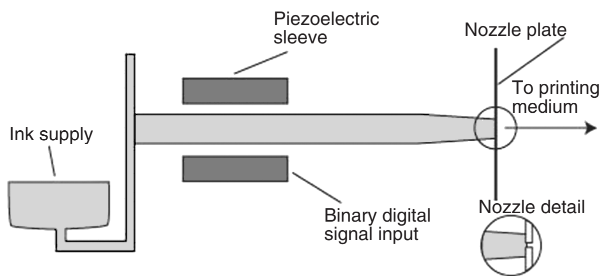


Figure 9 Illustration of piezo ink jet process.

The Printing Industry

Depending on the measure, the printing industry is between the fourth and seventh largest manufacturing industry in the world. Printing companies range from very large Fortune 500 organizations to small corner print shops. Because of the large number of small print shops and the large number of printing plants owned by the large companies, there are more printing manufacturing sites than for any other industry.

Types of Printers

Because of the diversity of the customer base, there are many different types of printing establishments. These are:

1. Commercial: commercial printers can vary greatly in size and can take on a wide variety of printing jobs. Their jobs can range from business cards to glossy color brochures.
2. Trade shops: trade shops provide services to the printing trade. They perform printing and finishing functions for printers who do not have all of the equipment for the job.
3. Special-purpose: special-purpose printing involves a limited type of job such as labels or forms.
4. Quick printing: quick printing includes copy centers such as Kinko's. These shops now employ direct digital printing devices as well as photocopying equipment. Many of these also still have small offset presses for larger numbers of copies.
5. In-plant: in-plant printing consists of any company which has its own print shop on site that performs printing functions for the organization.
6. Publishing: publishing involves printing of books, magazines, and newspapers. These usually employ very-high-speed web-fed printing presses.
7. Packaging: package printing involves printing on boxes, cans, and plastic films and foils.

There are also several related industries that provide services and materials to the printing industry. Related industries consist of ink companies and paper companies, along with film and plate material suppliers. Also included are the press and peripheral manufacturers.

Printing Inks

Printing inks are complicated mixtures of chemical compounds. The composition of printing inks varies by the printing process, by whether printing is sheet-fed or web-fed, and by the target substrate. The composition varies by the solvent base, be it oil or water. It varies by drying mechanism and by whether the drying is by primarily chemical, e.g., oxidation polymerization, ultraviolet cure, or physical processes, e.g., evaporation, absorption.

Inks are divided into liquid and paste inks. Gravure, flexo, inkjet, electrographic, and some electrophotographic inks (or toners) are liquid inks. Lithographic, screen, and letterpress inks are paste inks. The distinction between liquid and paste inks can be an arbitrary one, since it is based on apparent viscosity.

A printing ink consists of vehicle and pigment. Vehicle is all in the ink except the pigment. 'Varnish' is often used interchangeably with vehicle, but actually vehicle consists of varnish plus performance additives and solvent/diluent. As suggested by the name, the vehicle transports the pigment to the substrate. Varnishes must be chosen to wet the pigment. It they don't, suspension is virtually impossible and the ink will not have the desired rheological (flow) properties.

Pigments

Most pigments are used for all of the printing processes. Pigments are classified as carbon black, organic, white inorganic, and colored inorganic.

Carbon black is the major ingredient in black inks. Chemically it is mostly carbon, with small amounts of mineral matter and some volatile materials of the form C_xO_y. The typical particle size is 20–30 nm (10^{-9} m), the smallest of the pigments. Note that these may be truly nanoparticles. The smallest particles might be individual 'bucky balls' (single polymer molecules of carbon, possibly with other atoms encapsulated or bonded, e.g., C_{60}).

The C_xO_y improves the flow properties and serves as a natural wetting and dispersing agent. The amount of carbon varies between 90 and 99%, depending on the method of manufacture.

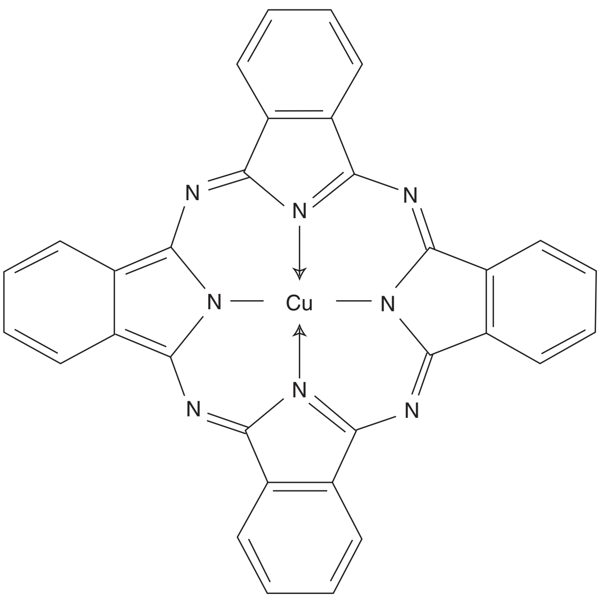
Organic pigments are used for process (photographic) color printing because they form transparent films. Most of these are derivatives of the aromatic hydrocarbons, benzene, naphthalene, or anthracene. The pigment molecules generally contain chromophoric groups such as $=C=NH$, $-CH=N-$, and $-N=N-$. The electrons in the double bonds selectively absorb some visible wavelengths and change energy levels. The color results from the wavelengths not absorbed. This is the subtractive color theory of colored objects.

The electrons in the chromophores are generally coupled to those in the conjugated aromatic rings. Dyes are soluble in the vehicle, while pigments are generally suspended in the vehicle. Pigments are preferred to prevent bleeding and fading. Dyes can be converted to pigments by reacting with phosphomolybdic and/or phosphotungstic acid.

Azo pigments, which have the $-N=N-$ group, include diarylide yellow, lithol rubine, red lake C, toluidine red, Hansa yellow, DNA orange, and napthol red. Phthalocyanine pigments are restricted to the blue and green regions of the spectrum. The phthalocyanine structure is given in **Figure 10**. Other pigments include pigment yellow 13, quinacridone magenta pigment, and pigment red 57, which are given in **Figures 11–13**.

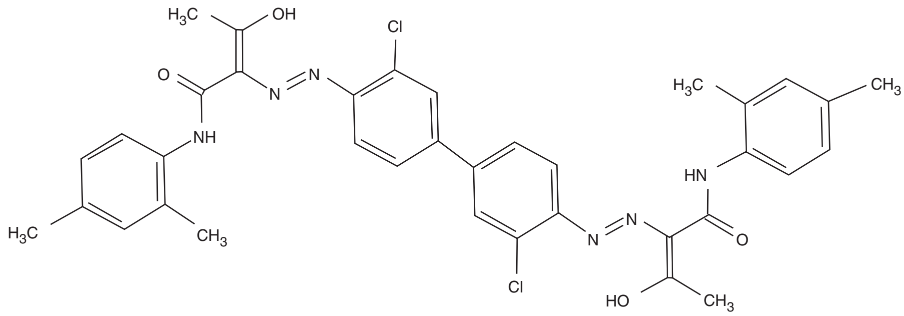
White inorganic pigments include titanium dioxide (TiO_2), calcium carbonate ($CaCO_3$), and clay. (There are no white organic pigments.) The clay used is a hexagonal plate-like form of aluminosilicate called kaolin. It has low opacity and is used as an extender for letterpress and screen inks. Barium sulfate and fumed silica are also sometimes used as extenders in inks. These white pigments are all also used to whiten paper.

Colored inorganic pigments are mostly the iron blues, which are based on ferric ferrocyanide. These are formed by oxidizing ferrous ferrocyanide with a strong oxidizing agent such as sodium dichromate or sodium chlorate. Different shades of blue are



Pigment Blue 15

Figure 10 Structure of phthalocyanine (pigment blue 15).



Pigment Yellow 13

Figure 11 Structure of pigment yellow 13.

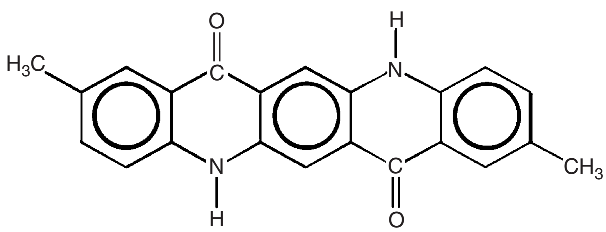
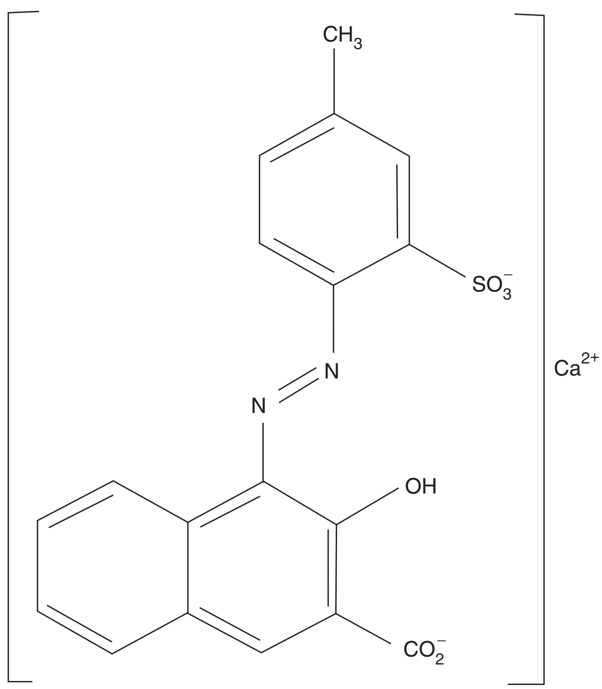


Figure 12 Structure of quinacridone magenta pigment.



Pigment Red 57:1

Figure 13 Structure of pigment red 57.

obtained by varying the pH, temperature, and time of heating during oxidation. These were used by printers for all printing inks through the mid nineteenth century, before the discovery of synthetic organic dyes.

See also: **Papermaking**: Paper Grades; The History of Paper and Papermaking; World Paper Industry Overview.

Further Reading

Adams JM and Dolin PA (2002) *Printing Technology*. Clifton Park, NY: Delmar.
DeJidas LP and Destree TM (1999) *Sheetfed Offset Press Operating*. Pittsburgh: GATF Press.
Dennis EA, Odesina O, and Wilson DG (1997) *Lithographic Technology*. Albany, NY: Delmar.
Eldred NR and Scarlett T (2001) *What the Printer Should Know about Ink*. Pittsburgh: GATF Press.
FFTA (1999) *Flexography: Principles and Practices*, 5th edn. Ronkonkoma, NY: FTA/FFTA.
Gray T (ed.) (2003) *Gravure Process and Technology*. Rochester, NY: GEF/GAA.
Kipphan H (ed.) (2001) *Handbook of Print Media*. Berlin, Germany: Springer-Verlag.
Levy U and Biscoe G (1998) *Nonimpact Electronic Printing*. Charlottesville, VA: Interquest.
Thompson B (1998) *Printing Materials*. Leatherhead, UK: PIRA.
Wilson LA (1998) *What the Printer Should know about Paper*. Pittsburgh: GATF Press.

Packaging Grades

G J F Ring, University of Wisconsin–Stevens Point, Stevens Point, WI, USA

Introduction

Nasiri Khosrau of Persia (now Iran) recorded the first use of paper as a packaging material in 1035 AD when he observed vendors in Cairo (Egypt) wrapping vegetables, spices, and dry goods in paper. Today, paper continues to be an important material used to transport, distribute, and market virtually every commodity and manufactured item. Paper competes very successfully with metals, glass, plastics, wood, and textiles, because it has many desirable properties including being biodegradable, recyclable, and renewable. Paper functions in many diverse packaging applications from heavyweight shipping containers to lightweight wrapping papers. This article will concentrate on lightweight specialty papers such as retail paper bags, food wrapping, gift wrapping, spiral-wound paper tubes, label stock, and other specialty items. The cut sheet size for wrapping papers is 24 in. by 36 in., giving a total ream area of 3000 ft^2. Types of paper used to manufacture boxes and containers are discussed elsewhere (*see* **Papermaking**: Paperboard Grades).

Retail Paper Bags

Retail bags are closed-bottom, flexible-walled containers that are capable of carrying many types of dry goods within them. Paper bags are manufactured from kraft paper due to the requirement for high strength. The paper may be bleached or unbleached depending upon the use. The grammage range for lightweight bags is 40–60 $g\,m^{-2}$. For heavier weight bags such as grocery bags that are required to carry as much as 12 kg the grammage range extends to 110 $g\,m^{-2}$.

Historically, bags were fabricated from textiles or animal skins with sewn bottoms. During the early nineteenth century, powdered goods such as flour or medicines were sold in hand-rolled paper sacks called 'pokes.' These early paper bags were actually inverted cones that required only folding to close the bottom. By 1877, paper bags were produced by machines that cut, folded, and either glued or sewed the sides from rolls of paper. Today, paper bags come in four basic shapes: flat, square, satchel-bottom, and self-opening.

Flat paper bags are made from kraft paper that has been glued with a starch-based adhesive to form a tube with its bottom folded and glued. This type of bag is commonly used for candy, greeting cards and many retail items that are small and lightweight. The square-bottom bag is similar to the flat bag except that the paper tube is first folded inwards along the sides to form an expanding gusset before the bottom is folded. When the square bag is opened or filled, the bag has a square or rectangular cross section. In this manner, the square bag can hold thicker and heavier items such as books and newspapers. The satchel-bottom bag also forms a square shape when opened but the bottom is folded into triangles and glued together to form a block bottom that is ideal for packaging flour, rice, sugar, and other dry food items. The satchel-bottom bags, when filled, can stand upright. Finally, self-opening bags have gussets to form square bags and specially folded bottoms that form flat-bottom squares or rectangles. These bags are folded flat but are designed to open with a snap of the wrist and stand by themselves for filling. Grocery bags and sandwich lunch bags are examples of self-opening bags.

Wet strength is an important paper additive for retail bags. Grocery bags in particular must be able to maintain a substantial portion of their strength when brought into contact with wet food and other products.

Multiwall Paper Sacks

Multiwall paper sacks are designed to be exceptionally strong and carry heavy and bulky materials for the building, food, and chemical industries. In essence, multiwall sacks are two or more separate sacks nested together to form a stronger and tougher sack. Five or six total plies of paper (60–110 $g\,m^{-2}$) may be necessary. For paper sacks, kraft paper is used; however, stretch and porosity as well as strength are critical performance criteria.

Stretch or extensibility is important because multiwall sacks are required to withstand numerous impacts during shipping and warehousing without rupturing and spilling their contents. Sack paper's ability to absorb shock during impact is measured by tensile energy absorption (TEA), which is a paper property that combines both strength and stretch. TEA can be thought of as a measure of 'work to burst.' Special extensible sack paper that has been produced through the 'clupak' process greatly enhances TEA and permits the use of lower grammage ranges (50–100 $g\,m^{-2}$) thus saving about 20% fiber by weight. The clupak process, invented by Sanford Cluett, produces extensible paper that is difficult to tear by passing wet paper through a steel and rubber nip that causes fiber crimping in the machine direction. Additional extensibility in the machine direction is produced on the paper machine through using slack draws in the dryer section. Slack draws prevent the sheet from developing dried-in drains leading to limited stretch.

Porosity is important for multiwall paper sacks because air needs to escape through the wall of the bag to permit rapid filling. Sack filling machines are able to fill a 25–50 kg sack in 1 second at temperatures that can exceed 100°C. Sewn-bottom and pasted bottom open-mouthed sacks are used for low pressure gravity-filling systems. Valve sacks are required when materials must be filled under pressure.

Multilayer sacks may be constructed with plastic liners to prevent moisture contamination. Plastic linings are important for foods and chemicals where the ingredients have to maintain a certain moisture level. Wet-strength resins are also used to control moisture penetration through the paper.

Food Wrapping Paper

Paper intended for the wrapping and serving of food must be manufactured from ingredients that do not adulterate food. This requirement necessitates the use of virgin chemically processed pulps along with paper additives and coatings that are recognized as safe to human consumption. These papers must have some form of wet strength and grease resistance as well as have reasonable printing properties. The basis weight range for food wrapping paper is 28–65 $g\,m^{-2}$. General categories of food wrapping paper include: greaseproof, metallized, and foil-backed papers. Special fruit wrapping papers impregnated with preservatives can also be found.

Greaseproof papers are papers that resist the penetration of grease and oils, and are also called moisture resistant papers. Vegetable parchment is a nonporous, homogeneous sheet of cellulose formed from sulfuric acid treating pulp. This material is the traditional form of greaseproof paper but is very expensive by present standards. Surface coating or sizing with wax or synthetic materials is now a more common method of manufacturing greaseproof paper from standard, bleached kraft paper. Food-safe paraffin wax is lightly applied to one side of the sheet. Thicker coatings of wax are also applied when a shiny surface is desirable. Synthetic surface treatments include silicone or polyvinyl alcohol based materials. Highly refined and supercalendered glassine, coated or uncoated, may also serve in this category. Grease or moisture resistance refers to surface treatments that have intermediate grease resistance between uncoated paper and greaseproof paper.

Metallized paper is an excellent packaging material for foods that are sensitive to moisture and light. The metal, usually aluminum, is applied in a very thin layer (0.02–0.05 μm) onto the paper sheet through vacuum deposition that involves vaporizing high purity metal. Due to the high surface free energy of paper, the vaporized metal bonds to the paper surface forming a moisture and gas impenetrable layer. The gloss of a metallized paper sheet is a function of the roughness of the paper. Rough paper surfaces produce matte or dull appearing metal layers, while smooth paper surfaces produce glossy metal layers. High-gloss metal layers are manufactured via indirect or transfer metallizing. In transfer metallizing a polypropylene web is initial metallized. Because the metal does not bond to the polypropylene, the entire metal layer can be transferred to the surface of an adhesive-coated paper sheet. The transferred metal layer has the surface smoothness of the polypropylene sheet. Thus, a high gloss metallized sheet is produced regardless of the original surface of the paper. Before printing, metallized paper is coated with a special primer layer to enhance adherence of the printing inks. Metallized paper is used as packaging materials for a number of food products that include chocolate bars, oily snack foods, candies, and chewing gums.

Foil-backed paper is produced by laminating aluminum foil to paper with an aqueous adhesive. The resultant sheet is attractive, easily printed upon, and has similar barrier properties to metallized paper. However, additional properties such as dead fold and heat retention capabilities that make it ideal for wrapping fast-food items such as hamburgers and other hot sandwiches. Dead fold is a direct property of the aluminum foil. Aluminum metal is very malleable and can be greatly deformed without cracking or losing its barrier capability. When fully annealed, aluminum maintains no 'temper' and retains its shape when deformed. Thus, dead fold gives foil-backed paper an ability to wrap around and temporarily seal a fast-food product from the time of purchase to the time of consumption.

Twisting paper is a novel food wrapping paper that is used primarily for personal-sized confections and cough drops. It has a high machine direction fiber orientation and a grammage range of 25–40 $g\,m^{-2}$. Some twisting papers may be metallized with aluminum to improve product attractiveness. Furnish additives include: titanium dioxide for enhanced opacity, and wet strength agents. Twisting papers are slit into very narrow widths to match the size of the confection. A heavier weight, non-food twisting paper is sometimes found making up the handles of paper bags used for shopping though it is now virtually obsolete.

An interesting paper grade that is frequently excluded as a packaging or wrapping grade is tea bag paper. Tea bag paper is a lightweight (grammage range 12–17 $g\,m^{-2}$) tissue paper made from very durable and long-fibered pulp such as abaca (banana leaf). This paper has to be porous yet hold the fine-sized tea leaves within the fabricated product.

Synthetic fibers such as polypropylene are frequently mixed into the furnish to produce a heat sealable bag.

Wrapping Papers

Wrapping papers are produced for a variety of purposes. Three major types include kraft wrapping paper, tissue paper, and gift-wrap paper. Kraft wrapping paper is sold in roll widths from 400 to 1200 mm with a grammage range of 50–90 $g\,m^{-2}$. It is produced from either unbleached or bleached pulp and is similar to kraft sack paper. When recycled pulp is used, it is sometimes called 'imitation' kraft paper and is dyed brown. Kraft wrapping paper is frequently used in retail transactions involving items that are not prepackaged or as an outer wrapping for food items that have flimsy, easily damaged food-grade packages.

Tissue wrapping paper is a lightweight paper sheet having a grammage range of 14–40 $g\,m^{-2}$. The standard tissue wrapping paper has a machine glazed finish due to the use of a high-temperature Yankee dryer that produces high gloss on the bottom side of the sheet. Unglazed tissue may also be produced using lower drier temperatures. Tissue wrapping paper is used to protect fragile or expensive gift items such as glass trinkets, ornaments, and jewelry. Wrapping tissue is made in colors running the spectrum from white to black. White wrapping tissue may have a brightness as high as 80. Special acid-free tissue is available to wrap items that are prone to tarnish, such as silver metal.

Gift-wrap paper is produced in grammages above 36 $g\,m^{-2}$, and is coated and calendered to maximize the attractiveness of the printed pattern. The paper's gloss is improved through the lamination of metal foil or the extrusion of a polymer coating. Rolls of gift-wrap are sold in widths of 500–800 mm and lengths of 1–5 m.

Paper Tubes

Spirally wound paper tubes are used in a myriad of packaging products. Some examples include: mailing tubes, snack food cans, and cores for paper roll products. The paper used is made from either virgin kraft or recycled fiber and has a grammage range of 35–95 $g\,m^{-2}$.

The process of producing a paper tube begins with slitting paper into narrow (minimally 2 inch) strips from a 50-inch roll. The strips of paper are then coated with a glue and several layers are wrapped into a spiral having an angle of approximately 45°. The final tubes can have typical diameters as great as 48 inches and wall thicknesses as much as 1/2 inch. Depending upon the final dimensions, the tube can be referred to as a tube, a can, or a drum. After gluing, the tubes are first rough cut, then cleaned, and precisely cut. Inside and outside layers can incorporate separate specialty papers that are optimized for barrier and printing properties. When tubes are used as cans or closed packages, the tube ends can be sealed by a variety of methods. In general, a paper top can be glued over the ends, the ends can be sealed by crimping and gluing, or a metal or plastic cap can be inserted.

Paper Cups

Paper cups are essentially single-wrap paper tubes with only one end sealed. The cup is sealed down the side similar to paper bags. The cup bottom may be sealed by either gluing a separate paper end cap or rolling the cup into a cone or convolute tube. Bleached, food-grade quality kraft paper similar to milk carton stock is required. The paper needs to have a high tensile strength, a low cross-machine stretch, and a low ash content. The top edge of a paper cup is rolled under to provide a smooth edge. This cup feature requires that paper cup stock have the ability to delaminate internally and hold the rolled edge.

Paper cup stock also needs to have a high moisture resistance for cold drinks. Wax coatings provide adequate moisture resistance as well as provide good sealing on the seam. However, wax coatings are likely to melt with hot drinks such as coffee and permit liquid leakage. Polymer laminations or extruded coatings are used on cups intended for hot beverages. The polymer coating is used only on one side to provide the moisture barrier and a sealable seam, while the outside of the cup is usually uncoated to provide better heat insulation. Clay coatings are frequently applied to increase printability and opacity. Miscellaneous paperboard items related to the use of paper cups in restaurants are insulating sleeves made from unbleached or recycled fiber and carrier trays. Many paper cups intended for hot drinks have paperboard handles glued to their sides.

Label Papers

Paper is an important method of labeling packages and containers that are nonprintable such as metal tins or cans and bottles. Paper is also an important method of labeling items in the office and at home with pressure sensitive labels. Paper designed for labels has one surface optimized for printing and the other optimized for the application of an adhesive. Flexographic, gravure, and offset printing are the most important commercial processes used for labeling retail products; however, blank labels used in the office and in the home must be receptive to pen inks and ink-jet printing. Paper label stock may also be clay coated, extrusion coated with plastic or laminated with metal.

Label stock intended for bottles and other liquid packages needs to be water resistant so that the label neither washes off the bottle nor losses its printing during normal usage. The label must also have wet strength sufficient to keep it intact if it is intended for use in recycled bottles where the label must be washed off with strong cleansing alkali. Paper used for these applications is white with ISO brightness above 80%, a gloss above 80%, and a high smoothness. The paper also needs to be stiff, dimensionally stable, and absorbent to adhesives. The paper furnish is derived from hardwood and softwood chemical pulps with a grammage range of 70–75 $g\,m^{-2}$.

Pressure sensitive labels are produced by laminating a printable face sheet on top of a 'release' liner using a suitable adhesive that completely peels away with the label allowing the label to be applied and adhered to another surface. Also known as 'peel and stick,' pressure sensitive labels come in either preprinted or blank forms that are die-cut to form individual labels on a roll or sheet. Pressure sensitive labels are used for: packages, cartons, mailing labels, computer disks, office labeling, and even postage stamps.

The release liner, also known as backing paper, is frequently silicone coated to create a smooth, pinhole-free surface that will not permanently bond with the adhesive of the face stock. The release liner can be either glassine or bleached kraft. Glassine is inferior to bleached kraft in regards to curl and dimensional stability, but its transparency makes it suitable where machine scanners are used to bring die-cut labels into position for printing and automatic labeling of packages. Glassine used for release liners has a grammage range of 30–80 $g\,m^{-2}$ and a caliper of up to 65 μm. Release liners made from bleached kraft have a grammage range of 30–130 $g\,m^{-2}$ with maximum caliper of 100 μm. The extra stiffness, dimensional stability, and bulk of the bleached kraft liners are required for high quality printing requirements. The need for high smoothness often necessitates supercalendering at about 20% moisture content. Silicone in the form of silicone acrylate is off-machine coated using a roll coater and then cured using either electron beam, ultraviolet or oven techniques. Solvent silicone systems are still used but flammability and environmental concerns are making newer aqueous systems more preferable. Modern machines that produce pressure sensitive labels coat and cure the backing paper and then apply the pressure sensitive adhesive directly to the silicone treated side. Simultaneously, the face stock is coated with an adhesive-receptive primer that is then dried. Both sheets are then laminated together to form the final product.

Face stocks can come in a variety of grades from lightweight (65 $g\,m^{-2}$) supercalendered paper to relatively heavy tag-grade paperboard (230 $g\,m^{-2}$). Face stocks may be either bleached or unbleached depending upon the application. Recycled fiber percentages as high as 100% may occur with post consumer waste percentages reaching as high as 50%. Face stocks are printed using a variety of methods including flexographic, letterpress and on-demand printing methods, such as direct thermal, thermal transfer, and laser/ink jet technologies.

See also: **Packaging, Recycling and Printing**: Paper Recycling Science and Technology. **Papermaking**: Overview; Paper Grades; Paper Raw Materials and Technology; Paperboard Grades; Tissue Grades; World Paper Industry Overview. **Pulping**: Bleaching of Pulp; Physical Properties.

Further Reading

Attwood B and Morre G (1995) *An Introduction to the Theory and Practice of Multiply Forming*. Leatherhead, UK: Pira International.

Biermann CJ (1993) *Essentials of Pulping and Papermaking*. New York: Academic Press.

Cakebread D (1993) *Paper-Based Packaging*. Leatherhead, UK: Pira International.

Hunter D (1947) *Papermaking: The History and Technique of an Ancient Craft*. New York: Knopf.

ISO (1998) *ISO Standards Handbook: Paper, Board and Pulps*. Geneva: International Organization for Standardization.

Kouris M (ed.) (1990) *Pulp and Paper Manufacture: Coating, Converting, and Specialty Processes*. Atlanta, GA: Joint Textbook Committee of the Paper Industry.

Paulapuro H (ed.) (1998) *Papermaking Science and Technology: Paper and Board Grades*. Helsinki: Fapet Oy.

Paulapuro H (ed.) (2000) *Papermaking Science and Technology: Papermaking*, Part 1, *Stock Preparation and Wet End*. Helsinki: Fapet Oy.

Savolainen A (ed.) (1998) *Papermaking Science and Technology: Paper and Paperboard Converting*. Helsinki: Fapet Oy.

Smook GA (1992) *Handbook for Pulp and Paper Technologists*. Vancouver, BC: Angus Wilde.

PAPERMAKING

Contents

The History of Paper and Papermaking

S AbuBakr, Western Michigan University, Kalamazoo, MI, USA
J R Thompson, Talo Analytic International, Inc., Duluth, GA 30096, USA

Introduction

It is difficult to imagine life without paper today. Paper has been a key factor in the progress of our civilization. The pulp and paper industry is nearly as old as civilization itself. Originating in the papyrus manufacturing discoveries of Egypt and the bonding of cellulose fibers in China, the industry has steadily marched forward. By the early part of the nineteenth century, paper manufacturing had stripped the supply of available cotton rags, the only known raw material. Serendipitously, the French, examining hornets' nests, leaped to the conclusion that paper could be made from wood, an event that happened shortly after the Fourdrinier brothers developed the continuous papermaking process. To this day, wood and continuous processes are used. The transformations in the past 200 years have evolved into an increased understanding of the sciences of forestry management, machinery foundations and dynamics, wood and papermaking chemistries, motive systems, computer control, logistics, and business finance and management. Thus we have moved from paper machines commonly as wide as the standard office desk using raw materials gathered within 1–5 km to machines one-third the width of the Panama Canal selling finished products around the world. We also have moved from the concept of print-and-distribute to distribute-and-print using the Internet.

Up to 1900

The oldest extant document, the 40-m long Prisse Manuscript written on papyrus was made by the Egyptians in about 2000 BC.

In AD 105, Ts'ai Lun proclaimed his great invention of true paper – a thin, felted material formed on a flat porous mold from macerated vegetable fiber. In AD 400, the Chinese invented ink from lamp-black and used it for writing on paper. Gypsum and starch flour were used as sizing agents in about AD 700 in China.

Paper was first made the Chinese way in Samarkand in AD 751 and in Baghdad in 793, during the era of Harun Al-Rasid. In about AD 900 paper was made in Egypt and by AD 950 was already being transferred and made in Spain. Paper for packaging and wrapping was reported in Egypt in about AD 1035.

Papermaking appeared in Sicily (1102), in Constantinople (1100), in France (1189), and in Germany (1228). The Fabriano paper mills were established in 1276 in Italy and by 1282 the first watermarks were introduced in Italy. The first paper money was issued in Tabriz, Iran in both Chinese and Arabic texts. The first use of paper in England was reported in 1309 and by 1495 the first paper mill was established there.

In 1440, Johannes Gutenberg introduced to the world his invention of printing with ink on paper, combining movable cast metal type, ink, paper and press to produce printing that very much changed the world. The first newspaper with regular publication dates was published in Germany in 1609; a similar one appeared in England in 1622.

The first English patent pertaining to papermaking was granted to Charles Hildeyerd in 1665, for 'The way and art of making paper used by sugar-bakers and others.' In 1680, the 'Hollander' or beater used in the maceration of materials for making into paper was invented in the Netherlands. In 1798, the paper machine for producing a continuous web of paper utilizing a wire mesh screen to form the paper was invented by Nicholas-Louis Robert in France.

A patent dated 24 July 1806 was taken out by Henry Fourdrinier under the following specifications:

> A number of molds, of the description called laid and wove, are hooked together to form one long mold. A platform to hold the said molds in such manner that the molds shall slide along backwards or forwards, but in no other direction. A vessel or trough from which the paper stuff or material is caused to flow upon the molds through holes, each provided with one or more registers to limit or mark the flow of stuff. A set of cylinders, upon which is passed, in the manner of a jack towel, an endless web of felting. There is a third cylinder in contact with one of these cylinders, and this third cylinder communicates by means of another web of felt with an additional pair of pressing cylinders. When the molds arrive at the first cylinder, the felt web takes off the paper and conveys it to the first pair of pressing cylinders, whence it proceeds to the second pair, and afterwards to any fit place of reception, so that continuing the process, paper of any length may be made, and with separate molds.

Other important examples of inventions and discoveries during this period include:

- The cylinder paper machine was first introduced by John Dickinson in 1809 and by 1817, he was the first scientist to introduce steam-heated drying cylinders.
- The first dandy roll was patented by John and Christopher Phipps in 1825.
- Papermaking from mechanical groundwood pulp was first introduced in 1840.
- Chemical pulping using caustic soda was introduced in about 1854.
- The first use of toilet paper in roll form in America was introduced in 1871.
- The first coating of paper on both sides was first introduced in 1875 by S.D. Warren.
- The largest and fastest paper machine by 1900 was in Rumford, Maine, with a wire 4.1 m (162 inches) in width and 18 m (60 feet) long running at about 150 m (500 feet) min^{-1}.

The total paper production in the USA at the end of the nineteenth century was about 2 million tonnes $year^{-1}$.

1900–1925

In the first quarter century of the twentieth century, the organization and development of the paper industry looked little different than that of the nineteenth century. Electricity was still a novelty and forestry practices had not become widespread. Hence paper was manufactured from either rags or locally harvested natural growth forests. Most likely, the mill was operated with a water wheel. As an aside, the Finnish suffix ‘koski’ means rapids and many Finnish mills were located in towns with names such as Kylmäkoski, Valkeakoski and so forth, as these were places on rivers and streams where water wheels could be built to power machinery.

In the USA, forestry management grew out of the keen interest of Gifford Pinchot (1856–1946) in the subject. His interest in Forestry Management led Pinchot to L’Ecole Nationale Forestière in Nancy, France for education on the subject, as academic work was not available at that time in the USA. Later President Theodore Roosevelt appointed Pinchot Chief Forester of the US Forest Service. Pinchot did much work in North Carolina, and in commemoration of his visionary work, the US Forestry Service, in cooperation with others, maintains the Cradle of Forestry Historic Site on US Highway 276 just outside of Pisgah Forest, North Carolina.

In this same time period, electric motors began to make an appearance in paper manufacturing. Along with light bulbs, which had been introduced in the later part of the nineteenth century, electric motors went a long way towards moving papermaking into the modern age. At last, papermills did not have to be sitting literally on top of a stream. It appears that electric motors first made their debut in paper mills in the USA, as that country was an early adopter of electric power. Additionally, at the same time, development had stalled in Europe due to World War I (except in Finland, where the Finnish Forest Research Institute was established in 1917). Interestingly, in those days, because there was no national power grid in the USA, there were few electrical standards, hence mills had voltages and alternating current frequencies of their own choosing. As late as the 1990s some older mills in the USA were still using their own power standards.

1926–1950

Paper Manufacturing moved forward on many fronts in this period. Professionals around the world were beginning to think of papermaking as a scientific endeavor rather than the ‘black art’ that it had been. In the USA, the Institute of Paper Chemistry was founded in Appleton, Wisconsin, for the study of wood and papermaking chemistry, and the granting of graduate degrees.

The malaise of nearly worldwide depression seriously affected development from 1929 until World War II. However, in the southern USA, a precursor to post-World War II paper industry expansion was developed. This was the Tennessee Valley Authority (TVA) project instituted by President Franklin Roosevelt. This project harnessed the power of the Tennessee River for the production of electricity and the establishment, coupled with developments elsewhere, of a national power grid.

During World War II, paper recycling became important nearly everywhere. The survival of cylinder board paper machines to this day is highly dependent on the recycling infrastructure developed during World War II in Europe and North America.

Following World War II, there was an explosion in paper demand in the civilized countries of the world. In most of Scandinavia, this started soon after the war, but in Finland and mainland Europe, it came along slightly later due to extensive infrastructure rebuilding efforts. In the USA, big (for the time) southern mills sprouted to take advantage of the forestry work that had been done with southern pine and the electrical grid infrastructure of the TVA.

1951–1975

The 1950s saw an explosion in paper usage throughout North America and Europe. As standards of living rose, paper goods were consumed by people experiencing higher levels of disposable income. The widespread introduction of flush toilets in small towns, another US government program of the 1930s, increased people's awareness of appropriate sanitation measures, driving the use of paper products specifically designed for this service.

In the late 1950s, Procter & Gamble, the consumer goods giant from Cincinnati, Ohio, purchased a small paper company headquartered in Cheboygan, Michigan named Charmin. Although the pundits of the day thought this would be the end of Procter & Gamble, the marketers in Cincinnati had a different idea. First, they began researching the taboo subject of what attributes made a toilet tissue desirable to the discriminating user. Next, they found a way, once such products had been developed, to market them to a public still firmly rooted in Victorian mores. An explosion in the demand for high-quality sanitary goods was the result.

Also in the 1950s and early 1960s other universities, especially in the USA, founded undergraduate and graduate programs of study in pulp and paper. By the 1990s, there were 11 such programs in the USA, with many more in Scandinavia, Canada, New Zealand, the UK, and Australia. Real pulp and paper scientists with a firm understanding of cellulose chemical and physical properties were being trained in substantial quantities.

At nearly the same time, precipitous events were happening in Finland and the United Nations. By the mid 1950s, Finland succeeded in completion of payment of war reparations to Russia. It was time to turn to repairing and renovating their own industry. A young engineer by the name of Jaakko Pöyry became head of engineering for the first renovation project. It was immediately followed by another, then another. Finland, even though a small country, has always been driven to being a major contributor to the United Nations. The United Nations, from its beginning, looked to development of natural resources, such as forests, to aid undeveloped countries in their move from the Third World. At nearly the same time Jaakko Pöyry was looking to expand his business, Max Jakobson was appointed Finnish Ambassador to the United Nations. Max Jakobson and Jaakko Pöyry had been in the same unit of the Finnish Army in World War II, fortuitous events indeed. The Jaakko Pöyry firm was engaged to do many studies for the United Nations around the world. Some of these studies led to the realization of actual projects, such as the Aracruz manufacturing and forestry site in Brazil, one of the world's largest producers of eucalyptus market pulp.

In 1962, Rachel Carson's book *Silent Spring* gained attention and had an impact on the pulp and paper industry, the degree of which no one could have imagined. This book turned the conservation movement into the environmental movement. Starting about 1970, environmental laws were implemented on a nearly worldwide basis. Although of little impact in the balance of this quarter century, this time closed with another event critical to the paper industry: the rise of the power of the Organization of Petroleum Exporting Countries (OPEC). Several oil shocks caused the industry to spend time and money on basic power generation sources, such as bark boilers, detracting scarce resources from improving the products which the industry made.

1976–2000

By The last quarter of the twentieth century, papermaking had clearly become science. Many aspects of the microscopic and atomic-level processes were well established. The development of other basic engineering disciplines and sciences, such as dynamics, metallurgy, process control, and so forth, developed to the level that many formerly misunderstood parameters became routine to manage and control.

New and unfamiliar challenges, however, strained the industry in ways not seen before. The industry responded slowly to growing environmental pressures, giving its detractors plenty of reason to seek control of it.

Plastics began to make serious inroads, along with reformulations of products formerly contained by paper (such as liquid detergents replacing powders). At the same time the Internet and the electronification of the office seemed to be a two-edged sword. No doubt more printers were making more copies than ever before, but it seemed as though certain paper grades were quickly obsolescing. No longer were printed stock certificates required, and interest in daily newspapers was waining. The impact of writing a letter on high cotton content paper was lost. Conversely, computers and associated software, coupled with changes in printing processes, led to many new and specialized magazines, as layout was easier and runs could be shorter. Overall, papermakers seemed lost as to how to distinguish their products and avoid falling into a commodity-only business. How to go from a production orientation to one of marketing?

By the end of the twentieth century, it can be said that the science of papermaking was firmly established. High-speed equipment operated by skilled professionals, using massive computing capacity, tamed the process. Today, we know how to make paper at high speed, efficiently and consistently, in an environmentally sound way.

See also: **Packaging, Recycling and Printing**: Packaging Grades; Paper Recycling Science and Technology; Printing. **Papermaking**: Coating; Overview; Paper Grades; Paperboard Grades; Tissue Grades; World Paper Industry Overview. **Pulping**: Bleaching of Pulp; Chemical Additives; Chemical Pulping; Chip Preparation; Environmental Control; Fiber Resources; Mechanical Pulping; New Technology in Pulping and Bleaching; Physical Properties.

Further Reading

Amigo E, Neuffer M, and Maunder E (1980) *Beyond the Adirondacks: The Story of St. Regis Paper Company,* Contributions in Economics and Economic History. New York: Greenwood.

Biermann C (1996) *Handbook of Pulping and Papermaking*, 2nd edn. New York: Academic Press.

Hunter D (1947) *Papermaking: The History and Technique of an Ancient Craft*. New York: Dover Publications, Inc.

Jakobson M (1987) *Finland: Myth and Reality.* Helsinki, Finland: Otava.

Miller C (2001) *Gifford Pinchot and the Making of Modern Environmentalism*. Washington, DC: Island Press.

Miller GK (2001) *Energy Northwest: A History of the Washington Public Power Supply System*. Philadelphia: Xlibris.

Minchin TJ (2001) *The Color of Work: The Struggle for Civil Rights in the Southern Paper Industry, 1945–1980*. Chapel Hill, NC: University of North Carolina Press.

Schurr SH, Buwell C, Devine W, and Sonenblum S (1990) *Electricity in the American Economy: Agent of Technological Progress*, Contributions in Economics and Economic History. New York: Greenwood.

Swasy A (1993) *Soap Opera: The Inside Story of Procter & Gamble*. New York: Times Books.

Waggener TR (1990) *Forests, Timber, and Trade: Emerging Canadian and US Relations under the Free Trade Agreement*. Orono, Maine: University of Maine Press.

World Paper Industry Overview

S AbuBakr, Western Michigan University, Kalamazoo, MI, USA

Introduction

Paper is one of our most important materials. It has been a key to the growth in human communications and commerce since invented by T'sai Lun in China. Various historians rank the Gutenberg Bible and the invention of the printing press as among the most important developments in history.

Changes in society have had a major impact on the use of paper around the world. However, despite predictions in the 1980s and 1990s that some combinations of technology would eliminate the use of paper for common uses such as the daily newspaper, there is little doubt that it will continue to have a key role in the future. Nevertheless, the paper industry must maintain its competitiveness and viability by continuing to develop new products that can compete cost-effectively with alternate means of information dissemination and alternate packaging materials, as well as seek out new end-use applications. Paper must also be produced economically and in an environmentally responsible manner. There are many challenges to paper that could reduce its use in some applications. Conversely, as the economies of Second- and Third-World nations continue to develop, paper consumption and growth will grow, driven by established uses and new and innovative applications. A driving force for its sustainability is a renewable and relatively low cost principal raw material, namely wood.

The following major areas are discussed in this overview:

- raw materials and major products
- demand and consumption
- long-term growth trends

- global trade
- major industry structural trends
- challenges to growth.

Raw Materials and Major Products

Paper for the most part is manufactured using softwood and hardwood trees to supply the fiber used in its manufacture. Globally, fibers from trees provide about half of the material used to make paper and paperboard, while recycled fiber provides about 20%. Most of the remainder is accounted for by various minerals and chemical additives used to impart optical and printing characteristics, water resistance, and strength characteristics to paper and paperboard grades. The remainder of the raw material used by the industry is composed of non-wood fibers, which are mainly used in parts of Asia and Africa.

Many grades are manufactured using recycled fiber, i.e., fiber that has already been used in a paper product, such as a box or as office papers, which is then recycled to provide the fiber for a paper or paperboard grade. As discussed later, trees are a renewable resource and this provides an advantage over many competitive materials. However, it also presents an environmental challenge due to society's perceptions of the pros and cons of the widespread cutting of trees to fuel the demand for fiber by the paper- and wood-consuming industries.

Common grades of paper and paperboard are used by people all over the world for a wide array of uses. Most major uses can be categorized as one of two applications: (1) communicating information or protecting and packaging products for shipment and end-use applications; (2) personal hygiene applications where a range of sanitary tissue grades is used for products such as toilet paper, paper towels, napkins, and facial tissues. Nonsanitary grades include products such as tissues for interleaving and electrical applications.

Common examples of paper used to store or communicate information range from the ubiquitous sheet of cut-size copy paper to the daily newspaper, direct mail, magazines, catalogs, promotional brochures, and books.

Paperboard grades are used to package food and to protect products for shipment. There are two major forms of packaging: folding cartons and corrugating containers. Frozen food, dry foods, milk products, and many other foods are packaged in paperboard folding cartons. Food is the largest use for folding cartons. Major folding carton applications include:

- bottled and canned beverages
- candy, biscuits, and crackers
- cosmetics
- carry-out food
- soaps and detergents
- hardware and household supplies
- tobacco
- bakery
- paper goods.

A wide array of products are packaged in corrugated containers, which is a paperboard box made of three plies, with the middle ply comprised of a wavy or fluted sheet called corrugating medium. The use of this fluted ply enhances its bending stiffness.

Among the major uses for corrugated containers (in order of the volume of boxes used) are:

- paper products
- electronics
- food
- hardware, tools, etc.
- consumer soft goods (e.g., clothes).

There is also a large and varied converting industry that uses paper and board as one of its key raw materials to produce a wide array of products. Some segments are based mainly on paper or paperboard, such as business forms converting, envelope converting, and box and corrugated container converting. An equally large and even more diverse segment is flexible package converting, where, for example, a plastic film may be used to cover an item for sale and is affixed to a backing sheet composed of recycled or bleached paperboard. Other examples include combinations of paper, film, and foil to manufacture bags or sacks with various barrier properties. Common examples include pet food packaging and aseptic juice containers.

The other major paper industry product is pulp. Many mills around the world do not make paper or paperboard: they simply make pulp. Pulp is the first product phase from the pulping of wood, and is the basic raw material for paper and paperboard. This market pulp is then shipped to paper mills that do not make their own pulp or those that only make part of their pulp requirements.

Demand and Consumption

The amount of paper consumed in the world is driven by a complex set of social and economic factors and the amount of paper products consumed or used by an individual, or on a per capita basis, varies widely around the world. However, as a general rule, consumption tracks fairly closely with per capita income and general economic levels. Persons having higher income buy more processed foods, consumer electronics, and toys. They also tend to be better educated and thus consume more newspapers, magazines, and books.

In more developed economies, such as in Europe and North America, large amounts of paper products are used. In developing countries, such as in Asia and Africa, very low levels of paper products are consumed. For example, per capita paper and paperboard consumption in North America approaches 330 kg, in Europe it varies from less than 200 kg to over 340 kg, and might average 230 kg, while in Asia and Africa it is less than 35 kg.

Consumption is also highly cyclical due to its close correlation with economic activity. Thus during periods of high economic growth, paper demand typically expands, while during slow economic growth, or during recessions, demand growth slows or demand can decrease.

Total world demand for paper and paperboard exceeds 300 million metric tons, based on data for 2001, the most recent year for which world data are available. The largest consumers are the USA, followed by China, Japan, Canada, and the major economies in Europe. Global demand contracted in 2001 versus the 2000 level due to weak economic conditions that prevailed in key economies, notably, the weakness in the huge US market, and the decline in Asian growth rates. At this writing, demand continues to be weak due to the ongoing weakness in the major world economies. For example, total US demand for paper and board fell 0.1% in 2002, a much more modest decline than the 6.1% drop in demand in 2001 and the 2.5% decline posted in 2000. The 3-year decline is one of the largest ever posted in the US market.

The Asian market, with the exception of Japan, has historically been a modest consumer of paper despite its large population due to its general lack of economic growth. However, this has changed somewhat in recent years as various countries have seen economic growth, and in some cases, removal or at least easing of restrictions on the dissemination of information. **Tables 1–3** give more detailed global information regarding growth and consumption.

In particular, change in China has been noteworthy. While currently the second largest individual market, demand is growing rapidly owing to strong economic growth in the last decade. It is projected that China may eventually become the largest market for paper products in the world due to its enormous population and movement toward a less controlled economy. Twenty years ago China was ranked sixth

Table 1 World paper and board production by grade 2000–2001 (1000 tonnes)

	Newsprint		*Printing/writing*		*Tissue*	
	2000	*2001*	*2000*	*2001*	*2000*	*2001*
European Union	9266	9336	32 649	30 847	5000	4902
Other western Europe	1196	1245	1440	1352	132	133
Total western Europe	10 462	10 581	34 089	32 198	5132	5035
East Europe	2214	2283	1961	2035	619	634
Total Europe	12 676	12 864	36 050	34 233	5752	5669
Asia	8520	8730	27 701	27 277	5360	6527
Australasia	782	738	562	586	255	261
North America	15 889	14 147	30 748	28 464	6922	7047
Latin America	947	928	3 529	3522	1985	1933
Africa	367	359	706	727	249	263
Total	39 181	37 766	99 296	94 810	20 522	21 699
	Containerboard		*Board*		*Total P&B*	
	2000	*2001*	*2000*	*2001*	*2000*	*2001*
European Union	18 280	18 215	10 652	10 450	84 655	82 222
Other western Europe	797	766	285	252	4153	4041
Total western Europe	19 077	18 982	10 937	10 703	88 808	86 380
East Europe	2902	3135	1599	1698	11 257	11 868
Total Europe	21 979	22 116	12 536	12 401	100 066	98 255
Asia	29 290	28 813	13 369	13 451	95 797	96 661
Australasia	1841	348	83	89	3526	3494
North America	33 917	32 347	14 577	14 095	106 603	100 433
Latin America	5331	5403	1395	1385	14 789	14 855
Africa	1357	1388	260	256	3200	3449
Total	93 714	90 415	42 221	41 677	323 981	318 147

Source: Pulp and Paper International (PPI), Annual Review Issue, July 2002, Paperloop.com.

Table 2 World's top 30 producers 2001 (000 tons). Source: PPI Annual Review Issue, July 2002

Paper and board production	*2001*	*% Change 2001/2000*
1. USA	80 759	–5.9
2. China, People's Republic	32 000	3.6
3. Japan	30 731	–3.4
4. Canada	19 686	–5.2
5. Germany	17 879	–1.7
6. Finland	12 503	–7.4
7. Sweden	10 534	–2.3
8. Korea, Republic of	9724	4.5
9. France	9630	–3.8
10. Italy	8924	–2.2
11. Brazil	7354	2.3
12. Indonesia	6951	0.3
13. UK	6204	–6.1
14. Russia	5599	6.9
15. Spain	5132	7.7
16. Austria	4250	–3.1
17. Taiwan	4211	–6.3
18. India	4049	5.2
19. Mexico	3811	–2.2
20. Netherlands	3174	–4.7
21. Australia	2656	0.3
22. Thailand	2445	5.7
23. Norway	2291	–3.5
24. South Africa	2268	6.8
25. Poland	1952	0.9
26. Switzerland	1750	–1.7
27. Belgium	1659	–3.9
28. Turkey	1513	–3.5
29. Portugal	1419	10.0
30. Argentina	1229	1.2
Pulp production	*2001*	*% Change 2001/2000*
1. USA	52 795	–7.3
2. Canada	24 918	–7.3
3. China, People's Republic	17 570	2.4
4. Finland	11 169	–6.3
5. Sweden	11 000	–4.5
6. Japan	10 813	–5.1
7. Brazil	7405	–0.8
8. Russia	6225	5.7
9. Indonesia	4326	5.8
10. Chile	2921	2.8
11. India	2645	2.5
12. Norway	2406	–1.8
13. France	2327	–5.7
14. Germany	2103	–5.1
15. Austria	1944	10.4
16. Portugal	1806	1.8
17. South Africa	1740	–23.0
18. Spain	1720	–1.7
19. New Zealand	1501	–6.5
20. Poland	933	0.8
21. Australia	921	4.2
22. Thailand	919	20.3
23. Argentina	791	0.5
24. Czech Republic	687	7.1
25. Italy	603	0.6
26. Korea, Republic of	554	–6.9
27. UK	492	–4.8
28. Belgium	405	–11.0
29. Mexico	384	–34.0
30. Taiwan	370	–3.9

Table 3 World's top paper and board consumers 2001 (000 tons). Source: PPI Annual Review Issue, July 2002

Paper and board consumption	*2001*	*% Change 2001/2000*
1. USA	87 933	–5.4
2. China, People's Republic	38 180	2.9
3. Japan	30 836	–2.8
4. Germany	18 543	–2.9
5. UK	12 516	–3.0
6. Italy	10 734	–3.1
7. France	9680	–14.4
8. Canada	7875	3.3
9. Korea, Republic of	7850	6.3
10. Brazil	6618	–2.7
11. Spain	6398	–6.2
12. Mexico	5313	0.1
13. Indonesia	4862	24.4
14. India	4444	6.8
15. Taiwan	4351	–14.8
16. Russia	3783	14.8
17. Australia	3661	0.2
18. Belgium	3380	–3.1
19. Netherlands	3355	–12.1
20. Sweden	2463	–2.2
21. Poland	2422	–0.3
22. Malaysia	2273	12.6
23. Austria	2103	7.1
24. Thailand	2070	5.6
25. Turkey	2017	–20.5
26. South Africa	1878	9.2
27. Denmark	1806	26.5
28. Argentina	1741	–5.6
29. Switzerland	1687	–4.8
30. Finland	1386	–9.1

in total consumption; 10 years ago, it only ranked behind the USA and Japan, and today it is number 2.

Long-Term Growth Trends

Demand for paper and paperboard products typically mirrors economic changes as measured by gross domestic product (GDP) or gross national product (GNP). Thus, as economic growth occurs, more paperboard packaging is required to ship industrial and consumer goods, more books and magazines are sold, and more paper is used in offices for copying, printing, and mailing.

Global paper and paperboard demand has typically expanded at about the same rates as world GDP, or about 2–3% annually. However, growth rates vary widely by grade as well as widely by region and country.

Based on two examples of growth in the future, **Table 4** outlines the growth in world paper and paperboard demand.

During the 1980s, rapid growth occurred throughout the world and in particular the huge North American market as the US economy expanded, and

Table 4 Increase in world demand at various growth rates (000 tons)

Annual demand growth (%)	*Growth in world demand per year*
2	6000
3	9000

Based on base consumption of 300 million tons per year. Source: PPI Annual Review Issue, July 2002.

throughout much of Asia, with Korea and China's consumption more than doubling. During this period, US growth was particularly strong for printing and writing grades due to enormous growth in the use of direct mail – referred to as junk mail by its opponents – which includes catalogs, as well as strong growth in newspaper inserts (also called free-standing inserts). In addition, demand for grades such as coated paper, uncoated free sheet, and uncoated groundwood grew at nearly twice the rate in growth of the general economy, i.e., at rates of 5–8% annually. Demand for packaging also posted strong gains, but not at rates matching printing and writing paper growth.

Growth continued into the 1990s but during the latter part of the decade the rapid growth in the use of computers began to have an impact on consumption patterns in the USA (for much of the 1990s growth in white papers was spurred on by computer printers and fax machines – in the later part of the 1990s paper consumption changed, but it is difficult to differentiate between the impact of computers and the internet and the general decline in the economy). In particular, the explosion in the use of the internet began to have a negative impact on various communication papers. During the 1990s printing and writing paper demand continued to grow rapidly in Europe.

During the last two decades, many people have spoken of the paperless office, where a wide array of computer and internet-based devices would essentially eliminate the use of paper. This remains a myth, and printing and communication paper demand continues to be large.

However, while the paperless office has never materialized, electronic information dissemination has had a major impact on the use of paper. This impact is caused by a wide array of forces, including direct substitution where paper is eliminated because another means of conveying information has replaced it. A good example is the reduction in the use of first-class mail correspondence, which has been caused by two factors. Initially, the use of the facsimile machine replaced the mailing of letters, but more recently, the explosion in the use of e-mail has had a much larger impact, as has the low cost of telecommunications.

Table 5 Total US advertising expenditure by medium

Medium	*%*
Daily newspapers[a]	19.2
Television	23.5
Direct mail[a]	19.3
Radio	7.7
Yellow pages[a]	5.9
Magazines[a]	4.8
Other	17.1

[a] Paper-related.

In other cases, the impact was more indirect. For example, advertising expenditure is a major driver behind the use of printing papers. When more money is spent on print advertising, more paper is used to print magazines, catalogs, and flyers. However, advertising dollars are spent on a variety of media, including print and electronic media such as television, radio, and more recently, internet-based advertising, and thus will potentially impact paper consumption.

Table 5 provides insight into the use of various advertising methods in the USA, based on 2001 data.

Printing and writing paper demand continues to grow strongly in areas such as in Europe, which have historically had various controls in place that limited the use of various media such as television, and where the use of sophisticated marketing approaches such as direct mail and catalogs is not yet as advanced as in more developed markets. Growth will continue to be strong in Asia where both literacy and economic rates continue to show rapid growth.

US demand is expected to continue to expand, but at much lower rates than during the 1980s and early 1990s. Projections by various forecasting experts peg growth at 1–3% annually over the next 5 years.

Global Trade

Paper and paperboard grades may be consumed in the country in which they are produced, or they may be exported to other countries. While the level of income, affluence, and lifestyle influences demand for paper, the production of paper products is often driven by a different set of parameters. Traditionally paper was produced in regions with abundant forest resources such as Scandinavia, Canada, and the USA, and appropriate economic resources (South America, Asia, and Russia all have large forest resources, but limited financial resources).

Historically, trade between various regions of the world was modest. Initially trade between countries began in areas such as North America and Europe when regions possessing abundant natural resources in terms of wide tracts of forestland and low-cost hydropower began to make paper and ship it to areas that lacked such resources. Thus, in the early parts of the twentieth century, Canada, which had huge tracts of virgin forest and numerous rivers, began to make paper to sell to the huge US market located to its south. In fact, this trend was encouraged by major consumers of paper in the USA that built mills in Canada. A prime example is the Tribune Company, which founded the first newsprint mill in Canada to supply paper to the large Chicago newspapers.

However, as noted below, paper trade has expanded due to the availability of low-cost wood in the southern hemisphere. In regions such as South America, and more recently in South-East Asia in countries such as Indonesia, the warmer climate and wide tracts of unused land have led to large growth in the use of 'forest plantations.'

Production has increased considerably in the last 10 years in Southeast Asia, notably in China, Indonesia, and Korea. Production is growing rapidly in China as the country attempts to meet its growing demand for paper and paperboard. Most of this is targeted at meeting domestic demand growth in these countries. However, considerable tonnage is also currently being exported to the USA and Europe, which is having the effect of displacing higher-cost locally produced paper. The growth in capacity in these countries has also to some extent replaced grades such as paperboard that were previously exported by the USA and Europe to the region.

Major Industry Structural Trends

Two fundamental changes, both economically driven, have radically altered the global forest products business in the last decade. They are: (1) huge growth in the use of plantations in warm climate areas of the world such as South America and South-East Asia to supply fiber; and (2) the huge growth in the economies of Asia, notably China, and in turn the rapid growth in the demand for paper and paperboard in these regions.

The global pulp and paper industry has been strongly affected by several key macroeconomic trends. Among the major ones are industry consolidation and shifting regional competition due to exchange rates.

One key trend that has been underway for some time in many industries, such as the automotive industry, has been a trend towards consolidation. Big companies buy up other companies as a method of increasing their market share, and for strategic reasons such as to extend their reach to other markets. Being large also provides the capital needed for investments and to ride out the notoriously cyclical nature of the industry.

Over the last 20–30 years exchange rates have played a major role in many industries, including the pulp and paper industry. During the early 1980s, the devaluation of Scandinavian currencies radically changed the competitive landscape of the world pulp and paper industry. The US industry, which for years had enjoyed a favorable competitive position due to the dollar, was suddenly at a disadvantage. This devaluation led to the initial expansion of exports of paper and board grades to the US market. The devaluation had effectively made a high-cost industry either a low-cost one, or at the very least, a competitive paper industry that was able to ship product to North America.

Similarly, in recent years, the weak Canadian dollar versus the US dollar has been a boon for the large Canadian forest products industry by allowing it to ship competitively priced products to the USA.

During the period 2002–2003, a large-scale change in the value of the dollar against the euro has begun to change the competitive position of the European and US industries. For much of the latter part of the 1990s, a strong US dollar has meant that it was difficult for US mills to compete globally and to export paper products. In contrast, it has meant a boon for European and, to some extent, Asian countries. As a result, US imports have risen considerably while exports have fallen. The decline in the value of the euro vs. the dollar which has occurred since 2002 is likely to slow the growth of imports to the US, although it is not likely that imports for certain grades will actually decrease.

Environmental Issues

One major factor impacting the availability of timber for industrial use has been environmental considerations. The largest and most notable example to date has been the withdrawal of millions of acres of federal land in the western USA due to environmental concerns. Environmentalists argued that the spotted owl was being damaged by excessive logging in national forests and were successful in getting the government to ban, or severely reduce logging in the region, which was traditionally one of the world's largest suppliers of fiber to the pulp and paper industry.

Other environmentally related issues include huge sums of capital spent by North American and European producers to meet stringent air and stream environmental standards.

Challenges to Growth

Most forecasts of growth in world paper and paperboard project that demand will continue to expand at modest rates of 2–3% annually for the foreseeable future. However, in some of the more developed economies of the world, notably in the USA, a wide array of forces have led to slower demand for certain grades. In fact, demand for a number of grades, such as newsprint and packaging papers, has either stagnated or has posted major declines due to competitive factors such as the growth in electronic media and electronic information dissemination and due to losses to competitive materials, notably plastics used for packaging.

Much has also been written about the impact of information technology on the use of and demand for communication papers. It presently appears that while demand for some products may decline, the negative impact of technology on paper use in the next 5–10 years will be limited to merely slowing the growth in demand, not actually causing it to decrease. And this negative impact is most likely to be the largest in high paper-consuming markets, such as Europe and North America, and less important in other markets.

There are several other challenges to the long-term growth and success of the pulp and paper industry worldwide. They include:

- The paper industry's image as a smokestack industry
- The image that the industry destroys old-growth forest and rainforests
- Competition for traditional paper uses from competitive information means and alternate packaging materials

The industry's record on the environment is beyond the scope of this article. However, what is important to recognize is the importance of how the public perceives these issues. In recent years, environmental groups have waged campaigns urging consumers to stop the use of paper and forest products due to various environmental reasons. They include the charge that forestry companies are cutting down old-growth northern forests as well as destroying tropical rainforests. The threat to the industry is that consumers will cease to buy and use paper products due to these concerns. While these groups have achieved some success, the global industry has met these challenges and others with large capital expenditures for air and stream improvement and a prodigious effort to plant more trees than are being consumed. As noted earlier, environmental concerns have previously been used to limit the use of forests as a natural resource in the production of paper and lumber products.

Competitive packaging materials are another key threat to the paper and forest products industry. Among the most notable losses that paper products have endured are the large-scale replacement of the common paper grocery sack with plastic sacks, and the shift in packaging automotive oil from oilcans to bottles.

Food packaging is another prime area where product substitution has impacted and reduced the use of paperboard packaging. For example, folding cartons and paper bags are being increasingly replaced by plastic pouches and sacks in a variety of foods.

The driving force behind almost all of these cases of substitution is lower cost. Lower-cost plastic is replacing a higher-cost paper product. In some cases the replacement product is also a better product.

A final element that poses a challenge to the industry has been the relatively poor financial performance of the paper industry in recent years. This has been due to several factors, mainly the weak global economy in the 1990–1991 and 1999–2002 periods, in addition to the industry's tendency to overinvest in capacity when times are good. In turn, this means that new and frequently excess capacity typically comes online just when demand is plummeting. Among the biggest challenges posed by this weak performance is the limit it places on the industry's ability to attract investment capital and to attract employees.

Another factor impacting established mills is that new capacity is frequently produced more efficiently, and at lower cost. These cost factors include labor rates, employees required per unit of production, cost of raw materials and energy, not to mention possible differences in cost of environmental compliance.

In conclusion, despite numerous changers in the global pape]r industry over the past few years, paper and board production has grown and growth will continue for years to come as economy throughout the world continues to grow – bringing increased literacy rates, an educated populace, and business commerce use of paper.

See also: **Packaging, Recycling and Printing**: Packaging Grades; Paper Recycling Science and Technology; Printing. **Papermaking**: Coating; Overview; Paper Grades; Paperboard Grades; The History of Paper and Papermaking; Tissue Grades. **Pulping**: Bleaching of Pulp; Chemical Additives; Chemical Pulping; Chip Preparation; Environmental Control; Fiber Resources; Mechanical Pulping; New Technology in Pulping and Bleaching; Physical Properties.

Further Reading

Biermann C (1996) *Handbook of Pulping and Papermaking*, 2nd edn. London, UK: Academic Press.

Paper Raw Materials and Technology

P P Bhojvaid and A K Rai, Forest Research Institute, Dehradun, India

Introduction

Paper and paper products in today's world play a very important role in everyday life. One cannot think of any activity without the use of paper; in fact paper is almost synonymous with development in the contemporary world. Per capita annual paper consumption is one of the indicators of economic development and the literacy rate of a country. Consequently the pulp and paper industry is one of the most important industries of the world, which provides employment to a very large number of people in most of the countries of world. Furthermore, the rising population and the recent change in lifestyles necessitate that paper should be available in plenty and at a very cheap price. Consequently, significant research and development has taken place for finding different raw materials for the manufacture of pulp (the basic constituent of paper) and for developing efficient, environmentally friendly, and economical technologies for papermaking. These two aspects will be the focus of this article, with special emphasis on non-wood fibers.

Definition and History

'Paper' is defined as the sheet or web formed by the deposition of (vegetable, animal, or synthetic) fiber from a suspension (in water, vapor, or gas) with or without the addition of sizing chemicals and filtered over a fine screen in such a way that the fibers are bonded and intermeshed together after pressing and drying. The raw material for these fibers is pulp, which is commercial cellulose, fibrous in nature and derived from wood, bamboo, grasses, or any other raw material by mechanical or chemical means. The paper thus formed may be coated or impregnated with the use of different materials to make it suitable for various specific end uses such as writing paper, packing paper, currency paper, and so on.

The use of non-wood fiber (NWF) for making pulp and paper dates back more than 2000 years. The oldest surviving piece of paper, discovered in 1957 in a tomb in Sian, China has been dated to between 140 and 87 BC. This paper and similar pieces of ancient papers are all made up of pounded and disintegrated hemp fibers. Furthermore, paper historians argue that the earlier Egyptian papyrus sheets, being woven and not 'wet laid' should not be referred to as true paper. Until the late nineteenth century the only source of fiber for papermaking was rags, i.e., worn-out clothes. Since at the time clothing was made of hemp and flax (occasionally cotton), it would not be wrong to say that almost all paper in history was thus made from NWFs. However, an increased demand for paper coupled with a shortage of rags and a scarcity of hemp and flax compelled the paper industry to look for alternative sources and modifications in papermaking technology. This led to the use of the world's most abundant and cheap source of fibers: our forests. Consequently, the usage of NWF as paper pulp has been reduced to 5% of total pulp production and is restricted to developing countries and some parts of Europe.

Characteristics of Non-Wood Cellulosic Raw Material and Paper Properties

All lignocellulosic fibrous raw materials used for pulp and paper essentially consist of cellulose and lignin along with some extraneous material called extractives such as gums and resins (**Figure 1**). Cellulose, a polymer of carbohydrates $(C_6H_{10}O_5)_n$, is the main constituent of the cell wall of plants and its natural source in pure form is cotton. The length of cellulose fibers affects various physical strength properties of paper, such as tensile, burst, and tear indices, and surface and optical properties, such as smoothness and brightness. Furthermore, the degree of polymerization (DP) denoted by n in the formula varies with the source of raw material and is also affected by chemical treatment during pulping and bleaching. DP in papermaking fibers varies from 600 to 1800. Decrease in DP during pulping results in a decrease in the strength properties of paper. Hemicellulose is another constituent composed of short-chain polysaccharides, which is a polymer of five different sugars, namely glucose, mannose, galactose, xylose, and arabinose. The hemicelluloses are chemically bonded with cellulose and lignin in a plant cell wall (**Figure 1**). Thus the total carbohydrate part of the fiber is referred to as holocellulose.

Lignin

Lignocellulosic material contains a polymerized hydrophobic substance lignin, which is amorphous, highly branched, and three-dimensional. It acts as a cementing material in woody plant fibers and is mainly concentrated in the intercellular portion called the middle lamellae and to a lesser degree

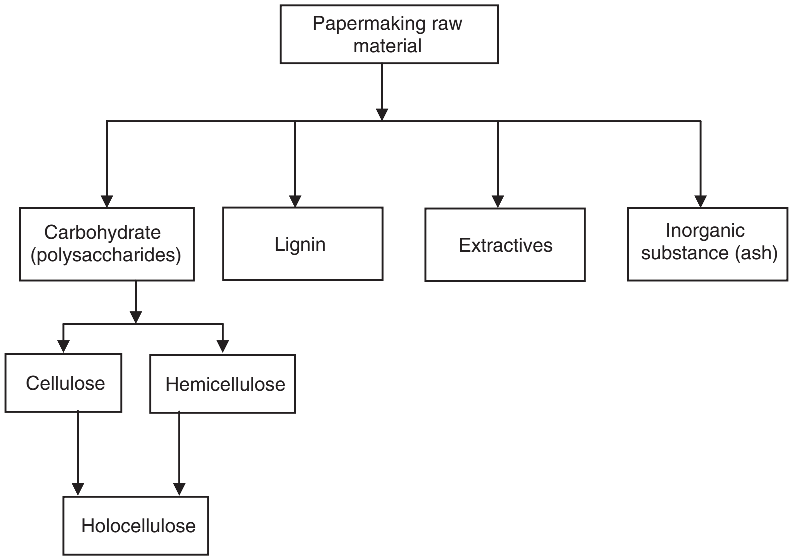


Figure 1 Components of cell wall of raw materials used for papermaking. The process of papermaking essentially comprises isolation of holocellulose and removal of lignin, extractives, and inorganic substances.

distributed in the cross-section of the cellulosic fiber. It imparts structural strength to wood but it is undesirable for papermaking as it inhibits interfiber bonding during the process of papermaking. Therefore, lignin is removed by treatment with acid or alkali, which results in its dissolution and facilitates fiber separation. The degree of lignin removal is dependent upon the desired quality and type of paper to be prepared.

In addition to cellulose, hemicelluloses, and lignin, the other group of chemical substances such as gum, resin, fatty acids, turpenes, and alcohols are also found in native fibers, depending upon the type of plant source. These substances, commonly referred to as extractives, are also undesirable for papermaking and are removed during pulping.

Most of the cellulosic raw materials due to their hydrophilic nature contain an appreciable amount of water either in green or air-dried conditions. It is, therefore, very essential to express the weight of raw material on a dry basis or wet basis. The common practice in paper mills is to express raw material weight on an oven-dried basis. This also helps in calculating the amount of various chemicals needed for wood or pulp processing. Further, wood specific gravity plays a very important role in the papermaking process and the properties of the end product. The specific gravity for softwood and hardwoods falls in the range of 0.29–0.57 and 0.30–0.70 respectively. High-density woods are harder to chip, require more energy for chipping, and are difficult for chemical penetration during pulping. Wood specific gravity strongly influences the fiber flexibility or collapse, which in turn influence the interfiber bonding and paper surface roughness. Low specific gravity wood will produce thin-walled, less coarse fibers, which collapse easily to give high physical strength properties with high paper sheet density. This makes softwoods suitable raw material for the manufacture of paper sheet of high density, low bulk, and higher physical strength. Therefore, it is clear that an ideal raw material for papermaking should have maximum holocellulose content, minimum lignin, and higher LD ratio, which is ratio of fiber length to fiber diameter. Accordingly softwoods are the best raw material for pulp making followed by hardwoods, bamboo, kenaf, and agricultural residues (**Table 1**).

Non-Wood Raw Materials for Pulp and Paper

Although any cellulose raw material can be used for the preparation of pulp and paper in the laboratory using the kraft pulping process, a proper selection of raw material is very important (from the vast source of vegetable kingdom) for commercial production. Wood, however, is the main source (60–70%) of raw material while non-woods such as bagasse, rice straw, wheat straw, reeds, bamboos and secondary fiber commonly known as recycled fiber (wastepaper) account for the rest of commercial production.

Bamboo

Apart from softwood and hardwood another most commonly used raw material for pulp is bamboo, which is used mainly in countries of the Asian

Table 1 Chemical composition, fiber dimensions, and global availability of wood and non-wood fibers for manufacture of various types of papers

Fiber source	*Cellulose (%)*	*Lignin (%)*	*Mean fiber dimension (mm)*		*Global availability in million tonnes (bone dry)*	*Types of papers*
			Length	*Width*		
Long fibers						
Cotton staple	85–90	0.7–1.6	25	0.02	18.3	Specialty papers, permanent document, banknotes, etc.
Seed flax	43–47	21–23	30	0.02	2.0	As reinforcement pulp to improve physical strength of paper, specialty papers
Hemp	57–77	9–13	20	0.022	0.12	Cigarette paper, tissue, lightweight paper, filter paper, greaseproof paper, security papers, tea bags, etc.
Abaca (manila)	56–63	7–9	6.0	0.024	0.08	Tissue and specialty papers
Medium long fibers						
Softwood	53–62	26–34	4.1	0.025	99.2	Almost all types of paper and board, and tissues of all grades
Sisal	47–62	7–9	3.3	0.02	0.50	Specialty papers
Bamboo	26–43	21–31	2.7	0.014	30.0	Printing and industrial grade papers
Kenaf	44–57	15–19	2.6	0.02	3.0[a]	Printing and industrial grade papers, tissues, etc.
Jute	45–63	21–26	2.5	0.02	13.7[b]	Most paper grades
Bagasse	32–37	18–26	1.7	0.02	120.20	Printing and industrial grade papers, greaseproof papers, and dissolving grade pulp
Short fibers						
Hardwood	54–61	23–30	1.2	0.03	41.6	Printing and industrial grades, tissues, etc.
Wheat straw	49–54	16–21	1.4	0.015	600.00	Printing and industrial grades of papers
Rice straw	43–49	12–16	1.4	0.008	360.00	Printing and industrial grades of paper
Esparto	33–38	17–19	1.2	0.013	-	Specialty papers
Rye straw	50–54	16–19	1.3	0.014	40.00	Printing and industrial grades of paper

[a] Bast fiber.
[b] Whole stalk.

subcontinents such as India, China, Malaysia, Indonesia, Thailand, Myanmar, etc. Bamboo fiber is longer than that of hardwoods but shorter than softwood and has a high silica content, which poses some problems in chemical recovery and papermaking. This is overcome by using desilication of pulping spent liquor and improved paper technology. The bamboo species most widely used for pulp and paper manufacture are *Dendrocalamus strictus*, *D. hamiltonii*, *Bambusa tulda*, and *Melocanna baccifera*.

Agricultural Residues

Growing demand for pulp, shrinkage of forests, and the consequent shortage of pulpwood experienced by pulp and paper mills around the globe have led to the search for alternative sources of raw material from agricultural residues such as sugarcane bagasse, rice straw, wheat straw, and cotton stalks. These raw materials are used for the manufacture of pulp and paper in the countries where forest-based raw material, i.e., wood is not available due to environmental considerations and to dwindling forest cover. The use of these raw materials has increased considerably and is expected to raise further the pulp and paper manufacture capacity particularly in countries like India, Pakistan, China, Egypt, Turkey, Indonesia, Bangladesh, Mexico, and Taiwan. The major sources of NWF in agricultural residue category are as follows.

Bagasse Sugarcane is an important annual crop grown primarily for the manufacture of sugar on a very large area all over the globe particularly in Asian countries, South America, South Africa, the USA, and the UK. The fibrous residues left after the extraction of sugar juice is known as bagasse and is a very promising pulping material for paper.

The greatest advantage in using bagasse as NWF lies in the fact there is no additional cost involved in growing and harvesting, and only the collection cost is borne by the paper industry. However, bagasse is usually used as fuel in the sugar mill's boiler furnace. Therefore only the surplus bagasse is available for use as a pulp material in the vicinity of sugar mills. Bagasse contains 25–30% pith, a nonfibrous material unsuitable for pulping. It is, therefore, removed by a wet or dry depithing operation and subsequently pulped either by soda or kraft process. Recent advances in pulping and papermaking technology have made it possible to use bagasse for the manufacture of cultural, industrial, and greaseproof grades of paper. It is also used for the manufacture of dissolving grade pulp for the manufacture of viscose rayon.

Rice and wheat straw Rice and wheat, like sugarcane, are annual crops grown in major areas of the globe. Their straw is used for the manufacture of pulp which is then made into various grades of paper using the soda process in minimills in various parts of the world. These agricultural residues yield short fiber and due to its higher silica and ash content, wheat straw is favored over rice straw as pulp material. Papers made solely from straws can be recycled only a few times due to weak fibers, which loses its strength properties after one or two pulping cycles. Therefore, these short-fibered straw pulps are occasionally blended with long-fiber reinforcement pulp to produce various varieties of cultural and industrial grades of papers of higher strength. These straws represent a promising source of fiber and are being used primarily in countries where wood is in short supply.

Other Non-Wood Plant Fibers

Other non-wood plant fibers are esparto, elephant grass, reeds, sabai grass, bast fibers of jute, hemp, kenaf, flax, and leaf fibers of abaca and sisal. In this class also comes seed hairs, e.g., cotton linter. Cotton is an extensively used raw material in the textile industry, so its use in pulp and paper is very limited and used only in the manufacture of specialty paper like currency paper and permanent papers. Some of the most abundant and widely used NWF in this category are described in brief in the following section.

Kenaf Kenaf (*Hibiscus cannabinus* and *H. sabdariffa*) belongs to the same plant family as cotton, okra, the ornamental hibiscus, and hollyhocks. It is an annual crop, which is normally cultivated in the tropics and subtropics where temperatures are greater than 20°C. It is harvested for fiber soon after its flowering. Under good conditions kenaf will grow to a height of 5–6 m in 6–8 months and can yield up to 30-35 tonnes ha^{-1} of dry woody material. It is grown in Thailand, China, India, Australia, and the USA. Kenaf fiber is classified as medium long fiber similar to bagasse; however, it has a higher cellulose content and lower lignin content as compared to bagasse, and is preferred as a pulp material over bagasse. Kenaf crops are more susceptible than trees to abnormalities in seasonal weather changes, e.g., droughts and floods. Further, the harvested raw material needs storage for a number of months to sustain the supply of pulp material and it is prone to decay. Moreover, kenaf has a mixture of long bast fiber (57%) and short core fiber (41%), which need separation and subsequent pulping in separate lots. Kenaf is used for the manufacture of almost all varieties of paper including specialty papers.

Hemp Hemp (*Crotoleria juncea*) is an annual crop, which can be grown on normal to poor soils and yields three to four times more useful fiber per hectare per year than forests. It attains 2.5–3 m in height after 4 months of growth and is widely grown in Asia, Central America, and Africa. Hemp fiber is classified as a long fiber material and is considered as one of the best pulping materials for the manufacture of expensive specialty papers such as cigarette paper and others lightweight papers, and also in blending with weak pulps as a reinforcement pulp in certain grades of cultural, industrial papers.

Jute Jute (*Corchorus olitorius, C. capsularis*) is also an annual herbaceous plant mainly cultivated in South and Southeast Asia. The average dry yield of jute fiber varies from 1.6 to 2.0 tonnes ha^{-1} $year^{-1}$. After extraction of fibers, the remaining jute sticks (core) are usually used to make fences and as fuel. However, the core fibers, which are shorter than bark fibers, are utilized for many other value-added industrial purposes and cheap-grade pulp and paper manufacture. The five major jute producing countries (namely India, Bangladesh, China, Nepal, and Thailand) account for about 95% of world production. Jute fiber is used for the production of high-quality writing and printing papers and a variety of specialty papers. Like the other NWF, using jute for pulp and paper has many advantages; it requires less chemicals for pulping and consumes less energy due to its lower lignin content than woody fibers.

Waste Paper (Secondary Fiber)

Waste paper has become a very important secondary source of raw material for papermaking in recent years. However, collection and sorting of various grades of waste paper, such as mixed waste paper, corrugated waste paper, white paper cuttings (waste from printing presses), waste news print and its conversion into paper, is important in those regions where it is difficult to get a large amount of cheap raw material on a sustainable basis for papermaking. Further the cost of collection, sorting, and transportation are practical problems, which limit its wide-scale use in papermaking. But due to easy recycling and emerging new technologies for de-inking by biological and chemical treatments, the use of waste paper is likely to increase in future. The recycling of waste paper is further preferred due to environmental reasons as it facilitates conservation of trees and other cellulose raw material for future use.

Papermaking Process for Non-Wood Fibers

Essentially the process of papermaking involves the breaking up of the raw material into small pieces, pulping, bleaching, washing, stock preparation, and preparation of paper sheets (**Figure 2**). A brief account of various aspects of these processes is explained below.

Pulping (from Raw Material to Pulp)

- Cleaning: This involves elimination of all undesirable components such as dirt, sand, and other contaminants.
- Cutting/chipping: Most of the NWF are too long or big in size. Therefore, to facilitate homogeneous chemical treatment or mechanical treatment raw material is cut or chipped to uniform size.
- Screening/classification: Fibers are screened or classified by centrifugal and gravitational processes to get a uniform sized fibrous material for further processing.
- Fiber separation: Cellulose fibers are separated either by chemicals that dissolve the lignin, or by mechanically separating the fiber structure. The material thus prepared is referred to as pulp and this process of fiber separation is called the pulping operation.
- Bleaching: This is an optional operation to achieve a higher brightness or whiteness for a better appearing sheet of paper. For some grades of paper manufacture such as packaging paper and board, bleaching is not required. Traditional bleaching has been done by chlorine compounds, which are being replaced gradually due to environmental considerations, by the use of oxygen, hydrogen peroxide, and ozone. Non-woods can be bleached relatively easily by hydrogen peroxide.
- Refining/beating: In this process fibers are subjected to mechanical action for the modification of the fiber structure and to facilitate fiber-to-fiber bonding. This process adds to the strength of the paper in the finished paper sheet.

Papermaking (from Pulp to Paper)

- Dilution: The pulp is diluted with a large amount of water to convert pulp into a dilute fiber suspension to facilitate formation of a uniform sheet.
- Formation: The dilute fiber suspension is injected on to a fine-mesh wire screen. This results in drainage of excessive water and settling of the fiber networks into a flat sheet.
- Pressing: Sheet consolidation and dewatering results by mechanical pressing.
- Drying: The wet sheet is dried over a steam-heated dryer cylinder by the evaporation of water.
- Calendering (optional): The dried sheet is calendered for surface smoothness.
- Sheeting/reeling: Finally the formed dried paper sheet is cut to the required size.

Conclusions

Rising concern about the 'greenhouse effect' demands that wasteful disposal of fibrous material

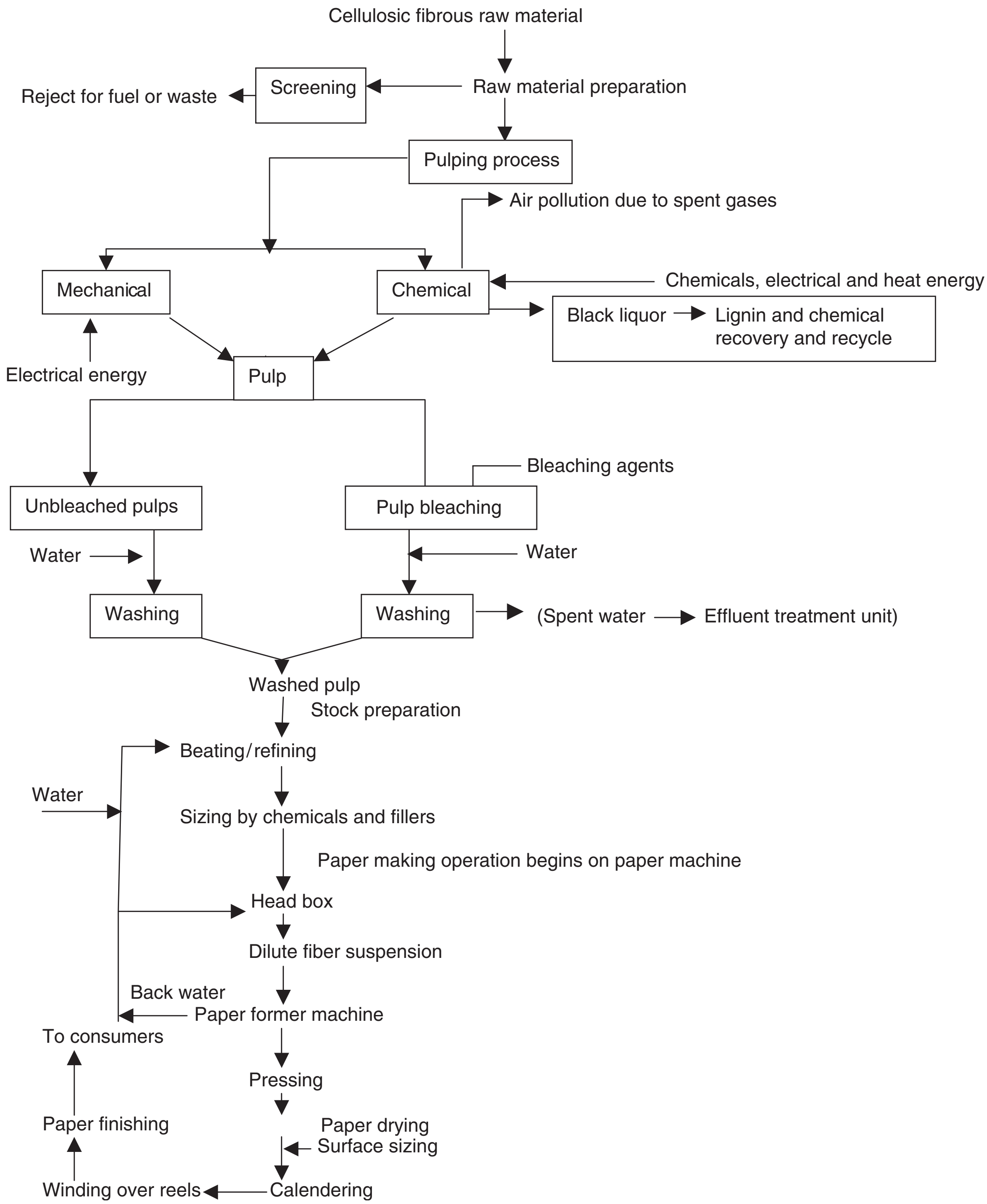


Figure 2 Flow diagram of pulping and papermaking process.

through carbon emission should be stopped. Consequently, efforts are being made to increase the use of non-wood fibers such as flax, hemp, rice, and wheat straw as valuable fiber supplements to the pulp and paper and allied industries. It has been suggested that such efforts will not only reduce demands on forest fiber supplies, but can also reduce greenhouse gas emissions. Further, carbon can be managed in a valuable material form as opposed to burning the agriculture residues as waste. Further, there is consensus all over the world that the non-wood fibers can be easily and quickly grown and are suitable for making paper of excellent quality. However, their usage is restricted to tropical developing countries due to the fact that contemporary papermaking in developed countries relies primarily on wood as the only significant source of paper fiber. The recent interest in using non-wood fibers, particularly hemp, in the Western world perhaps stems from strong environmental considerations.

Most of the forest resources in Europe, North America, Asia, and Australia have been utilized for paper production and other uses. So there seem to be valid reasons to look to NWF as a paper pulp source so that forests have sufficient time to rejuvenate and increase the forest cover. However, the research and development side of the papermaking industry has been focused on wood pulping technologies and equipment. Therefore, a lack of success and conservative attitudes with most non-wood initiatives stem from the application of wood pulping technology to non-wood fibers resulting in poor pulp quality and incorrect handling. This is generally true for digestion and refining operations, which tend to produce overcooked and over refined pulps due to the higher energy requirements of wood-based processes when they are used for non-wood fibers. Further, lack of will and financial support for the research and development wings of the paper industry, despite strong technical evidence of the potential of non-wood fibers, has resulted in the nonproliferation of this new concept. Nevertheless, there are many NWF-based paper mills already producing a wide range of paper grades. Finally, there is also a resurgence of initiatives for advancing the cause of the NWF paper industry to promote non-wood fiber as a cost-effective, high-quality competitive, and an environmentally friendly source for papermaking.

Further Reading

Casey J (1980) *Pulp and Paper Chemistry and Technology*, 3rd edn, vol. 1. New York: John Wiley.

Catling D (1982) *Identification of Vegetable Fibres*. London, UK: Chapman and Hall.

Dean WR (2001) Non-wood fibres, past, present and future. In: *Unpublished. Proceedings of the Pira Conference on Cost Effectively Manufacturing Paper and Paper Board from Non-Wood Fibre and Crop Residues*, Leatherhead, UK.

Deng M and Dodson CTJ (1994) *Paper: An Engineered Stochastic Structure*. Atlanta, GA: TAPPI Press.

Kocurek MJ (1993) *Pulp and Paper Manufacture*, vol. 3. Atlanta, GA: TAPPI Press.

Kocurek MJ (1996) *Pulp and Paper Manufacture*, vol. 5. Atlanta, GA: TAPPI Press.

Kocurek MJ (1997) *Pulp and Paper Manufacture*, vol. 1. Atlanta, GA: TAPPI Press.

Liu A (2000) *World Production and Potential Utilization of Jute, Kenaf and Allied Fibres*, Proceedings of the 2000 International Kenaf Symposium, Hiroshima, Japan.

McKinney RJ (ed.) (1995) *Technology of Paper Recycling*. UK: Blackie: Glasgow.

Paavilainen L (2001) Paper making potential of non-wood fibres. In: *Unpublished. Proceedings of Pira Conference on Cost Effectively Manufacturing Paper and Paperboard from Non-Wood Fibre and Crop Residues*, Leatherhead, UK.

Rance HF (1982) *Handbook of Paper Science*, vol. 2, *The Structure and Physical Properties of Paper*. Amsterdam, The Netherlands: Elsevier.

Roberts JC (1996) *The Chemistry of Paper*. Letchworth, UK: Royal Society of Chemistry.

Scott WE (1996) *Principles of Wet End Chemistry*. Atlanta, GA: TAPPI Press.

Singh SV (1995) *Advances in Pulp and Paper Research in India*. Dehradun, India: Indian Council of Forestry Research and Education.

Smook GA (1992) *Handbook for Pulp and Paper Technologists*. Vancouver, Canada: Angus Wilde.

Overview

G M Scott, State University of New York, Syracuse, NY, USA

Introduction

There is no denying that paper is very important in today's world. We use it for money, record-keeping, communication, personal hygiene, and many other uses personally, commercially, and industrially. We often take paper for granted: it is ubiquitous but essential in our lives. However, very few of us think about how it is made beyond that it is made from trees. Paper can be an extremely complicated product, both in its components and in its manufacture. For example, printing and writing paper has distinctly different properties from tissue. It is often difficult to use one type of paper for another purpose. (How many of us has tried to draw on a dinner napkin?) **Table 1** is a selected list of the variety of paper grades that are produced today.

Papermaking is ever-evolving and developing. As the needs of society change, the types of paper being produced have also changed. The personal computer revolution was supposed to bring about the 'paperless office' and make printed newspapers obsolete. Paper consumption has not decreased, however, due to the increased use and popularity of computers. The types of paper demanded by consumers have changed significantly. In keeping up with computer technology, grades of paper for use in ink-jet printers and for the home-printing of digital photographs have been developed. Per capita consumption of paper has been increasing steadily over the past decade. Worldwide, paper consumption is increasing at an even greater rate as developing countries make

Table 1 Examples of grades of paper made today. This list represents only a small fraction of the different grades of paper manufactured in the world

Printing and writing	Photographic
Facial tissue	Bathroom tissue
Tape backing	Grocery sack
Newsprint	Light-weight coated
Linerboard	Corrugating medium
Art paper	Parchment
Currency paper	Paperboard
Book	Index card
Construction paper	Paper cores
Cover paper	Electrical insulating
Envelope	Butcher paper
Medical paper	Glassine
Folder paper	Greeting card
Ink jet	Kraft
Label base	Laminating
Magazine	Napkin
Packaging	Tablet
Towels	Specialty

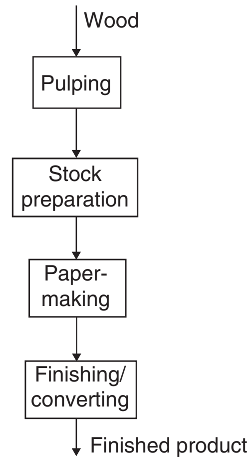


Figure 1 Overview of the papermaking process from wood to finished products. Pulping disassembles the wood into its component fibers while stock preparation prepares the fibers for papermaking. Papermaking reassembles the fibers into a sheet and finishing/converting makes that sheet into the final product.

increased use of paper. The paper industry is probably one of the most sustainable industries in the world. Its primary raw material, wood, is being replenished at a rate faster than consumption. Modern integrated paper mills are nearly energy self-sufficient. In addition, there is a well-established infrastructure for the recycling of paper.

Paper is typically defined as a 'felted sheet of fibers formed on a fine screen from a water suspension.' The key elements of this definition are that the raw material (pulp) has been previously reduced to individual fibers and suspended in water. This pulp is then treated and deposited on to a fine screen to remove the water, leaving a randomly oriented sheet that is subsequently consolidated and dried. In practice, modern paper also contains a variety of nonfibrous materials in order to give the paper its desired properties. These materials include clay, calcium carbonate, starch, and specialty chemicals that impart waterproofing, flameproofing, smoothness, and other properties. Paper thicker than 0.3 mm is often termed paperboard.

Figure 1 shows an overview of the papermaking process from wood to finished product. The wood is first pulped, or rendered into fibers, in one of two broad methods (*see* **Pulping**: Chemical Pulping; Mechanical Pulping). In stock preparation, mechanical action changes the surface properties of the fiber, allowing them to develop the papermaking properties that are desired. Different pulps (in terms of pulping methods and/or wood species) are blended with nonfibrous fillers and specialized chemicals. The papermaking process removes water from the sheet while forming and consolidating the sheet, which is dried to its final moisture content of approximately 5%. In the final step, finishing/converting, the final products of the process (e.g., envelopes, tablets, sheets, boxes) are produced from the large rolls of paper produced by the papermachine.

History of Papermaking

Given our definition of paper above, the first paper was reputedly made in China around AD 105 by Ts'ai Lun who was charged to find a new material for record-keeping. Papyrus, invented earlier by the Egyptians and not considered a true paper, was made by pounding strips of papyrus together to form a sheet. Ts'ai Lun pulverized the inner bark of mulberry tree, producing a pulp, and draining the fiber suspension using a fine screen. The resulting sheets were subsequently pressed and air-dried. For several centuries, China held a monopoly on papermaking, but eventually the technology traveled from China to Japan and Arabia, and into Europe by the eleventh century. By this time, cotton in the form of rags and linen was the primary source of raw materials for papermaking. A shortage of rags in the eighteenth century prompted papermakers to look towards other sources for fiber, especially wood. At this time, paper was still handmade one sheet at a time, using molds consisting of a fine wire screen (**Figure 2**). The invention in AD 1798 by Louis Robert of the papermachine, which could form a continuous sheet of paper, exacerbated the raw material shortage, prompting the development of the modern wood-pulping techniques in the nineteenth century. This century also saw many improvements in the continuous papermachine (**Figure 3**). While the basic concepts of papermaking remain unchanged since

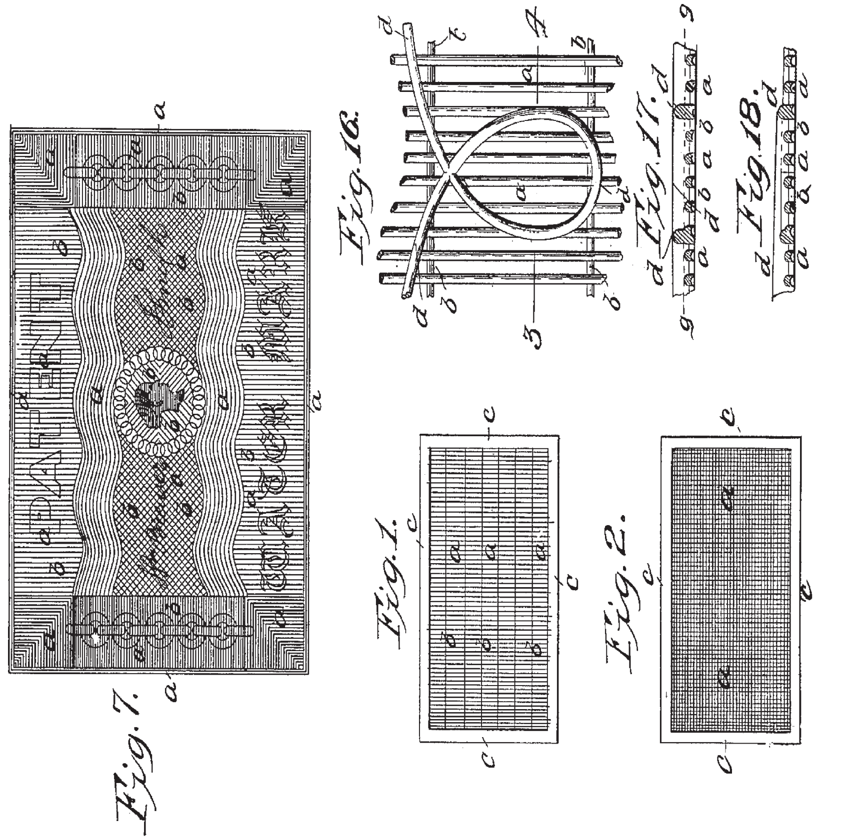


Figure 2 Patent drawing of mold for the handmaking of paper (US patent 7,979). This screen was hand-dipped into a slurry vat, drained, pressed, and removed for drying to produce paper one sheet at a time.

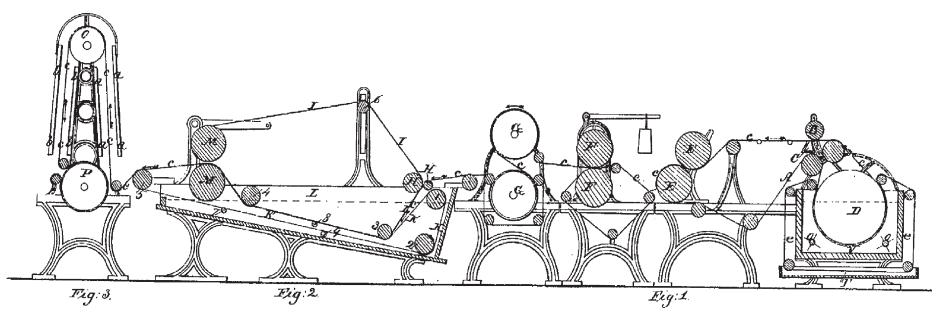


Figure 3 Patent drawing of early paper machine from the 1830s (US patent 8,698). All of the basic processes of a modern machine are present in this machine.

these developments, many refinements have led to the modern papermachine (**Figure 4**) that today operates at speeds of over 1800 m min^{-1}. **Table 2** summarizes the major historical milestones in the papermaking process.

Goals of Papermaking

Paper is an engineered product. The proper combination of raw materials and processing steps results in paper having the desired properties for a particular use. A large number of variables, from the raw materials to the type of equipment used, affect the final properties of the sheet (**Table 3**). It is the interaction of these variables that gives paper the properties needed for any particular grade. **Table 4** gives some of the desired properties of some common grades of paper as well as the typical pulp furnish used in that grade. As can be seen, different grades have significantly different properties, including printability, absorbency, and strength.

For example, newsprint must have excellent printability and opacity (so the writing on the back of the sheet does not show through). However,

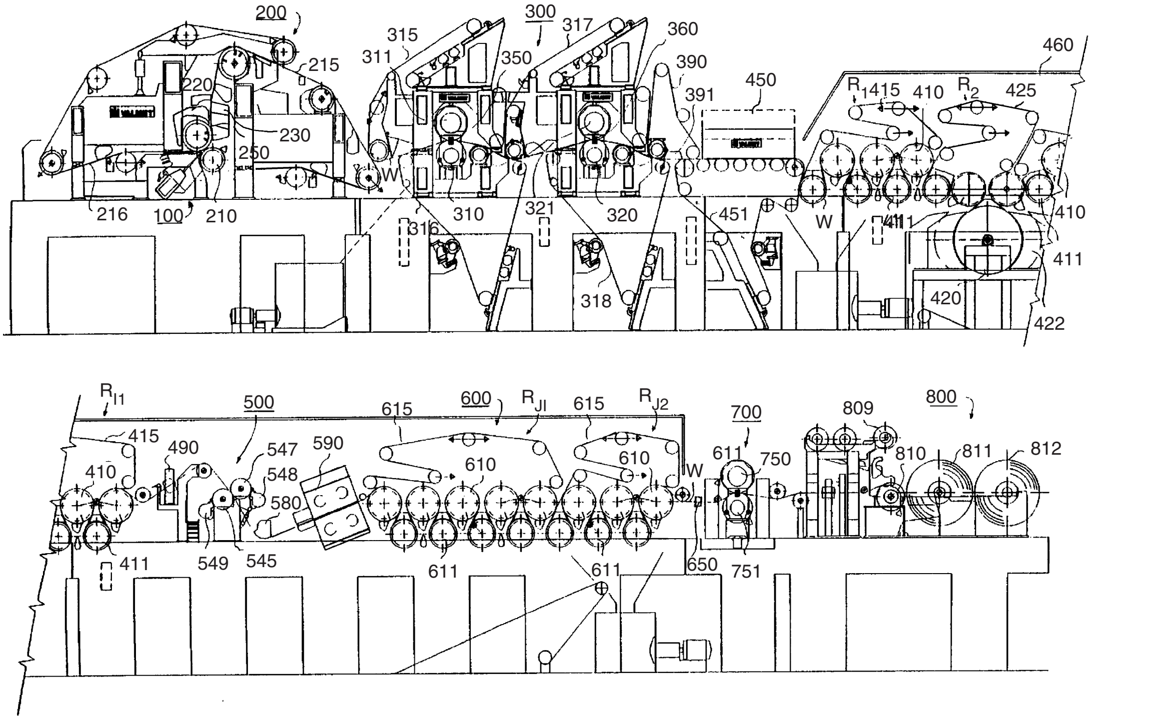


Figure 4 Patent drawing of modern paper machine (US patent 6,413,371). While much more complicated, this machine contains the basic operations of draining, pressing, and drying.

because of its limited life span of 1 day, it must be inexpensive. For newsprint, a thermomechanical pulp (TMP) is used. Printing and writing paper, having a much longer life span and higher brightness, uses more expensive bleached kraft pulp.

Papermakers use different raw materials for their furnish depending on the desired properties of the sheet. The different raw materials impart characteristic properties to the sheet (**Table 5**). While kraft (chemical) pulps are used for strength, they have relatively poor optical qualities. Mechanical pulps tend to be just the opposite. Fillers, such as calcium carbonate and clay, are inexpensive and impart excellent optical properties, but impart no strength to the sheet. Some specialty papers, such as paper for currency and bank notes, are made of nonwood fibers such as linen, flax, and cotton. Consumer demand has expanded the use of recycled fiber in many grades of paper. Some grades, such as tissue, toweling, and linerboard, are almost exclusively made from recycled fibers. Many other grades, such as printing and writing, have varying percentages of recycled fiber. Broke is internally recycled paper (e.g., off-specification paper) and is used in the furnish of most mills.

Paper Properties

The properties of paper can be divided into three main groups: physical, strength, and optical properties. **Table 6** summarizes the major tests that are performed on paper in these three categories. Physical properties are those that measure some structure of the paper such as grammage, thickness, and smoothness. Another physical property, density, ρ, is a function of the grammage, W, and thickness, t as $\rho = W/t$. Strength properties are those that measure the force or pressure needed to cause the paper to fail. Tensile, burst, tear, and folding endurance are all measurements of the ultimate failure of the paper in some prescribed manner. There are many more strength properties and measurement of paper; many of these are specific to certain grades of paper. Optical properties measure the paper's response to light, including brightness, color, and opacity. For some specialty grades of paper, some other properties are important, such as electrical properties. In other cases, the ability of the paper to resist water or oil penetration is very important. Each grade of paper has its own set of properties that must be met by the manufacturing process. The Technical Association of the Pulp and Paper Industry promulgates a complete set of testing methods for most of these paper properties.

Stock Preparation

Between pulping and the actual papermachine, the raw materials must be properly prepared. The

Table 2 Milestones in papermaking history

Year	*Milestone*
600 BC	Egyptians manufacture papyrus, which is not a true paper
440 BC	Greeks use parchment, the treated skins of sheep and goats
AD 105	Chinese invent the first true paper from the bark of the mulberry tree, reputedly by Ts'ai Lun in the court of Emperor Hedi
AD 610	Paper is made in Japan, where it becomes a part of the culture, being used for writing, fans, garments, and dolls
AD 704	Paper is made of cotton on the Arabian peninsula
AD 900	Paper (which was imported) used in Europe for papal proclamations
AD 1009	Papermaking introduced into Europe (Spain) and rags used as a raw material
AD 1330	Watermarked paper invented in Italy
AD 1411	First papermill constructed in Germany
AD 1453	Invention of the printing press greatly increases the demand for paper
AD 1588	Paper is made in England
AD 1680	Paper is made in Mexico
AD 1690	Paper is made in North America near Philadelphia
AD 1719	A shortage of rags for papermaking prompted investigations into other fiber sources, including wood
AD 1798	Invention of the continuous papermachine by Louis Robert
AD 1817	Development of the steam-heated dryer cylinders
AD 1840	Development of groundwood (mechanical) pulping process to allow paper to be made from wood
AD 1854	Development of soda process (chemical) which uses sodium hydroxide to digest wood
AD 1867	Development of sulfite process (chemical) which uses sulfites to digest wood
AD 1879	Development of kraft process (chemical) which adds sodium sulfate to the soda process
AD 1923	Development of twin-wire former
AD 1960	Development of the wet-end foil for dewatering
AD 1960s	Development of the synthetic press felts and nonmetallic wires

Table 3 Variables involved in papermaking from stock preparation to the paper machine

Raw materials	
Fiber furnish	
Type of wood	Softwood, hardwood
Time of harvest	Winter, summer
Location	Northern, southern, tropical
Pulping method	
Chemical	Kraft, sulfite
Semichemical	Chemimechanical pulp (CMP), chemithermomechanical pulp (CTMP), neutral sulfite semichemical (NSSC)
Mechanical	Groundwood, thermomechanical (TMP), refiner mechanical (RMP)
Recycled	Newsprint, old corrugated containers, mixed office waste, mixed paper
Fillers	Calcium carbonate, clay, titanium dioxide
Chemicals/ additives	Wet strength agents, dry strength agents, starch, retention aids, defoamers
Stock preparation	
Refining	Beaters, disk refiners, conical refiners
Cleaning	Hydrocyclones
Screening	Pressure screens, sidehill screens
Paper machine operations	
Headbox	Open, air-padded, hydraulic
Forming section	Fourdrinier, twin wire, multiply former, cylinder former
Press section	Solid roll, extended nip, suction roll
Dryer section	Two-tier run, single felt, single-tier run
Size press	Coating, surface treatment
Calender stack	Number of nips, heated nips
Finishing operations	Sheeting, converting, packaging

objective of the stock preparation step in papermaking is to process the fibers from the pulping step and combine them with the nonfibrous materials in a manner suitable for papermaking. Stock preparation consists of the processes summarized in **Table 7**. Consistency is a measure of the solids content of a sample of pulp. It is defined as the dry mass of the solid material over the original mass. In stock preparation, consistencies typically range from 0.5% or lower (in the final feed to the papermachine itself) up to 15% for high-density storage.

Repulping

For papermaking, the pulp fibers must be dispersed in water for pumping and the papermaking process. If a mill is integrated, the fibers will remain in a high-consistency slurry from the pulp mill. However, many paper mills do not have a pulp mill associated with them. So, these mills must take market pulp, often dried to 90% solids, and redisperse the fibers in water using a repulper. Repulpers or hydrapulpers are large mixing vessels with one or more revolving agitators to provide circulation and energy sufficient to disperse the fibers in the water.

Refining

The terms refining and beating are commonly used interchangeably in the paper industry and refer to the use of mechanical energy to develop papermaking properties of fibers. As with many processes, there are tradeoffs which depend on the products being made. In general, the strength properties, such as tensile and burst strength, increase with more refining. Tear strength tends to decrease with refining. Optical properties, such as opacity, tend to

Table 4 Properties and furnishes of common grades of paper

Grade	*Fiber furnish*	*Properties*
Newsprint	TMP	Printability, optical properties, inexpensive, short life
Printing/ writing	SWK, HWK, sulfite	Printability, whiteness, optical properties, ink holdout
Grocery sack	SWK	Strength
Tissue	Sulfite, recycled	Absorbency, strength, softness
Linerboard	SWK, recycled	Strength, printability
Corrugating medium	HWK, recycled	Stiffness, conformability
Paperboard	Recycled	Bulk, stiffness
Paper toweling	Recycled	Wet strength, absorbency

TMP, thermomechanical pulp; SWK, softwood kraft; HWK, hardwood kraft.

Table 5 Characteristics of various papermaking materials

Furnish	*Characteristics*
Softwood kraft (SWK)	Strength
Hardwood kraft (HWK)	Bleachability; optical properties
Sulfite	Bleachability; softer fiber
TMP/RMP	High yield; optical properties
Groundwood	Cheap filler; optical properties
Fillers	Good optical properties; inexpensive
Recycled	Consumer demand; mixed properties
Nonwood	Specialty products
Broke	Available; needs to be used; source of fiber

TMP, thermomechanical paper; RMP, refiner mechanical pulp.

decrease with refining as the fibers become more conformable and there are fewer fiber–air interfaces to scatter light. In all cases, the rate at which water drains from the fiber decreases. Slower drainage translates to lower production on the papermachine. Thus, it is necessary to refine such an amount that the necessary strength properties are achieved, while maintaining production rates on the papermachine.

The drainage rate of the pulp is often characterized by the Canadian Standard Freeness (CSF) measurement (Tappi test method T 227). In the test, water is drained from a known sample of pulp; freeness is the volume of water that overflows a calibrated orifice at the bottom of the collection cone. The greater the overflow, the faster the pulp drains. CSF is typically used in North American paper mills. Two other freeness tests used around the world include the Schopper Reigler and Williams. Typically, chemical pulps have a typical freeness of 400–700 ml CSF depending on the degree of refining. Mechanical pulps are much slower draining with freenesses in the range 100–200 ml CSF.

A variety of equipment is used for refining (or beating) in the paper industry. Early beating was done batchwise, using a Hollander beater or similar equipment (**Figure 5**). In this batch process, the pulp at 3–6% consistency circulates in an oval tank where it passes under a roller with bars against a bedplate. However, with the increasing production rates at many mills, the batch process became too slow, and mills changed over to conical and then to disk refiners. Both types of refiners operate similarly in

Table 6 Important paper properties and testing methods (Tappi)

Property	*Test method*[a]	*Description*
Physical properties		
Grammage	T 410	Mass per unit area of paper; also known as basis weight
Thickness	T 411	Single sheet thickness (caliper) of paper
Smoothness	T 538	Measurement of air flow between the surface of the sheet and two pressurized, concentric annular rings
Moisture content	T 412	Amount of water in paper
Strength properties		
Tensile	T 494	Force per unit width required to break a specimen in tension
Tear	T 414	Force perpendicular to the plane of the paper required to tear multiple sheets through a specified distance
Fold	T 423/T 511	Measures the ability of paper to withstand repeated bending, folding, and creasing
Burst	T 403	Pressure in a rubber diaphragm required to rupture a clamped sheet of paper
Optical properties		
Brightness	T 452/T 525	Measures the reflectance of paper
Color	T 524/T 527	Measures the color of paper with tristimulus filters (red, green, blue)
Opacity	T 425/T 519	Measures the ability of a sheet to obscure printing on a backing sheet

[a]Tappi test method published by the Technical Association of the Pulp and Paper Industry, Atlanta, GA, USA.

Table 7 Operations in stock preparation

Operation	*Description*
Repulping	Dispersion of the pulp fibers in water
Refining	Modification of the fibers and fiber surfaces through mechanical action
Cleaning and screening	Mechanical separation of undesirable materials in the pulp
Blending	Mixing of fibers and fillers to achieve desired sheet properties
Chemical addition	Use of specialized chemicals to achieve desired properties or operation

Figure 5 Jones–Bertram beater, which is similar to a Hollander beater. As the pulp circulates, it is refined in a batch process.

Figure 6 Small pilot disk refiner. Two facing rotating plates refine fibers in a continuous process.

Table 8 Effects of refining on papermaking fibers

Effect	*Description*
Fiber shortening	Cutting of fibers by the refining bars, producing shorter fibers
Fines production	Clipping and removal of fibrils from surface of fiber
External fibrillation	Increasing the fibrils on surface of fiber
Internal fibrillation	Increasing the swelling and hydration of the fiber

that the pulp passes between two surfaces that have bars over and between which the pulp must pass. In conical refiners (Jordan and Claflin refiners), the bars are on a tapered plug rotor which rotates inside the corresponding shell. In disk refiners, the pulp passes between two circular flat plates with bars. The two plates are either counterrotating or one plate is rotating while the other is fixed. Refiners operate with clearences of 0.1–1.0 mm between the bars on the two facing plates (**Figure 6**).

The passage of papermaking fibers through the close clearance of the refiners has several effects on the fibers, some beneficial to the development of the fiber properties and others that are detrimental. **Table 8** summarizes these effects on the fiber. In general, fiber cutting and fines (very short fibers) production are undesirable effects. One aspect of a fiber that determines the strength of a sheet of paper is the fiber length, especially tear strength. External fibrillation is the increase in the amount of fibrils raised from the surface. These fibrils, which look like 'hair' on the surface of the fiber, can interact and bond with similar fibrils on other fibers. The greater interaction between fibers leads to greater fiber-to-fiber bonding and greater-strength paper. Likewise, internal fibrillation, the delamination of the fiber structure, increases the flexibility of the fiber. Greater conformability also allows greater interaction between fibers and hence increased sheet strength. Refiners can be operated to favor internal and external fibrillation over fiber shortening and fines production by increasing the interaction between fibers in refining. With the greater consistency in the refiner, fibers tend to interact to a greater degree with each other rather than with the refiner plates. Gentler refining, using lower specific energies and wider plate separations, tends also to reduce the fiber cutting and fines production.

Different fibers refine at different rates. The degree of refining is typically measured through a drop in the CSF of the pulp. **Table 9** summarizes the energy needed per kilogram of pulp to drop the freeness by 100 ml CSF. Unbleached softwood kraft typically takes the most energy to refine. Bleaching the pulp weakens the fiber structure and makes it easier to refine. Hardwoods, which have shorter fibers than softwoods, also refine easier. Recycled paper, since it has already been refined at least once, also tends to require less energy to refine than the corresponding virgin fiber. Many paper grades are blends of different fibers. In the stock preparation step, it is usually necessary to refine these fibers separately as

Table 9 Energy required to change the freeness of the given furnish by 100 ml Canadian Standard Freeness (CSF)

Furnish	*Refining energy (kJ kg^{-1})*
Unbleached softwood kraft	280–360
Bleached softwood kraft	140–160
Bleached hardwood kraft	70–120
Mixed office paper	100–140
Old corrugated containers	100–180
Old newsprint	200–360

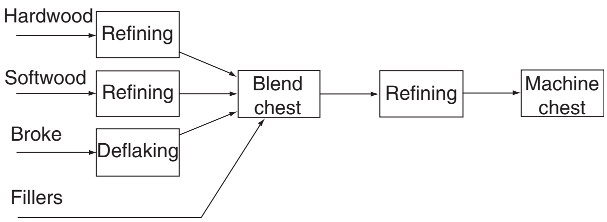


Figure 7 Overview of typical refining layout for stock preparation. Because of the different refining behavior of different fibers, they are often refined separately and then blended. A small amount of refining may be done after blending to 'fine-tune' the fiber properties.

they refine at different rates. For example, refining a blend of hardwood and softwood fibers together typically overrefines the hardwood and underrefines the softwood. As shown in **Figure 7**, the different furnishes are usually refined before blending. A small amount of refining ('tickler refining') based on feedback from the papermachine may be done after blending to meet the final requirements of the papermachine.

Cleaning and Screening

The cleanliness of the pulp going to the paper machine directly reflects on the quality of the final sheet. Most paper machines have one or more systems of screens and cleaners to remove contaminants that may affect the quality of the resulting sheet. While different fundamental processes are the basis for separation in different separation equipment, it is generally accepted that screens remove the relatively larger contaminants, while the various types of cleaners remove mid-sized contaminants. The smallest contaminants are generally removed in washing, thickening, and flotation operations, but these are not typically used on the approach flow to a papermachine.

Hydrocyclones Hydrocyclones, otherwise known as centrifugal cleaners, vortex cleaners, or centricleaners, came into widespread use in the paper industry in the 1950s. Prior to this, hydrocyclones were commonly used in the mining industry for separations. A hydrocyclone consists of a cylindrical-conical vessel with the inlet flow introduced tangentially at the top (**Figure 8**). The tangential inlet produces a helical flow of material in which centrifugal action and fluid shear force the denser material to the outside surface while the less dense material migrates to the center of the vortex. The outlet at the top of the hydrocyclone draws off the less dense material while the bottom nozzle removes the dense material that was thrown to the outside of the vortex. In the paper industry, the hydrocyclones tend to be 7.5–15 cm in diameter with the smaller-diameter cyclones developing the higher centrifugal forces.

Figure 8 Pilot plant hydrocyclone cleaners manufactured by Bird. Density differences allow the removal of the heavier contaminants.

As with any separation process, it is not a perfect separation. With hydrocyclones, there is a significant amount of fibers and other papermaking material in the reject stream to be recovered. **Figure 9** shows a three-stage system in which the accepts from the secondary and tertiary stages are returned to the previous stage while the rejects from each stage go to the subsequent stage. The primary purpose of the secondary and tertiary stages is not necessarily to

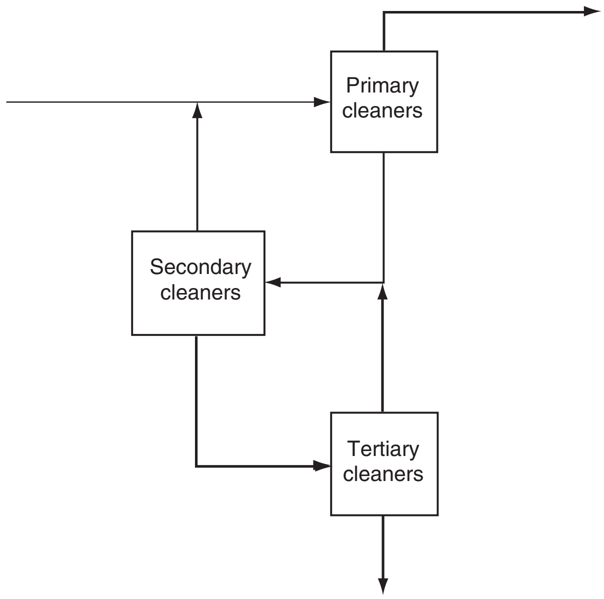


Figure 9 Three-stage cascade cleaner system. The accepts from each stage (top arrow) return to the previous stage, while the rejects (bottom arrow) go to the subsequent stage. The tertiary-stage rejects are removed from the system.

clean the pulp further. In fact, in most cases, a single stage produces cleaner pulp. However, the secondary and tertiary stages of cleaners recover usable pulp from the reject streams and return it to the primary screen. Some operations will even use four- and five-stage systems in order to recover the maximum amount of fiber.

Pressure screens Pulp is screened to remove oversized, unwanted particles before they can be incorporated in the sheet. While there are several types of screens, including vibratory and flat screens, most mills use primary pressure screens for the approach flow to a paper machine. Regardless of the type of screen, they all operate on the same principle: a barrier prevents the contaminants from passing through, while the pulp fibers and other desired papermaking materials pass through. **Figure 10** shows a pressure screen attached to a pilot paper machine. Depending on the type of contaminant that is being removed, the barrier screen can have either holes or slots. The slots in pressure screens typically have a width of 0.20–0.50 mm. As with hydrocyclones, pressure screens are usually arranged in a cascade arrangement (**Figure 9**).

Papermachine Operations

The most common basic form of the papermachine is the Fourdrinier machine, in which the paper is initally formed on an endless moving screen called

Figure 10 Pilot plant pressure screen manufactured by Black Clawson. The screen uses a slotted screen to remove contaminants from the pulp slurry.

a wire. There are a number of variations of the Fourdrinier machine in use today which use two wires with the sheet formed between them. After being formed on the wire, the sheet is conveyed through a series of presses to dewater the sheet further. Finally, the sheet is dried by evaporating the remaining water in the sheet (**Figure 11**). The papermachine has two main objectives: (1) to remove the water from the pulp, which is initially at approximately 0.5% solids to approximately 95% solids; and (2) to consolidate the sheet and form bonds, such that the sheet has the desired strength, optical, and other properties.

The following sections give an overview of the numerous processes that occur on a modern papermachine. Not all machines will have all the elements described, but most have many. In addition, the description of the approach flow, headbox, and wire section pertain to the most common form of the wet end of the paper machine: the Fourdrinier machine. A different type of former, the cylinder machine, is often used for heavier-weight paperboard grades.

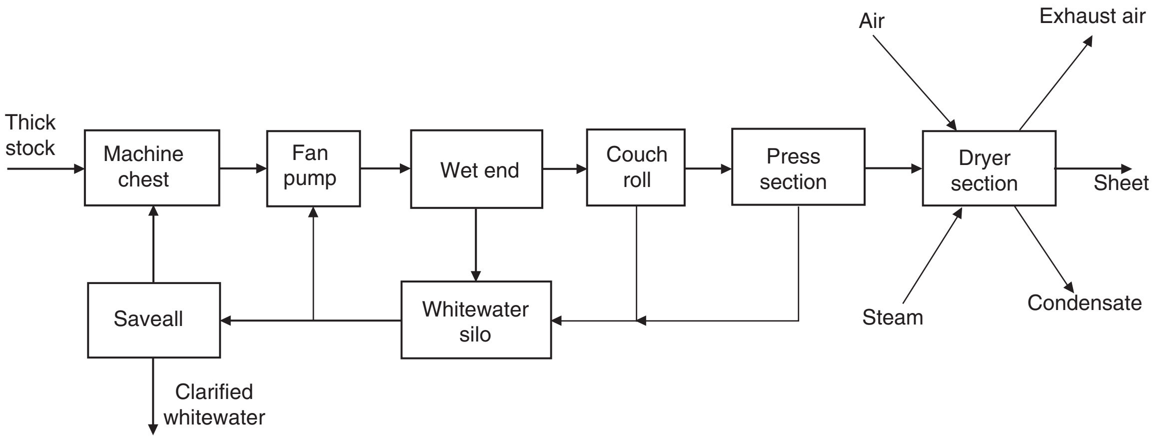


Figure 11 Flow diagram of typical papermachine. Note that the water drained from the wet end and press sections are used for dilution at the fan pump. Fiber from the excess water is recovered in the saveall.

For a description of this type of machine, the reader is directed to the further reading given at the end of the article.

Approach Flow and Headbox

The approach flow to the papermachine includes all the processes from the machine chest (where the pulp is held prior to use) to the headbox (which places the pulp suspension on to the wire). While every machine is different, most contain the hydrocyclones and screens described above, deaerators, and dilution to bring the stock to the headbox consistency. The fan pump, usually the largest pump in the papermachine, mixes the stock from the machine chest with the dilution whitewater returning from the wire, and delivers the stock to the headbox. Just prior to the headbox, the flow must be changed from a circular flow in a pipe to the flat flow evenly distributed across the machine. It is important for the uniformity of the final sheet that the pressure and flow pulsations be evened out. To accomplish this, a flow spreader, typically called a tapered header, distributes the flow evenly across the machine.

The headbox of the paper machine is the final element in the process before the pulp suspension is placed on the wire. The headbox, which can be either air-pressurized or completely hydraulic, accelerates the stock so that it hits the wire at approximately the same speed as the wire. In addition to accelerating the stock, the headbox also controls the flow rate of fiber on to the wire, thus ultimately affecting the weight of the sheet of paper. The headbox must also prevent flocculation of the fibers, which can cause nonuniformities in the final sheet. Baffles, internal mixing rolls, high stock velocities, and highly polished internal surfaces maintain the pulp dispersion.

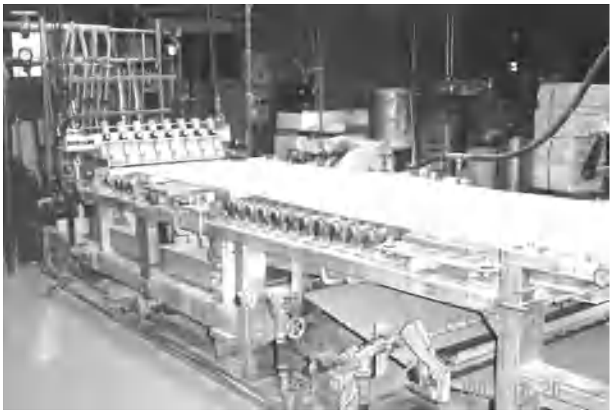


Figure 12 Wet end of the pilot papermachine at SUNY College of Environmental Science and Forestry. A hydraulic headbox is seen in the background and the forming sheet would move left to right while water drains through the wire.

Wire Section

The bulk of the water is removed at the wire section, or wet end of the papermachine (**Figure 12**). A good portion of this water is recycled for dilution of the incoming stock in the approach flow system. As the sheet moves with the wire, water is filtered through the wire, depositing the pulp fibers on the wire in a layered mat. However, as more and more fibers are deposited, the resistance to water flow is increased, thus retarding the drainage of water. With free drainage at the initial part of the wire, the only driving force of the height of the stock above the wire (on the order of 450 Pa) is quickly overwhelmed by the resistance. In some modern machines, multiple wires are used to dewater the stock from both sides of the sheet (**Figure 13**).

Table rolls and foils Table rolls and foils induce a vacuum under the wire, thus creating a greater

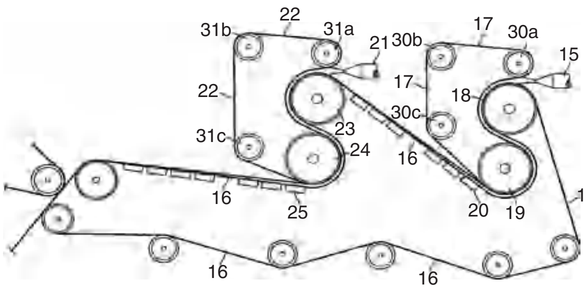


Figure 13 Patent drawing of a modern wet end of a papermachine using multiply, twin-wire forming (US patent 6,342,125). The pulp slurry is injected between two wires (15 and 21) and can be dewatered from both sides.

driving force to remove more water. Table rolls, originally used to support the wire, produce a vacuum that is proportional to the square of the velocity of the wire and related to the roll diameter and at moderate speeds on the order of 4500 Pa. Unfortunately, as speeds increased, a reverse pulse into the sheet at the front of the table rolls became too disruptive to the sheet. The foil was developed to address this drawback of the table roll. The foil is a stationary blade placed at an angle of 0.5–3° to the wire, with the larger angle causing a greater pressure drop. While the pressure driving force is approximately one-half that developed by the table roll, it does not have as great a leading pressure pulse into the sheet. Also, two to three foils can fit into the space of one table roll. However, since the foil is not rotating with the wire, they do tend to increase wear.

Vacuum boxes and vacuum couch At the final stages of the wire section, vacuum is applied to the underside of the wire to increase the driving force for water removal. As a series of vacuum boxes is often used, the vacuum level increases as one proceeds down the wire, with the highest vacuum being applied at the vacuum couch. The couch is the last roll before the sheet is removed from the wire and the wire is turned for its return. Vacuum levels can range from 20 000 to over 53 000 Pa of vacuum.

Forming fabric The fine screen on which the paper is formed is termed the wire, due to its originally being constructed of phosphor-bronze wire. Modern wires are basically a woven cloth of polyester monofilaments made into an endless loop. These fabrics are often woven into a double or triple layer construction in order to provide a wear surface on the bottom of the wire (for durability) and a smoother surface on the top on which the sheet is formed. In all cases, the wires are designed to maximize water flow from the sheet.

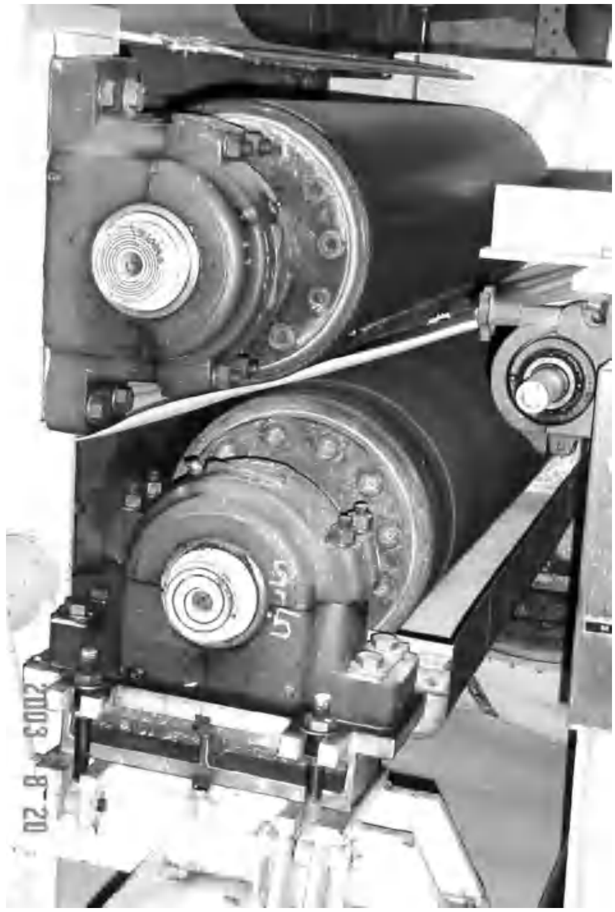


Figure 14 Press section of the pilot papermachine at SUNY College of Environmental Science and Forestry. The sheet together with its press felt would go through the nip, squeezing water from the sheet to the felt.

Press Section

The press section consists of a two to four press nips similar to the wringers on an old-fashioned washing machine (**Figure 14**). The objectives of press are to consolidate the sheet while removing water. Since the majority of the hydrogen bonding which gives paper its strength occurs at a solids content of 35–65%, pressing is key to the development of strength properties of the final sheet. Other properties that can be influenced in the press section include porosity, smoothness, and bulk. The sheet typically enters the press section at 20% solids and exits between 40 and 50%, depending on the grade of paper and pressing configuration.

In order to increase the amount of water removed, the sheet travels through the press together with a press felt, which also serves to support the weak sheet during pressing. The sheet and felt travel through the press nip in four distinct phases. In the first phase, the sheet and felt are compressed, removing air from both. When the air is removed and the sheet becomes saturated, water flows from the sheet to the felt. As the sheet passes mid-nip, the felt begins to expand and becomes unsaturated. However, hydraulic pressure still maintains water flow from the sheet to the felt. In the final phase the sheet is at maximum dryness and begins to expand and reabsorb moisture from the felt. It is important that the sheet and felt be separated as soon as possible after exiting the nip to prevent this reabsorption.

There are limits to the amount of pressure that can be applied to the sheet in the press section. In first presses in a section, the press is often 'flow-controlled.' That is, the limitation to pressing is the flow of water from the sheet to the felt. Overpressing under these conditions can lead to crushing the sheet, in which water flows backwards through the press nip, disrupting the incoming sheet. In 'compression-controlled' pressing, often found in the last press nips, the fiber web itself is the limiting factor in pressing. Under these conditions, increasing the nip pressure beyond a certain point has little effect on increasing the dewatering.

There are a number of ways of increasing the efficacy of the pressing operation; some are operational and require equipment changes. Increasing the nip pressure can increase dewatering in the early nips provided the sheet is not crushed. Double felting the nip can also increase the amount of water that can be removed. The press rolls themselves can be modified by grooving or drilling to allow water to pass through the felt. Suction press rolls can also increase water removal in the nip. Increasing the temperature of the sheet as it enters the nip reduces the viscosity of the water, making it flow easier. Finally, extending the length of the nip will increase the water removal of the nip (**Figure 15**).

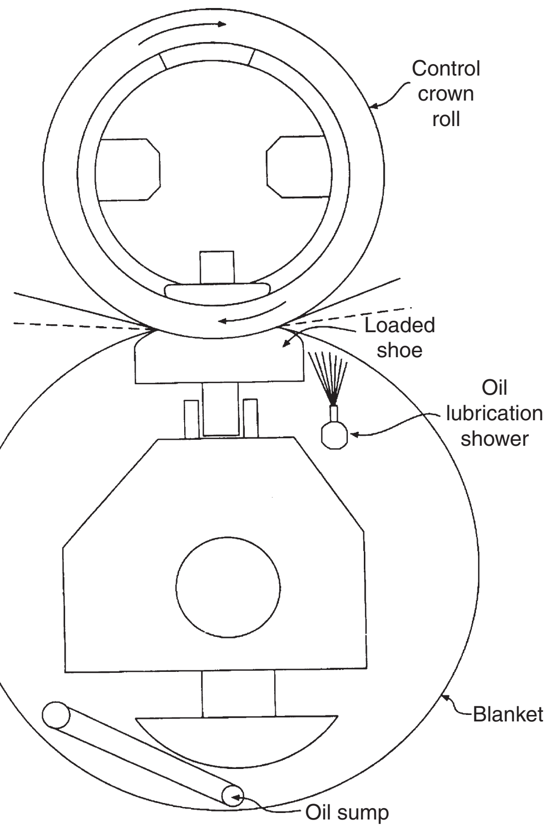


Figure 15 Patent drawing of prior art depicting shoe press used in many presses (US patent 6,458,248). Because of the loaded shoe, the sheet spends a much longer time in the press than with a nip produced by two rolls.

Dryers

The drying section is the most expensive part of the papermachine to run (**Figure 16**). About 78% of the energy used on a papermachine is used in the dryer section, with the remaining energy being split between the wet end and press sections. However, less than 1% of the water that enters with the stock at headbox is removed by drying. By contrast, pressing removes about 3% of the water, with the majority of the water being removed in the wet end. This last amount of water in the sheet is difficult to remove because of the fiber's strong affinity to water and the hydrogen bonds between cellulose and water that need to be broken. However, since this last water is so expensive to remove, small improvements in water removal at the wet end and press sections can translate into significant savings in the dryer section. Since the dryer section is also the most expensive part of the machine in terms of capital cost, paper machine production is often limited by dryer capacity.

Figure 16 Dryer section of the pilot papermachine at SUNY College of Environmental Science and Forestry. The sheet passes alternately over and under steam-heated cylinders in a serpentine pattern.

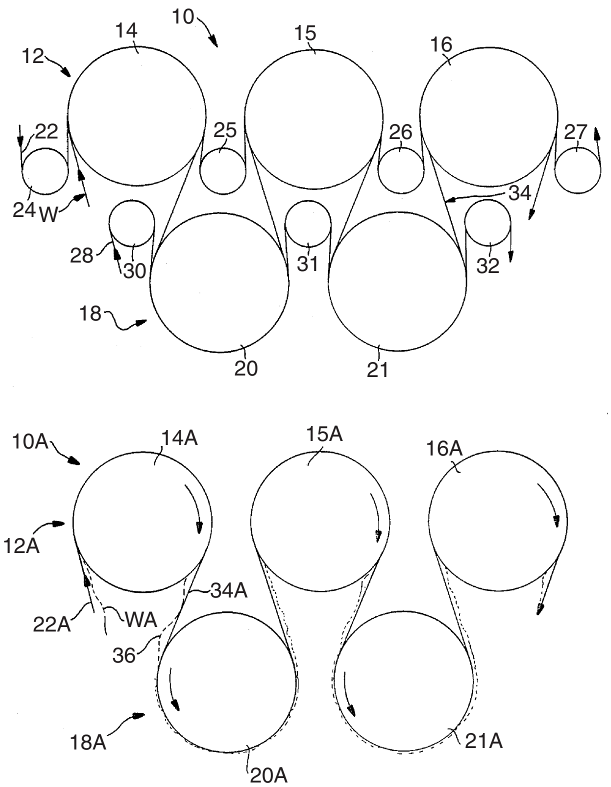


Figure 17 Patent drawing depicting prior art of dryer configuration. Top: double-felted dryer configuration; bottom: single-felted configuration (US patent 4,876,803).

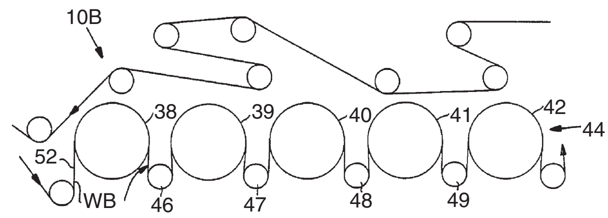


Figure 18 Patent drawing depicting modern dryer configuration. In this configuration, the sheet is completely supported by the felt through the entire run (US patent 4,876,803).

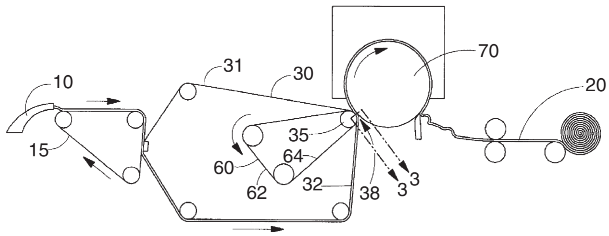


Figure 19 Patent drawing of modern tissue machine (US patent 6,447,642). Tissue machines, because of the light-weight sheet that they produce, tend to be smaller with a single, oversized dryer can (70).

The drying process consists of two main processes. First, heat is transferred from condensing steam in rotating cylinders to the paper sheet, evaporating the water in the sheet. Second, air is drawn through the dryer section to remove the evaporated moisture. The paper takes a serpentine path through the dryer section, passing alternatively over and under the steam-heated cylinders. Synthetic dryer felts hold the sheet in contact with the dryers which increases the heat transfer rate. A number of different configurations of dryers and felt are currently used in the industry. The top diagram in **Figure 17** shows the typical double-felted run in which the sheet transfers unsupported by the felt from one dryer can to the next. The bottom diagram shows a single-felted run in which the sheet is completely supported by the felt through the dryer section. However, in this case, the felt is between the sheet and the dryer can, retarding heat transfer. In **Figure 18**, the run is single-felted, so the sheet is supported and the rolls in which the felt is between the sheet and the roll have been reduced to unheated turning rolls. Tissue machines often use a single large dryer called a Yankee dryer to support and dry the sheet during the entire process (**Figure 19**).

Drying takes place in a number of stages. During the first part of drying, representing usually the first three or four dryer cans, the energy is mainly heating up the sheet. As the sheet proceeds down the machine, a constant-rate zone is entered that represents the bulk of the drying process. As the sheet nears complete dryness, the rate of drying decreases as the more difficult bound water is removed. In most paper machines, the paper is only dried to about 5% moisture, since this is the water content of paper in equilibrium with typical room air.

A size press is often located in the middle of the dryer section (**Figure 4**, item 500). The size press is used to put a surface coating or surface chemicals on to the sheet. Surface coatings can consist of clay, latex, and other materials depending on the grade of paper. Chemicals can also be added to retard moisture penetration or to provide fire resistance. After the application, which is often done as a slurry or solution, further drying is needed.

Calender

The final opportunity on the paper machine to change the paper properties is the calender stack (**Figure 20**). A calender stack consists of a loaded stack of steel rolls (or alternating steel and soft rolls) through which the paper takes a serpentine path. The paper thus passes through a number of nips depending on the number of rolls. The multiple nip passes tend to compact and densify the sheet. While some loss of strength is often evident in calendering, the process improves the smoothness and flatness of

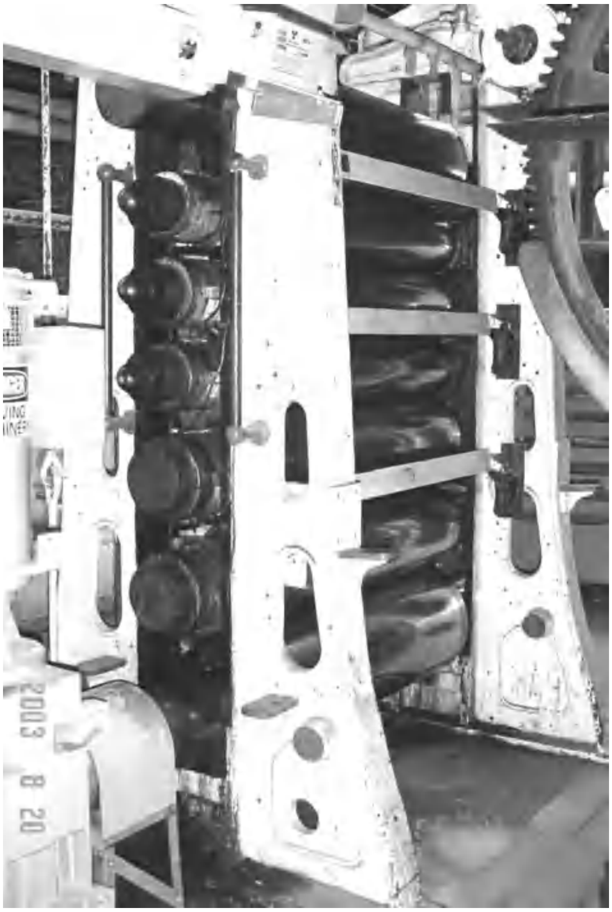


Figure 20 Calender of the pilot papermachine at SUNY College of Environmental Science and Forestry. The sheet passes through multiple nips to smooth the surface of the sheet.

the sheet and can correct some of the irregularities in the sheet. The effect of calendering on the sheet depends on a number of variables, including the sheet moisture, the type of coating applied at the size press, the calender stack loading, temperature, and number of nips.

Reel

The final step of the paper machine is to collect the paper that is produced on a reel (**Figure 4**, item 800). From here, the paper is rewound into smaller rolls needed for shipping or further processing in the finishing and converting operation. The type and amount of processing done after the reel depend on the grade of the paper and the customer specifications.

See also: **Packaging, Recycling and Printing**: Packaging Grades; **Papermaking**: Paper Grades; Paper Raw Materials and Technology; Paperboard Grades; The History of Paper and Papermaking; Tissue Grades. **Pulping**: Chemical Pulping; Mechanical Pulping.

Further Reading

Biermann CJ (1996) *Handbook of Pulping and Papermaking*. San Diego: Academic Press.

Borch J, Lyne MB, Mark RE, and Habeger Jr, CC (eds) (2002) *Handbook of Physical Testing of Paper*, vol. 2, 2nd edn. New York: Marcel Dekker.

Britt KW (1975) *Handbook of Pulp and Paper Technology*. New York: Van Nostrand Reinhold.

Clark Jd'A (1985) *Pulp Technology and Treatment for Paper*, 2nd edn. San Francisco: Miller Freeman.

Dieson M (1998) *Papermaking Science and Technology*. Atlanta, GA: Tappi Press.

Gavelin G (1998) *Paper Machine Design and Operation*. Vancouver, BC: Angus Wilde.

Hunter D (1978) *Papermaking: The History and Technique of an Ancient Craft*. New York: Dover Publications.

Karlsson M (2000) *Papermaking*, Part 2, *Drying*. Atlanta, GA: Tappi Press.

Kline JE (1991) *Paper and Paperboard: Manufacturing and Converting Fundamentals*. San Francisco: Miller Freeman.

Kojio M (1999) *Papermaking: Finishing*. Atlanta, GA: Tappi Press.

Levlin J-E and Söderhelm L (1999) *Pulp and Paper Testing*. Atlanta, GA: Tappi Press.

Mark RE, Habeger Jr, CC, Borch J, and Lyne MB (eds) (2002) *Handbook of Physical Testing of Paper*, vol. 1, 2nd edn. New York: Marcel Dekker.

Patrick KL (1999) *Primer of Pulping and Paper Making: Technologies and Production Practices*. San Francisco, CA: Miller Freeman Books.

Paulapuro H (2000) *Papermaking* Part *1: Stock Preparation and Wet End*. Atlanta, GA: Tappi Press.

Savolainen A (1998) *Paper and Paperboard Converting: Papermaking Science and Technology*. Atlanta, GA: Tappi Press.

Smook GA (1982) *Handbook for Pulp and Paper Technologists*, 3rd edn. Vancouver, BC: Angus Wilde.

Smook GA (1992) *Handbook of Pulp and Paper Terminology: A Guide to Industrial and Technical Usage*, 2nd edn. Vancouver, BC: Angus Wilde.

Thorp BA (ed.) (1991) *Pulp and Paper Manufacture*, vol. 7. *Paper Machine Operations*. Atlanta, GA: Tappi Press.

Paper Grades

G J F Ring, University of Wisconsin–Stevens Point, Stevens Point, WI, USA

Introduction

Paper is a sheet of dried cellulosic fibers and noncellulosic components formed from an aqueous suspension on a fine mesh screen. The ideal forming process deposits fibers on the screen in randomly oriented layers with a uniform mass distribution. Paper can make an enormous number of useful products. Approximately 2000 years ago, the Chinese invented paper as an inexpensive writing material. Because paper was also lightweight, flexible, and opaque, it became the material of choice for letters, manuscripts, and books, and it eventually replaced such writing materials as papyrus, parchment, and textiles. Paper later evolved to serve many other uses by changing the initial papermaking stock formulation, such as varying the type of fibers and additives, their relative proportion, and the total amount of these ingredients.

The term 'grade' signifies the manner in which one type of paper differs from another. Different papers can have different uses, appearances, qualities, and components. For example, paper can make books or boxes. Paper can be white or brown, smooth or rough, thin or thick, light or heavy. Virtually any plant can make paper, and virtually any noncellulosic material can be added to make specialty papers. Furthermore, different manufacturing processes can produce different grades of paper. This article will explore three typical categories of paper grades: printing, writing, and specialty grades.

Grade-Determining Paper Properties

Physical and strength properties of paper are important determiners of many paper grades. These properties include: grammage, caliper, density, strength, smoothness, porosity, lignin content, and pulp type. These properties are interrelated, and this section will describe the nature of this interrelationship and the fact that different stock formulations and production techniques can yield the same paper properties. For instance, uncoated supercalendered paper can successfully substitute for lightweight coated paper as long as the key material properties are identical.

A sheet of paper has dimensions of width and length dictated by its use. In general, the length is longer than the width. A common typewriter sheet size in North America is 8.5 inches × 11 inches (215.9 mm × 279.4 mm), while the equivalent size in Europe is ISO A4 (210 mm × 297 mm). The weight of a sheet determines the most basic physical measurement of paper: grammage or basis weight. Grammage is the ratio of sheet weight to area, and has units of grams per square meter ($g\,m^{-2}$). Basis weight is essentially the same measurement but uses English or United States Customary System (USCS) units. Basis weight is the weight in pounds of a ream or 500 sheets cut to a size specified by its ultimate use. A ream is an awkward and confusing measurement since the total area defined is different for many types of paper. Reporting basis weight in pounds per ream area (for example 34 pounds per 1000 square feet) can reduce potential confusion.

When all else is constant, changing the grammage of paper results in a change in thickness or caliper. Thicker paper will have correspondingly greater strength, bending stiffness and opaqueness. Paper having a grammage greater than 150 $g\,m^{-2}$ is usually termed paperboard. In the English system of units, paperboard is any sheet thicker than 12 points (1 point = 1 mil = 0.001 inch).

When caliper is held constant, changing the grammage of paper results in a denser sheet. Increasing density also results in increasing sheet strength with an accompanying loss in air volume. Sheet densification in papermaking occurs primarily through pulp refining, wet pressing, and calendering. Refining of pulp mechanically releases cellulose–cellulose hydrogen bonds inside the fiber walls by creating cellulose–water hydrogen bonds as water is drawn into the cell wall material. The net effect is a swollen fiber with a network of water-filled capillaries that exert considerable pressure inside the sheet during drying. The resulting surface tension pulls cellulose structures together both within and between fibers eliminating air spaces. As water in the capillary evaporates, the dimensions of the capillary decrease producing increasing surface tensions until the capillary disappears and the cellulose surfaces bond. Wet pressing enhances this bonding effect by mechanically reducing pore size before the dryer section thus increasing the average capillary pressure during drying. Calendering after drying collapses compressible air pores in the dry sheet without the same degree of hydrogen bonding and thus does not produce the same strength-enhancing effect. Calendered papers are smoother because of the reduced size of the surface pores. Calendered paper when compared to uncalendered paper at the same thickness will have a higher grammage or basis weight due to the increased density.

Paper has a surprisingly large percentage of air volume. Bulky groundwood paper has 63% air volume, while dense glassine (pergamyn) has only 13%. It is not surprising that glassine is the strongest class of paper since the underlying reason for the strength is maximally hydrogen-bonded cellulose. However, glassine is semitransparent and does not make good printing and writing paper. Transparency or its opposite, opacity, relates to the volume of air in paper. More precisely, opacity relates to the distribution of numerous small air pores with a large total surface area. Surprisingly, cellulose is a clear, transparent material, while paper composed of pure cellulose is a semiopaque white material. The appearance of whiteness comes from the visual effect of light scattering from the pore surfaces. This is identical to the visual appearance of either table salt or sugar: both appear white until microscopic examination reveals numerous clear crystals. Thus, paper is a matrix of transparent cellulose with a distribution of light-scattering pores.

For pure cellulose paper, increased opacity means a larger quantity of light scattered from the surfaces of numerous small pores. Correspondingly, increasing pore volume decreases the volume of cellulose thus reducing sheet strength. To produce equally strong yet more opaque papers, papermakers use inorganic fillers such as clays and calcium carbonates to increase the available light-scattering surface area inside the pores without sacrificing the volume and density of cellulose required for strength.

Pulp fibers play an important role in the structure of the paper sheet. The primary source of papermaking pulp fibers comes from wood because of its superior technical and economical factors when compared to other sources of plant fiber. Wood provides both short, fine fibers from hardwoods and long, coarse fibers from softwoods. Furthermore, wood fibers have lignin interpenetrating the cellulose material producing a controlled absorption of water. Different pulping methods yield different amounts of lignin. Chemical pulping has the least amount of lignin while mechanical pulping has the most. Lignin-free chemical pulps are pure pulps, free of biological contaminants, with quality high enough for food applications. Chemical pulps also have the highest absorption capacity.

Unrefined softwood chemical pulps (such as softwood kraft) by themselves do not make strong fine paper. These fibers floc excessively and produce bad formation with rough surfaces, high sheet porosity, and low sheet strength. Refining will increase sheet strength, reduce porosity, and reduce surface roughness, but only to a degree. Shorter, finer hardwood fibers are required to provide paper with superior properties. In paper, softwood fibers are the reinforcing elements producing adequate strength, while hardwood fibers fill in the spaces between the larger softwood fibers producing high-opacity, smooth paper.

Mechanical pulps with higher lignin contents produce inexpensive paper that has limited permanence. Lignin restricts the amount of fiber-to-fiber hydrogen bonding that can develop in the paper machine's dryer section. For this reason, mechanical pulps produce bulkier paper that has lower strength potential than refined chemical pulps. However, mechanical pulp produces paper that has greater porosity and opacity because of the greater number of pores left after drying. Smoothness is also a feature of mechanical pulps that results from the mechanical fracturing of wood yielding a large number of fines. These papers yield excellent surfaces for printing.

Lignin gives paper a yellow–brown color. Brightness is an optical test that measures the percentage of blue light reflected from the surface of paper. Brightness is sensitive to the presence of lignin in paper because the yellow color of lignin will absorb blue light. Chemical pulps tend to have dark brown colors due to the chemical modification of lignin even though the quantity of lignin may be very low when compared to brighter mechanical pulps. Bleaching of both mechanical pulps and chemical pulps is performed to increase brightness and improve the overall whiteness of paper.

Printing and Writing Grades

Printing and writing grades represent about 30% of the paper consumed in the world. The number of printing and writing grades is large and increasing due to both customer and technological demands. In general, where quality requirements are secondary to price mechanical pulps are used. Chemical pulps are used when higher quality is desirable and higher prices can be justified. Many grades are also coated and calendered to improve surface smoothness for higher printability. In general, printability can be defined as the combination of paper properties that result in a good printed image. Printability is a complex property related to the optical and strength properties of paper. It is also related to the manner in which ink chemically and physically interacts with the material substances of the paper. Furthermore, all printing grades have a high 'runnability' requirement, which refers to the efficiency with which the paper can run through the printing presses. Runnability is related to the strength properties of the paper sheet.

Uncoated Mechanical Grades

Newsprint is the grade used for the publication of newspapers, advertising supplements, magazines, telephone directories, and other similar publications. This type comprises uncoated papers with inorganic filler less than 8%, but may receive special calendering. Standard newsprint can range in grammage from 40–49 $g\,m^{-2}$ with a nominal caliper of 85 μm (3.3 mil or points). Lightweight newsprint may have a grammage as low as 28 $g\,m^{-2}$. The mechanical pulp used in this grade includes groundwood (SGW or GWD), pressurized groundwood (PGW), thermomechanical (TMP), and chemithermomechanical (CTMP). Recycled fiber (RCF) content may also be high depending upon region. Many manufacturers will add up to 30% chemical softwood pulp to ensure good runnability in printing presses. Newsprint needs to have good formation with a smooth, bright surface and be adequately thick for good opacity to avoid ink showthrough. Color printing in modern newspapers has necessitated one-stage chemical bleaching to improve brightness. Special grades such as those used for telephone directories may have dyes added to change the color of the sheet. The cut sheet size for newsprint grades is 24 inches × 36 inches (610 mm × 914 mm) giving a ream area of 3000 square feet (279 m^2).

Supercalendered (SC) papers are uncoated papers that have been supercalendered to achieve a high-gloss/nonglare finish and are used in magazines, catalogs, and other applications using rotogravure or offset printing. The amount of gloss is dependent upon the furnish ingredients. Filler content in these grades can reach as high as 35%. Fillers used include kaolin clay, talc, and calcium carbonate. Grammage can range from 39 to 80 $g\,m^{-2}$, but a range of 52–60 $g\,m^{-2}$ is typical. Furnish composition is 70–90% mechanical and 10–30% chemical pulp. Groundwood, pressurized groundwood, and thermomechanical pulps are the typical mechanical pulps used. Less premium grades of supercalendered paper have higher groundwood percentages and lower chemical pulp percentages. Recycled pulp may replace a portion of the mechanical pulp in these lower grades. Because these papers have exceptional brightness (68–70%), opacity (90–91%), smoothness, and strength they compete well with lightweight coated papers.

Coated Mechanical Grades

Coated mechanical grades are printing papers used for the production of magazines, catalogs, advertising flyers, and other printed materials that require high-quality four-color printing but still have a throwaway quality. The coating substance consists by weight: 80–95% pigment, 5–20% adhesive binder, and less than 2% miscellaneous additives that control the properties of the coating during and after application. Coating weights from 5 to 25 $g\,m^{-2}$ per side are applied with a thickness of 5–25 μm. Coating pigments may include: clay, calcium carbonate, titanium dioxide, aluminum hydroxide, barium sulfate, silicon dioxide, talc, zinc oxide, and plastic pigments. Sheet surface quality and production speed mandate the coating techniques used. Typical coating techniques include roll applicators with blade, rod, or air jet metering to control thickness.

Table 1 American Forest & Paper Association coated grades classification courtesy of the AF and PA

Quality	*Brightness*
Number 1	85.0–87.9
Number 2	83.0–84.9
Number 3	79.0–82.9
Number 4	73.0–78.9
Number 5	≤72.9

Coated papers are categorized primarily by brightness in the classification of the Technical Association of the Pulp and Paper Industry (TAPPI). **Table 1** lists the six American Forest & Paper Association (AF&PA) quality categories. Coated mechanical grades contain 50–70% mechanical pulp (GWD, PGW, TMP, or CTMP), and 30–50% chemical pulp. With 4–10% filler pigment content, these papers may have 24–36% total pigment content.

Coated mechanical grades are grouped into three main grammage classes: lightweight (LCW), medium weight (MWC), and high weight (HWC). LCW paper has a grammage range of 35–80 $g\,m^{-2}$, with a coating weight range 5–12 $g\,m^{-2}$ per side. MWC paper has a grammage range 70–130 $g\,m^{-2}$, with a coating weight range 12–25 $g\,m^{-2}$ per side. HWC paper has a grammage range 100–135 $g\,m^{-2}$ and may be double or triple coated. HWC are used in higher-quality publications and advertising. Other special grades exist such as ultralightweight coated (ULWC), machine finished coated (matte surface), and film coated offset (FCO). The cut sheet size for mechanical coated grades is 25 inches × 38 inches (635 mm × 965 mm) giving a ream area of 3300 square feet (306 m^2).

Uncoated Fine Printing Grades

Fine paper furnishes should have less than 10% mechanical pulp. Blends of chemical hardwood and softwood pulp with up to 25% filler are used. Papermakers sometimes apply the term ‘free sheet’ or the especially confusing term ‘wood free sheet’ to these grades to denote the absence of mechanical pulp, which gives the paper an archival quality. Alkaline or neutral papermaking conditions further enhance the permanence of these papers. High percentages of hardwood are necessary to achieve good formation in the paper, while fillers, such as calcium carbonate, are necessary for good opacity. On-machine calendering and soft-nip calendering provide surface smoothness. Size pressing may also enhance surface smoothness.

Another term for uncoated fine printing paper is uncoated offset paper used for book publishing, copy paper, and electronic printing. The important properties for offset papers are good internal bonding, high surface strength, dimensional stability, lack of curl, and low linting potential. Offset paper is surfaced sized with starch at 0.5–2 $g\,m^{-2}$ per side. The grammage range is from 32 to 300 $g\,m^{-2}$. The cut sheet size is 25 inches × 38 inches (635 mm × 965 mm) giving a ream area of 3300 square feet (306 m^2).

Uncoated book paper has a high requirement for appearance and printability. The brightness requirement is usually high. Color may run from blue–white to a natural yellow shade but must not change for the entire production run. Color may have to be consistent over several production runs so that different book printings will appear identical. Common surface finishes or textures are antique, eggshell, machine, English, and supercalendered. High opacity is crucial with low grammage sheets (i.e., $<75\,g\,m^{-2}$). Usually low gloss level is specified. High-quality book paper is known as text paper.

Bible paper is an example of a very low basis weight uncoated book paper (20–45 $g\,m^{-2}$). Because of its low weight, bible paper must be strong for good printability, but more importantly, it must be opaque. Highly refined chemical pulp is used to give excellent strength and high loadings of calcium carbonate are required for opacity. Frequently, non-wood pulps such as cotton, flax straw, and linen are used to provide superior strength.

Writing papers are a wide range of quality papers designed for pen and ink, typewriters, and personal printing uses. Some writing papers have well-identified brand names and watermarks. These papers may have very distinctive textures and colors. Many different types of pulps are used in this category for aesthetic reasons, and they may be made to simulate handmade papers. Tablet papers are part of this grouping. In general, they are hard sized for low-viscosity pen inks. The grammage range is from 48 to 90 $g\,m^{-2}$. The cut sheet size is 17 inches × 22 inches (431.8 mm × 558.8 mm) giving a ream area of 1300 square feet (120.7 m^2). Bond is a durable writing paper intended for stationery, legal documents, and other archival uses. Bond paper is manufactured from non-wood fibers such as cotton to increase its strength, durability, and permanence. Bond paper requires excellent printability. Onionskin paper is a lightweight (26–37 $g\,m^{-2}$) bond paper that has exceptionally low opacity and is used where low bulk is necessary. Other similar bond-type writing papers include: parchment, vellum, wedding, and ledger.

An important area for uncoated fine paper is copy paper and digital printing papers. These papers require good brightness (80–96%) and opacity, and must resist curling and cockling when subjected to heat from thermo-type printers. They must also be well sized to resist ink wicking in inkjet-type printers. Grammage range is 70–90 $g\,m^{-2}$.

Coated Fine Printing Grades

Coated fine paper grades are required for demanding printing applications. Products include magazines, books, and commercial printing. Grammage range is 55–170 $g\,m^{-2}$. General categories of coated fine papers include: low coat weight (55–135 $g\,m^{-2}$) with a total pigment content of 20–35%, standard coated (90–170 $g\,m^{-2}$) with a total pigment content of 35–45%, and art paper (100–230 $g\,m^{-2}$). Art paper has a highly finished and smooth surface with a coating weight of 20–40 $g\,m^{-2}$ per side or greater.

Specialty Grades

Specialty grade papers fit into a niche market where their enhanced value compensates for their low production volumes. All paper products begin as specialty grades until their production volumes make them commodity grades. Paper is extremely versatile and the number of paper products that fit into a specialty-grade category is prodigious making it difficult to completely describe the wide range of existing products. Paper's versatility is derived from the manner in which light, liquids, and air interact with it. Paper is also versatile because it is strong, yet light and flexible.

Paper's ability to carry an image led to its widespread use as a printing and writing material. However, the image carried need not be informational. Wallpaper is an example of this use. In practice, it is easier to create an image on paper using printing technologies and then apply the paper to surfaces that cannot be printed. Wallpaper is a decorative use of paper. High density laminates used for counter tops are another example of the decorative use of paper. Much like wallpaper, a sheet of paper with a color, pattern, or image is used in conjunction with other paper sheets that are saturated in resin polymers to form a waterproof veneer material that forms a very durable working surface. This technology is frequently used at lower densities in furniture-making to produce artificial woodgrain surfaces on top of compressed chipboard. Wallpaper is also an example of the use of paper as a carrier substrate. A carrier substrate can be defined as the employment of paper in a secondary role to assist the application of the primary product. In the case of wallpaper, the primary product is the decorative color, pattern, or image. It should also be mentioned that the backside of the wallpaper is coated with an adhesive glue to adhere the paper to the wall. Thus, the wallpaper acts not only as a carrier for the image, but as a carrier for the adhesive.

Many other materials can be carried on or in paper. Moist paper towels for hygienic purposes, household-cleaning tissues, and polish-saturated wipes are examples. It is also possible to imbed flower seeds in rolls of paper for planting purposes. Litmus paper is an example where paper carries chemicals for use in measuring pH. Medical test papers such as those used to determine blood sugar levels in urine are an extension of this principle.

An interesting use of paper as a carrier substrate is the manufacture of automobile brake pads. In this grade, paper is formed with a high loading of abrasive inorganic material and then saturated with phenolic resin. The sheet is glued to a metal backing and cured to form the brake pad surface that will provide the frictional forces to stop a moving automobile. A related range of products, where the abrasive is applied to the surface of the sheet rather than through the bulk, are sandpaper, finishing paper, and the base paper for grinder belts. Photographic paper carries the emulsion that forms a photograph when developed (before the acceptance of paper as the ideal carrier material, glass and metal plates were used). Release paper used as backing for self-adhesive labels is still another example. In many instances, the labels themselves are made of paper.

Because the porosity of paper can be controlled to a high degree by the selection of fiber type, additive, and processing, using paper as a filter material represents an important specialty grade sector. Paper filters are used to protect a wide range of automotive equipment as well as air handling, water purification, and electronic devices. Relative to the cost of the protected device, the paper filter is lowcost but can be sold for a premium. Coffee filters and tea bags are examples of these types of papers used daily by many people. Tea bags are made from a mixture of long banana leafstock (abaca) and synthetic fibers. The very open and thin sheet that is formed effectively filters the tea leaves from leaving the bag. It should be noted that air, water, and oil can all be filtered through paper because of the large quantity of surface area that provides ample surface free energy to adsorb and remove contaminants from the filtered fluid. Another home use for paper filters is the vacuum cleaner bag.

Food packaging at the wholesale and retail levels requires specialty grades. Cleanliness is very important to prevent tainting and spoilage. Recycled pulp, which may have significant contaminants, is not permitted to contact food. Generally, only chemical pulps are used. Sometimes the resulting paper is treated with fungicide to prevent molds as in fruit wrapping papers. Paper that contacts food often needs to be greaseproof. This property is provided by high density, low porosity paper such as glassine. Low opacity papers are used to wrap breads and bakery items to allow visual inspection of the product.

Many food products such as sugar and flour are packaged in bags made of sack kraft paper. These sacks need to be strong and resist rupture during handling. Sack paper also needs to be porous to permit air escape during rapid filling. Paper manufacturers will microcrepe sack kraft to increase elongation and enhance toughness. Square-bottomed kraft paper sacks are used as grocery bags. These bags are popular with consumers because they are recyclable. These bags need to have a high tensile strength to avoid rupture when filled with purchased items. A recent development to improve handling is the introduction of glued handles made of the same kraft paper.

Cigarette papers are required to be thin (16–24 $g\,m^{-2}$), strong, and porous. They are made from various textile fibers to ensure a white ash after burning. To achieve high opacities these papers are highly filled with calcium carbonate. Currency papers are also made from textile fibers for durability, but currency papers are also required to have high printability. Currency papers and related security papers must be refined enough to produce a good watermark. Many other security features are also incorporated to provide unique identification features.

See also: **Packaging, Recycling and Printing**: Paper Recycling Science and Technology; Printing. **Papermaking**: Coating; Overview; The History of Paper and Papermaking; World Paper Industry Overview. **Pulping**: Bleaching of Pulp; Chemical Additives; Chemical Pulping; Chip Preparation; Environmental Control; Fiber Resources; Mechanical Pulping; New Technology in Pulping and Bleaching; Physical Properties.

Further Reading

Biermann CJ (1996) *Handbook of Pulp and Papermaking*, 2nd edn. San Diego, CA: Academic Press.

Brandon CE (1981) Properties of paper. In: Casey JP (ed.) *Chemistry and Chemical Technology: Pulp and Paper*, pp. 1715–1972. New York: Wiley-Interscience.

Clark JDA (1985) *Pulp Technology and Treatment for Paper*, 2nd edn. San Francisco, CA: Miller Freeman.

Glassman A (1985) *Printing Fundamentals*. Atlanta, GA: Technical Association of the Print and Paper Industry.
Lebtinen E (ed.) (2000) *Papermaking Science and Technology: Pigment Coating and Surface Sizing of Paper*: Helsinki: Fapet Oy.
Oittinen P and Saarelma H (eds) (1998) *Papermaking Science and Technology: Printing*: Helsinki: Fapet Oy.
Parker JD (1972) *Sheet-Forming Process*. Atlanta, GA: Technical Association of the Pulp and Paper Industry.
Paulapuro H (ed.) (1998) *Papermaking Science and Technology: Paper and Board Grades*: Helsinki: Fapet Oy.
Scott WE and Abbott JC (1995) *Properties of Paper: An Introduction*, 2nd edn. Atlanta, GA: Technical Association of the Pulp and Paper Industry.
Smook GA (1992) *Handbook for Pulp and Paper Technologists*, 2nd edn. Vancouver, Canada: Angus Wilde.

Paperboard Grades

G J F Ring, University of Wisconsin–Stevens Point, Stevens Point, WI, USA

Introduction

Paperboard is a heavyweight paper that has a grammage or basis weight generally greater than 150 g m^{-2} and is thicker than 300 μm. The additional thickness results in a stiffer sheet that is ideal for boxes and containers providing protection for saleable products during transportation, handling, and storage. Paperboard grades include cartonboards, containerboards, and specialty boards, and are used in either food or non-food applications. The English units for paperboard are given in pounds per 1000 square feet (lb/1000 ft^2) and the thickness is measured in points or mils (thousands of an inch).

A box is a rectangular container with or without a top designed to transport and store a variety of goods and products in either liquid or solid form. A box must be strong enough to hold its contents not only during transportation and storage but also during the packaging operation. Because boxes are frequently stored in stacks, compression resistance in their vertical sides is required to avoid bulging and cracking that would result in loss or damage to the product contained within.

Boxes manufactured from paperboard are made to resist compressive forces by using stiff pulp fibers formed into thick sheets. Paperboard meeting these two requirements will have high levels of bending stiffness. Although the stiffness requirement for the pulp fiber is important, the greatest factor affecting bending stiffness is sheet thickness or caliper. Relatively small changes in thickness will result in large changes in bending stiffness since the effect of sheet thickness on stiffness is cubic rather than linear. Pulp selection for greater fiber stiffness leads papermakers to choose naturally thicker fibers such as softwood or hardwoods with noncollapsible, round cross-sections. High yield pulping processes such as thermomechanical pulp (TMP) or semichemical that produce pulp with high percentages of lignin are also desirable for paperboard because of their inherently stiffer fibers. High yield pulps are very desirable for the manufacture of paperboard because the fiber is not only stiff but produces bulky sheets that enhance bending stiffness through both fiber stiffness and sheet thickness. For these two reasons, recycled fiber is also used to a large degree in paperboard manufacture.

Manufacturing Multilayer Paperboard

The same basic paper machines used to produce writing and printing paper are also used to form paperboard. However, modern paper machines are limited in their ability to produce a single-layer paper sheet with a grammage above 150 g m^{-2}. There are a number of reasons for this limitation. Primarily, thicker single-layer sheets are more difficult to dewater requiring excessive reductions in machine speed. Furthermore, the increased drainage forces applied to thicker sheets in the forming section would cause greater fines removal from the bottom of the sheet resulting in a rougher surface. The topside of a very thick sheet would also be adversely affected since paper is formed on fourdrinier machines layer by layer from the wire side up, which would allow extra time for the fibers in the top layer to flock and produce a ‘hill and valley’ appearance. The combination of these two effects would produce an unacceptably two-sided product.

Manufacturing multilayered paperboard from separately formed sheets provides a solution to the above-mentioned problems. The forming section of paperboard machines are composed of two, three, or even four forming sections that bring individual sheets together at the wet press. Paperboard machines are for this reason large and complex having heights that are two to three times greater than single-former machines. Any one of the former sections in a multilayer machine can be either a traditional fourdrinier or a modified fourdrinier equipped with a top-wire unit for additional dewatering capacity. The use of different furnishes in each former produces a final sheet that is engineered for specific stiffness and smoothness requirements.

Although initially forming two to three separately formed sheets of paper, a multilayer machine forms a single sheet of paperboard when the individual sheets of paper are combined together in the wet press. The individual single-layered sheets prior to the wet press are 'vacuum dewatered' with a typical consistency of 20% (80% moisture) and are simply assemblages of fibers held together by capillary forces exerted by the continuous matrix of water surrounding the fibers. When the sheet continues it progress through the wet press and the dryers, this continuous matrix of water is decreased and the fibers are progressively drawn together through surface tension. Eventually, at the end of the drying process with a final moisture content of 4–8%, the surface tension forces between individual fibers will produce pressures sufficiently high enough to form fiber-to-fiber hydrogen bonds resulting in a mechanically strong sheet. During multilayer forming, a single sheet of paperboard is formed from the individual sheets of paper by merging the water matrices of each sheet into a single, hydraulically connected matrix in the wet press. The net result is that the multilayer sheet continues through the wet press and dryer section forming fiber-to-fiber bonds inside layers and between layers as if they were initially formed together. Theoretically, the fiber-to-fiber bonding between separately formed layers will be identical to fiber-to-fiber bonding within a single layer. Differences in interlayer bonding strength (measured by z-direction strength tests) will be found when the individual sheets are wet pressed at moisture contents lower than what is necessary to form a hydraulically connected matrix. (z-direction strength is the maximum tensile force per unit area which a paper or paperboard can withstand when applied perpendicularly to the plane of the test sample.)

The advantage of manufacturing a multilayer sheet is that key paper properties can be engineered into the paperboard that would not be obtainable by single-layer forming. Special top layers can be incorporated that are white and smooth, therefore, having excellent printing properties. Middle layers can be used that are bulky and thus inherently thicker producing the stiffest possible board. These middle layers can also contain recycle fibers or pulp fibers of lower quality that can be covered or masked by higher quality top and/or bottom layers.

Cartonboard Grades

Cartonboard produces consumer product packaging for food and retail items. The market for these grades is large and product development is great due to dynamic marketplace forces. Folding boxboard (FBB), white lined chipboard (WLC), solid bleached sulfate board (SBS), solid unbleached sulfate board (SUS), and liquid packaging board (LPB) are major types of cartonboard grades. Many of these grades will be pigment coated to produce a highly printable top surface. These paperboards need to be strong and stiff to form the walls of a carton. Because cartons are stacked during storage, compression resistance is also important. In particular, cross-machine direction (CD) stiffness is required to prevent carton bulging since the carton is manufactured with the CD parallel to its height. High-speed converting and mechanized packaging lines mandate excellent runnability; therefore, resistance to curl is also a necessity. Finally, folding these paperboards into containers must occur without cracking, which requires not only good strength, but also good stretch. The ream area for paperboard grades is 1000 ft^2.

Folded Boxboard

Folding boxboard grades are used to make packages for numerous products including: dry foods, liquid foods, frozen foods, confectionaries, cosmetics, detergents, and numerous other items. The grammage range for folding boxboard is 160–450 $g\,m^{-2}$. Folding boxboard is a multilayer sheet having three to four layers. The top and bottom layers are frequently made of bleached chemical pulp. The middle layers consist of either mechanical pulp or recycled fiber for stiffness enhancing bulk. The top layer is usually surface sized for good picking resistance in printing. Because the board must have a smooth top surface for good printability, yet have adequate thickness for good bending stiffness, smoothness is obtained through a combination of limited calendaring and coating. It is important for folding boxboard grades to also have good folding and scoring properties.

White Lined Chipboard

White lined chipboard (grammage range of 200–450 $g\,m^{-2}$) uses recycled fiber in its middle layers, and has many similar applications as folding boxboard except for certain food packaging applications where contaminants in the recycled pulp might spoil or taint the food. WLC grades may sometimes have four sheet layers. The fourth layer is actually an additional top layer used to maximize use of less bright recycled pulps, therefore minimizing the use of expensive highly bleached top layers. The top layer is frequently coated to increase printability and an optional bottom coating may be found.

Solid Bleached Sulfate Board

Solid bleached sulfate board is very similar to folding boxboard and white lined chipboard except that it is a single layer sheet (hence the term 'solid') made of virgin bleached kraft pulp. Hardwood is the predominant furnish but softwood is also used. Contamination and tainting of food and cigarette products is the primary reason for using virgin kraft pulp. SBS board may be coated on one or both sides with the topside receiving as many as three layers of coating.

Solid Unbleached Sulfate Board

Solid unbleached sulfate board is a heavier multilayer board (grammage $<500\,\mathrm{g\,m^{-2}}$) that uses unbleached pulps where extra board strength is required. For this reason, SUS boards are used in beverage and other packages intended specifically for carrying consumer items. Because SUS is not intended to come directly in contact with food, recycled pulps are frequently used in the middle layers. However, the high strength requirements (which includes tear strength) necessitate using kraft pulps in both the top and bottom layers. Sheet strength and surface smoothness are augmented through the application of surface size. Packaging applications for SUS require printing on the topside, which is accomplished by coating the topside two or three times to prevent 'show through' of the darker unbleached furnish. Where it is important to have high quality printing, high-whiteness pigments such as titanium dioxide (TiO_2) are used.

Liquid Packaging Board

Liquid packaging board is a multilayer board having a polyethylene-coated liquid barrier in conjunction with single or multiple layers of virgin chemical pulp. Milk, juice containers, microwave, and ovenable trays are typical uses for this grade. Polyethylene provides not only a liquid barrier, but also the ability to heat seal during container manufacture. The polyethylene is coated on only one side when a moisture vapor barrier is required for long shelf-life, but on both sides for liquid packaging such as milk. Aseptic packaging uses liquid packaging boards that have high cleanliness and purity standards.

Manufacturing Cartonboard Boxes

Cartonboard sheets or reels are converted into boxes through a process that involves cutting and creasing and then gluing the box into the final carton. Additional steps are frequently taken to produce a visually attractive box that may include printing, varnishing, film laminating, foil blocking, and embossing. Because cartonboard boxes are often an important part of the merchandizing of the contained product, rotogravure printing is necessary to provide the highest possible printed quality. Where self-advertising on store shelves is not critical, offset or flexography printing is used instead, or the box may be unprinted.

Printed boxes, unlike magazines and books, experience considerable abrasion during their use as a product package, which requires surface protection through either varnishing or plastic film lamination. Varnishing is accomplished through coating during the printing process. The varnishes of choice are usually aqueous dispersions that are cured on-line with ultraviolet light. Varnishing provides a gloss to the surface of the box further enhancing its attractiveness. When a more durable or glossier surface is required, off-line film lamination is also used.

Quality printing requires cartonboard grades to have a relatively high brightness from either the pulp or an applied surface coating. Printing also requires high smoothness, which is obtained from coating the sheet and using hardwood furnishes.

Cartonboard boxes are specifically designed for each product and have no standard sizes. Products such as cigarettes, camera film and software are sold in boxes that have unique sizes and designs, which may include intricate product-inspection windows or cutouts. These potentially complex designs are produced by die-cutting a cartonboard sheet in either a flat-bed or a rotary press that has cutting rules in the shape of the unfolded box mounted to a cutting die, which is then applied through the sheet against a counter die. The cutting rules or knives that are attached to the cutting die have compressible rubber gaskets on either side. These rubber gaskets hold the sheet motionless to produce an accurate cut and then expand to cleanly eject the sheet after the cutting compression stroke has taken place. Any cutouts are prevented from accumulating in the cutting die area by keeping them connected to the sheet through small 'nicks' or perforations that are produced with notched cutting rules. Cutouts are then removed in a stripping step that breaks the nicks and collects the waste material.

Die-cutting requires cartonboard sheets to have good strength properties to produce a clean cut. Poor fiber-to-fiber bonding, a function of low sheet strength, will result in fiber linting or dusting. Low-strength sheets are also more subject to tearing after cutting and exhibit poor runnability on converting machines. Moisture content is also important for converting machine runnability. Excessively dry sheets are harder and will wear out the die-cutting rules sooner. Drier sheets will also produce more cutter lint or dust.

Cartonboard sheets must also be creased to form folding boxes. Creasing is a step that occurs simultaneously with die-cutting on flat-bed machines, but after cutting on rotary machines. A folding crease is formed with a creasing rule that has a rounded edge rather than a cutting edge. Creasing rules are attached to the cutting die together with the cutting rules; however, the creasing rules work in conjunction with a creasing channel located directly opposite them on the counter die. A properly working creasing rule will form a sufficiently deep and narrow crease that will allow the cartonboard sheet to precisely fold where intended and produce a sharp attractive box corner. The creasing rule will be pressed against the side of the sheet that is intended to form the inside of the box.

Cartonboard grades that exhibit good creasing properties have good tensile strength and elasticity in order to survive the out-of-plane deformation during creasing. When a box is folded along its crease, the inside portion of the crease will undergo compression while the outside of the crease will undergo tension. Cracking will occur when the elastic limit is reached and the sheet fails in either tension or compression. In general, the compression limit is reached before the tension limit. Cartonboard sheets that resist cracking tend to have multilayered construction that delaminate around the crease with the inside layers buckling rather than undergoing compression failure.

Corrugated Containerboard Grades

Corrugated containerboard boxes are lightweight structures that can transport significant internal weight and withstand buckling and collapsing when multiple container units are stacked on top of each other. Corrugated containerboard boxes are manufactured by gluing a fluted corrugated medium between two strong outer linerboard faces. In this manner, maximum thickness is obtained with minimum weight to ensure high bending stiffness. Corrugated containerboard may also have two or even three corrugated layers sandwiched between alternating layers of linerboard when extra strength and rigidity is required.

Linerboard's primary characteristic is high bending stiffness and is usually produced with two or more plies from high-quality kraft or recycled pulp. To maximize bending stiffness, pulp fibers that will produce the highest tensile strength are placed in the outer or top layer that comprises about 30% of the total sheet. For example, the top layer will have the highest percentage of virgin fiber while the lower base layer will have a higher percentage of recycled pulp. As another example, the top layer may be a kraft pulp cooked to a lower degree of lignin content and refined to a higher degree than the bottom layer. Typically, compression testing such as the edge crush, flat crush, ring crush, and short-span compression is useful in predicting linerboard performance in the final containerboard product. Burst testing, which measures tensile strength in an empirical manner, has also been used to assess linerboard strength, but is now considered inferior to compression testing. Dry strength agents such as starch may be applied at a sizing press to increase linerboard's surface strength, and resin sizing may be applied in the headbox to enhance water resistance and wet strength. Printable top plies are made from bleached chemical pulps (either hardwood or softwood) that are sometimes pigment coated for more demanding printing requirements. The grammage range for linerboard is 125–350 $g\,m^{-2}$. Linerboard made from at least 85% virgin kraft pulp is called 'kraft linerboard.' Linerboard meeting the requirements of Rule 41 of the Consolidated Freight classification in the US is called 'test linerboard,' and meets either a minimum bursting strength or a minimum edge crush strength. Because kraft linerboard easily exceeds either minimum strength criteria, the term 'test linerboard' is usually applied to linerboard containing predominantly recycled pulp. Modern linerboard machines are multi-ply machines using twin-wire/gap-forming technology. Many new machines are being outfitted with the latest in shoe or extended nip wet presses.

Corrugating medium, used as the fluting between two linerboard layers, is a single-layer uncalendered sheet with a grammage range of 112–180 $g\,m^{-2}$. Compression resistance rather than tensile strength is particularly important for corrugated medium, because, as a composite structural material, corrugated containerboard boxes will fail at the box corners in an identical compression mode when either excessive external loads or excessive internal loads are present. In general, failure occurs in either condition because the containerboard is bending outwards and the linerboard on the inside of the bend is compressed to failure. The primary role of the corrugating medium in preventing containerboard failure is to provide adequate separation of the linerboard faces such that the degree of bending is minimized during loading. For this reason, the portion of the flute that spans from one linerboard face to the other must be stiff enough to resist compressive collapse. This particular property can be obtained in relatively low-cost, minimally refined, semichemical pulps where the fibers are naturally stiff due to the presence of lignin. Recycled pulps also having characteristically stiff fibers can be successfully used in this grade. These pulps produce sheets with bad formation and low tensile strengths. Handsheets made from these pulps are specified to be formed at 150 $g\,m^{-2}$ rather than

$60\,g\,m^{-2}$ to compensate for their lack of wet handling strength. Corrugating medium is also produced with a high machine-direction fiber alignment to enhance compression resistance in the direction of fluting.

Manufacturing Corrugated Containerboard

Producing corrugated containerboard requires converting machinery that combines separate rolls of linerboard and medium into a glued structure. The simplest structure is one sheet of linerboard glued to single sheet of corrugated medium and is known as single faced corrugated. Gluing an additional sheet of linerboard to the corrugated side of single face produces a single wall corrugated board. Gluing either two or three single faced corrugations together with a final linerboard face produces a double wall or triple wall corrugated board respectively.

During the production of single face corrugated, linerboard is unrolled and preheated to a temperature of 160–190°C in a unit known as a 'single facer.' In this unit, medium is also unrolled and preheated, but is passed over a corrugating roll to form the flutes or corrugations. During this operation, the medium must be held securely by either pressure or vacuum in the fluting roll to maintain the shape of the flutes. Glue, generally starch, is applied to one side of the flute tips, and then pressed firmly to the underside of the linerboard instantaneously bonding them together. The bond line formed by the glued tips is observable through the linerboard, and is preferably used as the inside surface of corrugated boxes. Single face is flexible, bending easily at the glue lines. As a material by itself, single face is used as a packing material due to its ability to wrap around items such as bottles providing them with excellent crush protection during shipping.

Single wall corrugated boards are produced in a converting machine where the single facer unit is coupled with a 'double facer' or 'double backer' unit. In this unit, the single face material is again preheated and glued to the remaining unbonded flute tips. The prepared single face is then pressed to another preheated linerboard sheet, which produces the rigid containerboard. Less pressure is applied in the double facer than in the single facer to avoid crushing the corrugations. However, because of the reduced pressure the linerboard glued in this manner does not have the same observable glue line as the single face material, and is more suitable for use as the printable outside surface of a containerboard box. Once the single wall board is produced, further heating to set the glue must take place over hot plates in order to convey the board flat through slitters and scorers before being cut into the final board sheet. Converting machines capable of producing double and triple wall container board operate in a similar manner to that just described with the exception that flutes on the corrugation side of a single face board can be glued to the linerboard side of a second single face board to form the final multilayer construction. Final boxes are manufactured using similar die-cutting, creasing, and printing techniques as described above for boxboard.

See also: **Packaging, Recycling and Printing**: Packaging Grades; Paper Recycling Science and Technology; Printing. **Papermaking**: Paper Raw Materials and Technology; World Paper Industry Overview. **Pulping**: Bleaching of Pulp; Physical Properties.

Further Reading

Attwood B and Morre G (1995) *An Introduction to the Theory and Practice of Multiply Forming*. Leatherhead, UK: Pira International.

Biermann CJ (1993) *Essentials of Pulping and Papermaking*. New York: Academic Press.

Cakebread D (ed.) (1993) *Paper-Based Packaging*. Leatherhead, UK: Pira International.

Hunter D (1947) *Papermaking: The History and Technique of an Ancient Craft*. New York: Knopf.

ISO (1998) *ISO Standards Handbook: Paper, Board and Pulps*. Geneva: International Organization for Standardization.

Kouris M (ed.) (1990) *Pulp and Paper Manufacture: Coating, Converting, and Specialty Processes*. Atlanta, GA: Joint Textbook Committee of the Paper Industry.

Paulapuro H (ed.) (1998) *Papermaking Science and Technology: Paper and Board Grades*. Helsinki: Fapet Oy.

Paulapuro H (ed.) (2000) *Papermaking Science and Technology: Papermaking*, Part 1, *Stock Preparation and Wet End*. Helsinki: Fapet Oy.

Savolainen A (ed.) (1998) *Papermaking Science and Technology: Paper and Paperboard Converting*. Helsinki: Fapet Oy.

Smook GA (1992) *Handbook for Pulp and Paper Technologists*. Vancouver, BC: Angus Wilde.

Tissue Grades

P Parker, Western Michigan University, Kalamazoo, MI, USA

Introduction

'Tissue' is a generic name for a variety of light-weight paper products. In normal use, the word refers to the hygienic or sanitary grades which collectively encompass products commonly known as bath or toilet tissue, facial tissue, napkin, and toweling. Other products in the tissue category include condenser paper, wrapping paper, and tea bags. The focus of this discussion will be on the sanitary grades, which account for the vast bulk of the production of tissue papers; the latter products will be discussed only briefly. In the remainder of this article, the word ‘tissue’ will refer to hygienic grades unless explicitly indicated otherwise.

Tissue use is very much driven by economic development. North America, western Europe, and Japan exhibit very high per capita consumption of tissue, while other regions have per capita consumptions that are small (**Figure 1**).

Growth rate data suggest that the North American market is close to saturation, as tissue growth is about the same as the population growth. Major tissue growth is expected in other regions (**Figure 2**).

Tissue production is dominated by two very large manufacturers (Kimberly-Clark and Georgia-Pacific), two medium-sized manufacturers (Procter & Gamble and SCA) and a host of smaller companies. Consolidation will continue to occur, as the four large companies have about 80% of the market in North America, 50% in western Europe, and 40% or less in other regions.

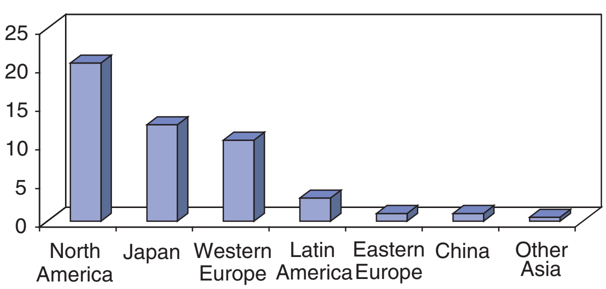


Figure 1 Per capita consumption of tissue products.

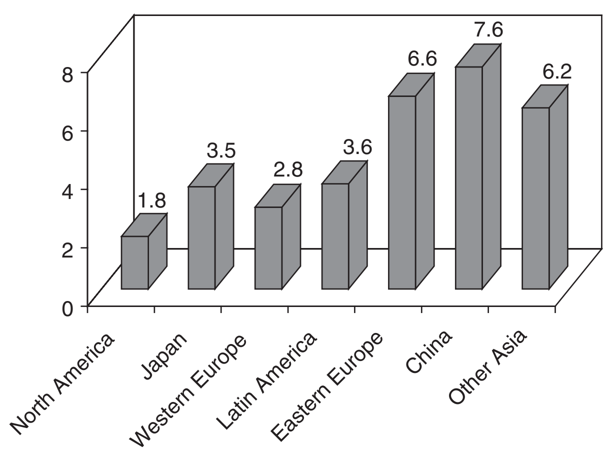


Figure 2 Forecast percentage per capita tissue growth (1994–2005).

In addition to categorization by use, the tissue market is often divided into two large distribution channel categories. Consumer tissue is that destined to the home user and brand-name recognition is critical to marketing success. Unlike most other paper products, manufacturers in the consumer tissue market channel product under their own names and do considerable marketing focused on brand-name recognition. The leading manufacturers (Georgia-Pacific, Kimberly-Clark, and Procter & Gamble) devote considerable resources to developing and protecting their brands (e.g., Brawny from Georgia-Pacific, Kleenex from Kimberly-Clark, or Charmin from Procter & Gamble.) The leading manufacturers, as well as the smaller producers, also supply products for private-label or ‘house’ brands. This latter market is growing substantially, especially in North America. While the consumer market is price-sensitive, product performance is paramount. The market can be segmented by performance/price expectations of the consumer as premium, value, or economy.

The away-from-home (AFH) channel distributes many of the same products as in the consumer channel, as well as some products made specifically for this distribution category. As indicated in the name, this category is for products not used in the home, and includes products distributed to hotels, food-service operations, health care, lodging, office, manufacturing, and institutions. Dispensing systems for product delivery with portion control and labor savings are an important factor. Specialty products in this channel include heavy-duty industrial wipes, heavy-duty napkins, and other specially treated products. This is a major channel for products made from recycled paper, as cost, rather than performance, may be the major selling characteristic. Performance is still important, but business owners who make the selection to service their business judge it. Tissue is generally a necessary cost and not a profit item for AFH.

Performance Characteristics

Performance of tissue products, in either the consumer or AFH segments, is critical. There are three major performance areas – softness, absorbency, and strength – that are common to virtually all tissue products. Visual appearance is an important characteristic, especially in the consumer channel. These four characteristics drive much of the manufacturing process. While the visual appearance can often be manipulated without affecting the other three to a significant extent, there are significant trade-offs in the other properties. Bulk is a key factor in product design as it signals to the user if there is enough product to do the job. Another key point is the bulk or absorbency per unit weight of fiber – getting the job done more efficiently.

Softness

Softness is a quality that is perceived by the user and, to date, has defied quantification. It is a critical property, especially for toilet and facial tissue in the consumer markets. It is becoming a more important characteristic for some toweling and for products in the AFH market where image is important. Softness has been studied extensively by the tissue manufacturers and they have drawn heavily on studies done in the fabric industry. There appear to be two components to softness as perceived by humans. A surface softness refers to the texture felt when the product is rubbed lightly across the skin (or vice versa). This characteristic appears to be related to the frequency, variability, and flexibility of the fiber ends that stick up from the surface of the tissue sheet. All three components are important. If there is no variability, then the user may perceive the product to be flat or smooth, but not soft. Similarly, if the flexibility is too low, then the product is rough. And if the frequency is too low, the product may be perceived as rough, even though the ends that stick up are very flexible. There is extensive work being done in this area, but to date the research work has not yielded quantitative models of human touch.

The other component of softness is bulk softness. This quality is related to the overall bulk and flexibility of the sheet and appears to be related to the tensile strength and modulus, tensile energy absorption (TEA), and thickness of the sheet. 'Hand' or 'drape' are similar terms from the fabric industry and the tissue industry has attempted to modify, with very limited success, test methods from the fabric industry. In general terms, bulk softness increases with the apparent thickness of the sheet and decreases with increasing tensile strength. Thus, manufacturers attempt to increase the thickness, or bulk, of the sheet while simultaneously decreasing the strength. Adding more fibers per unit area (that is, increasing the basis weight) will increase the bulk. Unless other steps are taken, however, this will also increase strength, as well as increasing cost. The goal, then, is to increase the bulk and decrease the strength at constant-basis weight. As fiber becomes more expensive, the goal becomes to reduce the basis weight without affecting other properties – a major challenge in the tissue industry.

Fiber type also plays a role in softness. Hardwood fibers tend to be short, thin, and flexible, contributing to a higher surface softness. Hardwoods also have a high number of fibers per unit weight, which contributes to a more uniform visual appearance. Softwood fibers tend to be long, bulkier, and somewhat less flexible, thus contributing more to the bulk softness component. Recycled fibers tend to be stiff, thus decreasing surface softness. However, their stiffness allows them to make a bulkier sheet, increasing the perception of bulk softness. The actual impact of recycled fibers on the tissue properties will depend upon their original source (e.g., high-yield pulp, bleached chemical pulp).

For the tissue industry, there are no agreed-upon, standardized tests for softness. Tissue manufacturers rely on human panels to measure softness and, while not truly quantitative, such tests do give relative rankings of products. Such tests can support advertising claims, but are not suitable for direct control of the process. A surrogate test that was rapid, accurate, and cheap would allow a tissue producer the ability to improve quality control of the process and lead to a competitive advantage. Such surrogate tests are under development by the major producers and hints of such work can be seen in the patent literature.

Absorbency

Absorbency is the ability of the product to absorb, or imbibe, a fluid. For most tissue products, the fluid of interest is water, and absorbency is normally measured with distilled or tap water. However, some products are required to absorb other fluids. Tampons, for example, must absorb catamenial fluids, while industrial wipes may need to absorb oils. Normal cellulose-based tissue products may need to be specially treated to meet these challenges.

For many products, the rate of absorption is of equal importance to the amount of absorption. The rate of absorption is, in general, related to the size and number of the surface pores. Relatively small pores give a high rate of absorption due to the high surface tension driving forces. Larger pores can hold more liquid. Multi-ply products attempt to deliver an optimal combination of both characteristics. The base paper of each ply can contain small pores to enhance the rate of absorption, while the space between the plies offers volume to hold the imbibed liquid.

Pore size is not directly controllable (or measured) by the tissue-maker. It is a function of the fiber type and how they bond to each other in the papermaking process. In general, low-basis-weight paper will have larger pores due to the larger spacing between the fibers, while higher-basis-weight paper, with more densely packed fibers, will have smaller pores. Increasing the basis weight to increase absorbency also increases cost.

As with softness, there is no standardized test for absorbency. Absorbency rate is usually measured by dipping a vertical strip of the product in water and observing how fast the liquid interface rises up the strip. Another option is to put a drop of water on the product and time the disappearance of the drop. Most tissue products are sufficiently absorbent so that this test is very inaccurate.

Total absorption is usually measured by placing a weighed piece of the product in water, waiting a fixed amount of time, and then extracting and weighing the test piece.

Fiber type and fiber processing are also important for absorbency. Cellulose fibers are hygroscopic and thus absorption of water into the fiber pores and on to the fiber surface are important components of the total absorption process. For most products, the bulk of the absorption is due to the physical spaces between the fibers, not absorption into the fiber pores. Absorption on to and into the fiber are probably significant components of the rate of absorption, but there is little work in this area. Virgin fibers have a much higher rate of absorption than recycled fibers due primarily to the hornification of the recycled fiber during repeated drying. Recycled fibers must be extensively treated, usually by refining, to make their absorption properties similar to that of virgin fibers. Unless recycled fibers are specially treated, products made from them will have relatively low rates of absorption. The total amount of water taken up may be equivalent to that of products made from virgin fibers as the total amount is related to the overall structure of the sheet, but they will require significantly more time to reach this final amount.

Strength

The importance of sheet strength depends upon the product. Bath tissue can be relatively weak, whereas toweling and napkin must be relatively strong. Sheet strength is primarily governed by the fiber-to-fiber bonding characteristics of the sheet. The more bonds that exist, the stronger the sheet. However, as indicated above, increasing the sheet strength generally leads to a stiffer, less soft sheet. The tissue manufacturer must balance the need for strength with the consumer's desire for softness.

Sheet strength is primarily controlled by the hydrogen bonds between the fibers. Fiber entanglement contributes in a minor way to sheet strength. As a result, when the sheet absorbs water, the hydrogen bonds are broken and sheet strength deteriorates rapidly. For bath tissue, this is not a serious problem, as it is generally used in the dry state and water absorption is not a major issue. For toweling and napkin, and facial tissue to a lesser extent, strength while wet is an important, consumer-driven property. Chemicals are added to the sheet during the manufacturing process to improve wet strength. These are normally long-chain polymers that bridge or cross-link between fibers during the drying process. Thus they impart additional dry strength as well as providing wet strength. Because they have significant wet strength, towel and napkin products are difficult to recycle as they will not break apart upon contact with water.

Visual Appearance

The visual appearance of the product, both in its roll form and as individual sheets, is an important marketing tool. This is especially true for the consumer distribution channel, but is playing an increasingly important role in the AFH distribution channel as well. The visual appearance can be affected in a number of ways. Until recently, the primary way was to treat the product during the converting process to impart a distinctive pattern on each sheet. Embossing, passing the sheet through a nip in which the opposing rolls contain a pattern, is a conventional way to impart a pattern on the sheet. This embossing could also be used to increase the bulk and absorbency of the sheet. Recently, manufacturers have developed ways to put patterns directly on the fabric used in the forming and/or drying processes.

Tissue products can also be printed to provide a distinctive visual appearance as well. Since the products are designed to absorb water (and other materials), high-resolution printing is difficult, as the ink tends to spread on the surface and creped tissue is not flat, thus destroying a crisp print pattern. Printed products tend to be slightly higher in price and are used primarily for special occasions.

Manufacture

The forming of a tissue sheet is very similar to that of other paper products. Fiber stock is prepared much like all other paper products. Virgin fiber is lightly refined to increase fibrillation; recycled fiber is more heavily refined to obtain the necessary fiber properties. The stock is cleaned, screened, and diluted to 0.5–1.0% consistency before being deposited on to a forming wire by the headbox. Both Fourdrinier and twin-wire formers are used. Modern machines are generally of the twin-wire type as they permit much higher speeds due to the two-sided drainage of the sheet. One unique modification for tissue manufacture is the crescent-former. This is a twin-wire-type machine, but the bottom 'wire' is not a true wire, but is a felt, similar to that used in dryer sections of other machines. The advantage of the crescent former is that the light-weight sheet can be carried from the headbox to the dryer without transferring the sheet. This is a significant advantage, given the light weight and low strength of tissue sheets. The combination of light-weight sheets, high drainage, and continuous sheet support allow tissue machines to reach high running speeds. Typical light-weight tissue machines will operate in the 5000–6000 ft min^{-1} (25.4–30.5 m s^{-1}) range and it is speculated that tissue machines will approach 8000 ft min^{-1} (40.6 m s^{-1}) in the not too distant future.

While the forming sections of tissue machines are very similar to that of other paper grades, it is in the pressing and drying sections that these machines differ dramatically from the other paper grades. For most tissue grades, there is no press section. One of the goals of the tissue manufacturer is to have a high-bulk, relatively low-strength product, so it is desirable to prevent the sheet consolidation and bonding that occur in pressing. Sheets are conveyed directly from the forming section at 20–45% fiber content, depending upon the forming method, to a drying section.

There are two types of drying systems in use: the Yankee dryer and the through-air dryer (TAD). The Yankee dryer is normally combined with a creping system to impart the desired properties. The TAD can be used alone or in conjunction with some form of Yankee dryer and creping.

Yankee Dryer and Creping

The in-line Yankee creping dryer was first pioneered by the Scott Paper Company in the early part of the twentieth century. Prior to their work, drying and creping were two distinct operations. The Yankee dryer removes moisture from the sheet, while creping breaks bonds and imparts bulk and softness to the sheet.

The Yankee dryer (**Figure 3**) is a large, cast-iron, steam-heated cylinder. Typical diameter is 16 or 18 ft (4.88 or 5.89 m) and the wall thickness is around 2 in. (0.051 m) to contain the pressure of the steam. The cylinder is the full width of the machine, sometimes exceeding 20 ft (6.096 m) in width, so these are massive items of construction. Steam (100–150 psia) is condensed on the inside of the cylinder and hot air (700°F (644 K)) is blown against the surface of the sheet to remove evaporated water as well as provide additional drying energy. The sheet is pressed against the Yankee surface and some water is removed in this light pressing operation. The sheet leaving the press nip is typically about 40% fiber. The sheet is then dried to around 95–98% fiber in the roughly 0.5 s that it takes to travel from this press nip to the crepe blade.

Figure 3 Yankee dryer. From *Pulp and Paper* (1978).

It is imperative that this drying process be as efficient as possible. As the sheet dries, it tends to lose contact with the drying surface, thus decreasing the ability of the Yankee to transfer drying energy to the sheet. To aid in heat transfer, as well as assist the creping operation, a small amount of an adhesive-type material is normally sprayed on to the surface of the Yankee just prior to the sheet nip. Manufacturers, both tissue and supplier companies, devote considerable resources to developing new and improved adhesives. A wide variety of materials have been patented, including polyvinyl alcohol, poly methyl methacrylate, and several types of poly amino amides. Exact formulation and application levels are protected by patents or kept as trade secrets. Application levels are small and the patent literature reveals application rates in the 0.5–1.0 lb (0.25–0.5 kg) of adhesive per ton of fiber.

The dried sheet is then creped off from the Yankee. The crepe blade is a thin steel blade that is pressed against the Yankee dryer and it 'scrapes' the sheet from the dryer. In effect, the sheet, traveling at about 60 miles per hour (26.82 m s^{-1}) impacts a solid-steel wall in the form of the crepe blade. The sheet buckles and fiber–fiber bonds break, imparting both surface softness and bulk to the sheet. This process is not well understood, but micrographs of a creped sheet show a large number of fiber ends, indicating broken bonds. Surface photographs show a large number of 'corrugations' or crepe bars. These run in the cross-machine direction and are up to a half-inch (0.013 m) in length. On a well-creped sheet, there will be 50–100 crepe bars per inch (1970–3940 crepe bars per meter) in the machine direction. While there is no proven theory for crepe bar formation, it is generally believed that the bars result from sheet buckling at the crepe blade. Thus the crepe process can be envisioned as repeated buckling of the sheet as it impacts the crepe blade. These crepe bars impart bulk to the sheet and affect surface softness in at least two ways. They provide some of the variability the sense of touch registers and they also provide hills and valleys for the free fiber ends to stick up and provide a component of surface softness.

Control of the creping process is critical to machine efficiency as well as producing the correct sheet attributes. If the sheet adheres too tightly to the Yankee, then it will not crepe cleanly and there will be holes in the sheet (which is a problem for later converting processes) or the sheet will tear altogether, resulting in machine downtime. If the sheet is not adhered strongly enough, then it will tend to float off the crepe blade and not provide the desired properties. At present, there is no automatic way of determining the quality of the crepe, although there are several laser-based instruments that have been tried. The current control is one of manual operation, with the machine operator judging both the sheet characteristics and the operability of the machine.

The crepe blade also plays an important role in the creping process. The crepe blade is pressed against the Yankee with a small level of force (about 10 lb (44.5 N) force per lineal inch or pli). It is believed that the crepe adhesive provides a very thin coat of organic material on the dryer and that the crepe blade cuts through part of this coating and rides on the remainder of the coating, thus protecting the Yankee surface. Thus, the crepe blade does not actually ride on the metal surface of the dryer. A new crepe blade has a very sharp corner that cuts into this adhesive layer, as shown in **Figure 4a**. As time passes, the corner is worn away and the blade starts to conform to the Yankee surface, as shown in **Figure 4b**. As this corner wears away, the surface contact area increases and the pressure applied drops, as the force pressing the blade to the surface remains constant. At some point, the pressure is insufficient to cut through the adhesive coating and the blade (at a localized point across the width of the machine) no longer crepes the sheet. This leads to holes in the sheet and indicates that the blade must be replaced. Also, as the blade wears, the crepe quality decreases. Changing the blade causes machine downtime, so blade life is a trade-off between machine efficiency and product quality. Typical blade life is in the 4–8-hour range, depending upon product type and product quality demands.

The angle the crepe blade makes with the dryer is an important part of the machine set-up, as it is difficult to adjust this angle. The set-up angle (α in **Figure 5**) is typically between 12 and 22°, resulting in a crepe angle (δ in **Figure 5**) of between 88 and 78°. The face of the crepe blade can also be beveled to adjust the crepe angle. Current belief is that the crepe angle is the critical angle for the process, not the set-up or take-off (θ in **Figure 5**) angles.

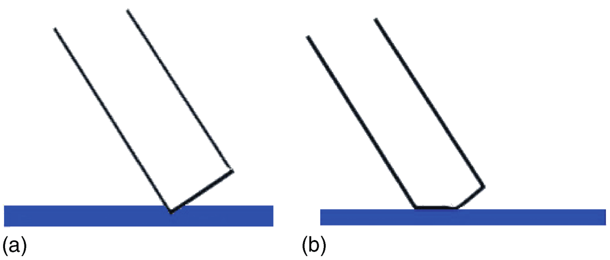


Figure 4 Crepe blades. (a) New blade; (b) worn blade.

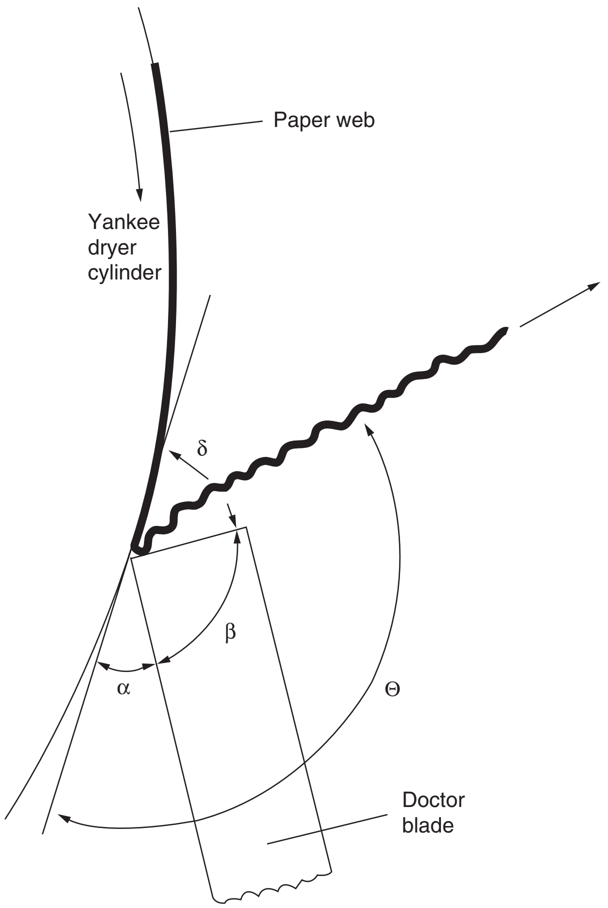


Figure 5 Crepe blade geometry. Reproduced with permission from Smook GA (1992) *Handbook for Pulp and Paper Technologists*, Angus Wilde, Vancouver.

Through-Air Drying and Uncreped Sheets

The Yankee dryer requires that the sheet be pressed against the dryer surface to assure good heat transfer for drying. The creping process is difficult to control and requires some downtime to change crepe blades. To overcome these issues and to provide a sheet with improved properties, the through-air-dried process was developed. This has recently led to a version in which the sheet is only through-air-dried (TAD) and is not creped.

The TAD is a large, open-type cylinder which is the full width of the machine. Hot air (400–500°F (477–533 K)) is blown through the sheet to dry it. Air can be blown from either the inside, with the sheet held against the TAD by a wire of some form, or it can be blown from the outside. This leads to two versions of TAD, commonly referred to as inside-out and outside-in. The main advantage of the TAD over the conventional creped Yankee dryer is that most, or all, of the water can be removed from the sheet by pressing the sheet. This leads to a bulkier sheet, as there is no press-related sheet consolidation.

In the early version of the TAD, the sheet was not completely dried on the TAD. Rather, it was taken to some intermediate dryness (around 60–70% solids) and drying was finished on a small, conventional-type Yankee dryer. The pressing necessary to adhere the sheet to the Yankee in this configuration was not damaging as the sheet was dry enough that the pressing did not consolidate the sheet. It did require a more complex machine, however, as now two drying cylinders (TAD and Yankee) were required and there was a need to transfer the sheet from the TAD to the Yankee. In addition to the drying, the Yankee was also needed to crepe the sheet to provide the desired surface characteristics.

A significant advance for the TAD process was the development of specialized forming and TAD fabrics. Conventional forming and early TAD fabrics were quite smooth, as the papermaking fabrics were designed to minimize the impression of the fabric design in the sheet itself. With TAD, it became possible, and even desirable, to leave some fabric impression in the sheet. These impressions can replace the crepe bars imparted by creping and contribute to desired bulk and surface characteristics. Operating the TAD at a slower speed than the forming section, called negative draw, can impart increased fabric impression in the sheet giving a surface with a visual texture similar to creping. This is commonly called fabric crepe and the negative draw may range from 3 to 15%. With the proper TAD fabric design, it is possible to eliminate the Yankee dryer altogether and impart surface characteristics with the fabric pattern, making full use of fabric crepe. This type of tissue making is called uncreped TAD.

While the uncreped TAD process eliminates the crepe dryer and the drawbacks associated with creping, it is not without some disadvantages. As currently practiced, it requires several fabrics and usually two TAD cylinders. This means that there are several sheet transfers, which increase the risk of sheet breakage. The additional wires are also an additional operating cost. The actual design and operation of an uncreped TAD machine is a closely held trade secret, as well as being protected by multiple patents.

See also: **Papermaking**: Overview; Paper Grades; The History of Paper and Papermaking; World Paper Industry Overview.

Further Reading

Adanur S (1997) *Paper Machine Clothing*. Lancaster, PA: Technomic.

Ampulski R, Spendel W, Sawdai A, and Weinstein B (1991) Methods for the measurement of the mechanical properties of tissue paper. In: *Tappi International Paper Physics Conference*. Kona, HI.

Biermann C (1996) *Handbook of Pulping and Papermaking*, 2nd edn. New York: Academic Press.

Carstens J (1981) US Patent 4,300,981. *Layered Paper Having a Soft and Smooth Velutinous Surface and Method of Making Such Paper.*

Costello P and Alberts C (1998) US Patent 5,753,076. *Method of Creping Tissue*.

Farrington T, Bahlman J, Burazin M, *et al*. (1999) US Patent 5,932,068. *Soft Tissue*.

Oliver JF (1980) Dry-creping of tissue paper – a review of basic factors. *Tappi* 63(2): 91–95.

Smook GA (1992) *Handbook for Pulp and Paper Technologists*, 2nd edn. Vancouver, Canada: Angus Wilde.

Coating

M K Joyce, Western Michigan University, Kalamazoo, MI, USA

Introduction

Coatings are applied to paper and paperboard for two essential reasons: to create a uniform surface for printing or to impart certain functional properties to the surface such as, grease resistance, water resistance, etc. Paper contains a series of holes formed by the overlaying of the fibers during the papermaking process. Coatings are applied to fill these holes and smooth the surface (**Figure 1**). Smoothing the surface enables the image carrier of the printing process to make more intimate contact with the surface, which results in better transfer of the image to the surface, hence better image quality. Coatings also provide a more uniformly porous layer for receiving the inks. Paper suppliers can use the coatings as a means to provide a product that has the desired optical and ink receptive properties needed by the printer for a given print job. Since the characteristics of the inks, means of image transfer, and ink setting and drying mechanisms change from printing process to printing process, the characteristics of the coatings must also change. Coated paper and paperboard manufacturers must therefore first understand the requirements of the coating for each of the printing process, before developing a coating formulation. A review of the four major printing processes (offset, flexographic, rotogravure, and nonimpact) is given elsewhere (*see* **Packaging, Recycling and Printing**: Printing).

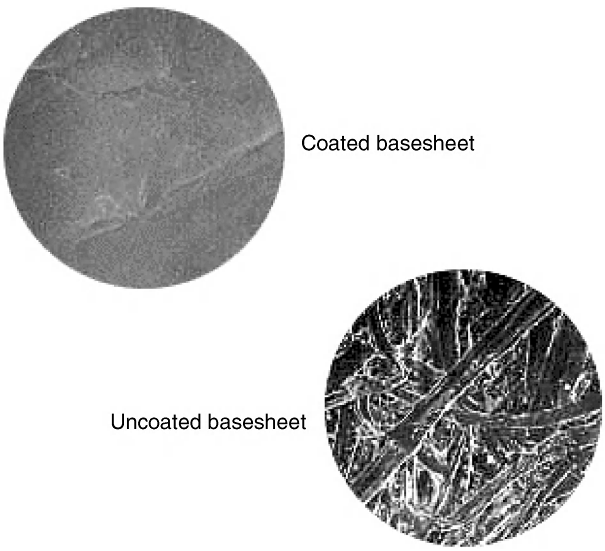


Figure 1 Microscopic views of a coated and an uncoated sheet of paper.

Ingredients and Properties of Coatings

Coating consists of three major components: pigment, binder, and water. It is the pigments that are used to fill the voids between the interlaying fibers. White pigments are chosen in order to provide the highest print contrast between the coating and printed image. The higher the print contrast, the more 'snap' the image will have. This is why high-quality photographic papers are now being sold with brightness values greater than 100%. How this is accomplished will be discussed in the upcoming section on coating additives. But for now, it is evident, that brightness is one property used to judge the quality of paper. Other important properties used to classify the grade of paper are furnish type, basis weight, smoothness, gloss, and opacity. A summary of the properties used in classifying coated North American paper and board grades are given in **Tables 1** and **2**.

Pigments

The optical properties, smoothness, and ink receptive properties of a coating are determined by the types of pigments used in the coating formulation. The most

Table 1 Summary of North American coated paper grade optical and smoothness properties

Paper grades	*Weight ($g\,m^{-2}$)*	*Brightness (%)*	*Smoothness (μm)*	*Gloss (%)*
MFC	55–60	75–78	2.0–2.5	25–30
FCO	52–60	68–70	1.0–1.4	45–50
LWC No. 5	45–70	69–71	1.0–1.4	48–50
MWC No. 4	74–118	75–78	1.0–1.4	58–62
No. 3 PUB	89–148	79–83	1.0–1.3	68–70
No. 2 PUB	89–118	83–85	1.0–1.3	78–82
No. 1 PUB	104–108	85–87	1.0–1.3	88–90

MFC, machine finished coated; FCO, film coated offset; LWC, lightweight coated; MWC, mediumweight coated; Pub, publication. Data from Gay JP, Al-Saimaani M, and Sharman P (1996) *International Papermaker* 59(5): 22–26.

Table 2 Summary of North American paperboard grade properties

Board	*Grade*	*Basis weight ($g\,m^{-2}$)*	*Stiffness*[a]	*Tear strength*[a]	*Surface finish*[a]
	Newsback CRB	200–800	4	1	3
Cartonboard	Carrier CUBK	300–600	5	3	3
	Solid bleached	150–600	4	1	5
Foodboard	Solid unbleached	150–500	4	1	2

[a] 5-Best, 1-Poor CRB, coated recycled board; CUBK, coated unbleached kraft. Data from Ouellet J, Viswanathan G, Sharman P, Cross C, and Johnson S (1997) *PIMA's International Papermaker* 79(5): 17–21.

commonly used pigments in North America are clays, while in Europe, carbonates are more commonly used. This is mostly because of availability. Europeans also tend to prefer more of a matte finish than a glossy finish, which is accomplished by using more carbonate in the formulation than clay.

The properties of the pigment that are most important to the papermaker are particle size and distribution, particle shape, index of refractivity, brightness, abraisivity, and of course cost. The particle size and distribution of the pigment(s) used influences the rheological qualities and runnability of the coating during application and metering and will influence the density of the coating layer after drying. The density of the coating layer influences the optical and ink receptive properties of the coating. The ink receptive properties of a coating are generally reduced when smaller particles, which pack more tightly, are used. However, the shape of the particle will also affect this property because it also influences the final packing density of the dry coating structure.

Gloss and smoothness generally increase with decreasing particle size. Smoothness tends to improve with decreasing particle size because the microdeviations on the surface decrease as the void spacing between the pigment particle decreases. There is some evidence that finer particle pigments require slightly more binder for sufficient adhesion and cohesion of the pigments to each other and the substrate.

Opacity will increase moderately with decreasing particle size, due to the increase in the number of air to pigment interfaces, which will refract more light. This holds true up to a particle size of about 0.3 μm. This has to do with the ability of light to see the pigment particle. For the most effective scattering of visible light, the diameter of the pigment particle should be about 40% of the light that is desired to be scattered. The visible light spectrum ranges 400 to 700 nm or 0.40 to 0.70 μm. Thus, a pigment particle diameter of 0.16–0.28 μm will scatter the incident light most effectively. The ability of a pigment to reflect light diminishes under 0.16 μm particle diameter.

So, as it may appear, the papermaker must balance the desired optical, smoothness, and ink receptive properties of the coating to the costs and processability requirements of the mill and customer.

Pigment Selection

Pigments are classified according to their brightness and weight percentage below 2 μm (**Table 3**). The particle size distribution and shape influence the ability of the particles to flow in the wet and to pack together in the dry state. So in the wet state, the rheological properties of the coating are greatly affected by the distribution and shape of the pigment particles.

The shape of a pigment is determined by the crystalline structure of the mineral from which it is obtained. The crystalline structure and chemical composition of the pigment are what also determines the refractive index and abrasitivity properties of the pigment. The surface finish characteristics of a sheet are heavily influenced by the shape of the pigment particle.

Clay

Clay is a naturally mined pigment. The most significant deposits of clay are found in Georgia (USA), Cornwall (UK), Jari River (Brazil), and southern and northeastern Australia. The major constituents of clay are koalinite and montmorillonite, hence the term kaolin clay. Chemically, clays are alumina silicates, Al_2O_3–$2SiO_2$–$2H_2O$, which have platy hexagonal structures (**Figure 2**). Its platy structure is what enables clays to develop gloss upon calendering. During calendering, the platelets align in the machine direction to improve the smoothness and gloss of the finished surface.

A perfect clay particle would be as shown in **Figure 2**. However, particles are rarely perfect and tend to be irregular six-sided platelets. Above 2 μm, they tend to exist as stacks of two to three platelets. By using a high shear extruding process (**Figure 3**), these platelets can be separated to produce a special grade of clay called delaminated clay. The individual platelets provide a smoother and more closed coating structure than standard clays upon calendering. For this reason, they are commonly used for solvent-based lightweight coated rotogravure printing grades.

Table 3 Classification of pigment

Premium brightness	*Solids (%)*	*Brightness (%)*	*<2 μm (%)*
Ultrafine	70	90–92	95–100
No. 1	70	90–92	90–94
No. 2	70	89.5–92	80–86
Standard brightness			
Ultrafine	70	86–88	94–98
No. 1	70	86–88	90–94
No. 2	70	85–87	78–84

Data from Hagemeyer R (1997) *Pigments for Paper*, TAPPI Press, Atlanta, USA.

Figure 2 Perfect rhombohexagonal clay platelets.

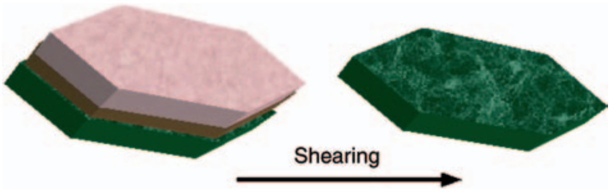


Figure 3 Shearing action to produce delaminated clay.

Selective fine clay particles can be structured into larger particles to enhance the light scattering and ink receptive properties of the particles. The structuring of clay can be performed by either a chemical or thermal treatment processes. The most commonly structured clay is called calcined clay. Calcined clay is obtained by calcifying the clay at temperatures above 1000°C. The high temperature treatment sinters the fine particles together and drives the hydroxyl groups from the chemical structure, which converts the clay to a noncrystalline aluminum silicate, Al_2O_3–$2SiO_2$. The new thermal structure can be described as a 'popcorn' type structure. Like popcorn, the structure contains many voids between the sintered particles. These voids improve the opacifying properties of the pigment, but rheologically make them more difficult to handle. Unlike standard clays, they can only be slurried up to 60% solids. Standard clays can be slurried up to 70% solids. The difference is significant to those wishing to apply high-solids coatings. Calcification also increases the abraisitivity of the pigment. They are most used in coated board grades where coverage is needed to cover the darker base sheet and to improve the absorption properties of grades to be printed with water-based inks.

Calcium Carbonate

Naturally ground calcium carbonate (GCC) is produced from chalk, limestone, or marble by either a wet or dry grinding process. The basic mineral of both chalk and marble is calcite, whose crystals are rhombic in structure. A rhombic structure is best described as a cube, which unlike the platelets of clay, do not produce gloss as readily during calendering. As a result, calcium carbonates are used more in the production of matte grades. However, fine ground and ultra fine ground calcium carbonates (UFGCC) are now available for gloss grades. Calcium carbonate reacts readily with acid and acid salts so carbonate coated broke can not be mixed with acid sized furnishes. They are therefore used in mills producing neutral or alkaline sized papers.

As a coating pigment, calcium carbonate produces a high brightness, high opacity coating. The rheological properties of calcium carbonate enables it to be supplied in slurry form at greater than 70% solids, which allows paper mills to run at higher solids. Unlike clays that have a yellow tint, carbonates have a bluish tint, which causes it to appear brighter in a coating. This property enables it to achieve a brighter coating more economically than clay. It is used significantly in wood free grades and matte grades. The rhombohedral particles pack more tightly than the two to three stacked platelets of standard clay. The resulting tight packing structure tends to dust more while printing. A blend of clay and carbonate is therefore more generally used for matte grades. Glossy grades are produced using little or no GCC or using an UFGCC with 90% finer particles less than 2 microns.

Another form of calcium carbonate that is being commercially sold in smaller quantities to the paper industry as a coating pigment is precipitated calcium carbonate (PCC). The switch from the acid to alkaline papermaking process has increased the usage of precipitated calcium carbonate in paper coatings, but its cost has limited its use. The conversion from acid to alkaline papermaking led to the development of satellite PCC mills next to the paper mills. PCC is produced from the limestone generated from the kraft chemical recovery process. The particle and shape of the PCC are determined by the precipitation conditions used, such as pH, temperature, degree of agitation, and use of additives. By controlling the conditions, either calcite or aragonite forms of PCC can be produced. The main advantage of PCC over GCC is the control of particle size, shape, and particle size distribution. They are mainly used for grades that can justify the increase in cost for the properties gained. The rheological properties of some of these grades also limits the ability to slurry them at high solids.

Specialty Pigments

Besides clay and calcium carbonate, there are many other types of pigments used in paper coatings that due to their lower usage levels are considered specialty pigments. These include titanium dioxide, plastic pigments, talc, alumina trihydrate, and silica, just to mention a few. The properties that prevent these materials from being used in larger quantities are one of cost and ease of application. Several of the above-mentioned pigments are difficult to disperse at high solids. They are therefore only used in applications where they have a special part to play.

Comparison of each pigment's properties in **Table 4** show the distinctive properties of some of these pigments. Besides differences in particle shape and refractive index, density is another distinguishing characteristic that can play an important role in the selection process for a coating. The density of a

Table 4 Summary of distinguishing pigment properties

Pigment	*Dry bright (%)*	*Refractive index*	*Specific gravity*	*Crystal form*
Clay	70–90	1.55	2.65	Rhombohexagonal
GCC	90–95	1.49–1.66	2.72	Rhombohedral
PCC	95+	1.49–1.68	2.72–2.94	Rhombic, acicular, scalenohedral
TiO_2	97–98	2.70 (Rutile)	4.20	Tetragonal
TiO_2	98–99	2.55 (Anatase)	3.90	Tetragonal
Solid plastic (polystyrene)	97+	1.59	1.05	Spherical

GCC, ground calcium carbonate; PCC, precipitated calcium carbonate; TiO_2, titanium dioxide.

pigment is especially important for lightweight coated grades of paper. In these grades, lower-density pigments are preferred to keep the weight of the coating down. For this reason, synthetic plastic pigments are often used for opacity and improved finishing and printing properties in these grades. Synthetic pigments are made from a variety of synthetic polymers, but styrene and copolymers that possess glass transition temperatures above 50°C dominate the commercial market.

The selection of pigment(s) for a coating will have a profound effect on the runnability, printability, and optical properties of the finished product. The right combination of pigments must be chosen to meet the end-use requirements and cost constraints of the customer. At the same time, it must be capable of being run on the manufacturer's available coating equipment. The same requirements must be met by the binder, which is the second largest component within any coating formulation (besides water).

Binders

The role of the binder is to provide the properties of cohesion and adhesion to the coating. Cohesion refers to the binding of two like surfaces, such as pigment-to-pigment bonds. Adhesion refers to the binding of two unlike surfaces, such as pigment-to-fiber bonds. The strength of the bond between any two surfaces strongly depends on the type of binder used and the amount of contact between the two surfaces. It is important to say that these are not the only factors, but since they are the two that can be controlled through the selection process, they are the only two that will be discussed at this time.

A summary of the different types of binders used in paper coatings is given in **Figure 4**. The bonding strength of the binder is to a large extent influenced by the length and flexibility of the polymer chain. The more flexible the polymer chain, the more flexible the bond. The chemical composition of the polymer and the amount and type of chemical conversions performed on the polymer control the flexibility and length of the binder's polymer chains.

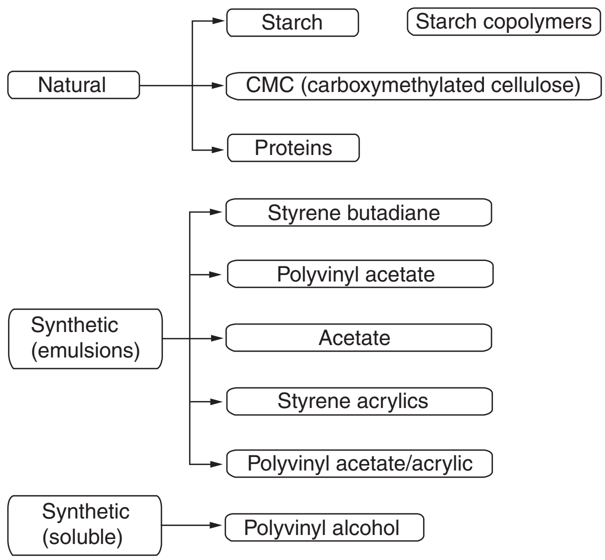


Figure 4 Summary of different paper coating binders.

A binder is a special kind of adhesive. Its role in a coating formulation is to adhere the pigments to one another and to the substrate. The binder also serves to control the porosity, and the water and solvent resistance of the coating. The gloss of the coating can also be greatly influenced by the type of binder used.

Binder Selection

When selecting a coating binder, the binding strength is not the only property that must be considered. The flexibility of the binder after drying is also very important as well as its film forming properties. A flexible binder will form a flexible, continuous film upon drying and flexible bonds between any two solid surfaces. A nonflexible binder will form a rigid film, resulting in rigid bonds that are nondeformable. A rigid structure that will not deform under the action of the calender will not attain a high level of gloss. On the other hand, a very flexible binder might become tacky and stick to the rolls of the calender. As a result, the two properties must be balanced to yield the final desirable coating properties.

The level of binder used depends on the 'binder demand' of the pigment. Binder demand means the amount of binder required to obtain the desired surface strength properties of a coating. Binding strength is very important, but it is very difficult to quantify because just as each binder has a particular strength, each pigment has its own binder demand. The binder demand of the pigment will depend on the shape of the pigment, particle size and particle size distribution.

So, when selecting a binder the formulator must consider the binder demand of the pigment, the bonding strength of the binder, the desired coating properties (optical and print properties), the demands of the printing process on the surface strength of the coating, and of course cost. Formulators seek to minimize the amount of binder needed not only for cost considerations, but also because the binder can interfere with the optical properties of the coating. The presence of excess binder reduces the number of air voids available to scatter light and receive the carrier solvents in the printing inks.

There are two major classes of binders used in paper coatings; natural and synthetic. The two predominant types of natural binders are starch and protein. Starch is composed of two high molecular weight polymers called amylose and amylopectin (**Figure 5**); it is easy to see that amylose is linear like cellulose while amylopectin is branched.

To enable the starches to be prepared at higher solids, the molecular weight of the starch can be reduced or the starch depolymerized. The depolymerization of starch involves the chain cleavage of the anhydroglucose units, which results in shorter, lower molecular weight polymer chains. Consequently, the viscosity of starch decreases and they can be prepared at higher solids.

Starches can be depolymerized (degraded) enzymatically with enzymes, or chemically using hypochlorite or hydrogen peroxide to oxidatively depolymerize the starch. Another chemical method is acid hydrolysis. The degradation can be made either on-site at the mill, or by the starch supplier. Hypochlorite, hydrogen peroxide, and acid hydrolysis are usually performed by the supplier. Starches can also be thermochemically modified. Thermochemical starches are prepared on-site by the mill using a continuous jet cooker. A starch slurry containing oxidizing agents, usually ammonium persulphate or hydrogen peroxide, is cooked in a jet cooker to a desired viscosity.

Another problem associated with using starch in comparison to synthetic binders is that it must be cooked to get it into solution and the temperature of the solution maintained at an elevated level to prevent retrogradation or gelling. To limit the effects of retrogradation and improve the solubility of starch, starches are chemically modified. The most commonly used derivatized starch in paper coatings

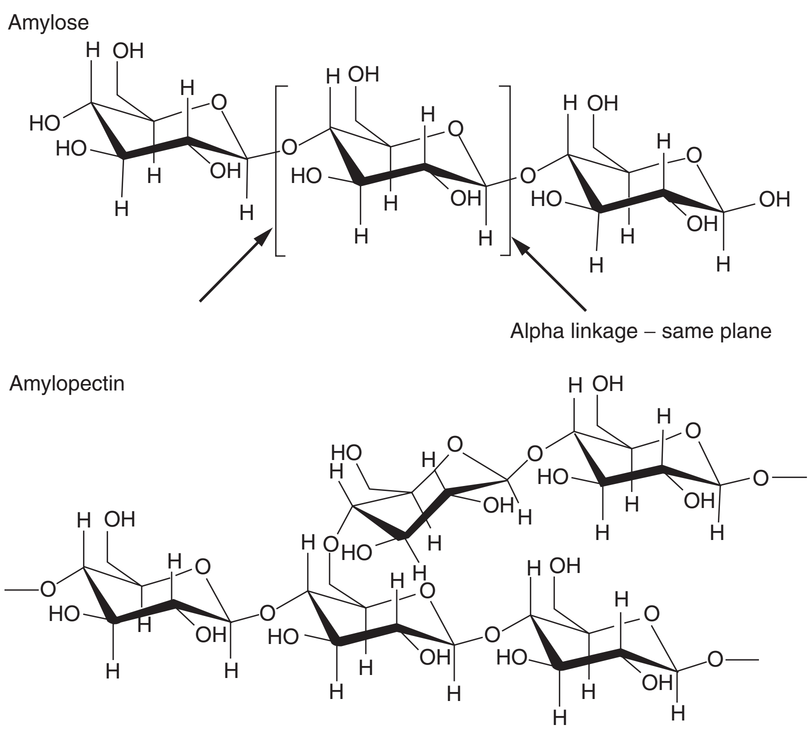


Figure 5 Structures of amylose and amylopectin.

is hydroxyethylated starch. Although more expensive, hydroxyethylated starch offers the advantages of more stable viscosity control, better film clarity and flexibility, and better water-holding properties.

Although these advantages come with a price, the economics are still better than that of synthetic binders. Unfortunately, regardless of the functionality added and the properties gained by the derivatization process, the solids at which these products can be made down are still limited to less than 30%. This limits the amount that can be used in high solids coatings.

Proteins

Proteins are obtained from natural sources such as milk casein and soybeans. But today almost all protein used by the paper industry is derived from soybeans.

The structure of protein is much more complex than starch. Protein contains 19 different amino acids, which are held together in a coiled structure by hydrogen and disulfide bonds. Proteins are amphoteric polymers. This means they contain positive (cationic) and negative (anionic) functional groups. Because most pigments are anionic, proteins interact strongly with pigments. This interaction causes a more open and bulkier coating to form.

Proteins can be modified to provide different bulking and viscosity characteristics. Like starch, they can be hydrolyzed to reduce the molecular weight, hence enabling them to be prepared at higher solids, due to less viscosity at given solids. They can also be carboxylated to improve their solubility and alter their degree of interactivity consequentially altering their bulking properties. They are mostly used in coatings for unbleached kraft board grades where bulk is needed to provide good coverage of the lower brightness base sheet.

Coating Additives

Additives are minor constituents that are added to a coating in relatively small amounts (less than 2% on weight of dry pigment) to improve the runnability of the coating on the machine or to enhance the final properties of the coatings. Some of the different types of coating additives used, just to name a few are defoamers, lubricants, rheology modifiers, crosslinkers, optical brightening agents, colorants, biocides, and dispersants. The name of the additive for the most part describes the role it plays within the coating. Although additives constitute only a minor part of the overall coating mix, their use is often critical to the overall performance of the coating in both the dry and wet state. A full discussion of their chemistry and application is too extensive to cover in this article.

Coating Processes

There are various methods for applying and metering a coating on to paper and board. Regardless of the method, the main objective is the same, to apply a uniform coating layer in a controlled manner.

All coating processes can be separated into three different operations: application, metering, and leveling. The type of application and metering devices used determine the stresses placed on the basesheet, the uniformity of the coating layer, the coat weight, range and possibility of operating problems such as scratching, ribbing, whiskering, misting, etc. Coatings can be applied on-machine and off-machine.

Size Press and Metered Size Press

The size press is the most common on-machine coater. It is mainly used to apply film forming materials such as starch and polyvinyl alcohol to the sheet to improve surface strength, alter the absorptive properties of the sheet, or impart a special functional property. When used to apply a pigmented coating, it is normally used to apply a low coat weight precoat. Three different flooded nip size press designs are shown in **Figure 6**.

The size press can be thought of as a simple roll coater or film transfer coater. Film transfer coaters all experience the same runnability problems at high speed, ribbing and misting. Both problems are influenced by the thickness of the wet coating layer as it is transferred from the roll to the paper. During the transfer process, the coating layer is split. As shown in **Figure 7**, part of the coating remains on the roll and part of the coating is transferred to the paper. The amount of ribbing and misting that occurs depends on the thickness of the wet coating layer before it splits, the rheological properties of the coating, absorptive properties of the base sheet and machine speed. Therefore to prevent the onset of ribbing and misting at higher speeds, it is desirable to minimize the thickness of the wet coating layer prior to the film transfer process. This understanding led to the evolution of the film transfer coater design from the flooded nip size press to the gate roll coater to the modern day premetered size press shown below in **Figure 8**. The premetered size press utilizes a short-dwell coating

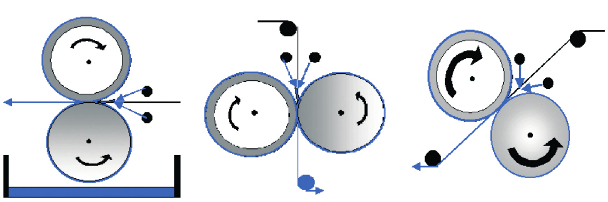


Figure 6 Three different size press designs: vertical, horizontal, and inclined.

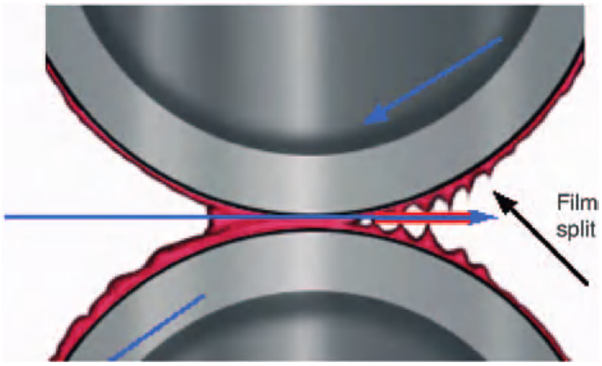


Figure 7 Film split between size press rolls and paper.

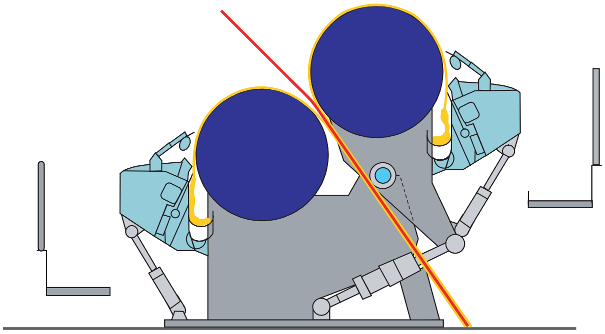


Figure 8 Modern metered size press.

head design, which holds a blade or rod metering device. In the short-dwell applicator, coating is pumped into a reservoir immediately upstream from the metering device. The pneumatic loading of the metering device controls the final coat weight.

Short-Dwell Coater

The short-dwell coater was originally designed as an off-machine coating method to coat lightweight grades of paper. The short contact time between the coating and paper surface reduced the number of sheet breaks experienced running these grades as a result of the loss in sheet strength due to the rewetting of the basesheet upon application of the coating. However, vortex flows in the low pressure reservoir have been linked to coating nonuniformities caused by the entrainment of air.

Blade Coaters

Although it provides the smoothest surface, the blade coater applies the greatest stress to the paper web. The stress applied to the web can cause web breaks, which results in costly machine down time. Scratches and streaks are also more prevalent with this method of coating.

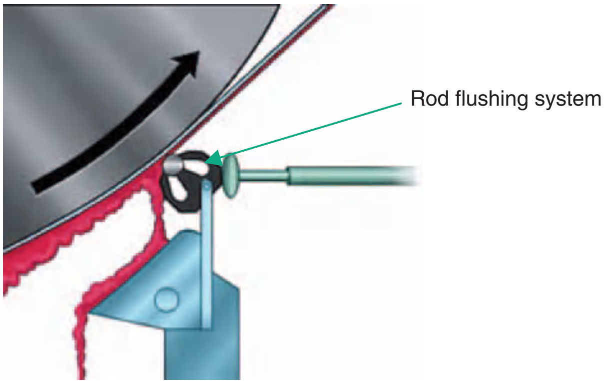


Figure 9 Example of rod holder and flushing system set-up.

Rod Coaters

Rod coaters are also rigid metering device coaters, but their cylindrical design stresses the base sheet less than a blade. It also enables the rod to be rotated against the web during its operation. This enabled a flushing system to be incorporated into the rod holder (**Figure 9**). This reduces the tendency for scratching and streaking which is especially beneficial to grades containing larger amounts of recycled fiber and lower surface strength, but the finished surface is not as smooth as a blade finished one.

Air Knife Coaters

Air knife coating is a noncontact coating application method, which uses a jet of air to meter the coating from the substrate. Since it is a noncontact coating method, it does not have the disadvantages of stressing the web and is not prone to scratching and streaking. The disadvantage to this coating method is in its limitation to applying low coat weights. It is mostly used to coat board. The smoothness of the coating layer is lower than that of a blade or rod coater.

New Coating Methods

Two new coating methods that are gaining industrial interest are curtain and spray coaters. Curtain coaters utilize a flow element, such as a die or extruder, to meter a coating onto the substrate. The coat weight is controlled by the slot width of the die and pressure drop in the coating line. New designs are currently being studied to reduce the problems associated with running these coaters at higher speeds and coating solids. The problems are mostly associated with the entrainment of air in the coating at higher web speeds. The advantage with this system is that good coating coverage can be achieved with little stress to the base sheet.

Spray coating is the newest commercially available coating method available. The method uses several spray nozzles that can be rotated during operation for cleaning to prevent down time. With spray coating, a wide range of coat weights are possible. Good coverage with minimal stress to the base sheet can be obtained. As with curtain coating, several issues remain with regard to formulation and uniformity of the final coating layer. However, each method shows promise as lower stress coating methods.

Concluding Remarks

The introduction of new coating technologies and new coating materials into the market place is increasing the level of competition between coated grades. Machines are running faster and more efficiently. Quality is improving and printers are reaping the benefits as they continue to demand and receive more from their suppliers. Advances in printing technology will continue to drive the coated paper markets as printers seek to print more colors using multiple printing technologies. To keep pace, the papermaker must stay knowledgeable of not only innovations in coating material and process technology, but also new printing technologies and trends.

See also: **Packaging, Recycling and Printing**: Packaging Grades; Printing. **Papermaking**: Overview; Paper Grades; Paperboard Grades.

Further Reading

Dean TWR (1997) *The Essential Guide to Aqueous Coating of Paper and Board*. Bury, UK: Paper Industry Technical Association.

Gay J-P, Al-Saimaani M, and Sharman P (1996) Making sense of the maze: guide to pulp and paper printing/writing grades. *International Papermaker* 59(5): 22–26.

Garey CL (ed.) (1997) *Physical Chemistry of Pigments in Paper Coatings*. Atlanta, GA: TAPPI Press.

Gullichsen J and Paulapuro H (2000) *Pigment Coating and Surface Sizing of Paper*. Helsinki, Finland: Fapet Oy.

Hagemeyer R (1997) *Pigments for Paper*. Atlanta, GA: TAPPI Press.

Hagemeyer RW (1983) Pigment coating. In: Casey JP (ed.) *Pulp and Paper, Chemistry and Chemical Technology*, vol. IV, 3rd edn. New York: John Wiley & Sons.

Kane RJ (ed.) (1995) *Paper Coating Additives*. Atlanta, GA: TAPPI Press.

Ouellet J, Viswanathan G, Sharman P, Cross C, and Johnson S (1997) Paperboard: all you need to know about classification. *International Papermaker* 79(5): 17–21.

Paulapuro H (2000) *Paper and Board Grades*. Atlanta, GA: TAPPI Press.

Pothier P and Je Y (1998) *Additives for Paper Coatings Description of Functional Properties and List of Available Products*. Atlanta, GA: TAPPI Press.

PATHOLOGY

Contents

Diseases of Forest Trees

M J Wingfield, University of Pretoria, Pretoria, Republic of South Africa

Introduction

Plant diseases have been recognized for as long as plants have been cultivated. There are many references to plant diseases in early Greek and Hebrew writings. In these early times, diseases were believed to result from the wrath of God and it is not surprising that the Bible contains many references to plant diseases.

The discovery that fungi could cause diseases of plants was made by the chemist Anton de Bary in 1853, when he showed that rust and smut fungi (Uredinales and Ustilaginales) were the causal agents of cereal diseases. De Bary was also responsible for showing that late blight of potato, a disease responsible for reducing the human population of Ireland by half in five years, was caused by the fungus *Phytophthora infestans*. This is perhaps the most famous (or infamous) of all plant diseases. De Bary is appropriately recognized as the 'father' of modern plant pathology.

Although understanding that plant diseases are caused by microbes might seem to be rather obvious to us today, the process of enforcing this understanding was by no means simple. During the first half of the nineteenth century, the doctrine of spontaneous generation was well established, with strong support for the view that microbes emerged from decaying plant and animal matter. Understanding that microbes were the cause and not the result of decomposition emerged relatively slowly. This was through substantial experimentation by scientists including De Bary and Pasteur.

Forest pathology and the study of diseases of trees followed relatively soon after the recognition that microbes can cause diseases of plants. The science of forestry had its origins in Europe and it is not surprising that the 'father' of forest pathology was German. Thus, Robert Hartig (1839–1901) produced the first textbook of forest pathology in 1874. The importance of this book was recognized rapidly as is evident from its rapid translation by the famous British plant pathologist Marshall Ward and the publication of an English edition in 1894.

Plant pathology is hugely important to human health and welfare, yet ironically it is not a subject that has attracted adequate support. It is difficult to know exactly how many active plant pathologists there are in the world but the International Society for Plant Pathology records approximately 6000 names. It is worrying to know that there are certainly no more than 300 active forest pathologists in the world today. These scientists are mostly specialists interested in particular groups of pathogens or aspects of forestry.

This article presents a brief overview of the role of pathogens in forests. This is clearly a very broad topic, which has been treated in various levels of detail and focus in a number of excellent textbooks. It is obviously impossible to provide detail concerning any particular disease. Rather, the aim is to present an introduction to other articles that deal more specifically with various categories of disease.

Diseases in Natural Forests and Plantations

Forest pathology generally treats three broad categories of trees:

- natural, generally undisturbed forests
- intensively managed plantations of native or exotic species
- amenity or ornamental trees.

Diseases tend to act differently in these distinct situations and their management is also generally different. This article specifically treats diseases of native trees, mostly in natural ecosystems or in managed woodlands or forests. Diseases in intensively managed plantations of exotic trees such as the millions of hectares of *Pinus*, *Acacia*, and *Eucalyptus* found in the tropics and the southern hemisphere are treated elsewhere (*see* **Pathology**: Diseases affecting Exotic Plantation Species).

Categories of Tree Disease and their Causal Agents

Virtually every treatment of tree diseases classifies them somewhat differently. If we use Manion's definition of diseases any 'disturbance in the normal physiological functioning of a plant,' then diseases include both those caused by biotic factors as well as those associated with abiotic factors. Biotic factors include microbes and other organisms that have the ability to spread and are thus considered to be infectious. Most forest pathologists study these diseases because they have the ability to cause devastating losses. Diseases caused by abiotic factors such as air pollution, soil contamination, and other environmental factors can also result in very substantial damage. Diseases associated with air pollution, for example, have grown in importance in recent years and this is a trend that is likely to continue as the world population grows.

Most biotic tree diseases are caused by fungi. These fungi include: (1) basidiomycetes such as the decay fungi with mushrooms and brackets as fruiting bodies and the rusts; (2) ascomycetes which are the most numerous causal agents of tree disease; and (3) the oomycetes or water molds such as species of *Phytophthora* and *Pythium* which are best known as root pathogens of forest trees. Tree diseases are also caused by many other biotic agents such as bacteria, phytoplasmas, viruses, nematodes, and parasitic plants.

Disease Epidemics

There are numerous examples of tree disease epidemics that have caused devastating losses to natural ecosystems. Most of these have occurred on trees in natural ecosystems into which pathogens have been introduced. Generally these pathogens occur on the same genera of trees in areas, separated geographically from those that are affected. Typical examples are Dutch elm disease caused by *Ophiostoma ulmi* and *O. novo-ulmi*, chestnut blight (*Cryphonectria parasitica*), white pine blister (*Cronartium ribicola*), and pine wilt caused by the pine wood nematode (*Bursaphelenchus xylophilus*).

The first recorded tree disease epidemics date back to the beginning of the twentieth century. That was also the time when worldwide trade in and movement of forest products began to increase. Today there are increasing numbers of tree disease epidemics appearing. This is likely to be a trend that will continue, with the increasing movement of people and products around the world.

Vascular Wilt Diseases

Vascular wilt diseases are broadly defined as those that result from a blockage of the vascular tissues. Symptoms generally include chlorosis of the foliage and a rapid wilt (*see* **Pathology**: Vascular Wilt Diseases). These diseases are best known in hardwood trees that have xylem vessels that are easily blocked, particularly in the case of ring porous trees where trees depend on large xylem vessels at the start of the growing season. Vascular wilt diseases are less clearly defined in the conifers that have tracheids, which are less easily colonized and blocked.

Blockage of the vascular tissues can be due to the physical presence of fungal structures. The production of tyloses in the xylem vessels is a typical response to infection by vascular wilt pathogens. Production of these structures represents an attempt to slow the movement of the invading pathogen and also blocks the vessels, giving rise to wilt symptoms. Some vascular wilt pathogens are known to produce toxins, which are also involved in the development of the wilt symptoms.

Vascular wilt diseases are caused by ascomycete fungi, nematodes, bacteria, and phytoplasmas. A large number of these disease agents are carried by insects and some are soilborne. Vascular wilt diseases tend not be caused by pathogens typically dispersed in water or via airborne inoculum.

Some of the best-known fungal vascular wilt pathogens are transmitted by insects. In this regard, there are two main categories of insects that carry these pathogens. Thus, the devastating Dutch elm disease pathogens *O. ulmi* and *O. novo-ulmi* are carried by bark beetles (Coleoptera: Scolytidae) which produce maturation feeding wounds in the branch crotches of healthy trees, enabling infection to occur. The same would be true for black stain root disease caused by *Leptographium wageneri*, which can be vectored by insects such as *Hylastes* spp. that undergo maturation feeding on healthy conifer roots. In contrast, various vascular wilt pathogens are carried by casual insects such as flies (various families of Diptera) and picnic beetles (Coleoptera: Nitidulidae) that are attracted to the sap produced by freshly made wounds on trees. Typical examples of this group of insect-vectored fungi causing vascular wilt are the oak wilt pathogen *Ceratocystis fagacearum* and *Ceratocystis fimbriata*, which causes vascular wilt on a wide range of hardwood trees.

Pine wilt caused by the nematode *B. xylophilus* is an extremely important disease of pines in Asia. This is an unusual disease because it occurs in the upper parts of trees and has many similarities to vascular wilts caused by fungi. The pathogen is vectored by longhorn beetles (Coleoptera: Cerambycidae) which, prior to the recognition of the cause of pine wilt in 1971, had been generally considered to be secondary wood-boring insects of minor importance. However, these insects and particularly species of *Monochamus* undergo maturation feeding on twigs of healthy *Pinus* spp. allowing the nematodes to enter the vascular tissues of the trees. The exact mechanism of tree death is not fully understood but is thought to include physical nematode feeding and the production of toxins by nematodes or bacteria associated with them.

Fungal vascular wilt pathogens that are typically soilborne include species of *Fusarium* and *Verticillium*. Both these genera of pathogens are also well known causal agents of serious diseases of agronomic crops. Thus, *Verticillium albo-atrum* is an important pathogen of potatoes but also causes a serious vascular wilt disease of hardwood trees such as maples and ash. Host specialized forms of *Fusarium oxysporum* also cause serious wilt diseases on a wide array of agronomic crops, such as panama wilt disease of bananas caused by *F. oxysporum* f. sp. *cubense*. There are fewer examples of this group of pathogens in forest trees, but they are relatively common on legumes such as species of Acacia.

Serious vascular wilt diseases are caused by various bacteria and phytoplasmas. A serious wilt disease of trees including for example *Eucalyptus* is caused by the bacterium *Ralstonia solanacearum*.

This pathogen occurs in various forms on a wide range of mainly agronomic crops and is generally recognized as being soilborne, entering wounds on roots. In contrast phytoplasmas such as the causal agent of the serious ash yellows disease are xylem limited bacteria and are typically vectored by leaf hoppers (Homoptera).

Root Diseases

Root diseases are most typically caused by fungi belonging to all the major groups, although perhaps the basidiomycetes are best known and most common. Root diseases are also caused by nematodes although there are few examples of serious nematode problems in native trees. Root diseases are often recognized by patterns of disease development arising from the gradual movement of the causal agents through the soil (*see* **Pathology**: Root and Butt Rot Diseases). Thus, for example, in the case of species of *Armillaria* and *Heterobasidion*, this movement is generally from a single point of infection resulting in discrete patches of dying trees, with the most recently killed trees at the periphery of the disease centers. Trees will die slowly or might appear to wilt and die rapidly, but they have generally been infected for a considerable time prior to the appearance of symptoms. Species of *Armillaria* are well known to produce huge infection centers caused by a single clone of the fungus, which has led to the discovery that these fungi represent the largest and the oldest living organisms.

Fungal root pathogens have various infection strategies. Some disperse through the production of large numbers of airborne spores. Typical examples are the species of *Armillaria* and *Heterobasidion annosum*. In the case of these pathogens, spores can infect the surfaces of stumps of freshly cut trees or wounds at the bases of these trees. The fungi then consume the stumps and roots of the infected trees to build up inoculum potential that enables them to move from tree to tree by root contacts or grafts. *Armillaria* species also produce bootlace-like rhizomorphs, which grow on the surface of roots and through the soil, facilitating infection of adjacent trees.

Waterborne and soilborne pathogens and particularly species of *Phytophthora* are amongst the most important root pathogens of trees (*see* **Pathology**: *Phytophthora* Root Rot of Forest Trees). These fungi produce motile zoospores which enable them to move through water. They also produce thick-walled sexual spores that facilitate their survival in the soil for extended periods. *Phytophthora cinnamomi* is by far the best-known tree pathogen in this category and its introduction into native woody ecosystems in Australia has resulted in severe disease epidemics.

An unusual and interesting root pathogen that requires heat to become active is the conifer pathogen *Rhizina undulata*. This pathogen is an ascomycete that disperses its spores actively and these appear to infest the soil, or possibly the fungus lives epiphytically associated with conifer roots. However, heat from fire and occasionally lightning is needed before *R. undulata* becomes active. The disease can result in substantial damage after forest fires and is also commonly associated with patches of dying trees, where camp-fires have been made; among forest workers in the UK it was often known as the coffee-break disease.

Insects can be responsible for the dispersal of tree root pathogens. The best examples are species of *Leptographium* that are asexual states of *Ophiostoma*. These fungi produce sticky spores in the galleries of bark beetles and weevils (Coleoptera: Curculionidae) and the fungi are thus transmitted to tree roots by these insects. The most serious pathogen in this category is the black stain root disease pathogen, *Leptographium wagneri*, which occurs in three forms and is restricted to conifers in western North America.

Canker Diseases

Canker diseases are most commonly caused by ascomycetes and occur on branches and stems of trees (*see* **Pathology**: Stem Canker Diseases). The most serious of these are stem cankers, which girdle the lower parts of stems, resulting in tree death. Canker pathogens tend to infect the cambium and trees can respond by producing callus to seal off the infected tissue. In the case of perennial cankers the pathogen is most active during one period and the tree responds during the remainder of the year. This results in target-like cankers with concentric rings of callus on the stems of trees. In contrast, annual cankers infect the cambium and in severe cases will often girdle the trees.

Although not strictly considered canker pathogens, many rust fungi cause perennial infections on the stems of trees. The rust fungi are unique obligate plant pathogens, having up to five stages in their life cycles, which can occur on two different hosts. Thus white blister rust caused by *Cronartium ribicola*, which has devastated white pine in the North America, gives rise to its most severe damage on the stems of white pines, but has *Rubus* species as alternate hosts. Likewise, serious damage is caused to the stems of various *Pinus* species by the fusiform rust pathogen *Cronartium quercinum* f. sp. *fusiforme*, while various species of oak serve as alternate hosts.

Most canker pathogens are dispersed by spores that are produced during moist weather and that are dispersed by wind. Certainly the best known and most devastating canker disease is caused by the chestnut blight pathogen which has virtually eliminated the American chestnut, *Castanea dentata*, from its native range. There are many other fungi that cause serious canker diseases and these include species of *Botryosphaeria*, the poplar canker pathogen *Hypoxylon mammatum*, and the pitch canker pathogen *Fusarium circinatum*, to name but a few. These pathogens all tend to infect natural or artificially caused wounds on trees, or they are endophytes in healthy trees that proliferate after the onset of stress.

Insects can be important associates of some canker pathogens. For example, the pitch canker pathogen is closely associated with twig and cone feeding insects. Pitch canker is one of the most serious diseases of pines and is responsible for a devastating disease of *Pinus radiata* in California. The pathogen occurs in countries such as Chile and South Africa but is restricted to nurseries. The absence of shoot and cone insects in these countries is thought to be the reason why the disease has not developed into a major problem on large trees.

An interesting recent example of an oomycete pathogen able to cause cankers on trees is *Phytophthora ramorum*. This pathogen is infecting many genera and species of trees in the western USA and is thought to have been introduced into that country from Europe where it occurs on leaves and shoots of *Rhododendron* spp. The sporangia of *P. ramorum* are dehiscent and dispersed by air, after which zoospores are produced in moisture and these directly infect the cambium of susceptible trees, to cause annual cankers.

Leaf and Shoot Diseases

As is true with all plants, trees have a very large number of leaf and shoot diseases (*see* **Pathology**: Leaf and Needle Diseases). These are most commonly caused by ascomycete pathogens but many are caused by rusts (Basidiomycetes: Uredinales) and in a small number of cases *Phytophthora* spp. These pathogens can infect shoots where severe dieback and damage can occur. They can also give rise to the death of large areas of leaf surface causing blight and severe defoliation. Although a single defoliation generally does not kill trees, repeated infections are common and can cause growth loss and even tree death. In other cases, leaf diseases cause discrete spots or localized symptoms on the leaves.

Ascomycete leaf and shoot pathogens have a number of different dispersal strategies. Some have exclusively airborne spores that tend to be actively discharged from fungal fruiting structures. Typical examples are for example in the sexual states of *Mycosphaerella* and the powdery mildews that cause leaf diseases on many trees. Many asexual states of ascomycete leaf and shoot pathogens produce spores that are discharged in association with rainfall. Typical examples amongst more serious tree pathogens are found in the needle blight pathogen *Dothistroma septospora* and the dogwood anthracnose pathogen, *Discula destructiva*.

The rust fungi cause leaf and shoot diseases as well as the cankers discussed above (*see* **Pathology**: Rust Diseases). Spores associated with most of these stages are powdery and windborne although moisture is generally required for the production of basidiospores and insects are known to be involved in fertilization of pycnia. Many rusts are important leaf and shoot pathogens of forest trees. These for example include needle rusts on conifers caused by *Coleosporium* spp., the aecial state of cedar apple rust on apples caused by *Gymnosporagium juniperi-virginianae* and eucalyptus rust caused by *Puccinia psidii*.

Insect Associated Diseases and Blue Stain

Many species of conifer infesting bark beetles are known to carry fungi that impart blue stain to the sapwood of infested trees (*see* **Pathology**: Insect Associated Tree Diseases). Most of these fungi are species of *Ophiostoma* and *Ceratocystis* and their asexual states. They are generally known to be nonpathogenic or only mildly pathogenic. However, their role in killing trees is poorly understood and deeply debated. Certainly some of these fungi such as *Ceratocystis polonica*, associated with the aggressive European spruce bark beetle *Ips typographus*, are highly pathogenic and appear to contribute substantially to tree death.

Irrespective of their pathogenic role associated with bark beetles, species of *Ophiostoma* and *Ceratocystis* that infest conifers impart substantial damage to timber products. After the insects have killed these trees, the sapwood typically becomes severely discolored with so-called blue stain. This discoloration is not strictly a stain in the sense that it is caused by a product of the fungi. It rather arises from the darkly pigmented hyphae of the fungi which colonize the tracheids and ray parenchyma. The fungi do not result in any weakening of the timber but the discoloration is aesthetically unattractive to wood markets and associated financial losses can be great.

Wood Decay

Decay and so-called heart rot in standing trees is most typically found in old-growth forest where trees are sufficiently old to develop columns of decay at their centers (*see* **Pathology**: Heart Rot and Wood Decay). Decay fungi enter wounds on the stems of trees or through broken branches and gradually consume elements of the heartwood. This decay is caused by basidiomycete fungi belonging to, for example, species of *Phellinus* and *Ganoderma*. Various important root pathogens such as species of *Armillaria*, *Heterobasidion annosum*, and *Phellinus weirii* also cause heart rot and decay after they have killed trees or roots.

There are various different types of decay and these arise from the different nutritional habits of the fungi that cause them. For example the white rot fungi consume approximately equal amounts of cellulose and lignin thus causing a relatively evenly spread softening of the wood, which is often stringy. Brown rot fungi utilize chiefly cellulose and the remaining wood is almost pure lignin that appears in a cubical pattern known as brown cubical rot. Another relatively common pattern of decay is white pocket rot where all the lignin is removed from small pockets that contain virtually pure cellulose.

Avoidance and Management of Tree Diseases

Management of diseases in native forests and woodlands is extremely difficult and in some cases virtually impossible. This is very different to disease management in plantations where many options exist for disease avoidance.

One of the most important components of tree disease management lies in excluding pathogens from new environments. As mentioned previously, some of the most devastating diseases have been caused by pathogens introduced into new environments. Exclusion of pathogens from new environments depends on quarantine regulations that ensure that they are not moved across borders. This objective can be very difficult to achieve, particularly where countries have large boundaries, especially with countries having less rigorous regulations. Island countries such as Australia and New Zealand have invested substantially in quarantine and they have achieved remarkable success. However, on the whole, plant quarantine commonly fails, and new and devastating diseases must be expected to continue to move between countries and continents as global trade and travel continue to grow.

Another strategy used to reduce the impact of disease is through eradication of pathogens after they have been introduced into new areas. This approach is complicated and depends on early recognition of the disease, a clear understanding of the biology of the causal agent, and intensive efforts to eliminate it. Various tree disease eradication programs have been launched and have failed. The best example was the program in the USA between 1930 and 1965 aimed at eradicating the alternate host of white pine blister rust. There are, however, more positive examples such as the virtual eradication of Dutch elm disease from New Zealand.

Chemical control or protection to reduce the impact of tree diseases is not commonly used in forestry. This is due to the fact that forests represent extensive, ecologically sensitive environments where most fungicides cannot be used responsibly. There are, however, some examples of very effective chemical control of tree pathogens. One of the best of these is the regular chemical control of *Dothistroma* needle blight in countries such as New Zealand, Australia, and Chile. Chemicals or biological products are used to protect conifer stumps from infection by the root rot pathogen *H. annosum*, and chemical control in nurseries is commonly applied.

An effective and commonly used strategy to manage tree diseases is through avoidance. Avoiding disease can be achieved through silvicultural methods aimed at reducing inoculum. For example, the efficient removal of dying elm trees that are infested with insects carrying the Dutch elm disease pathogen can be effective. Avoidance of wounds on trees at the time when they are likely to become infected is also an effective means of reducing diseases such as for example oak wilt. Natural forests can also be managed in such a way as to favor certain species that are not susceptible to the pathogens present, or management can include the removal of alternate hosts such as scrub oak, in the case of fusiform rust.

In the future, we might expect many new opportunities to reduce the impact of diseases. For example, DNA based techniques for disease diagnoses are becoming increasingly available and are likely to play an important role in quarantine. Biological control has not been particularly effective in tree disease management in the past, but new advances at the molecular level, for example in the use of fungal virus associated hypovirulence, are also likely to emerge in the future. Genetic modification of trees is also likely to advance to a point where trees previously eliminated from the landscape, such as in the case of the American chestnut, might be reintroduced. Furthermore, it is likely that new and nondamaging fungicides will be discovered in the future and that these will contribute to reduction in the impact of tree diseases.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Pathology**: Diseases affecting Exotic Plantation Species; Heart Rot and Wood Decay; Insect Associated Tree Diseases; Leaf and Needle Diseases; *Phytophthora* Root Rot of Forest Trees; Pine Wilt and the Pine Wood Nematode; Root and Butt Rot Diseases; Rust Diseases; Stem Canker Diseases; Vascular Wilt Diseases. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Boyce JS (1961) *Forest Pathology*, 3rd edn. New York: McGraw-Hill.

Manion PD (1981) *Tree Disease Concepts*. Englewood Cliffs, NJ: Prentice-Hall.

Peace TR (1962) *Pathology of Trees and Shrubs*. Oxford: Clarendon Press.

Sinclair WA, Lyon HH, and Johnson WT (1987) *Diseases of Trees and Shrubs*. Ithaca, NY: Cornell University Press.

Tainter FH and Baker FA (1998) *Principles of Forest Pathology*. New York: John Wiley.

Root and Butt Rot Diseases

M Garbelotto, University of California – Berkeley, Berkeley, CA, USA

Introduction

Diseases caused by root rots figure prominently amongst the most-studied pathologies of forest trees. Indeed, root and butt rots cause more economic damage to commercial forestry in the temperate world than any other known type of disease. While this notoriety underlines the negative impact of this type of disease on timber production, a much more dynamic and positive role can be assigned to root rots in natural ecosystems. Root rots are one of the driving forces ensuring spatial and temporal diversification of forests. While root rots as a whole encompass both generalistic and host-specific pathogens, aggressive primary microbes, and secondary opportunistic ones, their overall effect at the stand level is to accelerate, and sometimes cause, a patchiness in which some tree species are preferentially affected and weaker individuals culled. Because of their selectivity at the species and at the individual tree level, root diseases play a significant role in determining the structure and composition of a forest. Individual trees and/or clusters of individuals are taken out, and the gaps created allow for tree regeneration. Often, more resistant seral species will substitute the more susceptible pioneering species leading to forest succession. Ecotones between gaps and closed canopy offer rich and diverse habitats, home to a substantial amount of the local biodiversity. Finally, a further outcome of root rots is nutrient recycling: this is achieved by breaking down the chemically complex woody substrate in a synergistic activity with other wood decay fungi, bacteria, and wood-boring insects.

As stated above, concerns about root rots become serious when timber production is involved. Unfortunately, most habitat modifications, including but not limited to those related to logging, appear to increase the damage caused by root rots. In many cases, human activities allow for the establishment of or increase in root rots. Once disease is established, an irreversible process starts in which root rots will play a significant role in shaping the future of that forest. When root diseases affect ecosystems characterized by poor soils, limited host variability, or limiting climatic conditions, their impact may be significant even in the absence of further human activities.

Causal Agents of Root Rots: Establishment Strategies and Population Genetics

Root diseases can be caused by a wide range of organisms including oomycetes, ascomycetes, and basidiomycetes. Root and butt rots, instead, are exclusively caused by fungi belonging to the homobasidiomycetes. The three genera *Armillaria*, *Heterobasidion*, and *Phellinus* have broad worldwide distribution and probably are responsible for the majority of root diseases in temperate forests. Other less frequently encountered genera include *Inonotus* and *Phaeolus*.

All of the known root rotting organisms reproduce sexually. A fertile cell layer (called the hymenium) borne by the sexual fruit bodies of these fungi produces haploid meiospores. Hymenia can be porous or gilled (**Table 1**). Fruit bodies produced by root rot fungi can be an excellent diagnostic clue and include true mushrooms (*Armillaria*), bracket or shelflike conks (*Heterobasidion*), and relative inconspicuous resupinate fruit bodies entirely supported by the surface on which they are growing (*Phellinus weirii*) (**Table 1**). It should be noted that by the time the fruit bodies are produced, root rots are already in an

Table 1 A summary of characteristics of some important root rot diseases

Pathogen	*Disease*	*Hosts*	*Range*	*Decay*	*Fruit body*
Armillaria spp. complex	Oak root fungus; honey mushrooms	Very broad range, both angiosperms and conifers	Worldwide	White stringy	Fleshy gilled mushroom
Heterobasidion spp. complex	Annosus root disease	Primarily conifers, some angiosperms	Worldwide	White laminar	Perennial and annual porous brackets
Phellinus weirii spp. complex	Laminated root rot	Conifers	Western North America, Eastern Asia	White laminated decay, pitted	Resupinate porous
Inonotus tomentosus	Tomentosus root disease	Spruce, pines	Pacific Northwest, USA–Canada	White	
Phaeolus schweinitzii	Velvet top fungus	Conifers	Worldwide	Brown cubicle	Fleshy, velvety corrugated, porous, short or no stipe

advanced stage. Most root rot agents can be cultured, and in culture some produce asexual mitospores called conidia that may have diagnostic value.

In general, airborne basidiospores are the main means for primary infection by a root rot pathogen, and allow for the infestation of new areas. Vegetative or somatic spread of the fungal mycelium is the main means for secondary spread, allowing for the expansion of those individuals originally established through the primary infection process. This expansion may occur either by tree-to-tree contagion through root contacts and grafts, or by free growth of the pathogen in the soil through specialized structures such as mycelial cords or rhizomorphs. Root rotting basidiomycetes colonize a substrate and utilize it as they are growing. In this light, they can be considered territorial organisms, which physically occupy an area and do not easily allow other conspecific organisms to coexist in the same niche. While this phenomenon can be explained partially by the depletion of available nutrients by the pioneering individual, it has been shown that this exclusion of other individuals starts significantly earlier than nutrient depletion. Like most other wood-rotting basidiomycetes, species causing root rots have developed a multilocus system called vegetative (or somatic) incompatibility (VI). When two individuals belonging to the same species meet, a chemically mediated reaction results in the inhibition of growth of both individuals. The area between the two colonies is characterized by sparse or no fungal growth and represents one of the territorial borders of fungal clones or genets. Self-protection from viruses or pathogens present in other individuals is another function attributed to VI systems.

The VI system is active only in diploid ($2n$) and dikaryophytic ($n+n$) isolates. In dikaryons, the two parental nuclei pair up but do not undergo karyogamy. The lack of an active VI system in haploids allows mating to occur. Mating does not involve any specialized sexual structures but is attained by the simple fusion of vegetative haploid hyphae. The resulting $2n$ or $n+n$ thallus is long lived and leads to the production of fruit bodies and of meiospores. The haploid phase in nature is regarded as relatively short-lived and unfit, but some species, especially those relying heavily on primary infection (e.g., *Heterobasidion* spp.), are known to have long lived and virulent haploid phases.

Genetic studies on the clonal distribution of most root disease organisms have often shown complex patterns of colonization characterized by areas colonized by several individuals. In some cases both haploids and dikaryons coexist and there is evidence of genetic exchanges among individuals. VI barriers have thus to be interpreted not as absolute boundaries but as dynamic areas with potential interspecific interchanges.

Some root disease organisms, especially within the genera *Armillaria* and *Phellinus*, show a remarkable genetic homogeneity over large areas. In some cases, tens of acres have been shown to be colonized by a single individual, secondarily spreading among root systems of an entire forest for thousands of years. The case of a 33-acre (13.4 ha) genet of *Armillaria bulbosa* in northern Michigan has been reported as the largest living organism on earth. This case exemplifies a root disease organism for which secondary infection plays a very significant role and appears to be a much more frequent event than primary infection.

The relevance of primary vs. secondary infection is of paramount importance not only for understanding the biology and epidemiology of root diseases but also for management purposes. Pathogens like *Armillaria bulbosa* or *A. mellea* have the ability to spread secondarily over significant distances. When these organisms colonize woodlands extensively, there is often a carry-over of the pathogen into future generations; in these cases, new mortality may not necessarily be caused by new primary infection, but by the remnant of infections established at the site in previous rotations. The clear-cutting of infested stands may not resolve the problem, as most root disease organisms will survive for decades in larger woody debris and in stumps. A study of *Armillaria* infections in the south of France showed that the disease spread radially from a source point in all directions, causing a classic root disease center. Natural regeneration of the stand would always occur in the middle of the infection center, after the root disease had expanded and the pathogen in the oldest infection area was no longer viable. Interestingly, as the nucleus of regeneration expanded, its outer margins would eventually overlap with the outer margins of the disease center, where the pathogen was still viable. These regeneration patches would then become infected in the areas of overlap and start dying back inwards towards the center of the infection center.

Plantations of forest trees or woody crops in areas previously infested by a root disease like *A. mellea* may result in regeneration failures. In these cases, it may be important to identify and isolate sources of secondary infection, while ensuring trees are vigorous and less prone to become infected. When dealing with root diseases characterized by abundant primary infection events such as *Heterobasidion* spp., forest management should focus on minimizing those activities likely to create good primary infection courts, e.g., wounds on roots, stems and branches, and stumps. In general, heavy use of the land and logging will exacerbate these types of root diseases, with losses becoming apparent only after several years.

Symptoms Caused by Root Diseases

The lag between infection and the visible development of symptoms is due to the obvious fact that most symptoms caused by root diseases are in the roots. It has been shown that up to 50% of the root system needs to be affected before any symptoms of tomentosus root disease may be visible above ground. Colonization of the root system may thus go undetected for long periods of time. Although roots of all sizes can be infected by root pathogens, the most reliable underground symptom is the decay of woody roots. Root diseases are equipped with many enzymatic systems and can cause a brown (lignin not being utilized by the pathogen) or a white (lignin utilized by the pathogen) rot. Root rots can also be further characterized by being cubicle, pitted, laminar, and so forth. **Table 1** summarizes the types of rots caused by some important root diseases. Roots can be decayed in two ways: either by starting from the cambium (root girdling) and then proceeding inwards (sapwood rot) (**Figure 1**), or by decaying the central portion of the root (heart rot). The first pattern will result in the rapid death of infected roots and of the root collar, and in a relatively rapid death of the host by girdling. The second type may kill the smaller woody roots by physically breaking them down, but the larger ones may be hollowed and remain physiologically functional for long periods of time. Infection will proceed into the tree sapwood (or in some cases the heartwood), resulting in a physiological loss of vigor due to the loss of functional outer sapwood. Sapwood infection might make trees more vulnerable to other pests, diseases, and unfavorable climatic conditions. This type of decay, when advanced and extensive, may result in the significant weakening of the roots and lower bole of infected trees. Infected trees will be mechanically compromised and more likely to crash due to the effects of wind, rainstorms, or snowfall.

These two major patterns of root rotting are often determined not only by the pathogen species, but also by the host being infected. It is not uncommon

Figure 1 A section of the cut stump of a white fir (*Abies concolor*) in a California site infested by the root pathogen *Heterobasidion annosum*. A white laminated decay caused the rot pockets visible in the sapwood. Trees affected by sapwood rot will have reduced vigor and may decline rapidly at the onset of further problems.

to have the same pathogen species colonizing roots in two different ways when infecting two different hosts. Patterns of butt decay will also depend both on species of the pathogen and of the plant host. Not all root infections proceed into the tree butt. When surveying for incidence of root diseases, results have been different depending on whether surveys were based on root sampling or basal wood coring of tree buttresses. At any rate, root diseases figure as one of the most significant causes of cull in timber production, and the problem intensifies with each new rotation.

The time lag between root infection and the onset of symptoms above ground may vary depending on climate, host and pathogen species, and tree age. Smaller trees with smaller root systems may die rapidly after infection, even within the same season. In contrast adult trees may survive for decades after infection. When infection levels start affecting tree physiology and vigor, visible symptoms can be seen in the crown. Infected individuals will display slower growth. Tree crowns will appear thin as a result of both the slower growth and the shorter retention time of leaves. For instance, pines infected by a root disease may only keep needles produced in the current year while 2- and 3-year-old needles may be prematurely dropped. A single cluster of 1-year-old needles at the end of a barren branch gives these branches the so-called 'lion's tail' appearance. Root infection will also result in a shift in the color of the foliage, which generally appears less vibrant than the foliage of healthy individuals.

All of the above symptoms indicate trees with significantly altered physiology. The obvious question is whether such symptoms may always be considered as the effect and not the cause of infection by a root disease. The issue of causality is an important one and it has not been fully investigated. There are several studies indicating a strong correlation between physiological stress and infection by root diseases. These studies have shown that infected trees grow slower, that trees exposed to air pollution are more likely to be found infected, and that short-term draughts increase the frequency of trees with root diseases. Finally, trees affected by root diseases will be more attractive to bark and ambrosia beetles, and may provide an initial substrate for the growth of beetle populations that may then overflow and affect healthy trees. While there is enough evidence to suggest that these symptoms are the effect of infection by root diseases, there is still the possibility that these pre-existing symptoms may facilitate infection by root pathogens. Further research is needed to verify the role played by weakening agents in facilitating infection of trees by root rots.

An interesting perspective, when correlating root diseases and tree stress, may be to differentiate between primary aggressive pathogens and secondary less virulent ones. While primary pathogens can cause significant disease and alter the tree physiology with or without pre-existing tree stress, secondary ones require a pre-existing or concomitant stress factor (including other pathogens) in order for disease to develop. In the Sierra Nevada of California, for instance, rhizomorphs of the nonaggressive *A. gallica* can be found on the surface of the roots of large numbers of true firs (*Abies* spp.). Although the rhizomorphs are growing ectotrophically on the roots, there is no or little associated decay. *Armillaria* decay, though, may start soon after the same roots are infected by the more aggressive pathogen *Heterobasidion annosum*.

Those rhizomorphs could almost be interpreted as exploratory outposts ready to capitalize on the availability of weakened trees. This exploratory function of a secondary pathogen, although apparently extremely costly, allows for the rapid utilization of a substrate that may otherwise be fully colonized by the aggressive primary pathogen or other competitors. The above example highlights another important feature of root pathogens capable of secondary (vegetative) spread: i.e., their ability to maintain functional networks covering a sizeable area and several plants. Most of the network may be maintained at comparable levels until resources become available in one spot. At that point, most of the resources of the network are dynamically allocated to increase the utilization of that substrate. The apparent new attack on a host (e.g., a weakened tree), may be the result of energy reallocation through an already established network, rather than being the result of the advancement of an infection front.

At later stages, symptoms of root disease include progressive dieback of the crown, starting from the top downwards, and the presence of signs of decay. Fungal fruit bodies are produced either on the colonized woody substrates (normally at the root collar or on the roots) or on the duff layer thanks to the presence of masses of finer roots. Rhizomorphs are specialized structures produced by many *Armillaria* species; they consist of a strand of hyphae encased by a highly hydrophobic melanin layer. Rhizomorphs, commonly referred to as 'shoestrings' because of their appearance, can grow freely in the soil and allow the pathogen to move from tree to tree without the need to follow root contacts. The consistency, thickness, and cross-sectional structure of rhizomorphs can be a useful diagnostic tool to differentiate among *Armillaria* species. Rhizomorphs are commonly found on the roots and root collars of host trees, but they can also be found on several meters of the main bole, growing under the bark. Another sign of decay associated with root diseases is the presence of mycelial mats. *Armillaria* mycelial mats appear as fans radiating under the bark from the root collar. Wood in an advanced state of decay will present cavities often colonized by the white mycelium of root pathogens like *Heterobasidion* spp. or *Phellinus weirii*. The mycelium of the latter species is characterized by the presence of hair like structures called setae. Advanced decay also results in obvious punks and defects in the wood, often associated with resinosis, sap bleeding, or wetwood.

Root disease centers can be differentiated from clusters of trees killed by pest outbreaks or abiotic factors because tree mortality is not synchronous but occurs over a period of time. In the middle of the root disease center, there are those trees initially killed by the disease; some of them may have already been windthrown. More recent mortality may be present in a ring encircling the older mortality. Recently killed trees will still bear most of the dead foliage, while relatively older mortality will be characterized by trees made barren by winter storms. Symptomatic live trees may represent the visible edge of the root disease center (**Figure 2**). Studies on control options aimed at halting the secondary spread of the root pathogen *Heterobasidion annosum* in ponderosa pine (*Pinus ponderosa*) stands have highlighted the fact that the pathogen had already infected several tiers of apparently asymptomatic trees outward and beyond the apparently symptomatic ones. Root disease centers may thus be larger than judged by the presence of visible symptoms. It has been noted that enlargement of root disease centers does not proceed indefinitely but eventually stops. The factors regulating the spread of root disease centers are only marginally known.

Figure 2 A typical root disease center caused by *Heterobasidion annosum* in the mixed conifer forest of the Sierra Nevada, California. While true firs appear symptomatic or dead, pines (distinguishable by the longer needles) are not affected. This species of the pathogen in fact is specialized on true firs, Douglas-fir, and sequoias, and is very different from the species found on pines. Stumps and trees dead for several years are visible in the center, the location where the pathogen had originally established itself. Secondary growth leads to an expansion of the mortality center. Symptomatic trees and trees recently killed by the pathogen (note the brown–orange foliage still borne by the branches) mark the expanding edge of the pathogen.

The Ecology of Root Diseases

While root pathogens vary in their ability to freely grow in the soil (**Table 1**), their biology is intimately linked to soil properties. In general, loose, well-drained soils, poor in organic matter, are extremely conducive to the development of root diseases. The ecological and trophic requirements of these pathogens are rather species-specific, and root pathogens have evolved to minimize spatial overlap amongst individuals from the same species or from species having identical requirements. When requirements differ, spatial overlap may occur, as each species may be utilizing a different niche. In general, primary infection of root pathogens is successful only during the very initial stages of decay. In the case of conifer stumps infected by *Heterobasidion annosum*, infection rates drop dramatically each day after logging and become fairly minimal after 5 or 6 days. *Heterobasidion* spp. are not good competitors and need to arrive on substrates that are relatively available. Thus other wood-inhabiting fungi have the ability to exclude this pathogen from a substrate otherwise available. This basic observation has resulted in a biological control approach prescribing the application of strong competitors on the wood surface at the time of logging. Because with time there is a sharp decrease in infection success by spores of this pathogen, competitors only need to be active for a few days in order to be effective.

Precipitation requirements may differ among root pathogens but in general mild temperatures and good precipitation favor sporulation. Dry weather, or temperatures under 10°C or above 25°C, are in general unfavorable to sporulation and infection alike. Excessive rain may also be unfavorable to root pathogens relying mostly on airborne inoculum (e.g., *Heterobasidion*). In the case of pathogens relying more heavily on secondary spread (e.g., *Armillaria*), heavy rains can at times cause a temporary anoxia in the root systems and trigger a more aggressive root colonization by the pathogen. In areas with cold and dry winters, sporulation by *Heterobasidion* spp. is extremely low. Sporulation by the same species in areas with mild winters continues throughout the year; winter sporulation is relatively abundant in areas where precipitation, even if in the form of snow, occurs mostly in the winter season.

Although fruit bodies of most root pathogens produce unimaginably large numbers of basidiospores, the role of such spores is not always clear. This is particularly true for root pathogens relying heavily on secondary spread. While basidiospores can travel a long distance, sometimes on the order of hundreds of kilometers, spore densities undergo a huge dilution after the first few meters. The likelihood of primary infection is thus directly correlated with distance from a source point. While the migration of even a few spores may be significant for areas still not colonized by a root pathogen, it is unlikely the few spores from a distant source would have a huge impact on the large number of locally produced spores.

The presence of marked host specificity among morphologically indistinguishable populations of the same pathogen is prominent in root diseases. In fact the discovery of host specificity within the broad host range of pathogens *Armillaria* and *Heterobasidion* was a milestone towards the better understanding of the concept of biological species for the fungi. This host specificity was backed up by genetic studies indicating that populations specializing on different groups of hosts were genetically isolated from one another. The term intersterility group (ISG) was coined in the late 1970s to describe these host-specialized and reproductively isolated root pathogen populations. In the case of *Heterobasidion annosum*, a series of crosses between the two North American ISGs revealed for the first time the genetic system regulating intersterility and consequently speciation among these host specialized groups. Nowadays, thanks to the advancement of our genetic techniques, most of these biological species have been elevated to the rank of species (**Tables 2–4**).

Host specificity has several relevant consequences:

1. In a mixed forest not all trees species will be equally susceptible.
2. Disease severity in a mixed forest should be less than in a forest comprising a single susceptible species.
3. Susceptible species may be replaced by more resistant ones (succession).

It should be noted that host specificity might be relaxed when infection occurs on stumps rather than on live trees. This phenomenon has been reported for *Heterobasidion* species both in Europe and North America. In the case of this pathosystem, stumps may have a triple effect: (1) they greatly enhance primary infection, (2) allow for the establishment of a pathogen species once rare, and (3) allow for two or more species to grow in the same habitat. This close proximity, rarely present in nature, where different species are segregated on their specific plant hosts, has resulted in interspecific hybridization and gene introgression with unpredictable outcomes for California forests. Furthermore, as stated above, once stumps are infected, they can be the source of inoculum for several decades. Fruit bodies may in fact proliferate on stumps, and at the same time the infection of the stumps' root system represents a source of secondary infection.

Table 2 Details on some common taxa within the *Armillaria* species complex

Pathogen	*Main hosts*	*Range*	*Disease*	*Primary pathogenicity*[a]
Armillaria ostoyae	Conifers	Worldwide, circumboreal	Cambium and sapwood rot	+ + +
Armillaria borealis	Conifers	Northern Europe, Asia	Butt rot	+
Armillaria calvescens	Hardwoods	North America	Butt rot	+
Armillaria cepistipes	Hardwoods	Europe, North America, Japan	Butt rot	+ +
Armillaria mellea	Hardwoods, conifers	Worldwide, circumboreal	Cambium and sapwood rot	+ + +
Armillaria gallica	Hardwoods	Worldwide, circumboreal	Heartrot and sapwood rot	+ +
Armillaria sinapina	Hardwoods, conifers	North America	Heartrot and sapwood rot	+
Armillaria luteobubalina	Hardwoods	Australia	Heartrot and sapwood rot	+ +

[a] Refers to ability of killing hosts: + + +, more aggressive (primary pathogen); + +, less aggressive; +, secondary pathogen.

Table 3 Details on taxa within the *Heterobasidion annosum* species complex

Pathogen	*Main hosts*	*Range*	*Disease*	*Primary pathogenicity*[a]
H. annosum	Pines, spruce	Europe, Asia	Root and root collar girdling	+ + +
H. parviporum	Spruce	Europe, Asia	Heartrot	+
H. abietinum	True fir	Central and southern Europe	Sapwood rot and heartrot	+ +
H. annosum P ISG	Pines, incense cedar, juniper	North America	Root and root collar girdling	+ + +
H. annosum S ISG	True firs, sequoia, Douglas-firs	Western North America	Sapwood rot and heartrot	+ +

[a] Refers to ability of killing hosts: + + +, more aggressive (primary pathogen); + +, less aggressive; +, secondary pathogen.

Table 4 Details on taxa within the *Phellinus weirii* species complex

Pathogen	*Main hosts*	*Range*	*Disease*	*Primary pathogenicity*[a]
Phellinus weirii	Western redcedar	Western North America	Sapwood rot and heartrot	+ +
Phellinus henrichii, North American biological species	Douglas-fir, mountain hemlock, and other conifers	Western North America	Root girdling and sapwood rot	+ + +
Phellinus henrichii, Asian biological species	Conifers	Japan, Siberia	Root girdling and sapwood rot	+ + +

[a] Refers to ability of killing hosts: + + + more aggressive (primary pathogen), + +, less aggressive.

Root Rot Pathogens Shape our Forests

Forest management and the resulting forest structure and composition have a significant impact on root disease epidemiology, and conversely root disease will affect forest structure and composition. Disease severity tends to be higher in forests frequently logged and thinned, in forests with higher tree density, and in older forests. Logging and thinning provide either an abundance of primary infection courts (e.g., for *Heterobasidion annosum*) or may facilitate the secondary root colonization of the remaining stumps by *Armillaria* spp. Denser stands will facilitate secondary spread directly by making root contacts more abundant, and indirectly because of the overall reduced vigor of trees growing in overcrowded stands. Older stands are subject to greater amounts of root diseases; this is due to several factors including the greater availability of a substrate (i.e., roots) in larger trees, the tendency of older trees to be more prone to decay processes, and the loss of structural integrity allowing for some secondary root rots to colonize trees previously unavailable. Finally, larger trees will favor extensive secondary spread because of the presence of larger and far-reaching root systems. Furthermore it has been shown that some root rots grow faster in larger roots. This relationship appears to be true especially if the pathogen is not capable of growing ectotrophically on the root surface (*Heterobasidion*, *Phaeolus*): if ectotrophic growth is possible (*Armillaria*, *Phellinus*), the pathogen may not be limited by the presence of thin roots or the absence of root grafts.

Root diseases will in turn affect forest structure and composition. Root diseases create gaps where regeneration, often by different, light-loving, and more resistant plant species, will take place. Trees on the edge of the gaps will be released and their growth rates increased. In general, root diseases will create ecotones with increased biodiversity. It is clear that trees infected by root diseases become more attractive to bark and ambrosia beetles. Beetle attacks will generally significantly accelerate tree mortality. Diseased trees will also allow for the local growth of beetle populations. When beetle populations surpass certain thresholds, attacks may include neighboring healthy trees and expand tree mortality beyond that predictable solely by the effects of the root disease. Broad generalizations should be avoided when looking at the complex interactions between two natural disturbance agents such as root diseases and insects. In the case of *Inonotus tomentosus*, for instance, diseased trees were shown to be more attractive to beetles only where endemic beetle populations were present.

Droughts, pollution, and wind have been shown to interact with root diseases in increasing tree mortality. Root diseases will also affect nutrient cycling at the landscape level. In the case of ecosystems in harsh environment these effects may be long term. It has been determined that the openings in mountain hemlock (*Tsuga mertensiana*) stands caused by the pathogen *Phellinus weirii* in Oregon result in negative levels of carbon production for about 100 years. Increased nitrogen mineralization processes follow the edge of the expanding root disease center, with important consequences for growth rates of the regeneration and resistance of the remaining standing trees. In this case, therefore, the effects of root diseases may be long lasting.

In some instances, root disease centers are characterized by a complexity in the pathogen population that does not fit the picture of individual infections spreading radially in all directions as shown for *Armillaria* spp., *Inonotus tomentosus*, and *Phellinus weirii*. An alternative hypothesis has been formulated suggesting that initial infection processes may trigger a chain effect in neighboring trees (for instance by allowing more oxygen into roots of neighboring trees grafted to decayed roots) where resident infections may be latently waiting to be activated. Genetic data from true fir infection centers caused by *H. annosum* in California partially support this hypothesis.

Management Options for Root Diseases

Root diseases are virtually impossible to eradicate once they are established, and their introduction may have a long-lasting impact on forest ecosystems. These diseases may also shape the future of forests: once introduced and established they may make a return to the original type of forest an unlikely outcome. For instance, logging and fire suppression have allowed for the establishment of large mortality centers caused by *Armillaria* and *Heterobasidion* spp. in the Yosemite Valley in California. These pathogens will now in turn limit the possibility of regeneration of the forest, and are likely to lead the landscape towards a mosaic of open meadows interspersed by clusters of trees.

When forests are threatened by root pathogens, approaches can be taken to limit their establishment and spread. These interventions are often complex and long term and may be worth executing only if dealing with fragile ecosystems or when the disease has resulted in hazardous trees. Once the biology of the causal organism is understood, precautions can be taken to minimize levels of primary infection. For instance, in the case of *H. annosum* in pine, precautions include treating stumps (important primary infection courts) with chemicals such as borate or urea or, alternatively, applying the biological control fungus *Peniophora gigantea* at the time of cutting. In the case of *H. annosum* in true fir, thinning wounds may represent the most important source of primary infection courts, and thus a strategy aimed at limiting thinning entries or wounding of standing trees may be helpful. Operations should preferably be done when environmental conditions are unfavorable to the pathogen; this strategy has been adopted with some success by logging *Heterobasidion*-infested pine plantations in the southern USA during the hot summer months.

Lowering stand density may regulate secondary spread of the pathogen. Early precommercial thinning, when trees may be too small to be favorable infection courts, or the use of prescribed fires may help achieve this goal. When high-value sites are in question (e.g., campsites, public areas, etc.) a physical disruption of the vegetative growth of the fungus can be attempted. In southern California, trenching the soil and removing two tiers of apparently asymptomatic trees beyond the visible outer margin of an infection center successfully halted the spread of *H. annosum* in pine. In the case of pathogens capable of growing freely in the soil via rhizomorphs, this attempt may be futile, as portions of root systems left behind may actually be ideal colonization substrates for *Armillaria* spp.

If the removal of an individual tree is in question, pathogen identification is essential. For instance, the stump of a felled tree will provide an ideal substrate for *Armillaria* and become a source of inoculum if other trees are in the same vicinity. On the other hand complete removal of the tree, including the root system, may beneficially lower the amount of inoculum.

If a forest is affected by a pathogen with restricted or defined host range, it may be possible to increase the percentage of trees more resistant to the pathogen. Because resistance is often only partial, it may be a good idea to avoid complete removal of the susceptible species, as the resulting selection pressure on the pathogen may result in the infection of plants normally considered nonhosts.

When dealing with trees at the urban–wildland interface, avoid any horticultural treatment or practice that may result in physiological stress. Often even single events, e.g., the overwatering of a tree in the summer, may result in the colonization of that tree by a root pathogen that originally was growing ectotrophically on the roots. In some cases, when trees are affected by root disease but appear to decline very slowly, the application of insecticides on the bark before the tree is attacked may significantly prolong its life. The effects of such treatments are short-lived and valid only for conifers with a known beetle infestation. These treatments require the use of chemicals with a relatively broad spectrum of action and should be used sparingly and only in high-value landscape situations.

See also: **Entomology**: Bark Beetles. **Pathology**: Diseases of Forest Trees; *Phytophthora* Root Rot of Forest Trees. **Tree Physiology**: Root System Physiology; Stress.

Further Reading

Goheen DJ and Hansen EM (1993) Effects of pathogens and bark beetles on forests. In: Schowalter TD and Filip GM (eds) *Beetle–Pathogen Interactions in Conifer Forests*, pp. 175–196. San Diego, CA: Academic Press.

Hansen EM and Goheen EM (2000) *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in Western North America. *Annual Review of Phytopathology* 38: 515–539.

Otrosina WJ and Scharpf RF (eds) (1989) *Proceedings of the Symposium on Research and Management of Annosus Root Disease* (Heterobasidion annosum) *in Western North America*, 18–21 April 1989, Monterey, CA: US Department of Agriculture Forest Service.

Shaw CG III and Kile GA (eds) (1991) *Armillaria Root Disease*. Agriculture Handbook no. 691. Washington, DC: US Department of Agriculture Forest Service.

Slaughter G and Rizzo D (1999) Past forest management promoted root diseases in Yosemite Valley. *California Agriculture* 53: 17–24.

Smith ML, Bruhn JN, and Anderson JB (1992) The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. *Nature* 356: 428–431.

Woodward S, Stenlid J, Karjalainen R, and Hüttermann A. (eds.) (1998) Heterobasidion annosum: *Biology, Ecology, Impact and Control*. Wallingford, UK: CAB International.

Phytophthora Root Rot of Forest Trees

G E St J Hardy, Murdoch University, Murdoch, Western Australia

Introduction

As a genus *Phytophthora* can be considered as the most devastating group of plant pathogens on earth. Members of the genus cause huge economic losses in agricultural crops annually and are extremely destructive in a range of forest ecosystems worldwide. Their direct affect on plant losses is really quite well documented. The genus name is aptly derived from the Greek that means *phyto* (plant) and *phthora* (destroyer). There is still much debate over the taxonomy of *Phytophthora* and there are over 64 species, but this constantly changes with new species being described and others amalgamated as molecular diagnostics tools are used to characterize the genus. Some species such as *P. cinnamomi* have a wide host range whilst others have one to only a few hosts, consequently as a genus it is extremely plastic in terms of the range of plant species it impacts on. This article will provide a general but not a comprehensive overview of the major *Phytophthora* diseases of forest trees and cover impacts, threats, and methods of control.

Life History

The genus belongs to the class Oomycetes in the Kingdom Chromista and is more closely related phylogenetically to the heterokont algae than the true fungi or Mycetae. Oomycetes are diploid, have a coenocytic thallus or mycelium, and they reproduce asexually to produce chlamydospores or by the production of sporangia. Chlamydospores are formed terminally at tips of hyphae or are intercalary. They can be thin- or thick-walled and function as survival spores. Sporangia or more correctly zoosporangia are produced under warm and moist conditions from specialized hyphae or sporangiophores. The sporangia can germinate directly to produce a germ tube or indirectly to produce uninucleate, biflagellate zoospores within the sporangium. The zoospores emerge from the sporangium into a temporary vesicle that rapidly breaks, allowing the zoospores to swim away. The zoospores are propelled by two flagella; one is a long whiplash and the other a shorter tinsel. The zoospores can remain motile for hours and are attracted chemotactically to substrates where they encyst. The cysts germinate to produce a germ tube and if appropriately located will invade living organs of susceptible plant species to cause disease.

The sexual structures of *Phytophthora* consist of an oogonium (egg-containing female component) and an antheridium (male component). Reduction division (meiosis) of the chromosomes from the diploid to haploid in nuclei occurs in the coenocytic antheridium and oogonium (**Figure 1**). Sexual reproduction occurs when a fertilization tube from the antheridium deposits its nucleus inside the oogonium, fusion between the two nuclei occurs, and an oospore forms within the oogonium. Oospores like chlamydospores are survival spores and under suitable environmental conditions will germinate to produce single to multiple germ tubes at the tips of which sporangia can

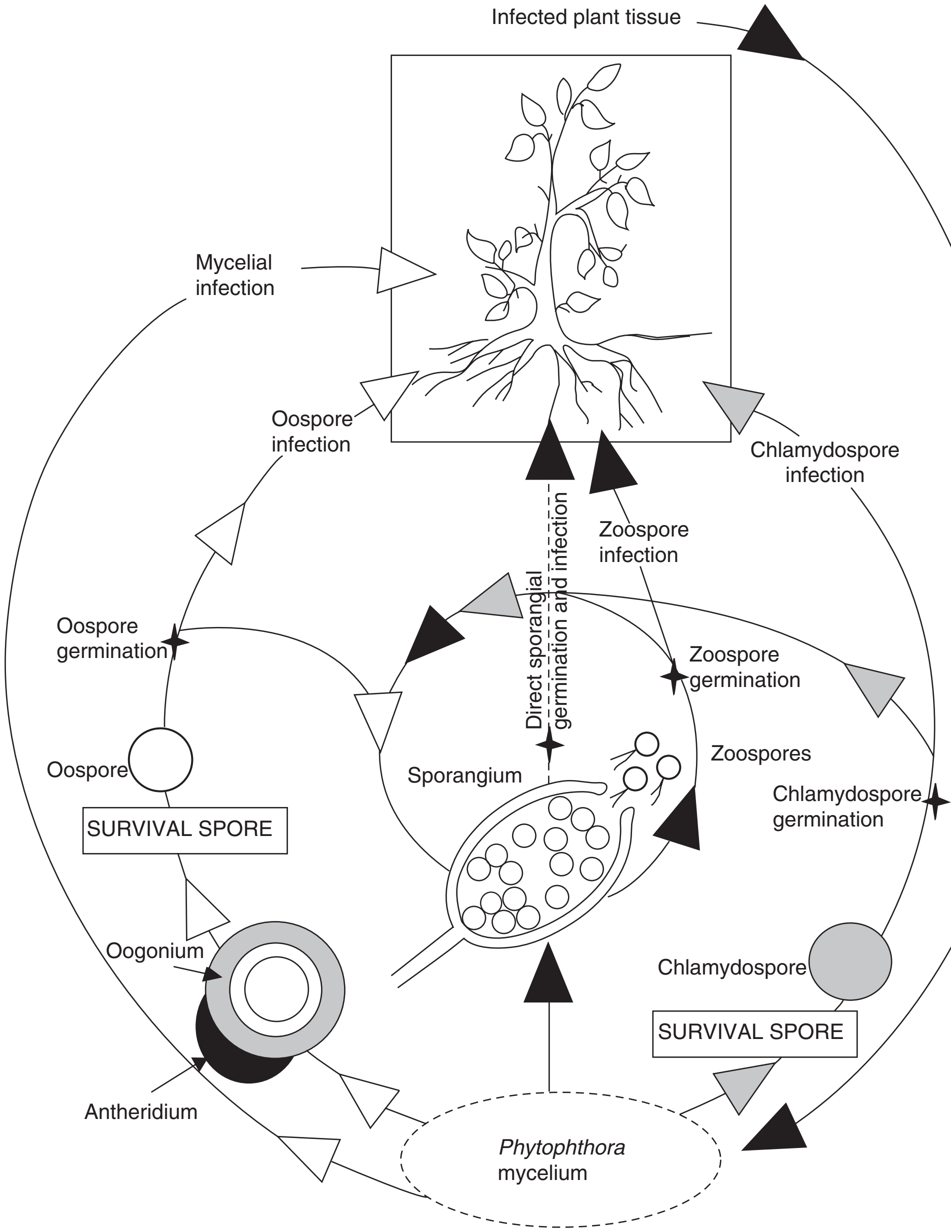


Figure 1 *Phytophthora* life cycle and infection strategies.

form. However, in some self-fertile (homothallic) species, oospores can be important sources of dissemination, germinating rapidly to produce sporangia under optimum conditions.

Phytophthora species are either homothallic or self-sterile (heterothallic). In the heterothallic species two compatible mating types must make contact before oospores will form at the point of contact between the two. In heterothallic species, the crossing of compatible (A1 and A2) mating types is likely to be the source of new races or biotypes, whilst in homothallic species, oospores function as survival propagules in plant debris.

The above characteristics of *Phytophthora* make it unique among pathogenic fungi since members within this genus are able to initiate and cause disease on nearly all parts of the host plants. In forest trees this includes the roots and collars (e.g., *P. cinnamomi*) and foliage (e.g., *P. ramorum*).

Spread

It is highly likely that many phytophthoras have been spread between countries and continents since the European settlement of the Americas, Australasia, Africa, and other countries. This would have occurred in the soil of containerized horticultural and ornamental trees being transported between countries. For example, *P. cinnamomi* was likely to have been introduced on planting stock into Australia on one of the first sailing ships from Europe. More recently, as trade barriers break down within the European Union, less stringent quarantine regulations will certainly provide avenues for the transfer of different *Phytophthora* species between regions. This introduces *Phytophthora* species to new hosts that previously have had no contact with a particular *Phytophthora* species and/or alternatively allows sexual reproduction to occur between compatible species allowing for new hybrids to develop. The latter is a likely scenario for the alder phytophthoras (see below).

Once in a region, phytophthoras can be spread through the movement of soil on vehicles, heavy earth-moving equipment, on the feet of hikers, feral or wild animals, surface water flow, and infested nursery stock. Consequently, once phytophthora are present, autonomous spread and spread through the movement of vehicles, people, and animals are extremely difficult to control.

Symptoms

In susceptible trees, many types of symptoms are observed and these depend on the *Phytophthora* species and the host species being colonized. In many trees, primary invasion is through the small absorbing roots and causes brownish to black firm roots with little progression into the larger lateral roots. In this case decline and death tends to be gradual and often associated with other predisposing biotic or abiotic factors. In other hosts, *Phytophthora* invades the lateral roots and colonizes the phloem girdling the roots and frequently moving up into the collars of the tree, where cankers are produced. Cankers can cause cracking of the stem or trunk, bleeding or exudation of kino or red sap, often with entire girdling of the trunk, leading to a restriction of transpiration, followed by tree death.

In broadleaved trees, invasion results in a gradual deterioration of the crown, with chlorosis, reduction in leaf size, absence or reduced new growth, wilting of leaves, and dieback of small branches usually being the first symptoms. These are followed by the development of epicormic shoots on large branches, which over time will die back resulting in a gradual decline leading to the eventual death of the host, although in highly susceptible hosts death can be extremely rapid.

In conifers, wilting does not usually occur and in 'littleleaf' disease of pine, for example, the first symptoms are yellowing of the foliage and needles that are smaller than usual; thereafter shoot growth decreases. In many tree species, decline can be slow and trees do not die until many years after infection.

Predisposing Factors

As with all plant diseases the key components of the *Phytophthora* disease – host, pathogen, environment, and time – are all necessary for a disease to occur. In the absence of the pathogen or a susceptible host disease will not occur. *Phytophthora* species generally require moist and warm conditions in order to cause disease; if these conditions are not present or present for too short a time, again disease will not occur. Consequently, it is critical to understand these factors when considering the biology, ecology, and pathology of a *Phytophthora* pathogen and the diseases it causes. For example, oak decline in Europe and adjacent parts of Asia has been associated with a variety of *Phytophthora* species (**Table 1**).

However, oak decline is also recognized to be a multifactorial disease syndrome with predisposing factors (e.g., industrial pollution, climatic extremes, and inappropriate site), inciting factors (e.g., drought, frost, waterlogging, insect attack, soil nutrient characteristics), and contributing factors (e.g., secondary pathogens) all contributing to decline in certain circumstances. Therefore, predisposition can and does play a role in disease syndromes associated with *Phytophthora* species. A predisposing factor such as drought will frequently speed up death of infected plants.

Phytophthora cinnamomi in Australasia

Over 31 *Phytophthora* species have been associated with plant deaths in Australia. The majority of these are horticultural, agricultural, or nursery pathogens with only *P. cinnamomi* causing major losses to forest trees. The loss of floristic and structural diversity, and consequential effects on faunal diversity are now considered a major problem of ecosystem breakdown and economic loss. As a result, *P. cinnamomi* has been listed as a 'key threatening process' to Australia's biodiversity in the Commonwealth's Environment Protection and Biodiversity Conservation Act 1999. *Phytophthora cinnamomi* is one of 11 key threatening processes and the only microorganism listed.

The major impact and threat is to open forests, woodlands, and heathlands of southern Australia. Its impact has been likened to that of the last ice age by botanists. For example, in the southwest of Western Australia alone it affects over 2000 of the approximately 7000 native plant species, of which 3000 are

Table 1 *Phytophthora* species isolated from some forest trees worldwide[a]

Host	Alder *Phytophthora*	*P. cactorum*	*P. cambivora*	*P. cinnamomi*	*P. citricola*	*P. cryptogea*	*P. drechsleri*	*P. ereugena*	*P. europaea*[b]	*P. hibernalis*	*P. inundata*	*P. lateralis*	*P. megasperma*	*P. nicotianae*	*P. syringae*	*P. gonapodyides*	*P. psychrophila*[b]	*P. quercina*	*P. ramorum*	*P. uliginosa*[b]
Acer macrophyllum																			+	
Acer sp.			+		+								+							
Aesculus hippocastanum											+									
Alnus cordata	+																			
Alnus glutinosa	+																			
Arbutus unedo				+																
Banksia spp.				+	+	+	+													
Castanea sativa		+	+	+	+											+				
Chamaecyparis lawsoniana						+				+		+								
Crataegus sp.																				
Eucalyptus marginata				+																
Eucalyptus seiberi				+																
Eucalyptus smithii														+						
Eucalyptus macarthurii														+						
Fagus sylvatica					+															
Fagus spp.			+																	
Lithocarpus densiflorus																			+	
Malus spp.			+																	
Nothofagus spp.				+	+	+							+							
Pinus echinata				+																
Pittosporum undulatum																			+	
Pseudotsuga menziesii				+															+	
Quercus agrifolia																			+	
Quercus cerris		+	+	+	+											+		+		
Quercus chrysolepis																			+	
Quercus ilex				+														+		
Quercus kelloggii																			+	
Quercus frainetto				+																
Quercus parvula var. *shrevei*																			+	
Quercus petraea				+	+				+								+	+		+
Quercus peduncularis				+																
Quercus pubescens				+																
Quercus glaucoides				+																
Quercus robur		+	+	+	+				+						+	+	+	+		+
Quercus rotundifolia				+																
Quercus rubra				+												+				
Quercus salicifolia				+																
Quercus suber				+			+													
Rhamnus purshiana																			+	
Rubus spectabilis																			+	
Salix matsudana (UK)											+									
Sequoia sempervirens																			+	
Taxus baccata				+	+	+														
Taxus brevifolia												+								
Thuja plicta					+	+														
Toxicodendron diversilobum																			+	
Umbellularia californica																			+	

[a]This list of *Phytophthora* species and hosts is not intended to be comprehensive but rather indicative of the number of each involved in tree decline and death.
[b]*Phytophthora* species isolated from soils in association with forest trees; pathogenicity still to be ascertained through further testing.

endemic; a number of these are important woodland or forest species.

On infested sites, resistant species that replace susceptible plant species tend to be wind-pollinated and do not produce nectar or nutrient-rich pollen and, therefore, do not attract or provide food sources for birds or smaller animals. Regeneration of such sites with susceptible species may never occur if seed reserves are lost; consequently many birds and animals may be lost from infested sites.

Phytophthora cinnamomi in the Americas

Phytophthora cinnamomi has been introduced into most forested regions of the western hemisphere and elsewhere in the world, where it has considerable impact in a range of forest species. It caused significant and catastrophic deaths of American chestnut and related *Castanea* species in forests and woodlands in the USA and removed much of the chestnut from the southern Appalachian foothills. Deaths were first reported in the early 1820s and it was not until 1932 that *P. cinnamomi* was associated with dying chestnut. Together with *Cryphonectria parasitica*, *P. cinnamomi* has essentially removed American chestnut from this region. *Phytophthora cinnamomi* is also the cause of 'littleleaf' disease in shortleaf pine (*Pinus echinata*), where it has caused decline across much of the tree's range in the southern USA. Unlike its association with *Castanea* and the many plant species in Australia where it attacks the main root system and stems of trees, *P. cinnamomi* is a fine feeder root disease in shortleaf pine. It plays a central role in 'littleleaf' disease as it causes severe fine root mortality, predisposing trees to other biotic and abiotic influences that contribute to the disease syndrome.

Phytophthora cinnamomi also causes the decline and death of oaks in Mexico. Although widespread in forests in the Pacific Northwest, *P. cinnamomi* does not impact severely if at all on many susceptible tree species since it is too cold in the wet winters and too dry in the hot summers for it to cause disease. This indicates the importance of the interactions of disease factors for disease to occur in the presence of the pathogen.

Phytophthora cinnamomi and other *Phytophthora* spp. in Europe

Phytophthora cinnamomi has been associated with oak decline throughout Europe and the Mediterranean region, and of all the *Phytophthora* species associated with oak, it is the most devastating. Oaks affected include *Q. cerris*, *Q. frainetto*, *Quercus ilex*, *Q. petraea*, *Q. pubescens*, *Q. pyrenaica*, *Q. robur*, *Q. rotundifolia*, *Q. rubra*, and *Q. suber* (**Table 1**). In Europe, the oak decline phenomenon is a complex disease with predisposing, inciting and contributing factors also contributing to the decline syndrome. *Phytophthora cambivora*, *P. citricola*, and *P. quercina* have also been associated with fine feeder root disease of oaks in Germany and are probably involved in oak decline, although their precise roles are still to be determined.

A total of 13 *Phytophthora* species has been recorded in Europe, with *P. cambivora*, *P. citricola*, and *P. quercina* being widespread. Frequently, *P. cinnamomi* and *P. cryptogea* are restricted to warmer climatic regions of Europe, *P. europaea*, *P. gonapodyides*, and *P. uliginosa* to wet sites, *P. pseudosyringae* sp. nov. to acid sites. There are infrequent isolations of *P. cactorum*, *P. megasperam*, *P. psychrophila*, and *P. syringae*. *Phytophthora* species are certainly associated with oak decline. However, more research is required to understand fully their interactions with abiotic and other biotic factors.

Phytophthora lateralis

The ecologically and economically important forest cedar, Port-Orford-cedar (*Chamaecyparis lawsoniana*) endemic to southwest Oregon and northwest California is severely affected by the introduced *P. lateralis*. It rapidly colonizes trees through the fine roots until it reaches the main stem. The pathogen also infects and kills the Pacific yew (*Taxus brevifolia*), but only when it grows in close association with Port-Orford-cedar. *Phytophthora lateralis* was rapidly spread throughout the native range of Port-Orford-cedar along the Oregon coast with road building and logging activities during the 1950s.

The endemic range of *P. lateralis* is still unknown. However, its introduction into Oregon and California before the 1920s, when deaths were first observed, illustrates how unregulated international plant movements in the horticultural trade has resulted in devastating forest tree epidemics. Deaths of Port-Orford-cedar along infested streams are especially high; however, today the impact appears to be less dramatic, as most of the vulnerable cedar stands are already infected.

Most disease management is directed around road management, such as wet season closures, and washing down of vehicles before moving between infested and noninfested areas. These sanitation activities reduce the likelihood of spread by reducing inoculum loads along roads. In addition, the most vulnerable trees growing along roads are removed. Recently, heritable resistance in Port-Orford-cedar has been shown to exist and breeding is a viable strategy to provide resistant planting stock into forest areas where the pathogen is present.

Phytophthora ramorum

Phytophthora ramorum was first described in 2001 from Germany and the Netherlands associated with blight disease in *Pieris* spp., *Rhododendron* spp., and *Viburnum* spp., although the disease caused by this pathogen had been observed since 1993. It is yet to be isolated from oaks in Europe, but pathogenicity experiments under controlled quarantine conditions indicate that a number of forest tree species (**Table 1**) including *Fagus* and *Quercus* species are susceptible to *P. ramorum*. Therefore, the risk to forest species in Europe is great.

In the USA, 'sudden oak death,' a rapid mortality of oaks (mainly tan oak and live oaks) in wildlands and the urban–wildland interface, has been observed since 1994 in the coastal fog belts of southern Oregon and northern California and is also caused by *P. ramorum*. The disease is currently in epidemic proportions in coastal California, covering an area that runs approximately 600 km south to north from central California to southern Oregon. It has a wide host range including a range of tree species (**Table 1**) and shrubs. In the oak family, all the susceptible species belong to the red oaks (section *Lobatae*), whilst so far no white oaks (section *Quercus*) or golden cup oaks (section *Protobalanus*) are found to be susceptible.

In Europe, only the A1 sexual compatibility type has been found which contrasts to the presence of only the A2 sexual compatibility type in North America. The internal transcribed spacer sequences of the European and American isolates are identical. In mating tests, the isolates rarely, if ever, mate together. Consequently, it is unclear whether *P. ramorum* has a normally functioning A1 × A2 outcrossing system. *Phytophthora ramorum* is exclusively aerial in its biology, unlike other *Phytophthora* species that cause disease in forest trees which are predominantly soilborne pathogens. Although recovered from soil and litter, *P. ramorum* has not been observed to cause symptoms below the soil line. It has been recovered from up to 20 m above the ground from stems with no basal cankers. However, it is still not understood how the pathogen has spread so widely, although it is recovered from rainwater indicating its possible dissemination by rain splash and wind-driven rain.

In northern America, the current geographic range of the disease includes a wide range of forest types within the Mediterranean climatic region of California receiving predominantly winter rainfall and with mean annual rainfall ranging from 85 to 200 cm. It is known to have a wide host range which includes members of the *Caprifoliaceae*, *Ericaceae*, *Fagaceae*, and *Lauraceae* and it is likely that other susceptible taxa will be found.

Of concern is the observation from pathogenicity tests that a number of Australian species from a range of families are susceptible to *P. ramorum*; this includes members of *Eucalyptus* spp. (Myrtaceae) a keystone plant genus of many plant communities. Therefore, if introduced into Australia, it is likely to be a major ecological threat to southern Australian forest or woodland ecosystems with a similar climate to California. The risk is real since *P. ramorum* has very recently been isolated from an ornamental *Rhododendron* species on the island of Mallorca (Spain), another Mediterranean environment. Consequently, it is critical that stringent quarantine measures are in place to ensure *P. ramorum* does not enter Australia or other countries where it is likely to be a problem.

Alder Phytophthora

In 1993, a lethal disease of alder (*Alnus* spp.) was observed in horticultural shelterbelts and along rivers in Britain. It was caused by a new *Phytophthora* species that superficially resembled *P. cambivora*, a common pathogen of European hardwood trees. The disease is now found through much of Europe, including Austria, Belgium, France, Germany, Hungary, and the Netherlands. Trees of all age classes are affected and symptoms include small and yellow leaves, tarry spots and exudations, top dieback, and death. The alder phytophthora is hard to isolate as it is considered a primary parasite and is soon replaced by other more opportunistic but secondary pathogens. Therefore, a range of insect pests and other pathogens are frequently isolated from alders but these are probably a result of the alder phytophthora predisposing the trees to secondary invasion.

The alder phytophthora comprises a range of species hybrids, with a common 'standard' alder phytophthora type found throughout much of Europe. The parents of the alder phytophthoras are probable hybrids between two developmentally different phytophthoras: *P. cambivora*, a fast-growing, sexually outcrossing species, and a phytophthora close to *P. fragariae*, a slow-growing, inbreeding and nutritionally fastidious species.

The standard alder phytophthora is extremely difficult to isolate from soil around diseased alder trees; thus its oospores are unlikely to contribute to survival or spread in the field. Local spread along river systems is probably via zoospores and through dispersal of infected alder debris containing healthy mycelium. International spread may have occurred through the distribution and planting of infested nursery stock. The alder phytophthora represents a serious threat to both natural and managed stands of alder and to the stability of riparian ecosystems in Europe and possibly elsewhere if introduced into other countries.

Currently, there are no clearly defined control strategies in place, although early coppicing of diseased trees is being considered. Trials are being established to evaluate whether differences in disease resistance are present within *Alnus* species.

Other *Phytophthora* Diseases

Many *Phytophthora* species have been isolated from the soils under rainforest, temperate forest, and Mediterranean forest plant species and have not been associated with plant deaths. For example, these include *P. katsurae*, *P. megasperma* var. *sojae*, and *P. palmivora* from rainforest in Papua New Guinea; *P. cactorum* in Australia; *P. europaea*, *P. psychrophila*, *P. citricola*, and *P. uliginosa* from under oaks in Europe; and *P. gonapodyides* in Australia, Europe, and North and South America.

Phytophthora gonapodyides does cause significant damage to fine roots of *Castanea* and *Quercus* in Europe; and with further research is likely to be associated with tree declines in Australia and North and South America. However, it is likely that these could become pathogenic as a result of climate change or through the breakdown of quarantine practices. If, for example, new species are introduced into a region it is possible that hybridization between these and existing species could occur resulting in destructive pathogens. This was the case observed for the alder pathogen in Europe.

Impact on Ecosystem Health and Function

Although it is reasonably well understood how different *Phytophthora* species impact directly on plant species, we have very little understanding on how they impact indirectly on ecosystem health and function. For example, we do not fully appreciate how the loss of the litter layer, changed soil-water status, loss of cover to shade-loving plant species, the loss of vertebrate and invertebrate pollinators, and the potential loss of the fruiting bodies of ectomycorrhizal fungi influence the function and health of ecosystems. These indirect effects are likely to be very profound. For example, in Australia, *P. cinnamomi* has been shown to impact adversely on fauna through the loss of habitat and food sources such as pollen, nectar, and possibly fruiting bodies of epigeous and hypogeous macrofungi, many of which are ectomycorrhizal. A number of small marsupial species rely almost totally on fungal fruiting bodies in their diet, so a decline in a fungal host species can result in loss of animals from an impacted environment. In turn, a loss of animals that turn over soil whilst digging for fungi can affect the incorporation of litter into the soil and result in the increased incidence of nonwetting soils. Reduced soil water uptake can result in increased erosion through increased surface water runoff and drought stress.

These are just a few examples of how *Phytophthora* species can impact on ecosystem function and health, and only very recently have researchers started to take a more holistic approach to examine the wider implications of plant diseases caused by *Phytophthora* diseases on communities in general.

Control

Effective hygiene and quarantine measures must always remain the primary methods of control and containment of all forest pathogens. These must include the stringent control of movement of plant material between regions, countries, and continents. The majority of *Phytophthora* diseases in forests today appear to be the result of new introductions into a region. Therefore, it is critical to stop the spread of the pathogen(s) into noninfested areas. Disease management aims to prevent and restrict spread and intensification of the pathogen and to protect and conserve conservation and economic values and includes:

- rating hazard or identifying levels of risk
- assessing risk or analysis of risk at the landscape level
- hygiene procedures
- manipulating conditions to disfavor the pathogen and to enhance host resistance
- education of the public and land managers and users
- appropriate use of research to address questions as they arise.

Chemical Control

Recently, in Australia, phosphonate compounds applied as foliar applications from aircraft, backpacks, or by trunk injection have been extremely effective in reducing the impact and spread of *P. cinnamomi* in forests and natural ecosystems. Control by one trunk injection have been extended beyond 6 years in some forest species and by 2–3 years with aerial applications. Consequently, applications along disease fronts or to plant communities containing rare or threatened plant species can be a viable and effective way of maintaining plant communities.

Phosphonate (also referred to as phosphite), the anionic form of phosphonic acid $(HPO_3)^{-2}$, controls many plant diseases caused by a range of *Phytophthora* spp., even at concentrations *in planta* that only partially inhibit pathogen growth *in vitro*.

Phosphonate is a systemic fungicide that is translocated in both the xylem and the phloem. In the phloem, phosphonate is trapped and therefore translocated through the plant in association with photoassimilates in a source–sink relationship. Phosphonate treatment induces a strong and rapid defense response in the challenged plant. These defense responses stop pathogen spread in a large number of hosts. Phosphonate exhibits a complex mode of action, acting directly on the pathogen and indirectly in stimulating host defense responses to ultimately inhibit pathogen growth. Recent work in the USA has also shown the chemical to be effective on *P. ramorum*.

It is critical to add an adjuvant when applying phosphonate as a foliar application, otherwise efficacy and persistence of the chemical are severely limited. These increase spray coverage by droplet spreading, promoting spray retention, and reducing spray drift, evaporation and wash-off. Care must be taken to ensure adjuvants are not phytotoxic in their own right.

It is important that plants are treated when they are actively growing and not drought-stressed otherwise uptake and distribution of phosphonate is substantially reduced. Rates of application vary significantly between plant species and communities. In Australia, foliar applications to runoff vary between 0.5% and 2.0% (5–$20\,g\,l^{-1}$), whilst aerial applications are normally in the range 12–$36\,kg\,ha^{-1}$ applied as ultra-low-volume sprays. Trunk injections vary between 5% and 20% (50–$200\,g\,l^{-1}$) depending on the species to be injected. Phosphonate can cause severe phytotoxicity and plant deaths if inappropriate concentrations are applied; consequently it is important to conduct preliminary trials before applying the chemical to large areas. It is important to note that although the chemical contains the spread of the pathogen *in planta* it does not always kill it. Therefore, the pathogen can still reproduce and disseminate its infective propagules under optimum environmental conditions. Reduced flowering, pollen viability, and seed viability have been observed in some species and more research is required to determine the long-term impacts of these. To date no adverse affects have been observed on mycorrhizal fungi. However, there is some evidence that repeated applications of phosphonate in horticultural situations does select for phosphonate-tolerant isolates of *P. cinnamomi*, and these isolates also appear to be more virulent. In natural ecosystems, where the chemical is applied infrequently it is unlikely that selection for tolerant *Phytophthora* isolates will occur. The main concern is the movement of supposedly 'pathogen-free' container plant stock from nurseries into areas where the pathogen can escape into forested regions. If these contain tolerant *Phytophthora* isolates problems may arise in the future. Irrespective, of these possible drawbacks, phosphonate provides us with a very viable control option for plant species or individual trees of importance whilst alternative control strategies are developed.

Conclusion

Phytophthora as a genus is extremely plastic in terms of genetic and phenotypic variability, pathogenicity, host range, and long-term survival strategies. As exotic pathogens they are devastating in forest and other plant ecosystems as has been observed in Australia, Oregon, Europe, and elsewhere. It is apparent that there are numerous *Phytophthora* species, with many still to be described in forests worldwide. The biology, ecology, pathology, and genetics of the majority of *Phytophthora* species are still poorly understood. However, it is clear that in addition to the presence of a pathogen and a susceptible host, conducive environmental conditions are critical for a *Phytophthora* disease outbreak to be triggered. Often only small shifts in environmental conditions whether biological, chemical, or physical are required to trigger a *Phytophthora* disease event. Therefore, with increasing global movement of humans and their associated plant produce, and climate change through global warming, new outbreaks of devastating *Phytophthora* diseases are likely to occur.

See also: **Pathology**: Diseases affecting Exotic Plantation Species; Diseases of Forest Trees; Root and Butt Rot Diseases. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Brasier CM and Kirk SA (2001) Differences in aggressiveness between standard and variant hybrid alder phytophthoras, *Phytophthora cambivora* and other *Phytophthora* species on live bark of *Alnus*. *Plant Pathology* 50: 218–229.

Erwin DE and Ribeiro OK (1996) *Phytophthora Diseases Worldwide*. St Paul, MN: American Phytopathological Society.

Guest D and Grant B (1991) The complex action of phosphonates as antifungal agents. *Biological Reviews* 66: 159–187.

Hansen EM and Sutton W (eds) (1999) *Phytophthora Diseases of Forest Trees*, Proceedings from the International Meeting on Phytophthoras in Forest and Wildland Ecosystems. Corvallis, OR: Forest Research Laboratory, Oregon State University.

Hardy GEStJ, Barrett S, and Shearer BL (2001) The future of phosphite as a fungicide to control the soilborne plant pathogen *Phytophthora cinnamomi* in natural ecosystems. *Australasian Plant Pathology* 30: 133–139.
Jung T, Blaschke H, and Osswald W (2002) Involvement of soilborne *Phytophthora* species in Central European oak decline and the effect of site factors on the disease. *Plant Pathology* 49: 706–718.
Rizzo DM, Garbelotto M, Davidson JM, Slaughter GW, and Koike ST (2002) *Phytophthora ramorum* as the cause of extensive mortality of *Quercus* spp. and *Lithocarpus densiflorus* in California. *Plant Disease* 86: 205–214.
Shearer BL and Tippett JT (1989) *Jarrah Dieback: The Dynamics and Management of* Phytophthora cinnamomi *in the jarrah (*Eucalyptus marginata*) Forest of South-Western Australia*, Research Bulletin no. 3. Como, Western Australia: Department of Conservation and Land Management.
Streito JC, Legrand PH, Tabary F, and Jarnouen de Villartay G (2002) Phytophthora disease of alder (*Alnus glutinosa*) in France: investigations between 1995 and 1999. *Forest Pathology* 32: 179–191.
Thomas FM, Blank R, and Hartmann G (2002) Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. *Forest Pathology* 32: 277–307.
Wills RT (1993) The ecological impact of *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. *Australian Journal of Ecology* 18: 145–159.
Zentymyer GA (1980) Phytophthora cinnamomi *and the Diseases it Causes*. St Paul, MN: American Phytopathological Society.

Vascular Wilt Diseases

K Jacobs and M J Wingfield, University of Pretoria, Pretoria, South Africa
J N Gibbs, Aberyail, Llangynidr, Wales, UK

Introduction

The vascular wilts include some of the most destructive of all tree diseases, in terms of both the scale of the damage and the speed of attack. Vascular wilt diseases mainly occur in angiosperms and only one example in a gymnosperm has been documented. True vascular wilts are caused by fungi, although there are some similar diseases caused by bacteria. Pine wilt disease caused by the pine wood nematode *Bursaphalenchus xylophilus* is covered elsewhere (*see* **Pathology**: Pine Wilt and the Pine Wood Nematode).

The Characteristics of Vascular Wilt Diseases

The fungi that cause vascular wilt diseases are initially restricted to the xylem elements. They can often achieve rapid dissemination within these elements through the passive movement of spores in the transpiration stream. Xylem anatomy can influence this process, with ring-porous genera, such as oaks and elms, that have large, long earlywood vessels which are particularly vulnerable to invasion. Vascular wilt pathogens often grow out from the xylem into the surrounding tissues after the tree has died. This enables them to establish contact with the outside world and, in particular, with insects that can act as vectors for transport to new hosts. Typically, vascular wilt pathogens do not have the capacity to survive long in the tissues of a dead host.

Generally, all vascular wilt diseases display similar symptoms. Leaves and young shoots on one or more branches suddenly wilt and die. If such a branch is cut, a marked discoloration can often be observed in the xylem of the current year. In a severe attack, symptoms can rapidly develop to kill the whole tree. Much still remains to be learnt about the process of pathogenesis. Vascular wilt fungi have the capacity to produce conidia in water-filled xylem vessels without causing cavitation (i.e., the breaking of the column of water). This can lead to rapid dissemination of the fungus throughout the tree in the transpiration stream. However, at some stage cavitation and an interruption to the water flow will occur. Gums, gels, and toxins may also be produced. In some cases the tree responds by producing balloon-like tyloses within the vessels by extrusion from adjacent parenchyma cells.

Ascomycetous fungi (and related mitosporic fungi) are responsible for most true vascular wilt diseases. Important examples are Dutch elm disease (*Ophiostoma ulmi* and *O. novo-ulmi*), oak wilt (*Ceratocystis fagacearum*), black stain root disease of conifers (*Leptographium wageneri*), and verticillium wilt (principally *Verticillium dahliae*). These diseases are discussed separately below.

Fungal Wilt Diseases

Dutch Elm Disease

Dutch elm disease has caused devastation to elms in Europe and North America. It is caused by two different, although closely related, species of fungi: *O. ulmi* and *O. novo-ulmi*. *Ophiostoma ulmi* was responsible for the first epidemic, which began in the

Netherlands (hence the name) in the late 1910s and quickly spread through much of Europe. In the late 1920s it was introduced to North America, where it proved to be particularly damaging on *Ulmus americana*. The second epidemic, caused by *O. novo-ulmi,* and proving to be very destructive in Europe, began in the late 1960s. It is now known to have developed from two centers, one in Eastern Europe and the other in the mid-west of North America. Two subspecies of *O. novo-ulmi* are associated with these two centers. Hundreds of millions of elms have been killed and huge sums spent in attempts at control and in the removal of dead trees. Most elm species are susceptible to the disease, with the American elm being especially vulnerable to both species of the fungus (**Figure 1**). Where there is some resistance, as in the Siberian elm, it is often found in trees that are lacking in aesthetic and silvicultural qualities.

The first symptoms of Dutch elm disease on a previously healthy tree typically take the form of the wilting or yellowing of the leaves on a vigorously growing branch in midsummer. Such a branch will show pronounced streaking in the vessels of the outermost xylem ring. The speed of subsequent symptom development down the branch and into the rest of the tree will depend, *inter alia*, on the species of host and pathogen involved. In some cases symptoms may remain relatively restricted in the first season, only to flare up throughout the crown early in the second season. Rapid general symptom development occurs if a tree becomes infected as a result of the transmission of the pathogen via grafted roots from an adjacent tree.

Various bark beetles act as vectors of the pathogen. The most important of these are *Hylurgopinus rufipes* and *Scolytus multistriatus* in North America and *S. scolytus* in Europe. (*see* **Entomology**: Bark Beetles). From the infection viewpoint, the key event is the establishment of the fungus within water-filled xylem vessels to which it has gained access by the feeding activities of the beetles. Early stages of colonization may be quite slow. However, once in the large, long, springwood vessels, spores of the fungus can be disseminated very rapidly under the influence of transpiration. They can also be drawn from a diseased tree to a neighboring healthy one if the trees have developed on a common root system or have grafted together (**Figure 2**).

Deleterious viruses may be present within the mycelium of *O. ulmi* and *O. novo-ulmi* and can lead to a reduction in pathogenicity. These viruses, known

Figure 1 English elm (*Ulmus procera*) killed by Dutch elm disease during the early 1970s. Photograph courtesy of J. Gibbs.

Figure 2 A hedgerow of English elm which has originated as sucker growth. Dutch elm disease is spreading rapidly through the common root system that links the trees. Photograph courtesy of J. Gibbs.

as d-factors, can spread from one unit of mycelium to another, provided that the latter is vegetatively compatible (i.e., belong to the same vc-group). Within *O. novo-ulmi,* one vc-group predominates, making it vulnerable to infection. However, hybridization between *O. novo-ulmi* and *O. ulmi,* once the former has moved into a new area, can lead to an exchange of vc-genes and hence to the formation of new vc-groups.

Management of Dutch elm disease requires effective removal and destruction of diseased or dead trees to reduce breeding material for the bark beetles. Disruption of root grafts between infected and healthy trees can restrict movement of the pathogen. In the case of trees of high value, fungicidal injections can be used. Breeding programs have resulted in the release of a number of resistant trees.

Oak Wilt

Oak wilt, caused by *C. fagacearum,* is a wilt disease known only in North America, where it mainly affects oaks (*Quercus* spp.) belonging to the red oak group. Currently the disease occurs in 21 states of the USA and has been recorded on 20 species of oak. *Ceratocystis fagacearum* is considered to be potentially as destructive as the fungi causing Dutch elm disease, but while they have effective vectors for dispersal, the oak wilt fungus currently lacks such vectors.

In red oaks such as *Q. rubra* and the northern pin oak (*Q. ellipsoidalis*), disease symptoms spread rapidly throughout the crown and trees can die within a few weeks. In contrast, white oaks such as *Q. alba* and bur oak (*Q. macrocarpa*) are substantially less susceptible. The disease progresses slowly with only a few branches being affected each year. In some cases trees may recover. In the live oaks of Texas (*Q. fusiformis* and *Q. virginiana*) the leaves become chlorotic or bronze, often with a yellow or brown color along the veins. Trees may defoliate and die quickly but commonly survive for several years (**Figure 3**).

Through experiments conducted in the USA, it has recently been discovered that the European white oaks *Q. robur* and *Q. petraea* are highly susceptible to *C. fagacearum*. This discovery, combined with the recognition that the European oak bark beetle, *S. intricatus*, has the characteristics to make it an effective vector for this fungus, has reinforced

Figure 3 (a) A red oak (*Quercus ellipsoidalis*) killed by oak wilt. A healthy tree can be seen in the background. (Courtesy of JN Gibbs; in Forestry Commission Collection.) (b) A white oak showing symptoms of oak wilt on one branch while adjacent branches remain healthy. Courtesy of JN Gibbs; now in Forestry Commission Collection.

concerns that the fungus could be extremely destructive were it to cross the Atlantic. Strict quarantine regulations are in force.

Ceratocystis fagacearum moves rapidly through the xylem, as spores are drawn along in the transpiration stream. This process is aided by the fact that the fungus commonly enters a tree via root grafts with a neighboring tree that is already diseased. After tree death, *C. fagacearum* grows out of the xylem and forms mats of mycelium just below the bark. The bark splits open as a result of pressure exercised by a special structure, the pressure cushion, and volatiles produced by the fungus act as attractants for insects such as sap-feeding beetles (Coleoptera: Nitidulidae). The insects become contaminated with conidia and ascospores from the fungus mats and, if they move to fresh xylem wounds on healthy trees, are capable of transmitting the pathogen. Trees are most vulnerable in late spring and early summer shortly after the new earlywood (springwood) vessels have become functional. There are several weak points in this association between insect and fungus. For infection to take place, wounds on susceptible trees have to be less than 3 days old. Moreover, relatively few of the insects visiting the wounds are carrying spores of the fungus.

Oak wilt is best managed by preventing infection. This is achieved through removing diseased stems on which sporulating mats might form (or by treating them to stop mat production) and by taking steps to minimize the creation of wounds on valued trees in late spring/early summer. Root grafts can be disrupted to prevent tree-to-tree spread. As with Dutch elm disease, high-value trees can be injected with fungicides, although this is very costly and is restricted to very specific situations.

Black Stain Root Disease of Conifers

Black stain root disease is caused by *L. wageneri*. The disease is restricted to the western USA and parts of western Canada where it has caused significant losses, particularly to Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). It is recognized to be of high quarantine significance as it is seen to pose a serious threat to both conifer plantations and indigenous forests elsewhere in the northern hemisphere.

External symptoms of the disease may develop gradually over several years. These include reduced height growth, reduced needle size, and premature needle fall. In the xylem of the roots and lower stems, a black stain can be found, typically in bands that follow the annual rings. Resinosis may be observed and the presence of the disease predisposes the tree to attack by bark beetles and other pathogens.

As in the case of other wilt pathogens, *L. wageneri* colonizes only the xylem elements of the host. Members of the Pinaceae do not have long vessels but only short tracheids, and hence rapid passive transport of spores is not a feature of this disease.

Rather, the fungus grows from tracheid to tracheid via the bordered pits. The dark mycelium of the fungus, together with a discoloration of the tracheids themselves, is principally responsible for the visible stain. In pines, the stained wood may be impregnated with resin and many tracheids may become occluded with tyloses.

Leptographium wageneri represents a species-complex including three different host specific variants, *L. wageneri* var. *wageneri* (occurring on pinyon pine), *L. wageneri* var. *pseudotsugae* (occurring on Douglas-fir), and *L. wageneri* var. *ponderosum* (occurring on jeffrey, lodgepole, and Ponderosa pines). Although all three varieties of *L. wageneri* can infect tree species other than those from which they were isolated, this rarely occurs in nature.

Black stain root disease spreads over relatively small distances through root grafts. Also, the fungus can grow for short distances (up to *c*. 15 cm) through the soil and infect healthy rootlets. For dissemination over longer distances, *L. wageneri* requires insect vectors, in particular bark beetles (Coleoptera: Scolytidae). It has been associated with two weevils *Pissodes fasciatus, Steremnius carinatus*, and the root-feeding bark beetles, *Hylastes nigrinus* and *H. macer*. These last species are thought to be the primary vectors on Douglas-fir and ponderosa pine respectively. These insects colonize declining roots of diseased trees and introduce the pathogen to the roots of healthy trees if attracted to them for maturation feeding or by the presence of preexisting wounds. Infection centers enlarge at the rate of about 1 m $year^{-1}$ but in Douglas-fir stands they tend to slow down markedly when the trees reach 30–35 years of age.

The incidence of black stain root disease is increased by environmental factors. The disease is prevalent near roads or railroad tracks, where logging has occurred or trees have been thinned. Management treatments for disease-prone areas should be those that cause least site disturbance and tree injury. In affected stands, resistant species should be favored.

Verticillium Wilt

Verticillium wilt caused by *Verticillium albo-atrum* and *V. dahliae* is widespread in both temperate and tropical regions of the world. In the northern hemisphere, many woody plants are affected, all in the class of Dicotyledons. Gymnosperms and woody monocotyledons are not susceptible. The two fungi differ in a number of characters and, where proper attribution to species has been made, almost all the cases of damage to woody plants involved *V. dahliae*. Verticillium wilt is principally a problem in nurseries and ornamental plantings, such as those in gardens, parks, and streets, and it rarely occurs in forests and natural stands. It affects several important shade tree genera, including maple (*Acer*), lime (*Tilia*), and ash (*Fraxinus*), as well as some orchard trees such as cherry and apricot (*Prunus* spp.).

Symptoms of this disease can vary depending on the host and the environmental conditions. Most species display wilting and browning of the foliage first, while others may exhibit rapid chlorosis and necrosis of the foliage. In some cases, symptoms develop rapidly to tree death, while in others they are chronic and include slow growth, sparse and distorted foliage, stunted twigs, and dieback. In some species, examination reveals marked xylem staining that varies in color with the host, e.g., in maples it is typically green (**Figure 4**). In others, such as ash, no discoloration can be seen. Most fatalities occur in nursery stock and small trees. In mature trees, chronic infection is more usual, with symptoms

Figure 4 Staining caused by *Verticillium dahliae* in the xylem of a small stem of the Indian rain tree (*Koelreuteria paniculata*). Photograph courtesy of J. Gibbs.

affecting just part of the crown, and recovery the following year being quite common.

Verticillium dahliae differs from the vascular wilt fungi described above in having considerable capacity to survive in the absence of its host. This survival is in the form of dark microsclerotia, which can persist in the soil for up to 10 years. Most information on the infection process comes from studies of herbaceous hosts. Hyphae from germinating microsclerotia invade via root tips and root wounds. In plants not immune to vascular infection, the fungus grows into the xylem where conidia are produced and disseminated into the stem. In the past, fungal toxins affecting leaf function were thought to be key to the development of symptoms but current views emphasize the importance of vascular disruption. Effective host resistance mechanisms are thought to depend on processes such as the rapid production of gels in the vessels to trap and immobilize the conidia, followed by the production of toxic secondary metabolites.

There is little evidence for host specialization in *V. dahliae* and some of the most dramatic disease outbreaks have occurred when tree nurseries have been established on old fields of susceptible species like potato or cotton. Such sites should not be used unless there is the option of carrying out soil fumigation. Once the disease is present in a tree, there may be some scope for promoting natural recovery by improving the growing conditions, although heavy irrigation and nitrogen fertilization should be avoided.

Other Fungal Vascular Wilt Diseases

Strains of *Fusarium oxysporum* cause important vascular wilt diseases on herbaceous and woody plants, particularly in warm temperate and tropical regions. A tree example is provided by *F. oxysporum* f. sp. *pernicosum* that has become a limiting factor in the use of mimosa (*Albizzia procera*) as an ornamental in parts of the USA. The fungus is soilborne, germinating from chlamydospores in the presence of host plants to penetrate both wounded and unwounded rootlets and then to colonize the xylem. Another race of the same fungus is known from *A. procera* in Puerto Rico. *Fusarium oxysporum* has also been implicated in the death of *Acacia koa* in Hawaii. *Ceratocystis albofundus* is the causal agent of Ceratocystis wilt on black wattle in South Africa and other parts of Africa. In the Seychelles, takamaka disease, caused by *Leptographium calophylli*, is a serious problem on takamaka (*Calophyllum inophyllum* var. *takamaka*), a broad-leaved evergreen tree that plays an important role in littoral habitats around the Indian Ocean. The bark beetle *Cryphalus trypanus* has been shown to act as a vector.

Bacterial Wilts

There are a number of wilt diseases of trees caused by bacteria in which the causal organism is restricted to the tissues of the xylem during pathogenesis, if not to the xylem elements. Most notable are bacterial wilt of willow and bacterial wilt of *Eucalyptus*.

Watermark Disease of Willow

This disease was first recorded in eastern England during the 1920s on *Salix alba* var. *caerulea* grown for the manufacture of cricket bats. In the 1930s it was recorded in the Netherlands but it is not known from any other European country. In 1993 it was found affecting several species of willow (*S. bakko*, *S. sachalensis*, and *S. kinuyanagi*) in natural forests in a mountainous part of Hokkaido, Japan. The symptoms involve the wilting of young leaves and shoots in early summer. The foliage turns a reddish-brown and the dead leaves are typically retained on the tree. Cross-sections of the stems of affected shoots show a marked brownish 'watermarking' of the xylem. In large branches and trunks this normally follows the position of one or more annual rings. On exposure to air, the discolored tissues darken and a brownish-black liquid may be exuded (**Figure 5**).

The causal bacterium is a Gram-negative nonsporing rod with peritrichous flagella. It falls within the *Erwinia amylovora* group and has been named *E. salicis*. Microscopic examination of the stained tissues of a diseased tree reveals masses of bacteria in some of the vessels, often in association with tyloses. Ray parenchyma cells show plasmolysis and become necrotic, and bacteria can also be seen in these.

Large numbers of bacteria can ooze from affected branches and it used to be thought that infection resulted from the dissemination of these bacteria by wind and rain to injured tissues on healthy trees. However, serological studies in the UK have shown that the bacterium can be detected in the wood of many healthy trees, and also in the coppice stools that provide cuttings for willow propagation. Isolates from adjacent diseased trees often fall into different groups on the basis of electrotyping and this supports the idea that the bacterium is disseminated within the cutting material in a latent or endophytic state, only developing to cause disease under the influence of some as yet unknown environmental factors.

In the UK a sanitation felling program for symptomatic willows is conducted in commercial

Figure 5 Cricket-bat willow (*Salix alba*) felled because of watermark disease. Staining due to the disease can be seen in the xylem of both trunk and stump. Photograph courtesy of J. Gibbs.

cricket-bat willow plantations. Although there was an initial fall in disease incidence following the introduction of this program in the 1930s, there has been little subsequent evidence for a further reduction in disease. In the Netherlands, serious losses in the 1960s can be attributed to the widespread amenity planting of a number of very susceptible clones of *S. alba*.

Bacterial Wilt of *Eucalyptus*

The bacterium *Ralstonia solanacearum* has been reported to cause bacterial wilt in commercial *Eucalyptus* plantations. This disease was first described in Brazil and later in China, Taiwan, Australia, Venezuela, and South Africa. *Ralstonia solanacearum* is divided in different biovars based on their nutritional requirements and in different races based on their host ranges. Biovars 1 and 3 are able to infect *Eucalyptus* and race 1 has been recorded from all the areas where the disease occurs on *Eucalyptus*.

Symptoms of bacterial wilt on *Eucalyptus* include wilting, leaf drop, reduced growth, discoloration of the vascular system, and death of stems. Infected trees may die within 6 months of showing the first signs of infection. Bacterial exudation can also be seen from the cut surfaces of the stems. Fortunately, only some *Eucalyptus* species are susceptible to this disease and it can be managed by planting resistant species or hybrid close.

See also: **Pathology**: Diseases of Forest Trees; Insect Associated Tree Diseases; Pine Wilt and the Pine Wood Nematode. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Appel DN (1995) The oak wilt enigma: perspectives from the Texas epidemic. *Annual Review of Phytopathology* 33: 103–118.

Ash CL (2001) Shade tree wilt diseases. In: Ash CL (ed.) *Proceedings from Wilt Diseases of Shade Trees: A National Conference*, August 25–28 1999, pp. 1–257. St Paul, MN: American Phytopathological Society Press.

Brasier CM (2001) Rapid evolution of introduced plant pathogens via interspecific hybridisation. *BioScience* 51: 123–133.

Coutinho TA, Roux J, Riedel K-H, Tereblance J, and Wingfield MJ (2000) First report of bacterial wilt caused by *Ralstonia solanacearum* on eucalypts in South Africa. *Forest Pathology* 30: 205–210.

Harrington TC and Cobb Jr FW (1988) Leptographium *Root Diseases on Conifers*. St Paul, MN: American Phytopathological Society.

Hessburg PF, Goheen DJ, and Bega RV (1995) Black stain root disease of conifers. US Department of Agriculture Forest Insect and Disease Leaflet 145. Washington, DC: USDA.

Jacobs K and Wingfield MJ (2001) Leptographium *Species: Tree Pathogens, Insect Associates, and Agents of Blue-Stain*. p. 206. St Paul, MN: American Phytopathological Society Press.

Roux J and Wingfield MJ (1997) Survey and virulence of fungi occurring on diseased *Acacia mearnsii* in South Africa. *Forest Ecology and Management* 99: 327–336.

Sinclair WA, Lyon HH, and Johnson WT (1987) *Diseases of Trees and Shrubs*, Ithaca, NY: Cornell University Press. p. 574.

Turner JG, Davis JML, and Guven K (1992) Watermark disease of tree willows. *Proceedings of the Royal Society of Edinburgh* 98B: 105–107.

Wingfield MJ, Seifert KA, and Webber JF (1993) Ceratocystis and ophiostoma: *Taxonomy, Ecology and Pathogenicity.* St Paul, MN: American Phytopathological Society.

Pine Wilt and the Pine Wood Nematode

K Suzuki, The University of Tokyo, Tokyo, Japan

Introduction

Pine wilt is caused by the pine wood nematode *Bursaphelenchus xylophilus* (**Figure 1**). This pine wilt disease, which is endemic to North America, has already spread epidemically to East Asia, and recently to Portugal in Europe (**Figure 2**). *Monochamus* spp. beetles (pine sawyer beetles) are the only insects that disperse the pine wood nematode. The incidence of the disease is closely related to environmental conditions such as high temperature with little rainfall. Pine wilt disease is becoming a serious threat to pine forests in the northern hemisphere.

Figure 1 The pine wood nematode, *Bursaphelenchus xylophilus*. The left image shows the head of a nematode. The right image shows the larvae in a cultural media.

History

Pine wilt was initially recognized as an unusual wilt of pines in 1905 in the port city of Nagasaki in southern Japan, which was the only port open to foreign culture in the nineteenth century. Pine wilt spread thereafter from many port cities in southern Japan. This suggests that the disease is artificially distributed by the shipment of infested logs. The loss of timber by pine wilt showed an abnormal increase in the late 1940s soon after World War II and then pine wilt became a matter of public concern. Thereafter, the damage was called 'matsukuimushi,' which is a general term covering more than 70 species of pine bark beetles and pine wood borers thought to be concerned with pine wilt in those days.

As a causal agent of pine wilt, the pine wood nematode was recovered from a dead Japanese black pine, *Pinus thunbergii*, in 1969. The pine wood nematode is associated with cerambycid beetles, the Japanese pine sawyer, which is a matsukuimushi (**Figure 3**). The pine species susceptible to the disease are Japanese red pine, *P. densiflora*, and the Ryukyu pine, *P. luchuensis*, in addition to Japanese black pine.

In 1979, the pine wood nematode was discovered in Missouri, USA. Most pine species in the USA are moderately resistant to the disease. The pine wood nematode is naturally found in diseased *Abies* spp., *Cedrus* spp., *Larix* spp., *Picea* spp., and *Pseudotsuga* spp. in the USA and Canada. It is hypothesized that

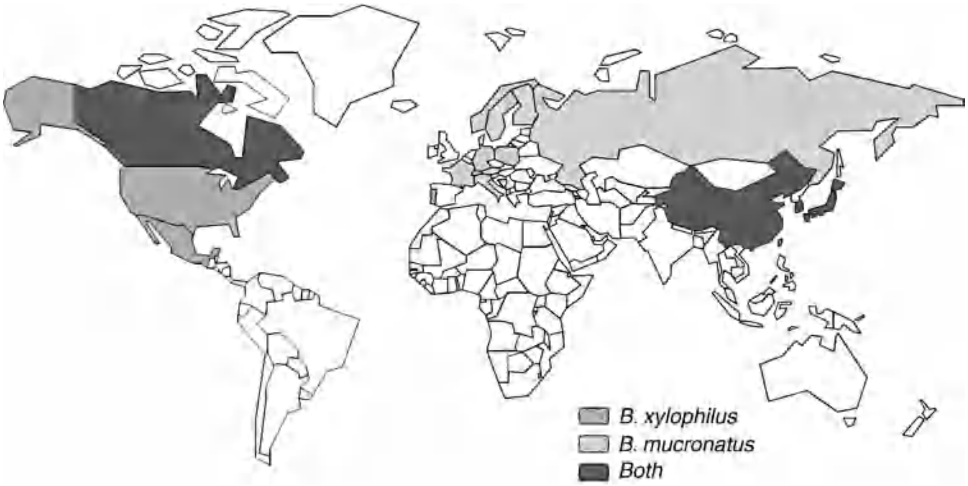


Figure 2 The distribution of *Bursaphelenchus xylophilus* and *B. mucronatus* in the northern hemisphere.

Figure 3 The Japanese pine sawyer, *Monachamus alternatus*.

the pine wood nematode was introduced in pine logs to Japan possibly from the USA early in the twentieth century.

Pine wilt disease had spread to Nanjing, China, by 1982 on Japanese black pine and southern red pine, *P. massoniana*, to Taipei, Taiwan, by 1985 on Japanese red pine and *P. luchuensis*, and to Pusan, Korea, by 1988 on Japanese black pine and Japanese red pine. Recently, pine wilt disease was found at Setubal, Portugal, in 1999 on maritime pine, *P. pinaster*.

The Pathogen, the Pine Wood Nematode

The pine wood nematode was first named as *B. lignicolus* in Japan in 1972, but was morphologically similar to the timber nematode, *B. xylophilus,* in the USA. The genus *Bursaphelenchus* belongs to the family Aphelenchoididae, and *B. xylophilus* was initially described as *Aphelenchoides xylophilus* from the wood of long-leaf pine, *P. palustris,* in 1934. Thereafter, *A. xylophilus* was transferred to the genus *Bursaphelenchus* in 1970. Based on genetic crossing between *B. lignicolus* and *B. xylophilus*, it was elucidated that they are the same species. Therefore, the name of *B. xylophilus* is valid based on the priority of nomenclature for a causal agent of pine wilt disease.

All species of the genus *Bursaphelenchus* have a relation with bark beetles and wood borers. As the pine wood nematode is mycophagous, it can propagate easily on cultures of *Botrytis cinerea* and other fungi. The pine wood nematode is also cultured on callus tissues of Japanese red and Japanese black pines grown on artificial media. This indicates that the pine wood nematode is able to feed on parenchymatous cells of living pine wood.

The pine wood nematode has four larval stages (L_1, L_2, L_3, L_4) and two different forms in its life cycle, that is, a propagative form (L_3, L_4) and a dispersal form (L_{III}, L_{IV}). The former develops under favorable conditions and the latter under unfavorable conditions. As to the propagative stage, females of the pine wood nematode lay an average of 80 eggs during a 30-day oviposition period. The pine wood nematode completes its life cycle in 3 days at 30°C, 4 days at 25°C, 6 days at 20°C, and 12 days at 15°C. No reproduction occurs at a temperature higher than 33°C and the limit of low temperature is 9.5°C for growth on *B. cinerea*. The dispersal stage is adapted to surviving unfavorable conditions, such as low temperature and lack of food. The larva of this stage, which is called the dispersal third-stage larva (L_{III}), is different in its morphological and biological features from the propagative third-stage larva (L_3). Larvae molt to become the dispersal fourth-stage larvae (L_{IV}) in wood under natural conditions. They have specific features such as a dome-shaped head, lack of stylet, degenerate esophagus, and subcylindrical tail. The fourth-stage larvae (L_{IV}, dauerlarvae) are adapted to being carried by the insect vector and are easily transmitted to healthy pines. When dispersal third-stage larvae (L_{III}) are placed under favorable conditions, such as on fungal culture at 25°C, they molt soon after to the propagative fourth-stage larvae (L_4) and multiply rapidly.

Meanwhile, a closely related pine wood nematode, *Bursaphelenchus mucronatus,* is found in declining pines, and is distributed over a geographically wider area than *B. xylophilus* (**Figure 2**). The hosts of *B. mucronatus* are *Pinus* spp. in Austria, Canada, China, Finland, France, Italy, Japan, Korea, Norway, Russia, and Sweden. In addition to *Pinus* spp., *Abies* spp., *Cedrus* spp., *Larix* spp., and *Pseudotsuga* spp., are its host species. *Bursaphelenchus mucronatus* has a similar life cycle to *B. xylophilus*; however, its pathogenicity is very weak. Based on hybridization and phylogeny of the pine wood nematode, the Japanese and the American strains of the pine wood nematode, *B. xylophilus*, are supposed to be derived from common stock of *B. mucronatus* originating in western Europe.

The Vector, the Pine Sawyer

Most species of *Bursaphelenchus* are associated with cerambycid beetles. *Monochamus* spp. called pine sawyer beetles are the only means for dispersal of the pine wood nematode in Asia and USA. *Monachamus alternatus*, the Japanese pine sawyer, is the major vector for *B. xylophilus* throughout Japan, and is widely distributed in Southeast Asia, including China, Korea, Laos, Taiwan, and Vietnam.

Japanese pine sawyer grows and develops each stage linearly in relation to effective temperature. The threshold temperature to commence development of overwintering larvae is 12.5°C. Japanese pine sawyer beetles often complete a single generation in 2 years in a cool climate in northern Japan. In this case, the larvae overwinter as immature larvae and become fourth-instar larvae in pupal chambers after feeding again in the following spring.

Before the emergence of the Japanese pine sawyer in the wood, the dispersal fourth-stage larvae (L_{IV}) of the pine wood nematode enter a body of the adult beetle through the abdominal spiracles and are held in the tracheae. The number of nematodes varies greatly in the body of the beetle. The maximum number of nematodes was recorded as 289 000 per beetle. The adult beetle emerges from May to July. Larvae (L_{IV}) have been observed on the body surface of beetles, mostly on the abdomen, with the largest numbers at the tail tip. The number of nematodes in a beetle's body decreases gradually with time after emergence. The Japanese pine sawyer has been shown to fly a maximum distance of 2.4 km by mark-recapture tests; however, most adult beetles are found around 100–200 m from the release point. Emerging adults of the beetle feed on the bark of pine twigs for maturation and the larvae (L_{IV}) of the pine wood nematode invade the living pine tree from the scars of maturation feeding.

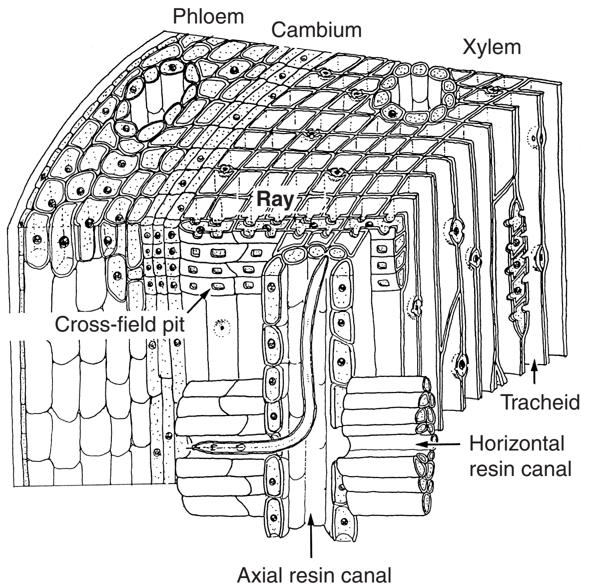


Figure 4 Main anatomical features involved in the movement of the pine wood nematode, *Bursaphelenchus xylophilus*, in Japanese black pine, *Pinus thunbergii*.

Symptoms and Development of Disease

Pine wood nematodes are introduced into the shoots of pine trees during maturation feeding of Japanese pine sawyer beetles. They move initially through cortical resin canals and then migrate rapidly into the whole trunk through xylem resin canals at a maximum speed of 40–50 cm day^{-1} (**Figure 4**). A slight reduction in the flow of oleoresin exudate is observed as a unique symptom at an early stage of the disease. This symptom is due to the destruction of epithelial cells around resin canals by the invasion of the nematode. The nematodes then eventually move from resin canals to adjacent rays, from rays to tracheids through cross-fields, and from tracheids to tracheids through pits. At the same time, enhanced ethylene production is observed 2–3 days after an invasion of pine wood nematodes. The ethylene increase is partially caused by an excretion of a considerable amount of cellulase by the pine wood nematode. The nematode density is very low at an early stage of disease development, often as low as a few nematodes per 100 g fresh weight of wood, even following highly concentrated inoculations.

As a general rule, disease developments following an invasion by the pine wood nematode are divided into two stages: an early stage and an advanced stage (**Figure 5**). In the early stage, cytological changes in the xylem parenchymatous cells occur, and these are soon followed by cavitation and embolism formation in tracheids, which cause dysfunction of conduction in the vascular system of the pine tree. Such internal symptomatology is induced not only in compatible but also in incompatible combinations of pine trees and nematode isolates. However, growth of the nematode population is not assured in pine trees under conditions unfavorable to the nematode, even if a high concentration of nematodes is inoculated. Therefore, this stage is considered to be latent, that is, denaturation of parenchymatous cells by a nematode invasion results in cavitation and embolism of some tracheids.

At the onset of the advanced stage, visible symptoms appear as a severe reduction of the oleoresin exudation rate and a chlorosis of 2–3-year-old needles, accompanied by a decrease in transpiration. This phenomenon is a unique characteristic of pine wilt disease, accompanied by a further increase in ethylene production. Furthermore, death of cambial cells and cavitation of tracheids occur within a large part of the outer xylem, and result in water deficiency, which induces a decrease in both transpiration and photosynthesis. At the same time, other pathophysiological phenomena are observed, for example, electrolyte leakage from pine tissues and production of abnormal metabolites such as benzoic acid. From the onset of

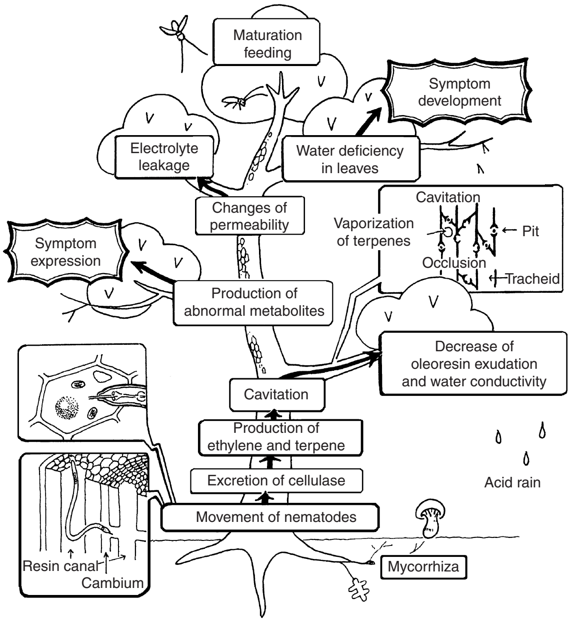


Figure 5 Schematic representation of the wilt mechanisms in the development of pine wilt disease.

water stress, caused by the cavitation of tracheids, the nematode population begins to increase rapidly.

In terms of disease development, the water status of pine trees plays a very important role in the pine tree–pine wood nematode relationship. Experimental results suggest that a lot of pine seedlings do not wilt solely by virtue of numbers of nematodes existing under conditions unfavorable to them, such as a well-watered environment. Empirically, pine wilt disease seems to occur more frequently and to be more destructive in high temperatures with little rainfall. Therefore, these two factors, physiological water status and nematode population density, are considered to be the decisive factors in the development of pine wilt disease.

Disease Control

Before the discovery of pine wood nematode as a causal agent of pine wilt disease, nobody knew an actual pathogen of the disease. However, felling, debarking, and burning of damaged pines immediately proved effective against the disease. Following the discovery of the pine wood nematode as a pathogen of pine wilt disease, the Japanese pine sawyer beetle, *M. alternatus*, was determined as a vector of pine wood nematode. Accordingly, control measures were directed to the Japanese pine sawyer by insecticide spraying.

A large-scale 5-year control project for pine wilt disease was initiated in 1977 by a special law in force in Japan. The project involved aerial spraying to prevent maturation feeding of the Japanese pine sawyer. In spite of these efforts, severe damage was not completely controlled and the disease spread widely from the south to the north of Japan. The reasons for incomplete control are thought to be the limitations of aerial spraying, relying too heavily on the special law in force, and failure to recognize the severity of the disease. In 1997, the special law in force came to an end after three revisions and having been enforced for 20 years since 1977, because considerable damage was continuing and it is still a great threat to the community and the landscape in Japan. Thus, the measures included in the special law in force were incorporated in the common law on forest pest control in 1997.

Control measures against the disease are aimed at breaking the pine tree–pine sawyer beetle–pine wood nematode disease triangle. Present control measures consist for the most part in aerial spraying of insecticides that are effective against the pine sawyer (to break the pine tree–pine sawyer relations), trunk injection of chemicals active against the pine wood nematode (to break the pine tree–pine wood nematode relations), and spraying of insecticides on timber damaged by infestation (to kill the Japanese pine sawyer).

Meanwhile, present control measures are classified under three categories: (1) direct control measures of felling and extermination; (2) preventive control measures of aerial/ground spraying and trunk injection; and (3) biological control measures of pathological microorganisms (*Beauveria bassiana*), predaceous insects (*Dastarcus longulus*), and predatory birds such as woodpeckers (*Dendrocopos major*).

Future Prospects for Pine Wilt Disease

It is generally believed that the pine wood nematode was introduced into Japan from North America a century ago. Subsequently it was introduced into eastern Asian countries and Portugal. European countries show great interest in avoiding the introduction of the pine wood nematode into Europe by timber imports. At present they impose an embargo on all raw softwood materials from North America.

The incidence of pine wilt disease is closely related to environmental conditions such as high temperature with little rainfall as mentioned before. Environmental changes such as increasingly warm and unusual weather conditions which are expected in the near future will most certainly affect the susceptilbility of pine trees. Changes in forest ecosystems resulting from the deposition of acidifying substances may significantly influence pine wilt disease. Pine wilt disease could become the most serious threat in pine forests in European countries, because Scots pine (*P. sylvestris*) and maritime pine (*P. pinaster*) are very susceptible to it.

See also: **Pathology**: Insect Associated Tree Diseases; Vascular Wilt Diseases.

Further Reading

Baojun Y (ed.) (1995) *International Symposium on Pine Wilt Disease Caused by Pine Wood Nematode*. Beijing: Chinese Society of Forestry.

Futai K, Tagashi K, and Ikeda T (eds) (1998) *Sustainability of Pine Forests in Relation to Pine Wilt and Decline*. Proceedings of International Symposium. Tokyo.

Kishi Y (1995) *The Pine Wood Nematode and the Japanese Pine Sawyer*. Tokyo: Thomas.

Kiyohara T and Tokushiga Y (1971) Inoculation experiments of a nematode, *Bursaphelenchus* sp., onto pine trees. *Journal of the Japanese Forestry Society* 53: 210–218.

Mamiya Y (1984) The pine wood nematode. In: Nickle WR (ed.) *Plant and Insect Nematodes*, pp. 589–626. New York: Marcel Dekker.

National Federation of Forest Pests Management Association (1997) *Matsukuimushi (Pine Wilt Disease) – History and Recent Research* (in Japanese). Tokyo, Japan: National Federation of Forest Pests Management Association.

Suzuki K (1984) General effect of water stress on the development of pine wilting disease caused by *Bursaphelenchus xylophilus*. *Bulletin Forestry and Forest Products Research Institute* 325: 97–126.

Suzuki K (2002) Pine wilt disease – a threat to pine forest in Europe. *Dendrobiology* 48: 71–74.

Suzuki K and Kiyohara T (1978) Influence of water stress on development of pine wilting disease caused by *Bursaphelenchus lignicolus*. *European Journal of Forestry Pathology* 8: 97–109.

Tokushige Y and Kiyohara T (1969) *Bursaphelenchus* sp. in the wood of dead pine trees. *Journal of the Japanese Forest Society* 51: 193–195.

Wingfield MJ (ed.) (1987) *Pathogenicity of the Pine Wood Nematode*. St Paul, MN: The American Phytopathological Society.

Leaf and Needle Diseases

J K Stone and M L Putnam, Oregon State University, Corvallis, OR, USA

Overview of Foliage Diseases

Foliage diseases of forest trees can be caused by a variety of biotic agents: fungi, bacteria, algae, phytoplasmas, and viruses, as well as abiotic agents such as air pollutants, chemical deposition (e.g., salt injury, acid precipitation), thermal injury, and nutritional deficiencies, both individually and in combinations. Recognition of the primary cause of diseased plants is often a difficult puzzle for the diagnostician, who must consider interactions between host plant, pathogens, environmental conditions, and management history to determine accurately the underlying cause of a foliar disorder. Often, unhealthy-looking foliage may actually indicate a root or stem disease problem.

Foliage diseases affect trees in nurseries and greenhouses, forest plantations, and urban and natural forests worldwide. Foliage pathogens, like their hosts, can occur either as natural components of a forest ecosystem or as exotics introduced through human activity. Exotic pathogens on endemic hosts, and endemic pathogens on exotic hosts, are often more destructive because host plants have no coevolved resistance to the pathogens. Diseases affecting trees in managed situations, such as nurseries and plantations, tend to be more uniformly distributed than in natural forests. Uniform host populations (with respect to species, clone, and age), i.e., monocultures, are more prone to damaging epidemics than plantations and forests managed for genetic diversity.

The inventory of pathogens that pose a threat to forest health is constantly expanding. The lists of forest foliage pests given below are a necessarily selective attempt to enumerate the most common and important foliage pathogens and their current known distributions, recognizing that forest pathogens and pests are constantly changing. New pest organisms are continually being discovered and described. Probably fewer than 20% of the pathogens that pose a threat to forest health have been recognized. Very little information is available on foliage diseases of several important forest trees such as dipterocarps, *Metrosideros*, and *Nothofagus*. Biological evolution continues to shape the interactions between plants and pathogens, as evidenced by development of pesticide resistance and the emergence of aggressive strains and races in pathogen species. Interspecific hybridization and resultant changes in host range have been documented for *Melampsora* and *Phytophthora* pathogens affecting forest trees. Despite international phytosanitary regulation, international trade involving plant and forest products continues to provide an avenue for introduction of insects and pathogens to new hosts and environments. The changing state of scientific knowledge also affects our understanding of pathogen distribution and importance. As increasingly powerful methods of population genetic analysis are applied to the study of forest pathogens, a more detailed picture of the dynamics in pathogen populations and species is revealed.

Diseases Caused by Fungi (Including Oomycetes)

Fungi are eukaryotic, heterotrophic microbes in the kingdom Fungi that occur either as single-celled (yeast) or filamentous forms. The filamentous fungi have evolved a variety of structural adaptations to penetrate directly and colonize plant tissues and cells to establish parasitic relationships. Fungal pathogens can also invade host tissue through wounds caused by breakage, insect feeding and freezing injury. Symptoms caused by fungal foliar pathogens can vary in severity from severe defoliation to inconspicuous leaf spots. Many have prolonged (1 year or more) incubation periods during which infected foliage remains symptomless. Symptoms of fungal foliage diseases include leaf spots, leaf blotch, scorch, anthracnose, needle blights, and needle casts. Typically, the presence of a fungal pathogen is indicated by minute fruiting structures characteristic of the pathogen species or taxonomic group.

Fungal foliage diseases rarely cause death of mature trees, although they can be responsible for serious economic losses due to decreased growth yield. Chronic fungal foliage diseases can weaken or stress trees so that affected hosts are outcompeted by other species, or are predisposed to attack by secondary agents such as bark beetles or opportunistic root diseases. Control of fungal diseases in forest plantations by protectant fungicides is feasible for certain pathogens and hosts. Successful control depends on timing of applications to coincide with optimum periods of pathogen sporulation and host susceptibility. Specific recommendations for control depend on approved materials, pathogen, tree crop, and local conditions, and are available from local pest management agencies. Judicious selection of planting stock and careful sanitation, where practicable, are often effective means of controlling fungal foliage diseases. The greatest diversity of fungal foliar pathogens of woody hosts are ascomycetes (phylum Ascomycota) and basidiomycetous rusts (Uredinales) (*see* **Pathology**: Rust Diseases).

Oomycetes

Because of their filamentous habit, parasitic oomycetes (kingdom Stramenopila) traditionally have been considered together with fungal pathogens, although they are more closely related to chrysophyte algae. Relatively few oomycetes are associated with foliage diseases of trees; those that cause tree diseases mainly attack roots. However, recent discoveries of foliage-inhabiting *Phytophthora* species, several as yet unnamed, suggest that foliar *Phytophthora* of woody hosts may be much more widespread than previously thought. *Phytophthora ramorum*, the causal agent of sudden oak death in the western USA, also infects foliage of species of *Acer*, *Lithocarpus*, *Quercus*, *Umbellularia*, and several other unrelated hosts, such as *Pseudotsuga*, and causes symptoms ranging from leaf spots and marginal necrosis to shoot blight and dieback. Other *Phytophthora* foliage pathogens include *P. palmivora*, which causes bud rot of coconut palm (*Cocos nucifera*) and other hosts throughout the tropics and subtropics. Littleleaf disease, caused by a suite of factors including the oomycete pathogen *P. cinnamomi*, affects short-leaf pine (*Pinus echinata*) in the southern Appalachians of eastern North America. Although *Phytophthora cinnamomi* infects rootlets, the primary symptoms are initially chlorotic, stunted foliage, and a progressively thinning crown.

Diseases of Conifers

Needle casts Foliage diseases of coniferous trees are usually categorized either as needle cast diseases, where affected needles are prematurely abscised, or needle blights, where needles are abruptly killed and typically remain attached. Needle cast pathogens generally have longer periods of development than those causing needle blights. Typical needle cast pathogens infect newly emerging foliage and complete their development to produce infective ascospores the following spring. An exception is the larch needle cast pathogen *Meria laricis*, which infects needles and sporulates in the same growing season. Needle blights typically attack and kill foliage and sporulate in a period of a few weeks. Important needle cast diseases are *Lophodermella*, *Cyclaneusma* and *Elytroderma* needle casts of pine, *Rhabdocline* and Swiss needle casts of Douglas-fir (*Pseudotsuga menziesii*), *Lirula* needle cast of spruce (*Picea* spp.), and *Meria* needle cast of larch (*Larix* spp.).

Pinus radiata is planted widely in forest plantations and hence *Cyclaneusma* needle cast is probably one of the most significant needle cast diseases worldwide. *Cyclaneusma minus* causes severe damage to *P. patula*, *P. ponderosa* and *P. radiata*, and *C. niveum* affects *P. nigra* and *P. pinaster* plantations in Europe, North America, South America, New Zealand, and southern Africa. *Elytroderma* needle cast of pines is unique in that the pathogen invades shoot tissue, causing hypertrophy and deformation, often killing branches. Although most damaging to young trees, *Elytroderma* needle cast can cause severe growth losses in medium-aged and mature stands, and can predispose mature trees to attack by insects and root diseases. *Elytroderma deformans* is a serious pathogen of *P. ponderosa* in western North America, and *E. torres-juanii* affects *P. brutia* in Greece, *P. halapensis* and *P. uncinata* in Spain, and *P. pinea* in Portugal.

Swiss needle cast of Douglas-fir, caused by *Phaeocryptopus gaeumannii*, is ubiquitous wherever Douglas-fir is grown worldwide, but generally is more destructive on trees grown outside their native range of western North America, and is more damaging on the interior (var. *glauca*) variety of Douglas-fir. The pathogen was first noticed on diseased Douglas-fir in plantations in Switzerland but later shown to be widespread throughout the natural range of Douglas-fir in western North America, where it is presumed native. Serious outbreaks of Swiss needle cast have occurred in Europe, New Zealand, and coastal Oregon; however in most of western North America the disease has negligible effects. *Rhabdocline* needle cast, caused by *R. pseudotsugae* and *R. weirii*, can cause severe defoliation of Douglas-fir, particularly on the interior form (*Pseudotsuga menziesii* var. *glauca*) in the Rocky Mountain region of western North America and in other regions where it has been planted as an exotic. The related asexual fungus *Meria laricis* is the cause of larch needle cast in western North America, northern Europe, and Siberia.

Lophodermella needle casts caused by *L. concolor* and *L. montivaga* affect *Pinus attenuata*, *P. contorta*, and *P. banksiana* in North America. In severe years entire hillsides of affected stands can aquire a reddish color due to the effect of these pathogens. Repeated years of severe defoliation can weaken trees, leading to mortality through attack by bark beetles and root pathogens. Tar spot needle cast is the most common needle cast of soft pines, mainly *P. strobus*, in northeastern North America. It is readily identified by the shiny black raised ascomata on the undersides of necrotic needles. *Ploioderma lethale* is the most damaging needle cast of hard pines (mainly *Pinus clausa*, *P. echinata*, and *P. elliottii*) in the southeastern USA.

The small (2–3 mm) but conspicuous gray to black, raised, elliptical fruiting bodies of several species of *Lophodermium* are very common on fallen needles of many species of pines, but most are considered harmless. One species however, *L. seditiosum*, is considered a serious pathogen causing *Lophodermium* needle cast. *Lophodermium* needle cast affects several species of pines, especially *P. sylvestris* in Europe and *P. resinosa* in North America. Attack by *L. seditiosum* kills young needles, and in nurseries and on young trees defoliation by this pathogen can be fatal.

Needle blights Important needle blights of conifers include *Dothistroma*, *Diplodia*, and brown spot needle blights of pine. *Dothistroma* blight, caused by *Mycosphaerella pini* (anamorph *D. septospora*), affects several important pine species, including *P. contorta*, *P. nigra*, *P. ponderosa*, and *P. radiata*, and has been especially damaging in *P. radiata* plantations in South America, southern Africa, and New Zealand. The disease has also recently caused severe losses in lodgepole pine (*P. contorta*) in northwestern British Columbia. Often a reddish band appears between the killed tips of needles and the green base and this is diagnostic for *M. pini*. *Sphaeropsis sapinea* (= *Diplodia pinea*) causes a needle blight and shoot dieback of many species of pine worldwide, notably *P. nigra*, *P. pinea*, *P. sylvestris* in Europe; *P. patula*, *P. pinaster*, *P. radiata* in southern Africa, where it has mainly been associated with hail damage; *P. nigra*, *P. palustris*, *P. ponderosa,* and several other pine species in New Zealand; *P. greggii*, *P. elliotii*, and *P. patula*, in Brazil; *P. canariensis*, *P. radiata*, and *P. sylvestris* in Argentina; several pine species in North America including *P. nigra*, *P. ponderosa*, *P. resinosa*, and *P. strobus*; *P. canariensis*, *P. elliotii*, *P. pinaster*, and *P. roxburghii*, in Australia; and *P. luchuensis* in Taiwan. Other hosts affected by *S. sapinea* include *Abies*, *Cedrus*, *Chamaecyparis*, *Juniperus* and *Pseudotsuga*. In addition to the needle blight and shoot dieback, *S. sapinea* also causes stem cankers and root disease in several pine species.

Other significant foliage blights include *Gleosporidina cryptomeriae* and *Cercospora sequioiae* which cause twig blight of *Cryptomeria japonica* in plantations in Japan and Brazil. Brown needle disease of pines, caused by *Cercoseptoria pini-densiflorae*, affects several species of pines including *P. pinaster* and *P. radiata* and can be particularly destructive to nursery stock. Young plantations and seedlings in nurseries are most severely affected. *Hypodermella laricis* causes a severe needle blight of larch and is distributed throughout the northern hemisphere. Tip blight and shoot dieback caused by *Kabatina juniperi* affect several Cupressaceae in North America and Europe.

Bud blights of conifers are caused by several pathogens. *Gemmamyces piceae* kills buds and causes abnormally twisted shoots of *Abies alba*, *Picea abies*, and *P. pungens* in Europe. In North America, severe bud and shoot blights of *P. englemanii*, *P. glauca*, *P. sitchensis* and *Pseudotsuga menziesii*, are caused by *Dichomera gemmicola* and buds of *Abies lasiocarpa*, and *P. glauca* by *Camarosporium strobilinum*. *Sirococcus conigenus* also causes shoot dieback of several conifer species, including *Picea sitchensis*, *Pinus resinosa*, *Pseudotsuga menziesii,* and *Tsuga heterophylla*, and can be particularly damaging to seedlings in nurseries. Shoot dieback of several conifer species, especially Douglas-fir, caused by *Botrytis cinerea* is most commonly associated with succulent young shoots damaged by late spring frost.

Felt blights and snow molds are diseases of alpine and boreal conifer foliage that is covered by snow for extended periods, typically affecting young trees and the lower branches of mature trees. The pathogens in the genera *Herpotrichia* and *Neopeckia* rapidly colonize snow-covered foliage in a distinctive wooly felt that binds needles together, initially gray and becoming brown as the foliage is exposed. The masses of brown felt mycelia are persistent and can survive summer desiccation, resuming growth when snow cover returns to cause a perennial blight. *Neopeckia coulteri* affects pines; *Herpotrichia juniperi* and *H. parasitica* affect various Pinaceae and Cupressaceae in North America and Europe, respectively. Snow molds (snow blights) similarly attack snow-covered foliage, but mycelia of these pathogens are evanescent, not persisting as felt mats after snowmelt. Several genetic variants of *Phacidium infestans* are recognized; var. *infestans* occurs on species of *Abies*, *Juniperus*, *Picea* and *Pinus*, throughout boreal Eurasia, mainly attacking *Pinus sylvestris*; a southern race mainly affects *P. cembra* in the Alps. Several different snow blight fungi attack conifers in North America. *Phacidium abietis* and *Sarcotrochila balsameae* are snow blight pathogens affecting *Abies* in western North America, *Hemiphacidium planum* attacks pines in the southern Rocky Mountains, and *S. piniperda* spruce, mainly in northeastern North America. Symptoms of snow blight are a progressive discoloration, eventually becoming gray-brown, with the dead needles remaining attached until the following year.

Diseases of Broadleaved Hosts

There is a bewildering diversity of foliage parasites of broadleaved woody hosts worldwide, the majority of which are ascomycetes or asexual states. Many occur as inconspicuous leaf spots and cause negligible injury to their hosts. Other than rusts, there are very few basidiomycetous foliar pathogens. One exception is *Chondrostereum purpureum*, which is primarily a sapwood rot, but basidiospores from nearby sporocarps are able to infect leaves of several broadleaved trees, causing a typical 'silver leaf' symptom due to the formation of air spaces between epidermal and palisade tissues. Silver leaf disease can be damaging to fruit orchards, but also occurs on maple, birch, willow, and *Eucalyptus* species.

Powdery mildew diseases are caused by fungi in the Erysiphaceae, which are specialized, host-specific ectoparasites of foliage of many plants, including broadleaved woody hosts. The mycelia of powdery mildews grow over the leaf surface, often appearing cottony, with intermittent penetration of epidermal cells by haustoria, specialized feeding structures by which nutrients are translocated from the host leaf to the superficial mycelia. The name derives from the masses of asexual spores (conidia) which can give the appearance of dusty patches on leaves. Important powdery mildews of forest trees include *Uncinula* species on maples and *Microsphaera* and *Sphaerotheca* species on oaks. In Europe, *M. alphitoides* causes death of leaves and shoot deformation of *Quercus petraea* and *Q. robur*, and also occurs on several species of oak in North America. Species in the *M. penicillata* complex affect a number of broadleaved host genera including *Acer*, *Betula*, *Carya*, *Castanaea*, *Cornus*, *Corylus*, *Fagus*, *Fraxinus*, and *Platanus*. Although powdery mildew is seldom seriously damaging to mature trees, nursery stock may need to be protected by fungicides.

Taphrina species are yeastlike ascomycetes that form a thin, superficial layer penetrating just the epidermis of leaves of several broadleaved hosts. Like the powdery mildews, *Taphrina* species are specialized, host-specific parasites. *Taphrina* symptoms are typically patchy swelling and gall-like deformations of leaves (leaf blisters), sometimes coalescing and causing 'leaf curl.' *Taphrina* gall of alder (*Alnus* spp.) also causes a hypertrophy in shoots and can be a persistent problem in nurseries, requiring control by fungicides. Other hosts commonly affected by *Taphrina* are *Quercus*, *Populus*, *Prunus*, and *Salix*.

Anthracnose diseases are characterized by sunken, often confluent, necrotic lesions on foliage, and are caused by several genera of ascomycetes, particularly those with acervular asexual states. In general, anthracnose pathogens infect foliage in spring, and more severe symptoms are associated with rain in late spring and early summer. Several anthracnose pathogens initially infect leaves and spread to shoots by hyphal growth, causing dieback. *Glomerella cingulata*, together with its anamorph *Colletotrichum gloeosporioides*, is one of the most widely distributed foliar parasites in temperate and tropical forests worldwide, and one of the most common fungi associated with anthracnose symptoms on numerous broadleaved woody hosts in nurseries, plantations, and forests. Some of the hosts affected by *G. anthracnose* include poplar, cashew, mango, citrus, papaya, *Robinia*, *Hevea*, and many others. *Glomerella anthracnose* has been reported as a particular problem in establishing plantations of *Gmelina arborea* in Malaysia.

Other fungus species associated with anthracnose symptoms include *Apiognomonia errabunda*, *A. tiliae*, *A. veneta*, and *A. quercina*, the causes of beech, lime (*Tilia*), plane (*Platanus*), and oak anthracnoses, respectively, in Europe and North America. *Kabatiella apocrypta* is common on several maple species in North America, causing interveinal necrosis and scorchlike blight of leaves and shoots. In Europe, *K. apocrypta* is associated with necrotic lesions around feeding sites of psyllid larvae on oak leaves. In North America, *A. errabunda* causes a damaging anthracnose of ash that can cause severe defoliation and shoot dieback when spring rain favors heavy infection. Oak anthracnose can also be particularly damaging in years when conditions are conducive to infection. Rain-dispersed spores produced on killed twigs infect emerging leaves and quickly generate more fruiting bodies, multiplying the amount of inoculum during rainy periods. Several oak species are susceptible, but white oak in the northeastern USA and California live oak are the most severely affected by shoot dieback and foliage blight from this disease. *Discula destructiva*, the cause of dogwood anthracnose in the USA, apparently was introduced almost simultaneously in the 1970s from an unknown source to both the eastern and northwestern USA, where it has spread rapidly, attacking the native species *Cornus florida* and *C. nuttallii*.

Tar spots of maple and willows are conspicuous, black, disk-like, 1–2 cm diameter spots, caused by *Rhytisma* spp. The tar spots are fungal stromata that complete their maturation during the winter and spring after leaves are abcised. Ascospores are released in the spring, coinciding with the emergence of new foliage.

A number of serious foliage diseases of broadleaved forest trees are associated with species classified in *Mycosphaerella*, or in the several genera of asexual states connected to it. *Septoria, Cercospora, Coniothyrium, Dothistroma, Lecanosticta, Ramularia*, and several other form-genera are used for different asexual forms of *Mycosphaerella*. A large number of *Mycosphaerella* species are associated with leaf spots of *Eucalyptus*. A recent monograph lists 55 *Mycosphaerella* species that cause leaf diseases of *Eucalyptus* worldwide, many of which are host-limited and cause injury only to certain species or hybrid clones. For example, *Mycosphaerella* leaf blotch disease has been shown to cause growth reduction in *E. nitens*, and also has been particularly damaging to *E. globulus* in South Africa and Australia. *Ramularia* shoot blight, caused by the fungus *Ramularia* (= *Quambalaria*) *pitereka*, causes a severe leaf and shoot blight of several of the *Eucalyptus* subgenus *Corymbia* species in eastern Australia.

Since *Eucalyptus* species are some of the most widely planted forest crops in Asia, Australia, South Africa, and South America, their pathogens are economically important. The emergence of specialized foliage pathogens on certain species and clones in plantations has forced changes in selection of *Eucalyptus* species in several regions where the diseases occur. The susceptibility of *E. globulus* to the leaf spot pathogen *M. nubilosa*, considered one of the most important leaf pathogens in South Africa, caused the planting of this species to be abandoned in parts of South Africa. *Phaeoseptoria eucalytpti* causes severe defoliation of lower branches and is particularly damaging to certain clones of *E. grandis*. It can also cause severe damage to seedlings in nurseries and hedges used for clonal propagation. *Eucalyptus* leaf and shoot blight caused by *Cryptosporiopsis eucalypti* is particularly damaging to *E. camaldulensis* in nurseries and plantations in Southeast Asia. An undescribed species of *Gleosporidina* has recently been reported associated with leaf lesions and shoot dieback of *E. nitens* and *E. globulus* in Tasmania, but apparently is infrequent.

Wattle (*Acacia* spp.), particularly black wattle (*Acacia mearnsii*), also has been planted in many parts of the world outside its native range in Australia, including India, Sri Lanka, and South Africa, and has led to the appearance of new pathogens of this host. Foliage pathogens of wattle include *Calonectria indusiata*, which caused complete defoliation of trees in parts of India and Sri Lanka. *Glomerella acaciae* is the cause of *Acacia anthracnose* in Japan.

Several important foliage diseases affect species of poplars (*Populus* spp.) and their hybrids grown for fiber. *Melampsora* rusts are probably the most significant foliage pathogens of poplars. Leaf and shoot blight caused by *Venturia macularis* on *P. tremuloides* and *V. populina* on *P. trichocarpa* can be particularly damaging in years with favorable mild wet weather in spring. Certain hybrid clones are resistant. Symptoms include discolored, blighted foliage and a characteristic blackened shoot dieback. *Septoria populicola* causes a severe leaf spot and defoliation of *P. deltoides* and susceptible hybrids in western North America. In eastern North America, *S. musiva* also causes severe leaf spots as well as cankers. The related *Venturia saliciperda* causes a similar dieback of willow, often in association with *Glomerella miyabeana*. *Linospora* leaf blight caused by *L. tetrasperma* affects *P. balsamifera* and *P. deltoides* as well as several hybrids, occurring across northern North America from eastern Canada to the Pacific Northwest. *Linospora* blight tends to be local in occurrence, but damage can be heavy in years when wet spring weather favors infection. Species of *Marsonnina* cause leaf spots and blights of several broadleaved woody hosts. The species *M. brunnea*, *M. castagnei*, and *M. populi* are particularly important as forest pests of *Populus* plantations worldwide, causing defoliation and dieback of several poplar species and hybrids. Subspecies and pathovars of *M. brunnea* differing in pathogenicity to different hosts are recognized.

Diseases Caused by Bacteria

Bacteria are single-celled microscopic prokaryotes of the kingdom Eubacteria. Unable to penetrate plants on their own, bacteria require natural openings such as lenticels, stomata, hydathodes, and leaf scars; or wounds due to events such as pruning, breakage, herbivory, or insects. Local dispersal of bacteria from an infected tree occurs via water splash, wind, insects, and rubbing together of infected and healthy foliage. Long-distance dispersal is primarily through transport of infected material such as seed, stools, and cuttings.

Although bacterial pathogens are widespread, information on bacterial diseases of forest trees is limited. In general, bacterial diseases of trees in mixed-forest systems (not trees isolated in landscapes, in fringes around cities, or in forest nurseries) are minor, often because they occur in low incidence or in more severe but sporadic outbreaks, during which they can cause heavy losses locally. The most serious losses occur in monoculture of same-age plantings, especially when derived from a single clone, or when the trees are exotic to the area.

Symptoms caused by bacteria on foliage range from small round leaf spots from which the tissue drops out, leaving a hole (shothole leaf spots); angular, water-soaked leaf spots; whole leaf blight; leaf scorch; and chlorosis or reddening of leaves, often associated with lesions or marginal necrosis. Bacteria can also cause blighting of small twigs or whole branches; cankers of twigs, branches and main stems; galls of branches, stems, or roots; vascular plugging leading to wilting; and death. Leaf spots and blights, occasionally leading to blighting and dieback of small twigs, are often caused by bacteria of the genera *Pseudomonas*, *Xanthomonas*, and *Erwinia*. Such blights are often limited to the current year's growth, and, in the case of *Pseudomonas syringae*, disease often follows cold injury. For this reason, leaf spots, leaf blight, and twig dieback are of minor significance, since complete defoliation is rare. Some bacteria can cause dieback of older branches, or, by infecting the trunk and causing large cankers, have a greater impact. This includes bacteria such as *Erwinia amylovora* (cause of fire blight), *Xanthomonas campestris* pv. *populi*, and some species of *Pseudomonas* on particularly susceptible hosts. Vascular diseases are caused by the xylem-inhabiting *Xylella fastidiosa* and *Ralstonia solanacearum* (= *Pseudomonas solanacearum*) and, by their systemic nature, can cause either rapid death or chronic stress via impedance of water movement throughout the canopy, rendering the tree more susceptible to additional stresses.

Specific bacterial pathogens of forest trees include *P. syringae* and its pathovars which affect a wide range of broadleaved hosts worldwide, including *Acer, Fraxinus, Populus, Quercus*, and *Salix*. *Ralstonia solanacearum* also affects a variety of hosts, primarily with tropical and southern distributions (China, South America, Australia, southern Africa) including *Acacia*, *Casuarina*, and *Eucalyptus*. Xanthomonads occur on both tropical and temperate woody hosts. *Xanthomonas populi* is widely distributed throughout Europe and causes a serious disease of *Populus* species and hybrids, resulting in blighted buds and shoots and the formation of persistent cankers. *Xylella fastidiosa*, a xylem-limited bacterium which causes Pierce's disease of cultivated grapes, causes leaf scorch and may contribute to a general decline in *Acer*, *Aesculus*, *Fraxinus*, *Platanus*, *Quercus*, and *Ulmus* in North America. Bacterial wilt of bamboo caused by *Erwinia sinocalami* has been reported from Fujian and Taiwan.

In situations where bacterial diseases require control, copper sprays and the antibiotics streptomycin and tetracycline have been used with varying success on cultivated trees with fire blight, but use in situations other than nurseries is extremely rare. Tetracycline is not as effective as streptomycin, and bacterial populations can become resistant to both streptomycin and copper. The loss of efficacy of these chemicals makes it imperative that sanitation measures be carried out, and sanitation is often the only option in situations where the trees are outside a nursery setting. This includes cutting and destroying affected limbs (with nonvascular diseases) or entire trees, establishing quarantines, clonally propagating from disease-free material, and preventing the reintroduction of the pathogen.

Diseases Caused by Phytoplasmas

Phytoplasma is the name given to microscopic, plant pathogenic, cell wall-less prokaryotes of the class Mollicutes that were formerly known as mycoplasma-like organisms or MLOs. Phytoplasmas are obligate parasites and have not been grown in axenic culture. Because of this, they have not been fully characterized and their pathogenic nature has not classically been confirmed, although it is assumed. Until the plant-inhabiting pleomorphic mollicutes can be cultivated and characterized apart from their hosts, they are provisionally classified as *Candidatus* Phytoplasma, with species delineated by genome size and phylogeny as inferred by the nucleic acid sequence of the 16S ribosomal RNA. Phytoplasmas cause 'yellows' diseases (named for the response of infected foliage) and other disorders in over 300 species of plants. Systemic and limited within the plant to the phloem cells, phytoplasmas are vectored by over 100 species of phloem-feeding insects, primarily leaf hoppers, plant hoppers, sharpshooters, and psyllids of the families Cicadellidae, Fulgoroidae, and Psylloidae. Parasitic plants of the genera *Cuscuta* and *Cassytha* may also transmit phytoplasmas.

Symptoms with which phytoplasmas have been associated may include several of the following: leaf stunting (little leaf); pinkish, or more commonly, yellow discoloration of the foliage (yellows); greening of flower petals; precocious or suppressed flowering; precocious shoot growth, proliferation of shoots or branches (witches' brooming); loss of apical dominance of the shoots, leading to deliquescent branching; phloem necrosis; branch dieback; progressive loss of vitality; suppressed root development; wilting; and eventual plant death. Phytoplasmas have also been detected in plants with no apparent symptoms, possibly indicating the existence of tolerance in the asymptomatic plants. Alternatively, it may be that plants with phytoplasmal diseases die due to multiple causes, with the phytoplasma being one of several contributory factors. Virus particles are often found in plants coinfected with phytoplasmas, as are other pathogens and pests.

Phytoplasma-affected plants may not be cured, although symptom remission does occur with treatment by tetracycline antibiotics. For this reason, effective disease management must consist of prevention, such as establishment of quarantines to prevent introduction into a new area, removal and destruction of infected trees, clonal propagation from only healthy trees, vector control, and breeding for genetic resistance.

Phytoplasma diseases are relatively rare in comparison with fungal diseases. Although important in agricultural production, the impact of phytoplasmal diseases in most forest ecologies is rather limited, probably due to the diversity of species present in most forests and the feeding preferences of the vectors. Phytoplasmal diseases will do most damage in situations where monoculture, especially of clonally propagated material, is predominant and where vectors flourish. Some phytoplasma diseases have been extremely important to the local economy, even while they are severely limited in geographic distribution (e.g., sandal spike, which only occurs in southern India). This is in contrast to diseases such as lethal yellowing of coconut, which has spread rapidly throughout the Caribbean, and a related disease of palms found in equatorial Africa, both caused by group IV phytoplasmas. It is difficult to assess the true distribution (and hence impact) of phytoplasmas on forest ecosystems, since many early reports of phytoplasma diseases are based on symptoms which are not exclusive to phytoplasmas. Commonly reported and substantiated (via light or electron microscopy, or molecular analyses) phytoplasma-caused diseases in forest trees include, from the tropics, witches' broom of *Paulownia* spp. in China (16S ribosomal RNA group I) and spike disease of *Santalum album* from India (group I). There are few reports of phytoplasma diseases in Europe, but alder yellows on *Alnus glutinosa* (group V) can cause problems. In North America elm yellows of *Ulmus* spp. (group V) occurs in the USA, whereas witches' broom of *Salix* spp. (group VI) and ash yellows of *Fraxinus* spp. (group VII) are widely distributed in the USA and southern Canada.

Diseases Caused by Viruses

Viruses are submicroscopic agents of disease composed of nucleic acids, either single or double strands of DNA or RNA, encased in a protein coat or capsid. Viruses are transmitted mechanically, by contact of infected plant material with healthy tissues (e.g., root grafts); by insect, fungal, or nematode vectors; by pollen; and via seed. Grafting of diseased material on to healthy trees is a primary means of spreading viruses in cultivated trees, but is less common in forest trees.

The mixed-species composition of most forests is a limiting factor to the impact of viruses in forest ecosystems. Viruses are often implicated in forest declines, in which a majority of trees exhibit poor vigor leading to reduced growth, decline, and eventual death. Although viruses may be detected in trees showing slow growth, poor color, branch dieback, and other nonspecific symptoms of poor performance, trees with these symptoms in the same area may not have any detectable levels of virus. The inconsistent association of virus particles in symptomatic trees has confounded the understanding of forest declines, and the role of viruses in these situations remains in many cases undetermined.

Sources of viruses in forest ecosystems include insect and nematode vectors, infected seed or pollen, forest soils, surface waters, and even fog, as with tomato mosaic tobamovirus in New York state. Many of the viruses documented in forest situations are nepoviruses, tobamoviruses, potexviruses, and ilarviruses. Cherry leaf roll nepovirus has been reported from several forest trees, including species of *Betula*, *Cornus*, *Fagus*, *Fraxinus*, *Juglans*, *Prunus*, and *Ulmus* in Europe and North America. Elm mottle ilarvirus affects *Ulmus* spp. in Europe. Tobacco necrosis necrovirus affects both conifer (*Larix*, *Picea*) and broadleaved (*Betula*, *Fagus*, *Populus*, *Quercus*) species. Bamboo mosaic potexvirus has been found in several species of *Bambusa* and *Dendrocalamus* from Taiwan and Brazil.

Trees infected with viruses may be asymptomatic or show one or more of the following: variations in leaf color, including light-green/dark-green mottling, striking rings or jagged lines of yellow or shades of red; leaf speckling; leaf spots; foliar distortion; shot hole; stunted leaves; reduced shoot or root growth; or branch dieback. Symptoms are best documented for domesticated trees which may also grow wild, such as apple mosaic virus on *Malus* or *Prunus* necrotic ringspot virus on *Prunus* spp. Virus infections are systemic, and there is no cure for infected trees.

Diseases Caused by Viroids

Viroids are the smallest known plant pathogens. Consisting of a single circular strand of ribonucleic acids a few hundred basepairs in length and without benefit of even a capsid, it is unknown exactly how these organisms are capable of infecting plant cells and causing disease. However, viroids can cause extensive damage in some hosts. There are fewer than 30 known diseases of viroid etiology, primarily of fruit trees, potatoes, and a few ornamentals. Their natural mode of transmission is largely unknown, but it is suspected that human activities play some part. In at least one temperate forest, trees showing symptoms of decline were assayed for the presence of viroids. None were found and so far there are no known viroid diseases of temperate forest trees. In contrast, in the Philippines, a viroid disease known as cadang-cadang of coconuts (*Cocos nucifera*) has been devastating. The disease has been spreading since it was first recorded in 1931; there is no known vector, no known means of control, and no known resistant coconuts. It is estimated that 30 million coconut palms died, as of 1980, from cadang-cadang. It is caused by a viroid of the potato spindle tuber viroid group, based on the sequence of their central conserved region, and exists as four distinct molecular forms which occur over the course of infection. A related viroid, causing tinangaja disease, has permanently destroyed the commercial coconut industry on Guam. Both diseases can be difficult to diagnose due to the long period over which the disease develops (7–16 years) and the similarity of symptoms to those produced by water stress, poor nutrition, typhoon damage, physiological sterility, and insect feeding damage. Foliar symptoms, which may take as long as 2 years after infection to develop, begin as nonnecrotic water-soaked spots which eventually enlarge with time. Spots may grow together to give an appearance of general chlorosis. With increased time, leaflets become brittle, the crown size is reduced, and death follows. Other palms found to be naturally infected with cadang-cadang include oil palm (*Elaeis guineensis*) and buri palm (*Corypha elata*). Artificial inoculations have resulted in disease of other members of the Arecaceae, but inoculations failed in 44 species from 12 other families. Viroidlike molecules have been detected in oil and coconut palms in other parts of the southwest Pacific, but cadang-cadang disease has not been identified in these areas.

Diseases Caused by Nutrient Deficiencies

Foliar abnormalities may be caused by factors other than pathogens. Insects, mites, and other arthropods may cause distortion, speckling, or the destruction of leaf or shoot tissues. However the arthropods are often present or at least leave evidence of their presence in the form of frass, eggs, or skins cast during molting. Abiotic factors of foliar problems, such as nutrient deficiencies and injury from air pollutants, are not as easily diagnosed or recognized. Symptoms of nutrient deficiencies appear when plants are grown in soils low in organic matter, in soils with extremely high or low pH, in heavily leached soils, or when growing in soils derived from native rock which is nutrient-poor. Nutrient deficiency symptoms are rarely diagnostic in themselves. Often one nutrient is essential in the metabolism of another, so that a deficiency in one will produce a concomitant deficiency in the other. Deficiency symptoms may be similar for more than one element and can resemble those caused by waterlogged soils, salt spray, drying winds, drought, compacted soils, or pathogens. Broadleaved plants will show symptoms differently than conifers, and even within a given species of plant symptoms may vary depending on time of year and plant maturity. If deficiencies are suspected, a leaf tissue and soil analysis can help target the insufficient element.

Diseases Caused by Air Pollution

Anthropogenic air pollution may also produce abnormalities in leaf color, size, and vigor, and has been implicated in forest decline, especially in northern temperate forests. Pollution may arise from point sources, e.g., power generation plants or industrial smelters, or from nonpoint sources such as automobiles. Injury may be due to long-term exposure of low levels of pollutants (chronic exposure) or from short- or long-term exposure to high levels of pollutants (acute exposure). Injury is most likely to occur when downwind from factory smokestack plumes, at edges of cities, or in areas of air inversions.

Diagnosis is difficult as pollutants are rarely present singly and symptoms often mimic those caused by other abiotic or biotic factors. Degree of injury will vary by species, physiological age of the tissues, and proximity to the source. Generally, chronic exposure results in yellowing, stippling, dwarfing, reduced vigor, and premature senescence. Acute exposure often results in well-defined areas of dead tissues, dwarfing, or plant death.

See also: **Pathology**: Diseases affecting Exotic Plantation Species; Diseases of Forest Trees; Rust Diseases. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Bulman L and Gadgil P (2001) *Cyclaneusma Needle Cast in New Zealand*. Rotorua, New Zealand: Forest Research.

Butin H (1995) *Tree Diseases and Disorders*. Oxford, UK: Oxford University Press.

Callan BE (1998) *Diseases of* Populus *in British Columbia: A Diagnostic Manual*. Victoria, Canada: Canadian Forestry Service.

Crous PW (1998) Mycosphaerella *spp. and their Anamorphs Associated with Leaf Spot Diseases of* Eucalyptus. St Paul, MN: American Phytopathological Society.

Crous PW, Knox-Davies PS, and Wingfield MJ (1989) A summary of fungal leaf pathogens of *Eucalyptus* and the diseases they cause in South Africa. *South African Forestry Journal* 149: 9–16.

Crous PW, Wingfield MJ, and Swart WJ (1990) Shoot and needle diseases of *Pinus* in South Africa. *South African Forestry Journal* 154: 60–65.

Hansen EM and Lewis KJ (1997) *Compendium of Conifer Diseases*. St Paul, MN: American Phytopathological Society.

Jacobson JS and Hill AC (eds) (1970) *Recognition of Air Pollution Injury to Vegetation: A Pictorial Atlas*. Pittsburgh, PA: Air Pollution Control Association.

Lee S-S (1999) Forest health in plantation forests in southeast Asia. *Australasian Plant Pathology* 28: 283–291.

Raychaudhuri SP and Maramorosch K (1996) *Forest Trees and Palms, Diseases and Control*. Lebanon, NH: Science Publishers.

Sinclair WA, Lyon HT, and Johnson WT (1987) *Diseases of Trees and Shrubs*. Ithaca, NY: Cornell University Press.

Wardlaw TJ, Kile GA, and Dianese JC (2000) Diseases of eucalpyts associated with viruses, phytoplasmas, bacteria, and nematodes. In: Keane PJ, Kile GA, Podger FD, and Brown BN (eds) *Diseases and Pathogens of Eucalypts*, pp. 339–352. Collingwood, Australia: CSIRO Publishing.

Rust Diseases

G Newcombe, University of Idaho, Moscow, ID, USA

Rust Fungi are All Parasites

Symbionts of forest trees may be parasites, mutualists, commensalists, amensalists, competitors, or neutralists. Rust fungi are unquestionably all parasites in that their interactions with plants are of benefit to their own fitness but detrimental to their hosts. There may be some, as-yet-unknown benefits to some hosts of rust infection, but detriments are obvious. Forest trees do not seem to constitute a special class of plant hosts for rust fungi, although herbaceous and woody perennials alike do afford opportunities for long-lasting infection unlike annuals.

Rust Fungi in Relation to Other Fungi

Systematists tend to accept between 5000 and 7000 species of rust fungi belonging to somewhere between 100 and 125 genera in from 10 to 15 families. Rust fungi constitute the order Uredinales, and they represent most of the species diversity in the class Urediniomycetes.

Some rust genera appear to be monophyletic, or natural groups of species descended from a common ancestor. *Chrysomyxa*, *Coleosporium*, *Cronartium*, *Gymnosporangium*, *Melampsora*, *Phragmidium*, and *Tranzschelia* appear to be in this category. However, some of the other genera that affect forest trees and woody plants and that are listed in **Table 1**, are not monophyletic: *Puccinia*, *Pucciniastrum*, *Thekopsora*,

Table 1 Distribution of rust fungi on selected genera of plants that are primarily of the northern hemisphere and 'woody'. 'Nonhost genera' are only genera that include species native to the US, for which the detailed databases of the US National Fungus Collections were consulted, and for which there were no rust records. Use of these databases also explains the North American bias that is evident in columns 3 and 4. The fifth column lists rust genera that are not necessarily Norh American in distribution.

Family	*Nonhost genera (no susceptible species)*	*Host genera (but N. American species appear to be non-hosts)*	*Host genera (at least one N. American sp. is a host)*	*Rust genera parasitizing susceptible hosts*
Aceraceae		*Acer*		*Aecidium*, *Pucciniastrum*
Anacardiaceae			*Rhus*	*Pileolaria*, *Uredo*
Aquifoliaceae			*Ilex*	*Chrysomyxa*
Berberidaceae			*Berberis*	*Aecidium, Cumminsiella*, *Edythea*, *Puccinia*, *Pucciniosira*
Betulaceae		*Corylus*		*Melampsoridium*, *Pucciniastrum*
			Alnus	*Melampsoridium*
			Betula	*Melampsoridium*
			Carpinus	*Melampsoridium*
			Ostrya	*Melampsoridium*
Bignoniaceae	*Catalpa*			
	Chilopsis			
	Paulownia			
			Tabebuia	*Aecidium*, *Prospodium*, *Sphaerophragmium*
Caprifoliaceae			*Lonicera*	*Aplopsora*, *Puccinia*
			Sambucus	*Puccinia*
			Symphoricarpos	*Puccinia*
			Viburnum	*Coleosporium*, *Puccinia*
Celastraceae	*Pachistima*			
		Celastrus		*Uredo*
		Euonymus		*Melampsora*
Cornaceae			*Cornus*	*Aplopsora*, *Puccinia*
Cupressaceae	*Thuja*			
			Calocedrus	*Gymnosporangium*
			Chamaecyparis	*Gymnosporangium*
			Cupressus	*Gymnosporangium*, *Uredo*
			Juniperus	*Gymnosporangium*, *Uredo*
Ebenaceae		*Diospyros*		*Aecidium*, *Uredo*
Elaeagnaceae			*Elaeagnus*	*Ceraceopsora*, *Puccinia*, *Ochropsora*
Ericaceae	*Kalmia*			
	Oxydendrum			
			Arbutus	*Pucciniastrum*
			Arctostaphylos	*Chrysomyxa*, *Pucciniastrum*
			Chamaedaphne	*Chrysomyxa*
			Gaultheria	*Chrysomyxa*
			Gaylussacia	*Pucciniastrum*, *Thekopsora*
			Ledum	*Chrysomyxa*
			Menziesia	*Pucciniastrum*
			Rhododendron	*Chrysomyxa*, *Pucciniastrum*
			Vaccinium	*Calyptospora*, *Naohidemyces*, *Pucciniastrum*
Fabaceae	*Cercidium*			
	Cladrastis			
	Gymnocladus			
	Robinia			
		Cercis		*Aecidium*
			Acacia	*Atelocauda*, *Endoraecium*, *Ravenelia*, *Sphaerophragmium*, *Uromycladium*
			Albizia	*Sphaerophragmium*, *Uromycladium*
			Amorpha	*Uropyxis*
			Gleditsia	*Ravenelia*
			Leucaena	*Ravenelia*

Table 1 Continued

Family	*Nonhost genera (no susceptible species)*	*Host genera (but N. American species appear to be non-hosts)*	*Host genera (at least one N. American sp. is a host)*	*Rust genera parasitizing susceptible hosts*
			Prosopis	*Ravenelia*
			Sophora	*Uromyces*
Fagaceae		*Castanopsis*		*Pucciniastrum*
		Fagus		*Cronartium*, *Pucciniastrum*
			Castanea	*Cronartium*, *Pucciniastrum*
			Lithocarpus	*Cronartium*
			Quercus	*Cronartium*
Ginkgoaceae	*Ginkgo*			
Grossulariaceae			*Ribes*	*Coleosporium*, *Cronartium*, *Melampsora*, *Puccinia*
Hamamelidaceae	*Liquidambar*			
		Hamamelis		*Aecidium*
Hippocastanaceae			*Aesculus*	*Puccinia*
Hydrangeaceae			*Hydrangea*	*Pucciniastrum*
			Philadelphus	*Gymnosporangium*
Juglandaceae	*Carya*			
			Juglans	*Gymnosporangium*
Lauraceae	*Persea*			
	Sassafras			
	Umbellularia			
Magnoliaceae	*Liriodendron*			
	Magnolia			
Moraceae		*Morus*		*Cerotelium*
			Maclura	*Cerotelium*
Myricaceae			*Myrica*	*Cronartium*, *Gymnosporangium*
Myrtaceae			*Eucalyptus*	*Puccinia*
			Melaleuca	*Puccinia*
Nyssaceae			*Nyssa*	*Aplopsora*, *Uredo*
Oleaceae		*Chionanthus*		*Aecidium*
		Osmanthus		*Aecidium*, *Zaghouania*
			Forestiera	*Coleosporium*, *Puccinia*
			Fraxinus	*Puccinia*, *Macruropyxis*
Pinaceae			*Abies*	*Calyptospora*, *Hyalopsora*, *Melampsora*, *Melampsorella*, *Milesina*, *Peridermium*, *Pucciniastrum*, *Uredinopsis*
			Larix	*Melampsora*, *Melampsoridium*, *Triphragmiopsis*
			Picea	*Ceropsora*, *Chrysomyxa*, *Peridermium*, *Pucciniastrum*, *Thekopsora*
			Pinus	*Coleosporium*, *Cronartium*, *Endocronartium*, *Melampsora*, *Peridermium*
			Pseudotsuga	*Melampsora*
			Tsuga	*Chrysomyxa*, *Melampsora*, *Naohidemyces*, *Pucciniastrum*, *Thekopsora*
Platanaceae	*Platanus*			
Rhamnaceae			*Ceanothus**	*Puccinia*
			Rhamnus	*Puccinia*
Rosaceae	*Cercocarpus*			
	Holodiscus			
	Physocarpus			
	Purshia			
	Pyracantha			
		Spiraea		*Triphragmium*
			Amelanchier	*Gymnosporangium*

continued

Table 1 Continued

Family	*Nonhost genera (no susceptible species)*	*Host genera (but N. American species appear to be non-hosts)*	*Host genera (at least one N. American sp. is a host)*	*Rust genera parasitizing susceptible hosts*
			Aronia	*Gymnosporangium*
			Chaenomeles	*Gymnosporangium*
			Crataegus	*Gymnosporangium*
			Malus	*Gymnosporangium*
			Prunus	*Thekopsora*, *Tranzschelia*
			Pyrus	*Gymnosporangium*
			Rosa	*Phragmidium*
			Rubus	*Arthuriomyces*, *Gerwasia*, *Gymnoconia*, *Hamaspora*, *Kuehneola*, *Phragmidium*, *Pucciniastrum*
			Sorbus	*Gymnosporangium*, *Ochropsora*
Rutaceae	*Poncirus*			
			Ptelea	*Puccinia*
			Zanthoxylum	*Aecidium*, *Coleosporium*, *Puccinia*, *Uredo*
Salicaceae			*Populus*	*Melampsora*
			Salix	*Melampsora*
Staphyleaceae		*Staphylea*		*Aecidium*
Taxaceae	*Taxus*			
			Torreya	*Caeoma*
Taxodiaceae	*Sequoia* *Sequoiadendron* *Taxodium*			
Tiliaceae		*Tilia*		*Pucciniastrum*
Ulmaceae	*Planera* *Ulmus*			
		Celtis		*Uredo*, *Uromyces*

*Only ever identified as *Ceanothus* sp.

and *Uromyces*. Such artificial groups of species cloud interpretation of host–parasite trends at the generic level, but these are presented regardless in **Table 1** so as to reflect current knowledge.

In spite of considerable research, even today rust fungi are far from fully known at the species level, and there are at least two reasons to believe that considerable species diversity in this group remains to be elucidated: (1) plants of many parts of the world, especially in the tropics, host rust fungi that have been little studied; and (2) even in North America, Europe, Japan, Australia, and New Zealand where rust fungi have received the most attention, single, poorly delimited taxa may actually represent large complexes of cryptic or sibling species. The latter may not be distinguishable morphologically but they may still be species that are reproductively isolated from their 'look-alike' congeners.

The host specialization of rust fungi is clearly a major factor in speciation, and thus evolution of such cryptic complexes. Specialization provides a special form of sympatric isolation for parasite populations; gene flow will stop in the absence of a common host. Divergence at many levels may then follow.

Rust fungi parasitizing the forest trees and woody plants of the tropics are only beginning to receive study that could add substantially to species diversity in the order. Perhaps even more importantly, discoveries of ecologically unusual rust fungi in the tropics could deepen understanding of the entire group.

Importance of Rust Fungi in Causing Diseases of Forest Trees

All reviews of the interactions of rust fungi with plants emphasize negative consequences for the plant hosts. Negative effects vary from mortality of seedling, sapling, and even mature trees to reduced growth in all age classes. Rust diseases of trees include foliar and needle rusts, cone rusts, limb rusts, stem rusts, and broom rusts. Cankers, galls, premature defoliation, and broken limbs and tops can all be the work of rust fungi.

Symptoms Caused by Rust Fungi

Signs (cells and tissues of the parasite itself) typically accompany symptoms of infection by rust fungi.

Timing is an issue in that symptoms such as chlorosis, or yellowing of normally green leaves or needles, may frequently precede signs. In stems, swellings or galls (symptoms) may be evident long before signs, and this is also true of abnormally dense clusters of stems or twigs that are called 'witches' brooms', or just 'brooms.' In some cases, genetic resistance of the host prevents signs from ever appearing (i.e., the host prevents the parasite from reproducing). When the host is susceptible, rust fungi parasitize its living cells, and their pustules may then frequently be surrounded by what appears to be healthy and normal host tissue.

In **Figure 1**, dark spermogonia are surrounded by orange, swollen tissue in which a *Gymnosporangium* rust has proliferated. However, the host tissue contiguous with the rust is typically green, even as it supplies the parasite with the products of photosynthesis. Once spermatia (**Figure 2**) from spermogonia of opposite mating type are transferred by insects to effect fertilization, aecia develop on the lower leaf surface (**Figure 1**). Once again, host tissue immediately surrounding the aecia typically appears green or 'healthy.'

When signs do appear in the form of sporulating structures or pustules (e.g., spermogonia, aecia, and subsequent uredinia, and telia), rusts are not easily mistaken for other fungi. This is especially true when spores from the pustules can be examined microscopically, either in the light microscope or scanning electron microscope, as in **Figure 2**.

Figure 1 Intimate association of spermogonia and aecia in the 'aecial host' of a heteroecious rust. Dark spermogonia embedded in orange rust tissue on the upper, adaxial surface of a leaf of the host, and following fertilization, aecial 'horns' emerging on the lower surface. A sp. of *Gymnosporangium* on *Amelanchier alnifolia* in mid-summer in the northern Rocky Mountains. Aeciospores released from the 'horns' must infect. *Juniperus*, the 'telial host' to complete the life cycle. Magnification × 10.

Life Cycle of Rust Fungi

Rust fungi are macrocyclic when their life cycle includes five spore states that are often designated by Roman numerals: spermatia (0), aeciospores (I), urediniospores (II), teliospores (III), and basidiospores (IV). A representative of each of the five is shown in **Figure 2**. However, it is important to note that the spore states are not recognized through morphology or appearance alone; the spore states are related to the nuclear cycle, as will be briefly explained.

Basidiospores, and the spermatia that follow them in the 'typical' sequence of spore states, are both genetically haploid and structurally small and simple with thin, smooth walls (**Figure 2**). They differ in that basidiospores are the haploid products of meiosis in addition to being unicellular and relatively ephemeral. Basidiospores must also infect and parasitize a host, whereas spermatia serve only in mating. In rust fungi, mating initiates a dikaryotic phase that encompasses the aecial (I), uredinial (II), and telial (III) states. It is only in the teliospore that the two nuclei of the dikaryon fuse to undergo meiosis to produce basidiospores once again.

Given the role of spermatia in mating, spermogonia and aecia are typically close together (**Figure 1**). Urediniospores and teliospores are sometimes closely associated also; they can even be produced in the same pustule. However, more often uredinia are produced in repeating cycles of infection until finally some host and/or environmental cue provokes the rust fungus to produce telia. Some rust fungi overwinter in a dormant telial state but others form teliospores that immediately produce infectious basidiospores. For example, non-dormant teliospores of the white pine blister rust fungus, *Cronartium ribicola*, produce basidiospores in fall that infect white pines. Those rusts that produce dormant teliospores require some ambient conditioning before they will produce basidia and haploid basidiospores.

Some rust fungi are heteroecious in that the so-called 'aecial host' supports the 0 and I phases of the life cycle, but an unrelated plant is the telial host for the II, III, and IV states. Whereas heteroecious rust fungi have alternate hosts, autoecious rusts lack

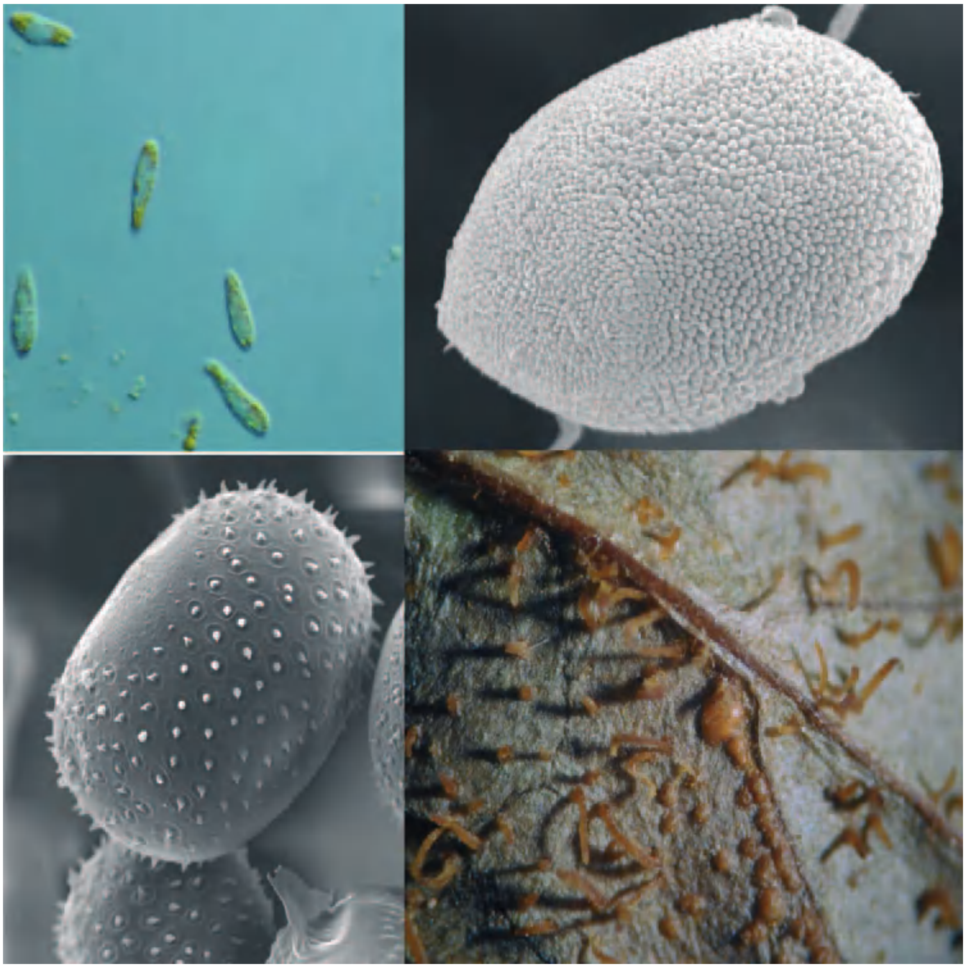


Figure 2 LM and SEM micrographs representative of different spore states, and of the association of uredinia and telia. The LM photo in the upper left is of spermatia from a spermogonium of **Figure 1**. In general, when spermatia of one mating type are transferred by an insect to a spermogonium of the opposite mating type, the aecia develop (× 1000). To the right of the spermatia is a 'warty' aeciospore, produced within an aecium (× 2500). Below the spermatia is a spiny urediniospore; these spores develop within uredinia and may repeatedly infect the same host (× 2000). However, not all aeciospores of rust fungi are warty and not all urediniospores are spiny. The LM micrograph at the lower right shows closely associated uredinia (round pustule in the middle) and telia (hairs or horns) or *Cronartium ribicola* on *Ribes* (× 10). The hairs are chains of teliospores that produce basidia and through meiosis, haploid basidiospores that infect white pines. Note the superficial but misleading, macroscopic similarity of aecial 'horns' and telial 'hairs'.

them. Life cycles from which some spore states are absent are commonly classified as demicyclic (no uredinia) or microcyclic (neither uredinia nor aecia). However, many other variations of life cycle are known. Finally, the life cycles of many rust fungi are still poorly studied.

Host Specialization

If current estimates were correct and there are from 250 000 to 300 000 species of plants, and 7000 species of rust fungi, one might calculate that the average rust fungus thus possesses a host range of roughly 35 to 43 host species. However, well-studied rust fungi are known to be specialists with much narrower host ranges. The discrepancy results from the following factors: (1) not all plant species are parasitized by rust fungi, and (2) not all species of rust fungi are known.

The first factor is demonstrated in **Table 1**. The 120 genera of woody plants in **Table 1** represent genera, primarily of the northern hemisphere, for which the research literature and the databases of the US National Fungus Collections could be used to summarize some major trends. Although rust fungi do parasitize a wide variety of angiosperms, gymnosperms, and even 'primitive,' vascular plants such as *Selaginella*, there are surprisingly genera of woody plants in which resistance to rust fungi has evidently become fixed in evolutionary time (i.e., nonhost genera). It is important to note also that within many genera that do host rust fungi (e.g., *Cornus*, dogwoods), there are many species that appear to be nonhosts. Interestingly, in *Cornus* it is the tree and shrub species that appear to be nonhosts, whereas the circumboreal, herbaceous species are hosts. The one exception is the giant dogwood, *Cornus controversa*, which in Japan hosts a rust fungus in the genus *Aplopsora*.

Another trend that is apparent in **Table 1** and is intriguing, has to do with the number of genera in which North American species are nonhosts for rusts in contrast to at least some of their Eurasian congeners: maple (*Acer*), hazel-nut (*Corylus*), bittersweet (*Celastrus*), *Euonymus*, persimmons (*Diospyros*), redbud (*Cercis*), chinquapin (*Castanopsis*), beech (*Fagus*), witch hazel (*Hamamelis*), mulberry (*Morus*), fringe-tree (*Chionanthus*), devilwood (*Osmanthus*), bladdernut (*Staphylea*), basswood or linden (*Tilia*), and hackberry (*Celtis*).

Among the 33 nonhost genera that are scattered across families that include woody plants of the northern hemisphere, there may be species that host rust fungi that have not been observed. However, most of these genera are quite well studied, and it would seem unlikely that rust infection has been missed. This seems especially true of the 10 nonhost genera that are endemic to North America (including Mexico): *Kalmia*, *Oxydendrum*, *Robinia*, *Umbellularia*, *Cercocarpus*, *Purshia*, *Sequoia*, *Sequoiadendron*, *Taxodium*, and *Planera*. The proportion of nonhost to host genera also seems significant: it is 33 to 87. In any case, there is evidently only a subset of the plant kingdom that hosts rust fungi. This fact transcends the artificial dichotomy between woody and herbaceous plants in that there are also many nonhosts among the latter although such plants are not the focus of this article. It is also true that many rust species or taxa are unknown or improperly delimited. In the latter case, complexes of cryptic or sibling species, among which morphological variation is subtle and continuous, present a considerable challenge to species delimitation.

Ideally, the host ranges of rust fungi would be experimentally determined so as to avoid the conflation of host ranges of cryptic species. To date however, few host ranges have been so determined. In any case, on the one hand there are fewer host species and on the other hand there are more rust species, than may be generally belived.

Rust Fungi Are Specialists in Relation to Plant Tissues and Age

Typically, woody plants are more susceptible to rust fungi when they are young. On a seasonal basis, young tissues are typically also more susceptible than older tissues. However, there may be exceptions to these generalizations about host ontogeny in relation to resistance. In the case of box rust (i.e., *Puccinia buxi* on *Buxus sempervirens* in the UK) there is at least circumstantial evidence that older individuals are more susceptible.

Rust fungi are not known to infect the roots of forest trees, but they may infect all portions of the aboveground shoot system. Similarly, there do not appear to be any clear examples of vertical transmission of seedborne rust, although introductions of rust fungi to new regions may cause the question to be raised.

Genes for Resistance to Rust Fungi

Most of what is known about genetic resistance to parasites of forest trees has been learned by studying rust fungi. Various researchers have identified major genes for resistance to the fungi causing white pine blister rust, poplar rust, western gall rust, and fusiform rust. If other rust fungi parasitizing forest trees received similar attention, it is likely that major genes for resistance would characterize those interactions as well.

Major genes that have been cloned can be proven to function in resistance in transgenic assays. Although major genes for rust resistance from forest trees have not been cloned, they would presumably be like such genes in crop plants in passing such a test. In contrast, partial resistance, that has also been described as quantitative or horizontal, is thought to be under polygenic control in that many genes of minor effect are thought to act in concert (*see* **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance).

Interactions of Rust Fungi with Other Fungi

Less is known about the effects of other fungi on rust infection. *Sphaerellopsis filum* parasitizes rust fungi, and can thus be described as a hyperparasite or mycoparasite. However, *S. filum* is not found on all rust fungi, nor is it always found in all parts of the geographic range of any particular rust fungus. Many other fungi are associated with rust pustules; these may be hyperparasites or opportunists that consume host cells parasitized or killed by the primary parasite, or rust fungus. Some fungal symbionts of forest trees could conceivably stimulate host resistance to rust fungi. However, in general, other fungi have not been developed as tools to control rust diseases of forest trees.

Control of Rust Fungi of Forest Trees

Forest pathology has been greatly influenced by attempts to control rust diseases. Avoidance of areas of high inoculum is generally recommended for new plantings of all forest trees. In the famous case of the introduced *Cronartium ribicola*, or white pine blister rust, extensive and expensive efforts were made to eradicate the alternate host (i.e., species of Ribes), albeit without much success. Pruning, avoidance of areas in which the environment favors infection by *C. ribicola*, nursery applications of fungicide, and programs to breed for resistance are all components of the arsenal deployed against white pine blister rust.

Breeding for resistance to the native, fusiform rust of loblolly and slash pines in the southern United States has also been combined successfully with silvicultural techniques of intensive management. Breeding for resistance to poplar rust is an ongoing battle both in Europe and North America, but again this subject is presented in more detail in this volume and elsewhere.

See also: **Pathology**: Diseases of Forest Trees. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Arthur JC (1962) *Manual of the Rusts in the United States and Canada*, *illustr.* Cummins GB. New York: Hafner.

Cummins GB and Hiratsuka Y (2003) *Illustrated Genera of Rust Fungi*, 3rd edn. St Paul, MN: American Phytopathological Society.

Gäumann E (1959) *Die Rostpilze Mitteleuropas*. Bern: Büchler.

Hansen EM and Lewis KJ (1997) *Compendium of Conifer Diseases*. St Paul, MN: American Phytopathological Society.

Hiratsuka Y and Sato S (1982) Morphology and taxonomy of rust fungi. In: Scott KJ and Chakravorty AK (eds) *The Rust Fungi*, pp. 1–36. London: Academic Press.

Littlefield LJ (1981) *Biology of the Rust Fungi*. Ames, IA: Iowa State University Press.

Littlefield LJ and Heath MC (1979) *Ultrastructure of Rust Fungi*. London: Academic Press.

Maier W, Begerow D, Weiss M, and Oberwinkler F (2003) Phylogeny of the rust fungi: an approach using nuclear large subunit ribosomal DNA sequences. *Canadian Journal of Botany* 81: 12–23.

Petersen RH (1974) The rust fungus life cycle. *Botanical Review* 40: 453–513.

Sinclair WA, Lyon HH, and Johnson WT (1987) *Diseases of Trees and Shrubs*. Ithaca, NY: Cornell University Press.

Swann EC, Frieders EM, and McLaughlin DJ (2001) Urediniomycetes. In: Esser K and Lemke PA (eds) *The Mycota*, vol. 7, part B, *Systematics and Evolution*, pp. 37–56. Berlin: Springer-Verlag.

Wilson M and Henderson DM (1966) *British Rust Fungi*. Cambridge, UK: Cambridge University Press.

Ziller WG (1974) *The Tree Rusts of Western Canada*. Victoria, BC: Canadian Forestry Service.

Stem Canker Diseases

T R Gordon, B J Aegerter and C J Friel, University of California, Davis, CA, USA

Introduction

Canker diseases are caused by a diverse array of pathogenic fungi, and are grouped together based on similarities in the symptoms they produce on their host plants. Our treatment will be restricted to diseases caused by fungi in the group known as Ascomycetes. This includes most of the biotic pathogenic agents responsible for cankers, but does exclude at least one noteworthy group: the obligate parasites known as rust fungi, some of which cause diseases referred to as cankers (*see* **Pathology**: Rust Diseases). Even with this limitation, canker diseases represent a heterogeneous grouping, which is unified more by the nature and location of the damage on the tree than the appearance of the diseased tissue.

Pathology

A canker would typically be defined as a more or less sunken area on a stem or branch where pathogen growth has killed the underlying cambium, and which is often bordered by host-produced callus tissue. Thus, it is the combination of no growth where host tissue is killed and a somewhat elevated border of callus produced in response to infection that defines a depressed area known as a canker. However, many so-called canker diseases do not have symptoms at all similar to the forgoing description, and among the pathogens that produce typical cankers, some will do so only on certain plant parts, such as large-diameter branches, because younger branches die too quickly after infection for a canker to develop.

To account for variation in the appearance of cankers induced by different pathogens, three subgroupings have been recognized: perennial, annual, and diffuse cankers. Perennial cankers would most closely match the description given above. As the name implies, perennial cankers persist for many years. Their appearance may change over time, reflecting the dynamic nature of the interaction between host and pathogen. For example, the sunken appearance becomes increasingly apparent as surrounding healthy tissue expands while growth has ceased in the cankered area. Concentric rings may develop around the canker due to annual production of callus tissue in response to infection (these have been termed 'target cankers'). In some cases the callus may expand into the interior of the canker and even cover it completely. The appearance of the canker may help to identify the causal agent, and many publications and internet resources provide photographs that are useful for diagnostic purposes.

Annual cankers are those that do not persist past a single year, so there is insufficient time for differential growth of infected and healthy tissue, and/or production of callus to produce the distinctive appearance of a perennial canker. Annual cankers are often associated with an effective host response that contains the infection, and the affected area may be overgrown with callus, which effectively 'heals' the wound. On the other hand, those in the third category, diffuse cankers, expand rapidly and outpace radial growth of the tree. The inability of the host to contain the pathogen effectively often results in girdling of the affected branch or stem. This type of canker would commonly be found in young tissue on a highly susceptible host.

In summary, canker diseases are those that affect branches and stems of various age and size classes, where growth of the pathogen leads to death of the colonized tissue, which, combined with structural alterations to the bordering healthy tissue, may or may not lead to a sunken appearance. Where cankers occur on young branches near the growing tip, the end result will likely be girdling of the affected branch and the disease might well be placed in the category of 'shoot blight' or 'tip dieback.' The same pathogen growing on larger diameter branches may produce a more discernible canker; *Diplodia pinea*, described below, is one example of a pathogen that produces both types of symptoms.

Economic Impact of Cankers

Where damage is restricted to tip dieback, the principal economic impact will be reduced growth due to loss of photosynthetic tissue and redirection of resources to defense and away from growth. This effect will be greatly magnified when cankers form on larger branches, increasing the proportion of crown affected. Cankers on the main stem can affect the entire tree by compromising transport of water to the canopy and photosynthate to the roots. Cankers on the main stem can also lead to differential rates of radial expansion, enhancing the risk of structural failure and providing points of entry for other wound-infecting pathogens, such as wood-decay organisms. Wood quality is affected as well. A higher proportion of non-woody cells reduces the strength of the wood, whereas discoloration and resin accumulation (two commonly co-occurring symptoms) impair the appearance of the wood and reduce its permeability to preservatives.

In general terms, one might ask how canker diseases developed into problems for forest trees, and if there are common features that can explain these syndromes and thereby suggest ways in which their impacts can be minimized. A first step toward answering such questions is to consider the diversity of pathogens that are associated with canker diseases and the nature of their relationships with host trees. Not surprisingly this exercise quickly exposes our lack of knowledge of pathogen biology and the host–pathogen interactions that give rise to disease syndromes. In particular, we are largely ignorant of how contemporary associations came to be; i.e., what was the relationship between host and pathogen prior to human intervention and how has the latter altered the situation? Although the information available on these subjects is incomplete, some well-studied examples provide a basis for speculation on hypothetical pathways to pathogenicity that may account for much of the present inventory of canker diseases.

Ecology of Canker-Causing Pathogens

We can begin by considering the ecological role of canker-causing pathogens in a native forest. Trees are primary producers in forested ecosystems and as such represent a source of fixed carbon to be exploited by other organisms, including fungi. In principle, fungi could access the nutrients available in standing trees through overt pathogenesis, leading to death of the host and assimilation of its constituent parts. No doubt fungi have pursued this strategy at various times, but it has not led to associations of long duration, for obvious reasons. Host trees susceptible to such an onslaught would be eliminated from the forest and leave relatively few propagules to seed later generations. Populations would thus be extirpated or, through natural selection, enriched with individuals more resistant to the aggressive pathogen. In the latter case, presumably either the pathogen would be eliminated for lack of a suitable host or a more stable relationship would ensue. Such a relationship could involve limited colonization of living trees, whereby the pathogen obtains nutrients without severely impacting the host.

Weakly parasitic associations could develop as described above, or more directly through selection from strictly saprobic fungi for strains that are sufficiently invasive to gain limited access to host tissue prior to its demise. Regardless of how it came about, fungi employing this strategy can persist, albeit with limited growth in most cases, at the expense of their host, and may further benefit from their proximity to the underlying tissue, which can support more extensive growth when the tree, or a part of it, is no longer living. Such a relationship is obviously beneficial to the fungus, with a more variable and less predictable impact on the host. The literature on forest pathology clearly shows that many fungi exploit trees in this way and they are regarded as benign colonizers of nonliving tissue or minor pathogens of little consequence.

Relationships between organisms are inherently dynamic as they are subject to alteration due to physiological or genetic changes in either participant, and to changes in the ambient environment. These factors provide a framework within which pathways to pathogenesis can be recognized. In the context of a native forest, trees growing on sites to which they are well adapted could be expected to tolerate the presence of weakly parasitic fungi in their bark and to a lesser degree in more internal tissues. In fact, healthy trees commonly support the growth of many fungi within their living tissues and may never suffer ill effects from them (such fungi are often referred to as endophytes). On the other hand, trees growing under less suitable circumstances may be unable to devote the resources necessary to limit growth of parasitic fungi, and one or more of them may thus be allowed to grow aggressively and cause visible damage to the tree. Such parasites are generally referred to as opportunistic pathogens, and it seems likely they serve as one means by which the geographic range of a tree species is enforced. It follows from the nature of this relationship that its pathogenic manifestation is seldom observed, but its historical role in shaping biogeographical patterns in the forest may be profound.

Incidence and Severity of Canker Diseases

Evidence for an effect of growing conditions on the incidence and severity of canker diseases may be found in observations of numerous host–pathogen combinations. For example, in a US Forest Service publication on diseases affecting native conifers on the Pacific Coast, 12 of the 14 canker diseases included are described as being more severe on trees growing on poor sites and/or subjected to drought stress; the absence of this qualification in two cases may be due only to incomplete information on the diseases. A particularly dramatic example of site effects on disease severity is provided by cypress canker, caused by *Seiridium cardinale*. This disease is unknown in native stands of Monterey cypress, which are found on the California coast where temperatures are moderate and fog is frequent, but is common and often fatal to planted Monterey cypress in warm, dry environments farther inland. Thus, for a forestry enterprise and for landscape plantings, proper site selection is an important component of managing canker diseases.

Physical location will not be the only determinant of the growing environment to which trees are subjected. For example, stand density can impose limits on access to light and soil moisture, which may lead to stress that, in turn, may promote the activity of otherwise minor pathogens. This density-dependent effect of plant pathogens provides one mechanism for natural thinning, which will tend to promote stocking levels that are more sustainable. Just as dense stands can render light-deprived trees more prone to damage from canker diseases, shade-suppressed lower branches on otherwise vigorously growing trees are often preferred sites for development of these pathogens. As a result, weakly parasitic fungi participate in the early stages of nutrient cycling by initiating the breakdown of plant parts no longer making a positive contribution to the carbon economy of a growing tree.

Many factors that influence tree health and vigor can render the impact of canker diseases more severe. One commonly cited predisposing factor is water stress brought about by an abundance of neighboring trees and/or insufficient precipitation. *Diplodia pinea*, for example, is known to be more damaging on trees subjected to drought. Additional predisposing factors reported to be important for some canker diseases include: extremes of weather such as frost and hail, and infection by other pathogens such as dwarf mistletoe. Any of these factors could lead to elevated incidence of a disease in a native forest. Obviously exotic plantations invite the possibilities of more severe and persistent problems.

The foregoing discussion implies that vigorous, healthy trees growing under conditions to which they are well-adapted should not sustain serious damage from canker causing pathogens. This generalization is reasonably well supported, but is predicated on a critical assumption: that the depredations of pathogenic fungi have been moderated through a long history of association between host and parasite. Thus, weakly parasitic saprobes in-waiting are a part of the environment to which native trees are adapted. Such adaptations will not necessarily be applicable to foreign microbes, which can expose inherent genetic susceptibilities of native trees, with catastrophic consequences.

Long-distance movement of parasitic fungi offers an alternate path to pathogenesis for tree-associated fungi. Here too the pathogen may have originated as a weak parasite, but in this case it has been moved to a new host to which it is preadapted for virulence. Whereas in its native environment the fungus was a benign associate of its host tree, it has the potential for more aggressive growth on a related host species that has not previously been exposed to the parasite, and lacks the ability to contain its growth. It should be added here that it is probably the exception when introduced fungi become successful pathogens; the failures are likely to be far more numerous but they are difficult to document.

In the sections that follow, we will provide a detailed account of three canker diseases, all of which have become problematic due to movement of the pathogen to new areas. For the first of these diseases, chestnut blight, the historical impacts have been particularly dramatic, whereas the second, pitch canker, is a more recent development that continues to unfold. For the third disease, *Diplodia* canker, pathogen introductions have been important, but movement of the host to suboptimal growing sites can also be a critical determinant of disease severity. The three diseases differ in the extent of the damage they have caused and the manner in which the host–parasite relationships have stabilized. Although this is but a small sampling of the many canker diseases known to affect forest trees, it will serve to illustrate key features found among pathogens causing this type of disease.

Chestnut Blight

The causal agent of chestnut blight, *Cryphonectria parasitica*, infects species of chestnut (*Castanea*) as well as several species of oak (*Quercus*) and chinquapin (*Chrysolepis*). The fungus is a weak pathogen on some live oak species in the southeastern USA. It is more damaging to European and eastern US white oaks and other *Quercus* species, causing twig and branch dieback and perennial cankers on larger trunks leading to mortality in some cases. In species of *Chrysolepsis* from the eastern USA, similar symptoms accompany more extensive mortality, whereas *Chrysolepsis* species in California are unaffected by *Cryphonectria parasitica*. All species of *Castanea* are susceptible to some extent. On Asian species (*C. crenata* and *C. mollissima*), the pathogen is predominantly an opportunist, living as a saprobe and infecting pruning wounds and weather-induced injuries, causing deformations and some canker damage, but rarely death.

The manifestation of chestnut blight on American and European chestnut species (*C. dentata* and *C. sativa* respectively) is infamously more serious than on those described above. The fungus was introduced to the USA in 1904 and rapidly spread through the entire native range of American chestnut in the eastern third of the country. Presumably, the disease was introduced on infected young trees or seed from Chinese chestnut planted as an ornamental in New York. The chestnut blight pathogen isolated from those trees was also known from Asia where it had little effect on native trees; but by the mid-1950s *Cryphonectria parasitica* had devastated native stands of American chestnuts, reducing the trees to dense collections of vegetative shoots emerging from the bases of otherwise dead trees, and ruining the vast economy supported by products harvested and manufactured from this once-dominant tree species. Similarly, introduction to Europe is thought to have occurred in the 1920s when Japanese chestnut trees, resistant to a disease which had plagued the local chestnut industry, were planted among the extant European chestnut in Italy, Spain, and France. *Cryphonectria parasitica* was first reported in Italy in 1938 and quickly spread throughout European stands causing severe and sometimes total crop losses over a 25-year period.

Development of the Disease

Chestnut blight is initiated when spores are introduced into wounds on stems primarily by the actions of insects and birds. The fungus grows to gain access to the inner bark and cambium layers and eventually, sunken cankers form on the bark. The cankers are characterized by long cracks and the orange–brown color of stromata (a mixture of fungal and plant tissue) that hold spore-containing pycnidia (**Figure 1**). Orange strands of asexually produced spores ooze from pycnidia during moist weather and are again spread by insects and birds and by rainsplash. Brown mycelial mats form under the bark, and eventually callus tissue forms at the margin of the elongated canker and the bark sloughs off. Successive callus formation and sloughing sometimes leave a bull's-eye appearance to the cankers. As the disease progresses, perithecia form in the stromata and produce ascospores (i.e., sexual spores) that are forcibly discharged and dispersed by the wind. Both

Figure 1 A stem canker, caused by *Cryphonectria parasitica*, on American chestnut (*Castanea dentata*). Photograph courtesy of Swiss Federal Institute for Forest, Snow and Landscape Research. Reprinted with permission from the *Annual Review of Phytopathology*, Volume 32 © 1994 Annual Reviews.

pycnidia and perithecia can be present within the stromata at the same time. The fungus continues to grow until it ultimately girdles the stem, restricting the flow of water thus killing the affected part distal to the infection.

On American and European chestnuts, the early stage of disease reveals yellow and brown leaves that remain on the branch for the first year of infection. Bare branches appear as a result of earlier infections. The disease affects twigs, branches, and trunks but not the roots, which continue to live and send up numerous vegetative shoots. These shoots are eventually subjected to infection by the pathogen, canker development, and dieback. New shoots soon form and the cycle continues; the roots never produce a mature tree.

Genetic Resistance

There is no control for chestnut blight on *Castanea dentata* in the USA. Breeding programs are plagued by a high frequency of disease escapes in resistance trials. Furthermore, many Asian varieties and Asian hybrids that are resistant or show tolerance to the pathogen are grown as ornamentals and for nut production, but also provide potential reservoirs of inoculum that threaten extant American chestnut trees that were previously protected by isolation from the native stands. Outbreaks in small, isolated plantings located in California, Oregon, and southwestern Canada have been kept in check only through sanitation and early intervention to eradicate affected trees. Also, small plantings of *C. dentata* in Wisconsin, 200 miles west of the westernmost boundary of the native range, have remained intact until the relatively recent appearance of *Cryphonectria parasitica*. Intensive research efforts are focused on controlling the disease there.

Biological Control

Biological control efforts hold considerable promise for management of chestnut blight in Europe. These measures follow from observations of natural recovery of European chestnuts in southern Europe in 1951. Strains of the fungus isolated from cankers on recovering trees had a different appearance in culture and were not as virulent as strains recovered from active cankers. This phenomenon was termed hypovirulence, and is now known to be conferred by a mycovirus that infects the pathogen and can spread to uninfected strains, thereby allowing diseased trees to recover. Transmission of the mycovirus requires hyphal fusion, which can only occur between genetically compatible strains of the fungus. In Europe, interstrain compatibility is common, and natural spread of hypovirulence led to recovery of diseased trees in some areas (**Figure 2**). This has been augmented with artificial inoculations of active cankers with hypovirulent strains of *C. parasitica* to provide effective biological control of chestnut blight. As a result, chestnut is still profitably cultivated in Spain and Italy. Hypovirulence has not proven to be an effective control measure in the USA, where the genetic structure of fungal populations is much more diverse. This limits compatibility between strains, and thereby restricts transmission of the mycovirus. As a result, hypovirulence is not widespread in the pathogen population and the recovery observed in Europe has not occurred in North America.

Pitch Canker

Pitch canker is caused by *Fusarium circinatum*, an asexual form (anamorph) that also produces a sexual stage by the name of *Gibberella circinata*

Figure 2 Callus tissue grows over 'healed' cankers that were inoculated with hypovirulent strains of *Cryphonectria parasitica*. Photograph courtesy of Swiss Federal Institute for Forest, Snow and Landscape Research. Reprinted with permission from the *Annual Review of Phytopathology*, Volume 32 © 1994 Annual Reviews.

Figure 3 Pitch canker on *Pinus radiata*; multiple infections caused by *Fusarium circinatum* lead to death of the affected branch distal to the girdling canker. Diseased branches are identifiable as naked tips or by the associated killed (brown) needles, where these have not yet fallen.

(teleomorph). Although the sexual stage is readily produced under laboratory conditions, it is rarely, if ever, seen in nature. Pitch canker was first described in the southeastern USA where it came to be regarded as a chronic problem affecting a number of southern pine species in plantations, seed orchards, and nurseries. In 1986, the disease was discovered in California as a cause of extensive damage and mortality to planted *Pinus radiata* (common names: Monterey pine and radiata pine). Soon thereafter, pitch canker was reported in both native forests and plantations in Mexico, in pine seedling nurseries in South Africa, and among planted pines in Japan. More recently, pitch canker has been documented as a cause of seedling mortality in Chile and Spain.

The nature of the damage caused by pitch canker varies with the tree species and the circumstances under which it is growing, but commonly involves dieback in the canopy to varying extents (**Figure 3**). Death of a branch tip results from a girdling canker on the current year's growth. Disease severity increases due to multiple tip infections and independent infections on larger branches. Complete girdling of the main stem can occur as well, most often probably as a result of multiple coalescing cankers rather than a single infection. Resin accumulates in and around infection sites, this being especially pronounced on older branches and the trunk of the tree (**Figure 4**). Cones and pollen-bearing strobili may also be infected.

Although pitch canker is a relatively minor problem for plantation forestry in the southeastern USA, it represents an evolving and increasingly serious problem in other parts of the world. In California, native *P. radiata* forests have been badly affected, and damage to the extensive landscape plantings of this species is a continuing problem. Although *P. radiata* has suffered by far the most damage from this disease, most pines native to California are also susceptible, and some of these have become severely diseased where they are exposed to the pathogen. Perhaps the greatest concern about pitch canker lies in its potential to attack exotic pine plantations in the southern hemisphere, where *P. radiata* is a critically important species.

Figure 4 Resin streaming from multiple cankers on the main stem of *Pinus radiata* caused by *Fusarium circinatum*. Reprinted with permission from Gordon TR, Storer AJ, and Wood DL (2001) The pitch canker epidemic in California, *Plant Disease*, 85: 1128–1139.

Although pitch canker was first described in the southeastern USA, it is not known if this constitutes the site of origin of the pathogen, or if it was introduced there. One other possibility for the aboriginal home of the pitch canker pathogen is Mexico, which is a center of diversity for the pine genus and where the population of *F. circinatum* is genetically quite diverse. In any case, most accounts of pitch canker in the southeastern USA suggest that the disease has 'stabilized' in this area, being widespread but rarely severe. On the other hand, where the pathogen is a more recent arrival, its geographic range may still be expanding. Thus pitch canker is regarded as an endemic problem in the southeastern USA but an invasive pathogen in California, South Africa, Chile, and Spain.

Factors in Susceptibility

The potential for pitch canker to pose problems for forest trees can be assessed by considering the basic elements required for a pathogen to cause disease: a susceptible host and a permissive environment. This is well illustrated by *P. radiata* which, as a species, is highly susceptible but does include some resistant individuals (**Figure 5**). In addition, some trees that become infected may eventually recover from pitch canker. This results from a loss of symptomatic branch tips through breakage in the vicinity of the canker and a lack of new infections, which has been attributed to systemic induced resistance. Thus, the damage caused by pitch canker to a stand of *P. radiata* will be determined, in part, by the proportion of trees that manifests inherent and/or induced resistance to the disease.

Figure 5 A stand of *Pinus radiata* that includes many pitch canker-infected trees, one of which (large tree on the right) has been killed by the disease. An adjacent tree (left of the dead tree) has remained free of symptoms due to genetic resistance.

Where trees are fully susceptible to pitch canker, disease development may be constrained by environmental limitations. The pathogen requires a wound and ambient conditions that allow wounds to remain moist long enough for infections to become established. In the southeastern USA, weather-related events are regarded as the important cause of wounds for infection, whereas in California pine-associated insects appear to be the most important wounding agents. Where aboveground damage caused by pitch canker is a problem, atmospheric moisture is plentiful during periods of moderate temperatures. Such conditions are provided by warm summer rains in the southeastern USA, and by rain and fog along the California coast. Movement of the disease to more northerly locations in North America may be limited by progressively lower temperatures. In California, drier conditions in more inland areas are likely to be restrictive. It is noteworthy, however, that most of the approximately 4 million ha planted to *P. radiata* elsewhere in the world are in regions where the climate should be conducive to development of pitch canker.

As noted earlier, pitch canker can be a problem in seedling nurseries. Under these conditions it infects roots and may kill seedlings at or before emergence or almost anytime thereafter. In very young seedlings, symptoms of the disease are not distinctive, but in older seedlings (1–3 years) tree death is associated with girdling of the main stem near the soil line, where the accumulation of resin is similar to what is seen in the aerial phase of the disease. Where *F. circinatum* is operating as a soilborne pathogen, the environmental limitations described above are not likely to pertain.

From a global perspective, management of pitch canker should emphasize prevention, by avoiding importation of the pathogen into areas where forest resources would be at risk from this disease. Although *F. circinatum* can survive in association with various infected plant materials (and in soil), seed probably represents the most efficient vehicle for dissemination. Seed can be infested externally or internally and may give rise to seedlings that die quickly or survive without symptoms for 6 months and possibly much longer. Sowing infested seed will contaminate soil, which may thereafter serve as a reservoir of the pathogen, and subsequent shipment of symptomless seedlings provides an ideal mechanism for establishment of the disease in plantations or landscapes.

Genetic Resistance

In the long term, genetic resistance to pitch canker may have a role to play in disease management. In native forests, practices that promote regeneration may facilitate natural selection for more resistant genotypes, which are known to be represented within *P. radiata* populations, for example. In managed plantings, it may be prudent to avoid highly susceptible pine species altogether, in favor of those less prone to severe damage. However, where industries are heavily committed to *P. radiata*, as in Chile, New Zealand, Australia, and Spain, it should be possible to enhance the level of resistance in improved varieties. This can be accomplished through vegetative propagation of known resistant clones, but it is as yet unknown how many different genetic combinations may confer resistance. As a consequence, it may not be possible to deploy an array of clones that is sufficiently diverse to avoid undue risk of catastrophic failure due to selection for more virulent strains of the pathogen. Likewise, the heritability of resistance has not been established so the prospects for increasing resistance through family-level selection cannot yet be assessed. Research is needed to better understand the genetic basis for resistance to pitch canker and facilitate its application to disease management.

Diplodia Shoot Blight and Canker

Diplodia shoot blight and canker, caused by *Diplodia pinea* (syn. *Sphaeropsis sapinea*) is common in temperate regions worldwide. This pathogen infects conifers in both the Pinaceae and Cupressaceae, including various species of *Cedrus* (cedar), *Juniperus* (juniper), *Picea* (spruce), *Pinus* (pine), and *Pseudotsuga* (Douglas-fir). The disease is most frequently seen on two- and three-needled pines, on which tip dieback is the most common symptom (**Figure 6**). Cankers caused by *D. pinea* are characterized by elongated, depressed areas on branches or stems, often with resin flow on the outer bark. When the bark is removed, resin-soaked wood is visible (**Figure 7**). In older infections, callus growth may be observed around the edges of the canker. Where young branches are infected, needles and shoots stop expanding and are quickly killed, later appearing stunted and necrotic. Infected stem tissues are initially water-soaked in appearance, later becoming purplish-brown and necrotic. Repeated tip and/or stem infections can lead to branch death. The seedling phase of the disease, called collar rot, is characterized by similar infections, which may girdle the stem and cause mortality of seedlings.

Figure 6 Shoot tip dieback on ponderosa pine (*Pinus ponderosa*) in California caused by *Diplodia pinea*. Photograph courtesy of M.H. Morris.

Figure 7 Resinous cankers, caused by *Diplodia pinea*, on a branch tip (a) and the main stem of pine (b). In both cases, the bark has been removed to show resin-soaking and discoloration in the underlying wood. Photograph 7b courtesy of US Department of Agriculture Forest Service, North Central Research Station.

Figure 8 Perennial canker caused by *Diplodia pinea* on trunk of radiata pine (*Pinus radiata*) on a plantation in South Africa. Photograph courtesy of M.J. Wingfield.

Economic Importance

Diplodia shoot blight and canker is seldom damaging to trees planted within their natural range and as such it is rarely important in native forests. On the other hand, exotic pine species in plantations or in landscape plantings can be severely affected. For example, this disease has caused economic damage to *Pinus patula* (Mexican weeping pine) and *P. radiata* in plantations in the southern hemisphere (**Figure 8**) and to both exotic (e.g., *P. nigra* and *P. sylvestris*) and native (*P. resinosa* and *P. banksiana*) pines in the north central USA.

Two subgroups of the pathogen have been described, morphotypes A and B, which are differentiated on the basis of colony morphology and growth rate in culture as well as by isozyme profiles and DNA polymorphisms. The two morphotypes also exhibit differential aggressiveness to pine, with A being more aggressive. Recent work indicates the two morphotypes should be considered separate species, with the A morphotype being associated with the binomial *D. pinea* and the B morphotype designated as a new species, *D. scrobiculata*.

Life Cycle

The fungus produces spores in fruiting bodies (pycnidia), visible with a hand lens, on needles, fascicle sheaths, cone scales, and bark. Even apparently symptomless trees may harbor spores formed on cone scales. Pycnidia typically form in the spring of the year following infection. Spores contained in pycnidia are transparent at first and later become brown. These are released during wet weather and are spread by rainsplash or wind-driven rain. Spores can infect expanding needles and shoots, and second-year cones, where surface wetness persists for 12 h at 12–36°C. Infection of mature current-year and older shoots and stems can occur through fresh wounds, such as those caused by insects, hail, or pruning.

This fungus is also considered an endophyte because it can be associated with symptomless infections. Such infections are thought to become damaging when the host is predisposed by some form of abiotic or biotic stresses. Drought stress in particular has been well-documented to induce damage in *D. pinea*-infected trees. The ability of *D. pinea* to exist within its host as a latent pathogen suggests that this fungus has a long history of association with pines. The observation of more severe disease on off-site or stressed trees and on exotic species in plantations fits the pattern described above for weak parasites that become opportunistic pathogens when conditions are altered to the detriment of the host.

Management

Management of diplodia shoot blight and canker in plantations depends primarily on avoidance of the disease. Careful selection of the planting site and of a timber species appropriate for that site are important to minimize stress. High soil fertility should be avoided as this has been shown to aggravate the disease in some situations. Should the disease reach severe levels within a commercial stand, replanting or early harvest may be warranted. In nurseries, seedling beds should not be established in the vicinity of older trees as these may serve as a source of inoculum. Seedlings can be protected by frequent fungicide applications until shoots and needles are mature. On Christmas-tree farms, fungicides may also be employed to protect trees, but control depends primarily on avoiding shearing operations during wet weather.

Conclusion

The three canker diseases described above illustrate ways in which movement of plants and pathogens can lead to new or significantly altered host–parasite relationships, with devastating consequences. Chestnut blight in North America offers an extreme example of an exotic pathogen preadapted for virulence, where susceptibility of the host was complete and the result was disappearance of a dominant tree species throughout a vast forest ecosystem. Pitch canker is also caused by an exotic pathogen, but one that has not found a host as devoid of resistance as the American chestnut was to the blight pathogen. Susceptibility to pitch canker is the rule in *P. radiata* and mortality has been widespread, but a small percentage of individuals proved to be highly resistant and many others have sustained relatively minor damage. This, combined with remission in some severely diseased trees, suggests that the host–pathogen relationship will stabilize in a way that allows *P. radiata* to remain a defining feature in forests that bear its name. Likewise, chestnut blight in Europe show signs of stabilizing, not through a response of the host but because the pathogen is itself debilitated by a parasite. Thus, various mechanisms can serve to constrain the aggression of an invasive species, imparting a resilience to forested ecosystems that has no doubt been critical to their persistence.

Diplodia pinea offers a contrast to chestnut blight and pitch canker in that native forests suffer little damage from it. In this case, too, introduction of the pathogen into new areas has created problems, but primarily for exotic plantation forestry. Thus, movement of the host to suboptimal sites is the primary reason *D. pinea* is a damaging pathogen. The genetic constitution of most potential hosts prevents aggressive growth of *D. pinea*, except where trees are compromised by stress. In a broad sense, all three canker-causing pathogens are opportunists that differ in the nature of the opportunities they have exploited.

In terms of management, these diseases illustrate the importance of prevention, especially where this can be achieved on a regional scale by limiting new pathogen introductions. Unfortunately, historical barriers to the spread of plant pathogens, such as spatial gaps in host distribution, are increasingly likely to be breached through steadily increasing trade and travel. Ever-present threats include not only known major pathogens but also untold numbers of minor pathogens that await their opportunity to flower into full virulence. Thus, the implementation of any new and effective measures to limit more widespread distribution of plant-associated microbes offers great potential to reduce the risk of major new disease problems for forest resources worldwide.

See also: **Health and Protection**: Diagnosis, Monitoring and Evaluation. **Pathology**: Diseases of Forest Trees. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Gordon TR, Storer AJ, and Wood DL (2001) The pitch canker epidemic in California. *Plant Disease* 85: 1128–1139.

Hansen EM and Lewis KJ (1997) *Compendium of Conifer Diseases*. St Paul, MN: American Phytopathological Society.

Heiniger U and Rigling D (1994) Biological control of chestnut blight in Europe. *Annual Review of Phytopathology* 32: 581–599.
Swart WJ and Wingfield MJ (1991) Biology and control of *Sphaeropsis sapinea* on *Pinus* species in South Africa. *Plant Disease* 75: 761–766.

Insect Associated Tree Diseases

J N Gibbs, Aberyail, Llangynidr, UK
J F Webber, Forestry Commission Research Agency, Farnham, UK

Introduction

The causes of tree diseases range from the simple – with one principal damaging agent – to the complex – where a number of damaging agents interact.

A key role for insects in some simple diseases is that of vector for a pathogen. This is particularly important for certain fungal diseases. However, insects also play a vital part in the dissemination of some tree-pathogenic nematodes, phytoplasmas, xylem-limited bacteria, and viruses.

In complex tree diseases insects may play a variety of roles. At an early stage, leaf-eating insects may act as agents of stress. At a later stage it may be bark- or wood-inhabiting beetles that deliver the final death blow to the tree.

Fungal Diseases Vectored by Insects

Among the fungi, there are three main taxonomic groups: the Oomycotina, the Basidiomycotina, and the Ascomycotina (plus the closely allied Fungi Imperfecti). The majority of fungal pathogens with known insect vectors are either Ascomycotina or Fungi Imperfecti, and most of the ascomycetes fall within two genera of the family Ophiostomataceae – *Ophiostoma* and *Ceratocystis*. In addition, most of the imperfect fungi are *Chalara*, *Leptographium*, or *Verticicladiella*, genera that would be expected to have *Ophiostoma* or *Ceratocystis* perfect states. The nature of the insect–fungus relationship with this group of pathogens is discussed in some detail later in this article. Among other ascomycetes, recent attention has focused on the role of insects as vectors of *Fusarium circinatum*, the cause of pitch canker. This major pathogen, first recognized in the eastern USA, was reported from California in 1986. Studies there on *Pinus radiata* have focused on the twig-feeding bark beetles *Pityophthorus* spp., but other beetles, including the cone beetle *Conophthorus radiata*, have also been implicated. In southern Europe, a cone-feeding insect, the seed bug *Orsillus maculatus*, has been found to transmit the important canker pathogen *Seiridium cardinale* to *Cupressus sempervirens* cones. Once the cones are colonized by the fungus they become a source of inoculum for branch infection. Interestingly, it seems that when *S. cardinale* arrived in Europe, it took over a long-established relationship between the insect and a nondamaging fungus *Pestalotiopsis funerea*.

Although the Basidiomycotina include many fungal pathogens of trees, the only indubitable case of insect transmission concerns the *Amylostereum* species that are transmitted by woodwasps in the genera *Sirex* and *Urocerus*. In most parts of the world these organisms do little damage but in Australia and New Zealand, *Sirex noctilio* and *Amylostereum areolatum* can cause significant losses in *Pinus radiata* plantations, especially during periods of drought.

The fungus is carried by the adult siricids in a pair of small invaginated intersegmental sacs protruding into the body. These are connected by ducts to the anterior end of the ovipositor. During oviposition (**Figure 1**), spores of the fungus are 'injected' into the sapwood of trees and developing mycelium then invades the wood around the oviposition hole and larval tunnels. As is commonly the case with xylem pathogens, a zone of reduced moisture content develops around the tissue occupied by *Amylostereum* and this ensures that the *Sirex* eggs hatch and the larvae develop in relatively dry wood. In addition, host resinosis is reduced in colonized tissue, and this also favors larval development. Female larvae, from the second instar onwards, carry the

Figure 1 *Sirex* woodwasp, vector of basidiomycete *Amylostereum* ovipositing on pine. Courtesy of Forest Commission.

Figure 2 A soil tent (arrowed) produced by ants, causing *Phytophthora megakarya* infection of cocoa pods. Courtesy of CM Brasier.

fungus in deep skinfolds called hypopleural organs sited in the abdomen. The young adult then acquires the fungus during eclosion when, by reflex actions, it breaks up the hypopleural organs in the cast-off larval skin. Interestingly, inoculation with the fungus alone has relatively little effect and the insect's mucus secretions are believed to play an important part in 'conditioning' the tree for invasion by *A. areolatum*.

The only oomycetes known to be insect-vectored are *Phytophthora palmivora* and *P. megakarya*. They cause black pod disease of cocoa and can also cause stem cankers and wilt of flower cushions. Although these fungi can be disseminated via rain splash and contact with plant litter, several species of ants have been found to act as vectors. Transmission occurs when ants collect particles of soil contaminated with *Phytophthora* and build them into tents on the cocoa plants, including on the pods (**Figure 2**). These can then become infected with the pathogen, which appears to be capable of invading both wounded and uninjured pods.

The Ophiostomoid Pathogens of Standing and Freshly Felled Trees and their Insect Dispersal

Because of their economic importance, diseases caused by this group of fungi have been subject to detailed research, evaluation of which has thrown much light on the principles underlying the process of insect transmission.

Two contrasting patterns of host invasion can be found in the Ophiostomataceae and these have a significant influence on the nature of the relationship with potential insect vectors. In the vascular wilts the fungus shows extensive vertical distribution in the xylem elements (vessels or tracheids), but is unable to colonize xylem parenchyma, the medullary rays, the cambium, and the inner bark (phloem tissue) until the host becomes moribund. Examples from temperate regions of the world include Dutch elm disease caused by *Ophiostoma ulmi* and *O. novo-ulmi*, oak wilt (*Ceratocystis fagacearum*), and black stain root disease (*Verticicladiella wageneri*), which affects pines and Douglas-fir. A tropical example is takamaka wilt in the Seychelles caused by *Leptographium calophylli*. By contrast, in the vascular stains the fungus invades the rays, ray parenchyma, and inner bark at the same time as it colonizes the xylem elements. Some vascular stain diseases occur in standing trees. Examples are the *Ceratocystis* canker of deciduous trees caused by *C. fimbriata* and the pathogenic bluestain, caused by *C. polonica*, that develops in Norway spruce following trunk invasion by *Ips typographus*. Another pathogenic bluestain occurs in *Pinus contorta* in western North America following attack by the mountain pine beetle *Dendroctonus ponderosae* (**Figure 3**). Here two fungi, *C. clavigera* and *O. montia*, are carried to the trees on the beetles and are strongly implicated in overcoming host resistance. Other bluestains only develop if the trees lack active host resistance following felling or windblow. A European example is the stain caused by *Leptographium wingfieldii* that develops in *Pinus sylvestris* logs following attack by *Tomicus piniperda*.

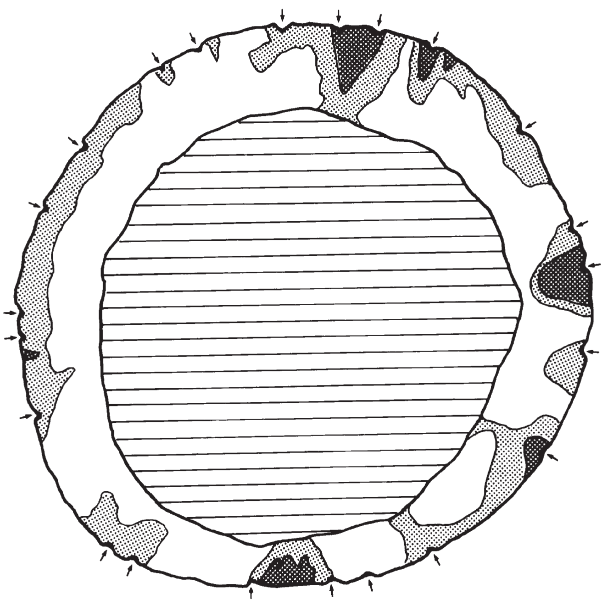


Figure 3 Cross-section of xylem of a lodgepole pine a few weeks after it has been successfully colonized by *Dendroctonus ponderosae*. Arrows show the position of egg galleries. The zone of blue-stained wood and the surrounding zones of wood with reduced moisture are shown with different degrees of stippling. The heartwood is hatched. Some of the patterns are due to the presence of other egg galleries above or below the section. Reproduced with permission from Reid RW, Whitney HS, and Watson JA (1967) Reactions of lodgepole pine to *Dentroctonus ponderosae* and blue stain fungi. *Canadian Journal of Botany* 45(7): 1115–1126.

Establishment of the Link Between Insect and Ophiostomoid Fungus in the Diseased Tree

Specialized plant pathogens are characterized by an expanding phase of parasitic growth in the living host and a declining phase of saprotrophic growth in the dead host. This is because qualities which fit the fungus for parasitism tend to put it at a disadvantage when it comes to prolonged survival in competition with other microorganisms. Any potential vector must have a life cycle that is completed before the disappearance of the fungus, and some likely candidates can prove to be of no significance.

An example is provided in myrtle wilt, a vascular stain disease of *Nothofagus* in Tasmania caused by *Chalara australis*. Very large numbers of the mountain pin hole borer, *Platypus subgranosus*, breed in trees killed by the fungus but while the *Platypus* has a 2–22-year life cycle, *C. australis* survives in the stems of dead trees for only 12–18 months. Hence, the lack of synchrony between the two species prevents the borer from vectoring the pathogen.

Of course, it is not enough for the fungus just to survive in the tree. It also needs to produce propagules that are suitable for insect dispersal. The ophiostomatoid fungi are typically very well adapted for this purpose, as illustrated in **Figure 4** for the Dutch elm disease pathogen *Ophiostoma novo-ulmi*.

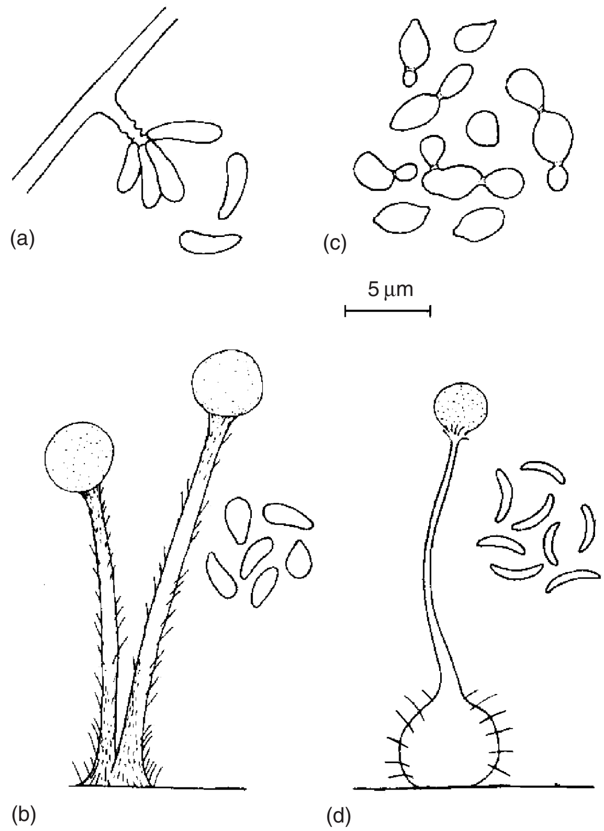


Figure 4 Spore forms and fruit bodies in *Ophiostoma novo-ulmi*. The scale applies to the spores only: (a) conidial or sporothrix stage; (b) stalk-like coremium (c. 1 mm tall) and coremiospores; (c) budding yeast-like stage; (d) flask-shaped perithecium (0.5 mm tall) and ascospores. The coremium and the perithecium are particularly well-adapted for insect dispersal. Courtesy of CM Brasier.

Transport of Ophiostomoid Fungi from Diseased to Healthy Trees

By definition a vector must move from a diseased to a healthy tree, or at least from a diseased part to a healthy part of the same tree. Scolytid beetles act as vectors of Dutch elm disease because, following emergence from their pupal chambers, the young adults often fly to feed in the twig crotches of healthy trees (**Figure 5**) before seeking out suitable fresh bark for breeding.

The method of spore transport, the behavior of the vector and the environmental conditions during dissemination can all influence the chances of successful disease transmission. With some vectors, spores are simply carried externally on the insect's exoskeleton and so are directly exposed to desiccation and ultraviolet radiation during flight. Studies on *Scolytus scolytus* in the UK during the 1980s showed that the mean percentage of beetles carrying *O. novo-ulmi* was over 89% in the pupal chambers but only 17% after emergence and flight.

Although fungi are much better protected if they are contained within the specialized carrying organs, mycangia, possessed by many bark and wood-boring beetles, it is a matter of record that few of the fungi transported in this way have much ability to cause tree disease or bluestain.

Temperature may also play an important part in disease transmission by regulating insect behavior. Although most vectors are commonly assumed to fly, the threshold temperatures for flight can often be quite high – at least 20°C in the case of the Dutch elm disease scolytid vectors. Indeed, the very temperatures which encourage insect activity can often be detrimental to the fungi they transport. For this reason, crawling may be more important than is generally recognized, and is crucial in the dissemination of *Verticicladiella wageneri* by various root-inhabiting beetles and weevils, which actively seek out stressed and diseased roots for oviposition.

Transfer and the Establishment of Infection with Ophiostomoid Fungi

Once the vector has reached a potential host tree, successful transfer of the fungus to susceptible plant tissue and the initiation of sustained disease again

Figure 5 (a) Larger European elm bark beetle *Scolytus scolytus*, vector of Dutch elm disease; (b) feeding grooves (arrowed) produced by *S. scolytus* on *Ulmus procera*. Courtesy of Forestry Commission.

depend on several factors. These include the nature of the infection court, and the quantity of inoculum that is introduced to it.

Wounds are required in all known cases of infection by the Ophiostomataceae involving insect transmission, and, where bark beetles and weevils are involved, the insects are able to make the wounds themselves. However, with other kinds of insects, such as the sap-feeding nitidulids that vector the oak wilt pathogen *Ceratocystis fagacearum*, there is a dependence on wounds made in other ways, e.g., through the use of pruning tools or tree-climbing irons.

The depth of the wound may also be important. With the vascular wilt diseases like Dutch elm disease and oak wilt, the wound must reach the wood if the pathogen is successfully to penetrate and invade the xylem elements, whereas with a vascular stain disease like the *Ceratocystis* canker of fruit trees, a wound exposing live inner bark is all that is required.

The arrival of viable fungal spores in a suitable wound does not necessarily lead to disease. Infection depends on the number and physiological condition of the spores, and on the effects of competing microorganisms. Simultaneous host invasion from many infection points may also be necessary to overwhelm the resistance of a host which might otherwise be able to check the development of a single infection. This has been shown to be important with the vascular stain pathogen *Ophiostoma polonica* on Norway spruce, where doubling the number of inoculation points produced an almost eightfold increase in the amount of wood which succumbed to the pathogen.

Relationships in the Brood Galleries Between Insects and Ophiostomoid Fungi Causing Vascular Wilt Diseases

In a vascular wilt disease like Dutch elm disease, the pathogen can move rapidly away from the point of infection as spores are carried along in the transpiration stream. The result is that symptoms arising from a single infection can appear rapidly throughout the crown. Bark beetles can successfully establish breeding colonies in the trunk and major branches of such trees and, as the larval brood develops, there is the opportunity for a link to be reestablished with the fungus in the xylem. At the same time colonization of the inner bark can also take place from propagules of the pathogen still present on the parent beetles as the latter begin to establish breeding galleries. The subsequent ecological interactions between the beetle larvae and the various ‘sources’ of the fungus are quite complicated.

The survival of the fungus on the parent beetles also means that it can establish itself in brood galleries that are made in the bark of logs or windblown limbs from healthy trees. Young beetles emerging from such material can be just as effective in spreading the pathogen as beetles emerging from diseased trees. Failure to recognize this point greatly hampered early attempts to eradicate Dutch elm disease from the USA in the 1930s.

Insects as Agents for Fertilization in the Ophiostomoid Fungi

It is important to realize that, in the Ophiostomataceaea, as in many other groups of fungi, spore dispersal may be as important, or more important, for fertilization as for infection or substrate colonization. This is because they comprise two mating types and these have to be brought together for the sexual stage of the fungus to be produced. There may also be a link between dissemination for fertilization and dissemination for transmission. For example, in *C. fagacearum*, the cause of oak wilt, the switch from asexual spore to sexual spore production following fertilization prolongs the period over which inoculum is available for disease transmission.

Pine Wilt Disease: Caused by a Nematode, Vectored by Longhorn Beetles

The pine wood nematode *Bursaphalenchus xylophilous* is a native of North America where it causes little damage. However, following its introduction to Japan and subsequently to other countries in Asia, it has caused enormous losses to the native pines. Transmission is by several species of *Monochamus* (longhorn beetles in the Cerambycidae), and, as with the scolytid vectors of Dutch elm disease, these insects can introduce the pathogen both during maturation feeding and during oviposition (**Figure 6**). Within the vector, the nematode exists as a special larval stage, the dauerlarva, but once in the xylem of the healthy tree, the dauerlarvae molt to reproductive adults that mate and begin egg-laying. The first-stage larvae molt while still in the egg and then hatch as second-stage larvae that feed on host parenchyma cells. The larvae molt to third and fourth larval stages and then to adults that continue feeding and breeding. Once the tree dies, the nematodes survive on fungi (principally ophiostomoid bluestain fungi) before forming an overwintering stage. In the same trees, *Monochamus* larvae develop through various instars before pupating and emerging as adults in spring. The overwintering form of the nematode changes into dauerlarvae and these enter the tracheae of the callow *Monochamus* adults via the thoracic spiracles.

Diseases Caused by Phytoplasmas, Xylem-Limited Bacteria and Viruses and their Insect Vectors

These diseases are caused by a loose grouping of tree pathogens that share the characteristic of being unable to replicate except within living host tissue. *Inter alia*, this means that transmission from one host to another is essentially a passive operation. Insects

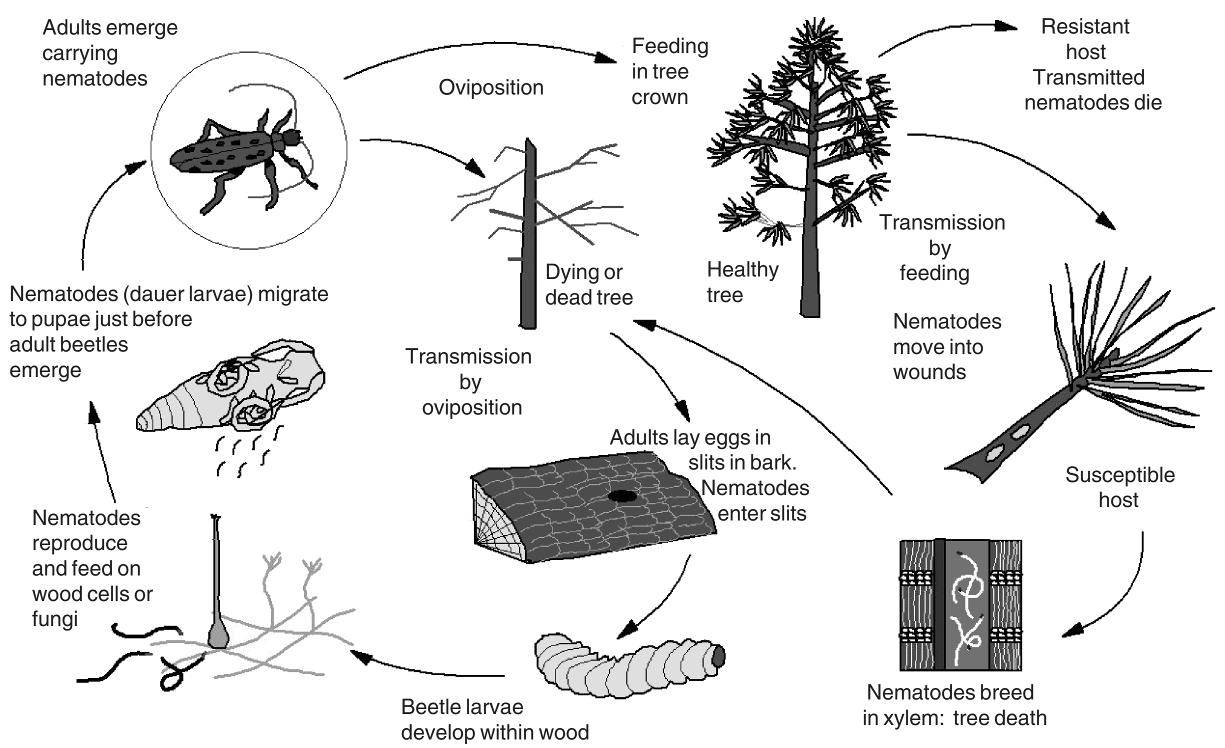


Figure 6 Diagram of the pine wilt disease cycle showing transmission of the nematode both by twig feeding and oviposition. Courtesy of HF Evans.

implicated in the process are all in the Homoptera, a group (suborder) that contains sucking insects such as aphids, leaf-hoppers, psyllids, and spittlebugs. However, only in comparatively few cases are the vectors known with certainty. Phytoplasmas, formerly known as mycoplasma-like organisms (MLOs), have the general characteristics of bacteria but lack cell walls. They can only invade the phloem where they replicate in the sieve tubes. Symptoms typically involve a yellowing of the foliage, followed by progressive dieback. Shoot proliferation resulting in the formation of witches' brooms may also occur. Important examples include elm and ash yellows in North America, lethal yellowing of coconut (widely distributed in the tropics) and, recently, sudden death of cabbage tree in New Zealand.

Detailed knowledge of the role of insects in transmission has been obtained from studies on elm yellows where the white-banded leafhopper, *Scaphoideus luteolus*, is known to be a vector. The pathogen is picked up by the insect during feeding on phloem sap in the leaf veins. It multiplies in the insect's salivary glands and is transmitted to the phloem of healthy trees during further feeding. Almost a year can elapse between infection and the development of symptoms. A planthopper *Myndus crudus* appears to be the principal vector of lethal yellowing of palms. This insect often lives among the roots of various grasses by day but migrates to palm trees at night.

The xylem-limited bacteria are smaller than other plant-pathogenic bacteria and, as the name indicates, are restricted to the host xylem. Strains that cause diseases of trees have been given the name *Xylella fastidiosa*. Symptoms in genera such as elm, plane, and oak include delayed leaf expansion, late-season leaf scorch, and dieback. Given the biology of the pathogen, it follows that their vectors are all xylem-feeding sucking insects. Many species have been identified through studies of the pathogen in the economically important Pierce's disease of grapevine but those involved in transmission to trees are not yet known. However, it is probable that nymphs as well as adult insects will be able to acquire and transmit *X. fastidiosa*. It is suggested that the bacteria form a plaque in the foregut and are flushed out by the sucking pump.

Many of the above-mentioned diseases were originally thought to be caused by viruses. When it comes to tree diseases caused by the true viruses (viruses consist of a nucleic acid core and a protein coat), very few have important insect vectors. One exception is plum pox where up to 20 species of aphid are thought to be involved in transmission.

Role of Insects in Complex Tree Diseases

Tree diseases of complex cause often go under the names of diebacks or declines. A good model for this type of disease involves various agents of stress acting on the tree which is then so much altered that it becomes vulnerable to organisms of secondary action, i.e., organisms that would be unable to cause significant damage to a healthy tree. Defoliating insects very often act as agents of stress, preventing the tree from carrying out photosynthesis and hence causing a depletion in essential food reserves. For example, the introduced gipsy moth (*Lymantria dispar*) plays this role in the condition known as oak decline in the northeastern USA, and so does the native oak roller moth (*Tortrix viridana*) in the somewhat similar condition in northern Europe known as oak dieback. Similarly, sucking insects can act as agents of stress by removing large quantities of sugars from the phloem. Thus in the condition known as beech bark disease, the scale insect *Cryptococcus fagisuga* builds up huge populations on the trunks of beech (*Fagus sylvatica* in Europe and *F. grandifolia* in North America) and renders the bark vulnerable to attacks by fungi (*Nectria* spp.) that would not normally be capable of damage.

Insects often also act as organisms of secondary action. Thus many beetles that are incapable of initiating a successful attack on a healthy tree will quickly establish breeding galleries in one that has been altered by various agents of stress. In North American oak decline, for example, it is the two-lined chestnut borer *Agrilus bilineatus* that often delivers the coup de grâce to a tree weakened by successive gipsy moth defoliations. Similarly many of the conifer bark beetles can cause mortality in trees weakened by drought.

See also: **Entomology**: Bark Beetles; Foliage Feeders in Temperate and Boreal Forests; Sapsuckers. **Pathology**: Diseases of Forest Trees; Pine Wilt and the Pine Wood Nematode; Vascular Wilt Diseases. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance. **Wood Formation and Properties**: Biological Deterioration of Wood.

Further Reading

Ash CI (ed.) (2001) *Shade Tree Wilt Diseases*. St Paul, MN: American Phytopathological Society.

Evans HF, McNamara DG, Braasch H, Chadoeuf J, and Magnusson C (1996) Pest risk analysis for the territories of the European Union (as PRA area) on *Bursaphalenchus xylophilus* and its vectors in the genus *Monochamus*. *EPPO Bulletin* 26: 199–249.

Houston DR (1992) A host-stress-saprogen model for forest dieback-decline diseases. In: Manion PD and Lachance D (eds) *Forest Decline Concepts*, pp. 3–25. St Paul, MN: American Phytopathological Society.
Schowalter TD and Filip GM (eds) (1993) *Beetle-Pathogen Interactions in Conifer Forests*. London: Academic Press.
Webber JF and Gibbs JN (1989) Insect dissemination of fungal pathogens of trees. In: Wilding N, Collins NM, Hammond PM, and Webber JF (eds) *Insect–fungus Interactions*, pp. 161–194. London: Academic Press.
Wingfield MJ, Siefert KA, and Webber JF (eds) (1993) *Ceratocystis and Ophiostoma: Taxonomy, Ecology and Pathogenicity*. St Paul, MN: American Phytopathlogical Society.

Heart Rot and Wood Decay

F W M R Schwarze, EMPA, St. Gallen, Germany

Introduction

In natural ecosystems, there is a dynamic equilibrium between the accumulation of woody biomass and its breakdown. In this way, a permanent cover of trees or shrubs is maintained, while the carbon and minerals that they have fixed are recycled. At the same time, the survival of a range of woodland plants is fueled by the energy released in the breakdown of wood. Decay fungi play a major role in the processes of breakdown since, alone among microorganisms, they have evolved the means to break down large volumes of wood completely.

The balance between trees and decay fungi represents the state of play in a coevolutionary battle that has lasted for hundreds of millions of years, and in which wood has been the main prize. The success of trees as a dominant form of land vegetation has depended on their being able to maintain a perennating woody structure, which is their means of attaining both height and longevity. This defensive strategy protects the woody stem against loss of integrity of both its water-conducting and its mechanical properties. A range of agents, especially decay fungi, whose mode of attack is the degradation of the woody cell wall, can cause such damage.

Colonization of the Standing Tree

Heart rots were for a long time regarded as the primary cause of decay in standing trees. Whilst it is now clear that this is a considerable oversimplification, it remains true that in high forest and mature amenity trees heart rots are still a major cause of economic loss and deterioration. Based on the concept that either the distribution of water and its mutual relation with aeration are primary determinants of colonization patterns, five distinctive colonization strategies are recognized:

- heart rot
- active pathogenesis
- specialized opportunism
- unspecialized opportunism
- desiccation tolerance.

Most heart rot fungi have a stress-tolerant colonization strategy, i.e., they colonize the tree via exposed heartwood or ripewood (**Figure 1**). Although the heartwood of many tree species does exhibit a high concentration of antifungal extractives (e.g., polyphenols, tannins), heart rot fungi have adapted to the adverse conditions (low oxygen concentrations, high carbon dioxide concentrations, low moisture content). Thus, those features that render functionally intact sapwood nonsusceptible to decay are avoided. Moreover, after colonization of the tree via infection courts such as logging scars, branch stubs, fire scars, broken tops, pruning wounds, and severed roots, decay fungi can degrade the heartwood without inducing the host response system of the tree.

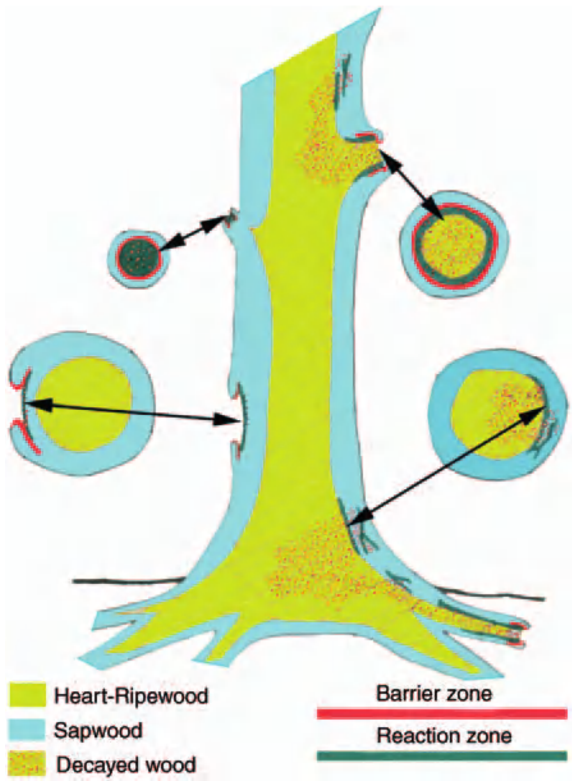


Figure 1 Infection points for decay fungi and associated host response mechanisms within the tree.

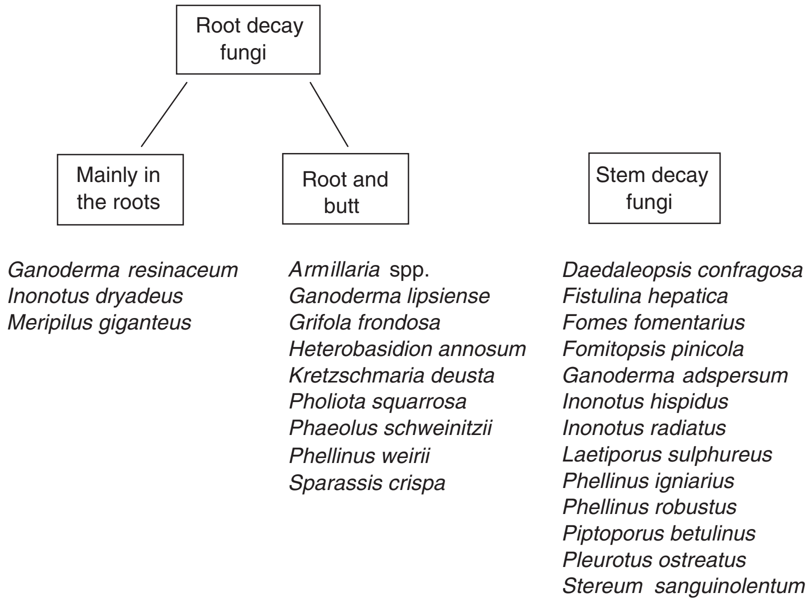


Figure 2 Classification of decay fungi according to the position of rot within the tree. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

Wood decay fungi are separated into top rots and root or butt rots depending on which part of the tree is affected. Important agents of decay in trees are listed in **Figure 2**. Top rot decay fungi are found in the wood of the upper parts of trees. They seldom progress very far into the roots and therefore do not spread from one tree to another via roots. Root and butt rot fungi colonize the lower stem and roots of trees. Some parasitize the cambium of roots while others remain within the central xylem and can be classified as saprophytes.

The Construction of the Woody Cell Wall

A full understanding of the interactions between decay fungi and living trees requires studies at various levels; anatomical, physiological, and biochemical. In order to understand the alterations caused in woody cell walls by decay fungi, the micromorphological aspects of the sound wall will therefore be briefly described.

Conifer wood is relatively homogeneous in structure and consists primarily of tracheids, uniseriate xylem rays, and, in some genera, also axial parenchyma and epithelial cells surrounding resin canals. Tracheids are dual-purpose cells combining properties of both mechanical support and water conduction. By comparison, dicotyledonous wood is more heterogeneous, and its mechanical and water conducting functions are served by vessels, while fibers or fiber tracheids mainly supply strength and support. Parenchyma is a more prominent feature in dicotyledonous wood than in coniferous wood, with most genera having multiseriate xylem rays and varying amounts of axial parenchyma.

The structure of woody cell walls can be seen in **Figure 3**. The cell wall proper consists of a thin primary wall, to which a much thicker secondary wall consisting of three layers (S_1, S_2, and S_3) is added after the initial formation of the cell. As in plant cells generally, the walls of adjacent cells are bonded together by a layer termed the middle lamella (**Figure 3**). The main structural component of the walls of juvenile wood cells is cellulose, whose long threadlike molecules are aggregated in microfibrils which provide the tensile strength of wood and are held within a matrix of other polysaccharides, known loosely as hemicellulose. The cellulose microfibrils in the various secondary layers show different orientations in relation to the cell wall axis (**Figure 3**).

During the maturation of wood cells, all the layers of the wall together with the middle lamella become to a greater or lesser extent impregnated with lignin, a hard polymer that provides stiffness and resists compressive forces. Of these, the two phenylpropanoid units guaiacyl and syringyl are the most important monomers of the lignin of trees. Conifer wood lignin consists almost exclusively of guaiacyl monomers, whereas hardwood lignin consists of approximately equal proportions of guaiacyl and syringyl. The proportions of these monomers vary between individual cell types. For example, water conducting cells such as the vessels and tracheids, and the middle layer in the cell walls, have a very

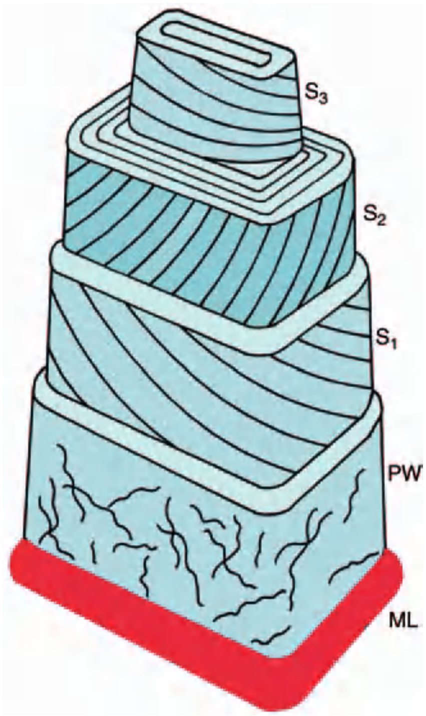


Figure 3 Conventional cell-wall model which distinguishes five cell-wall layers. These are the middle lamella (ML), the primary wall (PW), and the three-layer secondary wall (S): outer (S_1), middle (S_2), and inner secondary wall layer (S_3). The sloping lines indicate the angle of cellulose microfibrils. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

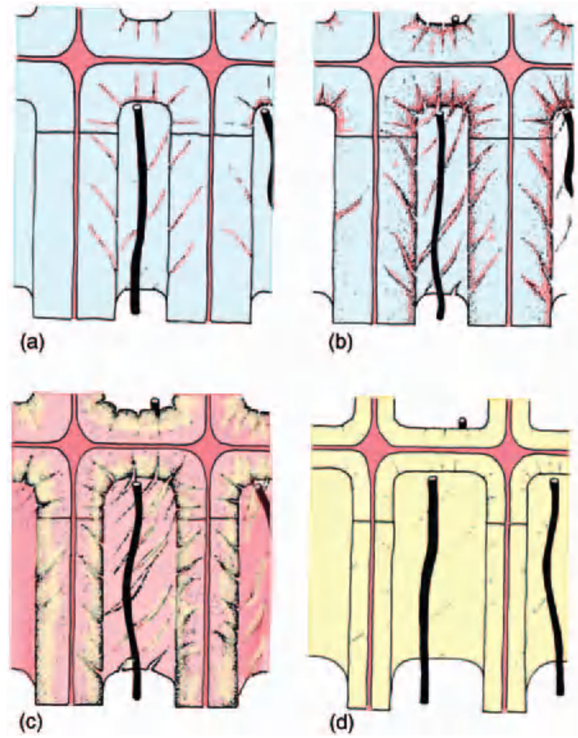


Figure 4 Different stages of brown rot. (a) In early stages enzymes (stippled) penetrate radially into the cell wall from hyphae of *Fomitopsis pinicola* growing in the lumen. (b) At a more advanced stage, enzymes have penetrated into the secondary wall, resulting in the extensive degradation of hemicellulose and cellulose. (c) As cell-wall volume decreases many cracks and clefts appear. (d) At an advanced stage a matrix of modified lignin persists. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

high concentration of guaiacyl and thus are particularly resistant to most soft-rot fungi.

Types of Wood Decay

Brown Rot

Brown rots, in which cellulose and hemicelluloses are broken down with little or no overt breakdown of lignin, are caused exclusively by basidiomycetes. This class contains many families, though the majority of the brown rot fungi belong to the family of the Polyporaceae. Moreover, they are predominantly associated with conifers, whereas most white rot fungi are associated with broadleaved trees. The correlation of brown rots with conifers coincides with the predominantly northern distribution of these fungi compared with the preferential tropical distribution of white rots. In brown rot, cellulose and hemicelluloses are broken down in the wood substrate, while lignin remains preserved in a slightly modified form. In contrast to white rot fungi, most brown rot fungi lack extracellular phenoloxidases. Because of the preferential degradation of carbohydrates, the decayed wood acquires a brittle consistency, breaks up into cubes, and finally crumbles into powder. The modified lignin gives the decayed wood its characteristic color and consistency.

The breakdown of cellulose by brown rot fungi has been postulated to involve not only enzymes but also a nonenzymic system. In this system, hydrogen peroxidase and iron cause oxidative reactions in the cellulose molecule, thereby enhancing the activity of enzymes (endocellulases) which split the molecule at random points along its length. As a result, the cellulose microfibrils are cut into short lengths, so that a dramatic loss of tensile strength occurs within a very short period of exposure to the brown rot process. The enzymes can then make energy and carbon available to the fungus by further breaking down the remaining short chains and their constituent glucose subunits.

Brown rot fungi cause some alterations of lignin, but lack the enzymes to break it down substantially. Their hyphae cannot erode the lignified cell wall from the lumen outwards, especially since the innermost layer of the wall, the S_3, is especially resistant to physical penetration (**Figure 4**). Thus the cellulose-degrading secretions of brown rot fungi have to diffuse into the cellulose-rich S_2 layer within the cell wall. Sufficient diffusion can occur from even a single hypha to cause breakdown of a substantial proportion of the cell wall material (**Figure 4**). The partial alteration of lignin may facilitate this diffusion, since the intact cell wall is thought to be impervious to large molecules such as enzymes. However, the molecules of the nonenzymic system, which break open the cellulose chain, are thought to diffuse through the cell wall even when lignin is unaltered.

The ontogeny of wood decay by brown rot fungi is uniform, apart from a few exceptions such as *Fistulina hepatica*. The reason for this is presumably the adaptation of these fungal species to the relatively simply structured softwood of conifers, and their restricted ability to degrade lignin. In contrast, white rot fungi, which preferentially occur on broadleaved trees, exhibit an extraordinary diversity in the ontogeny of wood decay.

White Rot

White rots are caused both by basidiomycetes and by certain ascomycetes. The common feature of all these fungi is that they can degrade lignin, as well as cellulose and hemicelluloses. However, the relative rates of degradation of lignin and cellulose vary greatly according to both species of fungus and the conditions within the wood. As with brown rots, there is additional variation related to the preferential decay of different zones within the annual ring. The adaptation of white rot fungi to the much more heterogeneously structured wood of broadleaves, plus their ability to degrade all the cell wall constituents extensively, leads to a multiplicity of different patterns of wood decay. Within this range of variation, two broad devisions are widely accepted: selective delignification and simultaneous rot. White rot fungi degrade lignin by an oxidative process which involves phenoloxidases such as laccase, tyrosinase, and peroxidase. They degrade cellulose in a less drastic way than brown rot fungi, since their cellulolytic enzymes attack the molecule only from the ends, splitting off glucose or cellobiose units. This reduces tensile strength only gradually, unlike the breakdown of cellulose in brown rots, which occurs at random points.

Selective delignification In selective delignification, lignin is degraded earlier in the decay process than cellulose or hemicellulose. The hyphae, which are responsible for secreting the lignin-degrading enzymes, grow in the cell lumina in some cases, so that the lignin is dissolved out of the adjacent cell wall. In other cases, the hyphae penetrate the compound middle lamella between the cells and delignify it so that the cells tend to separate. As indicated above, cellulose is left relatively unaltered during selective delignification, at least in the early stages of decay. The resulting residual material is stringy in texture, having lost much of its stiffness and hardness while retaining considerable tensile strength. This contrasts very much with brown rots in which cellulose is removed while lignin remains, leaving a very brittle residue.

Many of the fungi that cause selective delignification tend to do so in discrete pockets which show up paler than the surrounding wood due to the high concentrations of cellulose that remain within them. An example of this 'white pocket rot' is caused by *Phellinus pini* or *Grifola frondosa*. When present in otherwise dark-colored heartwood, such pockets are particularly striking, showing up as bright, white scattered zones. It is not surprising that this remarkable pattern was one of the first types of decay investigated.

The different patterns of cell wall degradation during selective delignification can be observed in

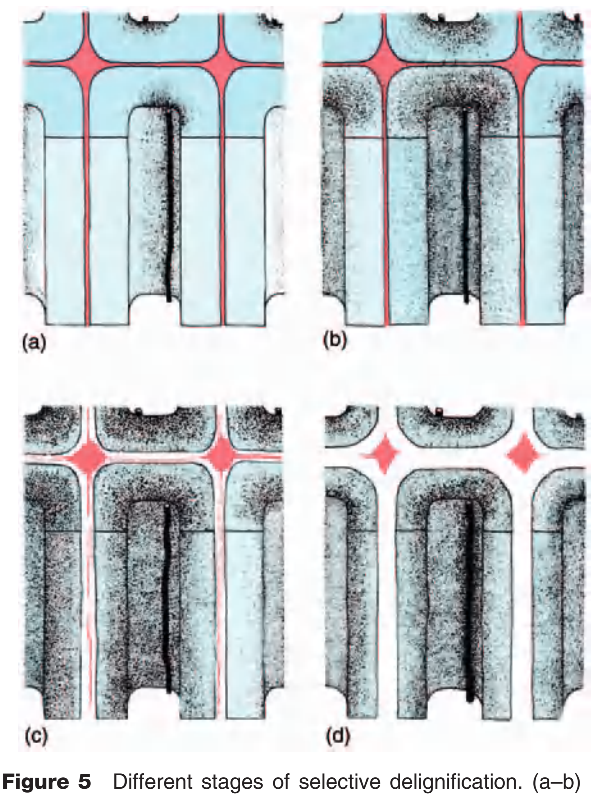


Figure 5 Different stages of selective delignification. (a–b) In early stages enzymes diffuse into the secondary wall from hyphae of *Heterobasidion annosum* growing in the cell lumen. Delignification extends from the secondary wall into the middle lamella. (c–d) During advanced stages, preferential degradation within the highly lignified middle lamellae results in the separation of single cells from one another. Cellulose remains intact during initial stages of decay. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

Figure 5. Initially degradation of the middle lamella, occurring in conjunction with extensive lignin degradation in the secondary wall, is apparent. At an advanced stage individual cells become separated from their matrix. Moreover, extensive delignification may occur in the S_2 layer, leading to the accentuation of radial structures within the secondary wall (S_2).

Although selective delignification is usually associated with cellulose degradation in wood, extreme forms of this type of decay are well known. From the temperate rainforests of southern Chile a type of wood decay which is called *palo podrido* is known. This is a name for decayed tree stems which are used as cattle fodder in southern Chile. Chemical analyses have shown that the wood of some decayed tree stems consists of 97% cellulose and merely 0.9% lignin. Native peasants in southern Chile use the term *palo blanco* for this incredibly white wood, whereas *palo podrido* is a general term for delignified wood.

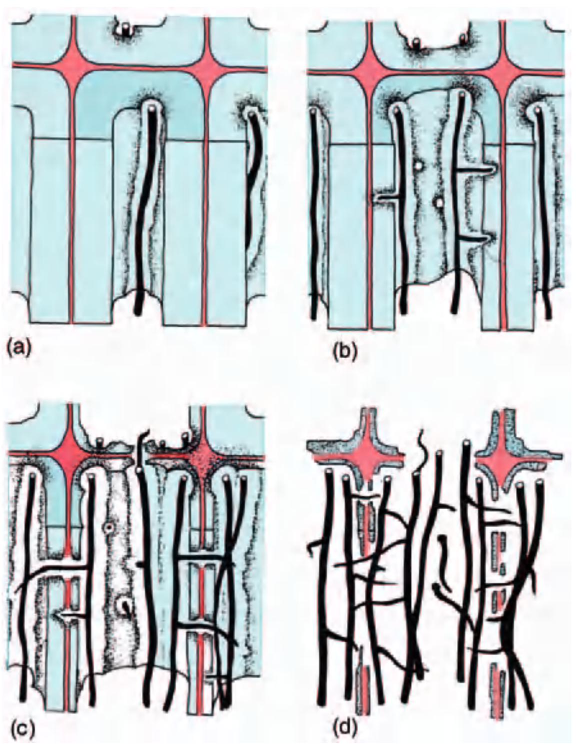


Figure 6 Different stages of simultaneous rot. (a) In early stages, degradation of the secondary wall occurs in the immediate vicinity of the hyphae. (b) The cell wall is progressively broken down from the lumen outwards. Individual hyphae of *Fomes fomentarius* penetrate into the cell wall at right angles to the cell axis. (c) The cell wall becomes increasingly thinner, and numerous boreholes appear between neighboring cells. (d) At an advanced stage, degradation of the compound middle lamella commences. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

Simultaneous rot In simultaneous rot, lignin and structural polysaccharides including cellulose are degraded at similar rates by enzymes secreted by hyphae growing in the cell lumen (**Figure 6**). This form of degradation takes place close to the hyphae involved, and results in the formation of erosion troughs where they lie on the cell wall. Fungi causing a simultaneous rot comprise a large group of species which occur commonly in hardwoods, but only rarely in softwoods. The enzymes that they secrete are able to decompose all substances of the lignified cell wall. As the degradation of cellulose, hemicelluloses, and lignin occurs at nearly the same rate, the term simultaneous rot is appropriate, although the general term white rot is often applied. The coalescence of the erosion troughs induced by numerous hyphae results in a general cell wall thinning from the lumen outward (**Figure 6**). Unlike selective delignification, simultaneous rot can lead to a fairly brittle fracture because of the loss of tensile strength from cellulose degradation.

Soft Rot

Soft rots are considered to be chemically more similar to brown rots than to white rots, since they strongly decompose cellulose while leaving lignin only partially altered. Another common feature of both brown rot and soft rot fungi is the demethylation of methoxyl groups. However, the degradation of wall materials at the hyphal contact surface in soft rots is more reminiscent of white rot than of brown rot.

Although soft rot fungi are also able to degrade the lumen surface of the wood cell wall adjacent to the hyphae by erosion (type 2 attack) the formation of cavities within the S_2 layer of the secondary wall (type 1 attack) is the characteristic mechanism of cell wall degradation. Soft rot cavities are initiated by fine penetration hyphae formed from hyphae in the lumina of wood cell walls. The penetration hypha grows through the innermost S_3 layer of the cell wall to the cellulose-rich S_2 layer where it either branches and grows axially within the cell wall following the orientation of the cellulose microfibrils (**Figure 7**). Fine hyphae that exhibit branching continue hyphal extension for a short period, but then cease apical growth. At this stage a cavity is formed within the secondary wall around the fine hypha, which increases in diameter as the cavity develops. This is then followed by a further phase of apical growth at the hyphal tip, producing a needlelike proboscis hypha. This process repeats itself many times over, leading to the formation of a spiral chain of cavities within the wood cell wall, all orientated to the angle of the cellulose microfibrils and each showing different stages of cavity expansion (**Figure 7**). The repetitive start and stop pattern of apical hyphal

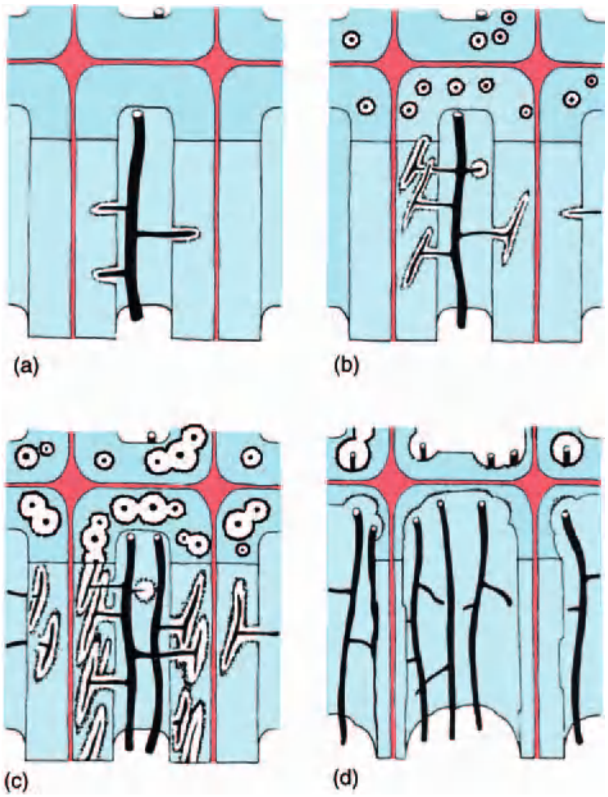


Figure 7 Different stages of soft rot type 1. (a) Penetration of hyphae into the secondary wall. (b) Branching and growth of the hyphae parallel to the alignment of the cellulose microfibrils in the S_2 layer. (c) Enzymatic degradation of the secondary wall around the hyphae results in the formation of cavities with conically shaped ends. (d) At an advanced stage of degradation by *Kretzschmaria deusta* the secondary wall is completely broken down, whereas the compound middle lamella persists. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

growth of results in gradual breakdown of the wood cell wall as the cavities expand and the secondary wall is destroyed.

Traditionally, soft rots has been attributed to deuteromycete and ascomycete fungi (e.g., *Chaetomium* spp.) and have been generally thought not to be caused by basidiomycetes. A major supposed difference between soft rot fungi and wood-degrading basidiomycetes in general is that until recently only the latter were considered to occur deep within large volumes of wood and in the living sapwood of trees. Fungi of the types that are commonly associated with soft rot are active only in the outer layers of dead wood or timber, although they can progress inwards as the surface layers become eroded. In living trees, the most significant role so far attributed to soft rot fungi has been the decay of the bases of dead branches, which results in a form of natural pruning.

Various ascomycetes are known to cause limited amounts of decay in living trees, particularly members of the Xylariaceae such as *Hypoxylon* spp. However, one member of this group, *Kretzschmaria deusta* (syn. *Hypoxylon deustum*) is exceptional in being able to cause deep-seated and extensive decay in large volumes of wood. It causes a distinctive pattern of decay in all its host species, in which many fine dark zone-lines can be seen. The ability of *K. deusta* to function as a soft rot fungus in living trees is of considerable interest, since this type of decay has not been previously thought to occur within living trees. However, one important aspect of the soft rot decay mechanism is that once fungal hyphae have penetrated into the cell wall and branched along the orientation of the cellulose microfibrils, they are able to avoid toxic compounds that may be present in the wood cell lumen. This can apply to wood preservative chemicals impregnated into the wood, but equally to natural products and extractives deposited in the lumen.

Soft rot caused by basidiomycetes Recent work has shown that the cavity-forming soft rot decay process is not exclusive to members of the lower acomycetes and deuteromycetes, but can be demonstrated in some wood-decay basidiomycets. Thus, diamond-shaped or rhomboid cavities have been found in the cell walls of wood decayed by basidiomycetes causing white or brown rots. As in true soft rots, such cavities may follow the helical course of cellulose microfibrils. However, soft rot patterns have not until recently been found in the wood of living trees degraded by basidiomycete decay fungi. Observations showed that, the basidiomycete *Inonotus hispidus*, which occurs on living trees of several genera, causing a white rot of the heartwood and sapwood, could produce internal cavities both in artificially incubated wood blocks and naturally infected wood of London plane (*Platanus* × *hispanica*) and of ash (*Fraxinus excelsior*). Other conditions that seem to favor soft-rode mode of degradation in living trees by *I. hispidus* are found within reaction zones, i.e., regions where the living cells of sapwood have reacted to fungal invasion.

Development of Decay within the Tree

As the growth of decay fungi can effectively only be observed at the anatomical level, microscopical investigations of their modes of action are essential for a better understanding of their behavior within reaction zones.

Many studies attempting to explain the limitations of colonization at the host–pathogen interface have been restricted to the description of discoloration and decay patterns in wood. Alex Shigo's CODIT-model ('compartmentalization of decay in trees') proposed that, following fungal colonization of the xylem of trees, decay columns are confined within defined compartments in the wood. Such compartments have recognizable boundaries within xylem between a region of decay and surrounding sound wood. Different types of boundary have been identified representing regions of anatomical modification and deposition of materials. Within these zones, tyloses or gummy deposits are found blocking the lumina of vessels and fibers adjacent to parenchyma. In many cases, toxic phenolic substances are present, so that hyphal growth is both physically and chemically deterred within the cell lumina, which would otherwise provide easy pathways for fungal colonization and surfaces for cell wall erosion (**Figure 8**). In response to wounding, reaction zones are apparent as areas of discoloration between healthy and infected tissue. Material deposited by the host as a defense mechanism and barrier to invasion is therefore viewed as a form of containment against ingress of air and subsequent colonization by decay fungi. Dynamically, the invasion of living sapwood at a reaction zone margin has been envisaged as a continuous process, the host tissue passing through the sequence functional sapwood, drier transition zone, reaction zone, incipient decay, and decayed wood. More recently, evidence has been obtained showing that in some

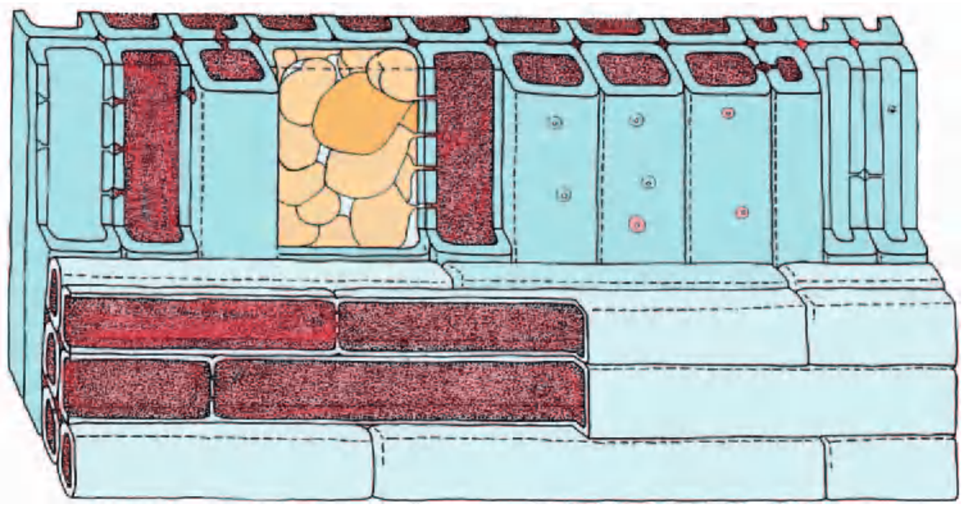


Figure 8 Schematic diagram illustrating the modified wood structure within a reaction zone of beech. Tylose formation is apparent within vessels. The inner cell wall of axial parenchyma cells is encrusted with a polyphenolic layer, whereas cell lumina fiber tracheids are occluded with abundant polyphenolic deposits. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

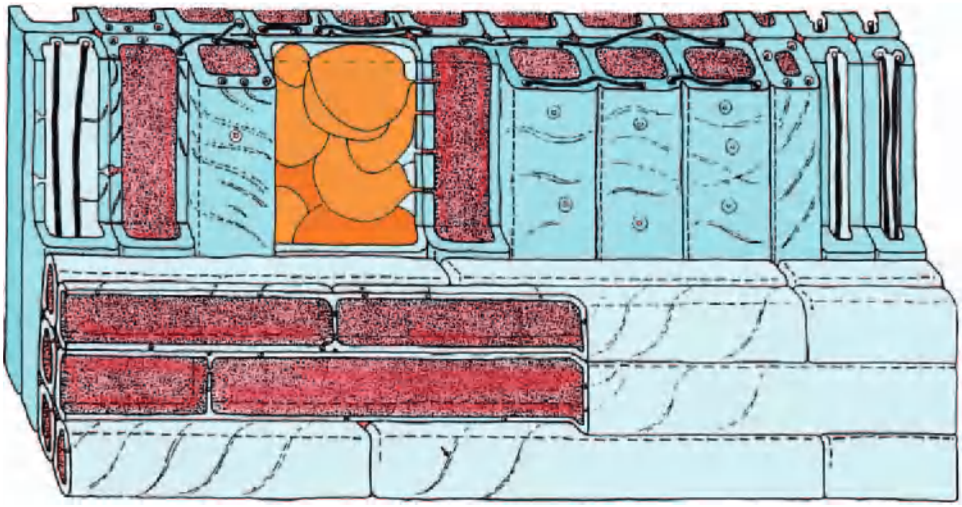


Figure 9 *Inonotus hispidus* defeats reaction zones by penetration hyphae and a soft rot mode within secondary walls of xylem ray parenchyma. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

angiosperms this sequence of continuous pathogen advance does not seem to occur. Thus, it appears that rather than forming a dynamic barrier, reaction zones essentially act as static boundaries to decay. Furthermore, this is supported by the presence of reaction zone relicts within decayed wood, indicating that the invasion of functional xylem tissues by decay fungi in these trees is discontinuous.

The fact that reaction zones can be breached by fungi and the nature of the mechanisms by which this occurs have particular relevance in understanding the invasive potential of decay fungi in standing trees. Knowledge of these mechanisms greatly improves interpretations of the dynamic interactions at the host–pathogen interface. It seems that some decay fungi can partly escape the adverse conditions within reaction zones by switching their mode of action towards hyphal colonization within the cell walls. Reaction zone penetration by *Inonotus hispidus* in London plane (*Platanus* × *hispanica*) is accomplished by forming soft-rot-like tunnels through the cell wall (**Figure 9**). A soft rot mode of growth within reaction zones apparently enables hyphae to circumvent impedances within the cell lumina. Invasion of reaction zones in beech (*Fagus sylvatica*) by *Ganoderma adspersum* is characterized by the preferential degradation of polyphenols (**Figure 10**). In contrast, *Kretzschmaria deusta* defeats reaction zones in beech by soft rot and preferential degradation of the secondary walls without decomposition of polyphenols

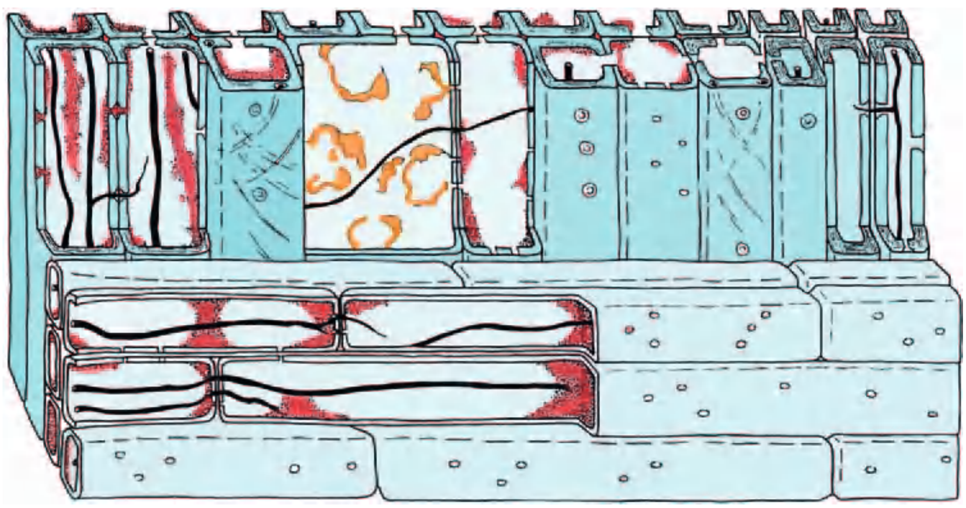


Figure 10 *Ganoderma adspersum* initially degrades polyphenols allowing subsequent hyphal growth through the cell lumina. At advanced stages of decay the fungus causes a selective delignification of the cell walls. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

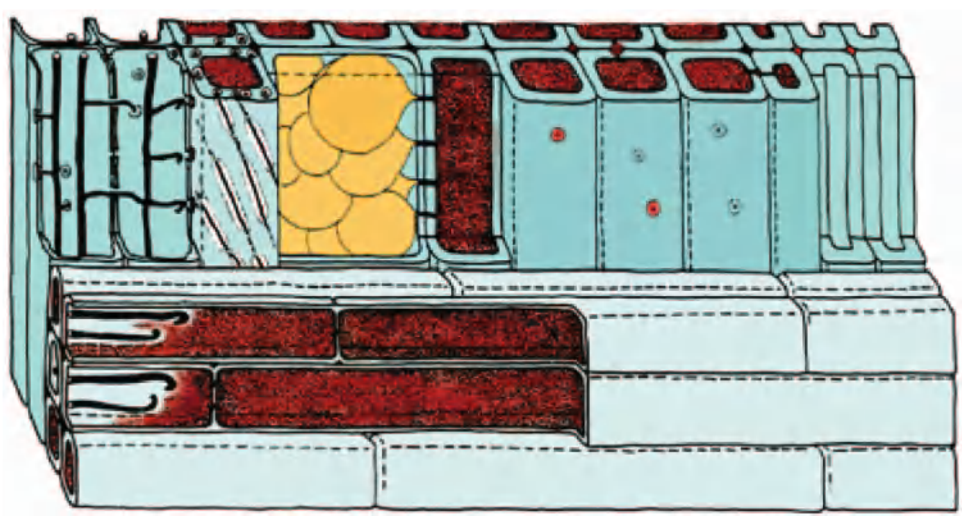


Figure 11 *Kretzschmaria deusta* defeats reaction zones by a soft rot mode without significant degradation of polyphenols. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

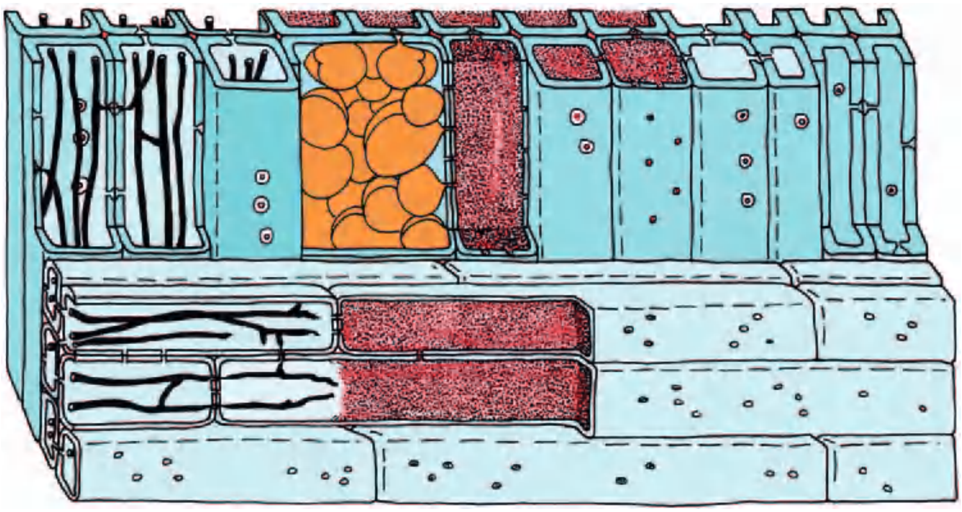


Figure 12 Hyphae of the brown rot fungus *Fomitopsis pinicola* can readily colonize and degrade cell walls of the unaltered sapwood. Due to their limited enzymatic ability they cannot readily penetrate reaction zones in beech. Reproduced with permission from Schwarze FWMR, Engels J and Mattheck K (1999) *Hozzersetzende pilze in Baümen – Stralegien der Holzzersetzung*. Rombach, Freiburg, Germany.

(**Figure 11**). Failure of *Fomitopsis pinicola* to invade and defeat reaction zones in beech is apparently related to the limited enzymatic ability and inflexible behavior of brown rot fungi (**Figure 12**).

On the basis of these observations, it is postulated that *I. hispidus* and other basidiomycetes have the ability to cause a soft rot either in addition or alternatively to their more typical mode of action, i.e., a white rot may be a common phenomenon, which may play a significant role in lesion expansion for a range of other decay fungi. By contrast, more aggressive decay fungi may have a broader enzymatic potential capable of degrading polyphenols deposited in the wood cell lumina.

The relative aggressiveness of decay fungi seems to be a function of their ability to degrade both lignin and polyphenolic compounds formed in response to lesion expansion in the wood. The fact that less-invasive fungi appear to avoid polyphenolic deposits by tunneling into the cellulose-rich regions of the wood cell wall and do not display an ability to penetrate through the lignin-rich middle lamella adds weight to this view.

See also: **Pathology**: Diseases of Forest Trees; Root and Butt Rot Diseases. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Eriksson KEL, Blanchette RA, and Ander P (1990) *Microbial and Enzymatic Degradation of Wood and Wood Components*. Berlin: Springer-Verlag.

Pearce RB (1997) Antimicrobial defences in the wood of living trees. Tansley Review no. 87. *New Phytologist* 132: 203–233.

Rayner ADM and Boddy L (1988) *Fungal Decomposition of Wood: Its Biology and Ecology*. Chichester, UK: John Wiley.

Schwarze FWMR and Baum S (2000) Mechanisms of reaction zone penetration by decay fungi in beech wood. *New Phytologist* 146: 129–140.

Schwarze FWMR, Engels J, and Mattheck C (2000) *Fungal Strategies of Wood Decay in Trees*. Heidelberg, Germany: Springer-Verlag.

Schwarze FWMR, Lonsdale D, and Fink S (1995) Soft rot and multiple T-branching by the basidiomycete *Inonotus hispidus* in ash and London plane. *Mycological Research* 99: 813–820.

Shigo AL and Marx HG (1977) *Compartmentalization of Decay in Trees*. Durham, NH: US Department of Agriculture Forestry Service.

Disease Affecting Exotic Plantation Species

M J Wingfield, University of Pretoria, Pretoria, Republic of South Africa

Introduction

Tree pathogens in natural forests are typically in balance with their environment. This delicate balance can easily be disturbed through the introduction of an exotic pest or pathogen (*see* **Pathology**: Diseases of Forest Trees). In natural forests, pathogens play an important role in maintaining genetic diversity of the tree species in these ecosystems. They are also important in removing weak trees from the forests and contribute to decomposition of forest biomass. Thus, management of natural forests, especially for commercial forestry, is complicated and often poorly understood.

Plantation forestry is a relatively modern undertaking and has been practiced for just over 100 years. These forests are primarily propagated to produce solid-wood products for construction, fuelwood, or secondary products such as charcoal, pulp, and paper. Demand for some of these products has grown rapidly during the course of the last century and huge commercial industries are now based on plantation forestry.

Plantations are established either using native or exotic species. In the northern hemisphere, the tendency has been to establish plantations of native species such as loblolly (*Pinus taeda*) and slash (*P. elliottii*) pines in the southeastern USA, scots pine (*P. sylvestris*) in Europe and various species of *Populus* in North America and Europe. In contrast, huge plantation areas have been established in the tropics and southern hemisphere using primarily exotic species of *Pinus*, *Eucalyptus*, and *Acacia*. These include *Pinus radiata* in Australia, Chile, and New Zealand, *P. patula* in Southern Africa, *P. taeda* in Brazil, hybrids of *P. elliottii* and *P. caribaea* in Australia and South Africa, *Eucalyptus grandis* and hybrids of this and other species in Brazil, South Africa and Southeast Asia, *E. globulus* and *E. nitens* in Chile, and *Acacia mangium* in various parts of Southeast Asia.

There are fundamental differences between natural forests and trees grown and managed intensively in plantations. Natural forests are typically made up of a mixture of species. In some ecosystems, such as the boreal forests, this can be a relatively small number of species, while others such as tropical forests include a great diversity of species. This is very different to the composition of plantations of exotic species where uniform families or even single genotypes are planted across extensive areas.

The establishment of plantations of exotic tree species in the tropics and southern hemisphere has been hugely successful. Growth and yield generally surpass those obtained in plantations using native species and the performance of the exotic trees has been likened to that of weeds. Although the reasons for the superior performance of exotic trees in plantations can be debated, there is substantial evidence to suggest that this is strongly linked to the so-called pest and pathogen release hypothesis. Here, the trees have been released from their natural enemies and are able to grow vigorously in the absence of competition. Indeed, in many cases, a problem with exotic tree species is that they commonly ‘escape’ from plantation lands and establish themselves as serious weed plants in natural ecosystems.

The absence of pests and pathogens has provided forestry companies growing exotic trees with a valuable window of opportunity. However, pathogens have gradually appeared in these plantations and in some cases they have resulted in considerable loss. These losses are usually exacerbated due to the large areas planted to single species where the trees are often genetically related. There are thus examples where the tree species being grown has had to be abandoned due to the appearance of a serious disease problem.

Examples of Diseases in Exotic Plantations

Diseases affecting exotic plantation forestry occur in two distinct categories. These include those caused by exotic pathogens, which have usually originated on the trees or related tree species in their areas of origin. Alternatively, they are caused by pathogens native to the new environments in which the trees have been established. In some instances, the pathogens are well known in their areas of origin or elsewhere in the world and their appearance in new environments might even have been predicted. However, in many situations, native pathogens are unknown in their areas of origin because they are not associated with an obvious disease problem or a commercially important species of tree. This often means that the source of a pathogen affecting exotic tree species is unknown and complex molecular genetic studies are required before its origin can be discovered.

Generally, when plantations of exotic tree species have been established in areas where very closely related native species grow naturally, serious disease problems have emerged. Thus, although different, the exotic tree species are sufficiently similar to the native trees to enable pathogens to move on to them. For example, where European *Pinus* spp. have been planted in areas of the USA that has a diverse ecosystem of native *Pinus* spp., serious disease and pest problems have been experienced on the exotics. Likewise, where *E. globulus* has been planted as an exotic in western Australia, these trees have been severely infected by a wide range of pathogens, presumably originating on nearby native *Eucalyptus*.

Diseases Caused by Native Pathogens

There are many examples of diseases of exotic plantation trees that are caused by native pathogens. Amongst the first of these to be discovered were root pathogens such as species of *Armillaria*, *Ganoderma*, *Heterobasidion annosum*, and *Phytophthora* that tend to have wide host ranges. However, in recent years, numerous examples of native stem and shoot pathogens that infect exotic plantation trees have emerged. Some of these were thought to be reasonably host-specific but this is clearly not the case. Now it is of particular concern that these 'new' pathogens that have become adapted to infect the exotic species might be accidentally introduced into areas where the trees are native. Such situations where native trees are invaded by exotic pathogens could lead to epidemics of a magnitude equivalent to chestnut blight and Dutch elm disease, discussed elsewhere (*see* **Pathology**: Insect Associated Tree Diseases). This section includes a selection of examples of native pathogens that have caused serious disease problems in plantations of exotic tree species.

***Armillaria* root rot** Armillaria root rot is a well-known disease of woody plants that can be caused by one of numerous species of *Armillaria*. Most of these fungi have wide host ranges and are best known in the northern hemisphere, where disease centers in native forests caused by single clones of the pathogen can become very large. *Armillaria* spp. such as *A. ostoyae* have thus gained notoriety for representing the largest and oldest living organisms on earth.

Armillaria spp. are native in natural woody ecosystems, generally killing weakened trees and moving through the soil via bootlace-like rhizomorphs. When trees have been felled to provide land for planting exotics, stumps are colonized by the *Armillaria* spp. The fungus thus acquires energy (inoculum potential), enabling it to infect healthy trees adjacent to the colonized stumps. Large numbers of newly planted seedlings can be killed in this way and it can be virtually impossible to establish stands without removing the source of inoculum.

In more established trees, infection centers usually originate from colonized stumps of felled trees. Infection passes from one tree to another via root contacts or by rhizomorphs. This can result in large disease centers that continuously increase in size, during the rotation.

Armillaria spp. have been amongst the first pathogens noted after the establishment of exotic tree species, generally but not exclusively in plantations of *Pinus* spp. For example, *A. limonea* and *A. novae-zealandiae* have resulted in serious losses to newly established stands of *P. radiata* in New Zealand. Similarly, *A. limoneae* and *A. luteobubalina* are associated with *P. radiata* establishment problems in Chile. In South Africa, *A. fuscipes* has caused serious losses in newly established plantations of various *Pinus* spp., but especially *P. elliottii* and *P. patula*.

Eucalyptus rust Rust diseases are caused by a group of pathogens generally known to be highly host-specific. These fungi tend to have complex life cycles and many have both primary and alternate hosts, which bear different parts of these life cycles. Amongst the three most important genera of trees grown as exotics in plantations, *Pinus* spp. have the largest number of rust diseases. It is thus interesting that none of these have appeared on exotic *Pinus* spp., grown in the tropics and southern hemisphere. *Eucalyptus* is a very large genus including more than 600 species, mostly native to Australia. It is thus interesting that no rust diseases are known on these trees in their native environment.

Puccinia psidii that causes eucalyptus rust is an unusual pathogen. This fungus is native in South and Central America where it occurs on various genera and species of native Myrtaceae. The fungus has, however, developed the capacity to infect *Eucalyptus* spp. In countries such as Brazil and Uruguay it has caused severe damage to these trees, especially in young plantations of susceptible species. As trees become older, they are less severely damaged by the pathogen and thus, established plantations are not considered at risk due to rust.

The eucalytpus rust pathogen is widely considered to be amongst the most important threatening organisms linked to forestry. This is collectively because rust fungi have powdery spores that facilitate spread, and the fact that some native Myrtaceae, especially in Australia, are highly susceptible to this pathogen. Accidental introduction of *P. psidii* into that country could have disastrous consequences for the natural environment.

***Ceratocystis* wilt** *Ceratocystis* species are well-known pathogens of woody plants and many cause important wilt diseases. Examples include the causal agents of oak wilt, *Ceratocystis fagacearum*, and sapstreak of sugar maple and other hardwood trees caused by *C. virescens*. These fungi are primarily dispersed by casual insects such as flies and picnic beetles (Coleoptera: Nitidulidae), which are attracted by the fruity aromas produced by the fungi, sporulating on infected trees. The insects are attracted to the sap produced by fresh wounds, and in this way the fungi enter the vascular systems of trees (*see* **Entomology**: Sapsuckers). Because infections lead to the blockage of sap flow, these fungi tend to kill trees relatively rapidly.

Ceratocystis wilt is a relatively newly discovered disease in plantations of exotic trees. *C. albofundus* was the first species belonging to the group shown to cause a rapid wilt disease of trees. This fungus infects wounds on exotic *Acacia mearnsii* (black wattle) and *A. dealbata* (green wattle) in South African plantations. Large numbers of trees can be killed rapidly and this is the most important disease of *A. mearnsii* in South Africa. There is good evidence to show that *C. albofundus* originated on native Proteaceae in South Africa. This is unusual given that Proteaceae are very distantly related to *Acacia* spp. The fungus has not been found in Australia and might pose a threat to native *Acacia* spp. in that country.

Ceratocystis fimbriata is a well-known wilt and canker pathogen on many forest and fruit trees. This fungus has recently been discovered to cause rapid wilt and death of *Eucalyptus* spp. in Brazil, Uruguay and the Congo. Phylogenetic studies have shown that the fungus in the former two countries is probably native, but it appears to be exotic in the Congo. There is no evidence that *C. fimbriata* occurs in Australia. Thus, strains of the fungus that infect *Eucalyptus* elsewhere in the world are clearly threatening to native stands of these trees.

Diseases Caused by Introduced Pathogens

Many pathogens found on exotic plantation trees are thought to have been introduced from the areas of origin of these trees. As mentioned previously, these assumptions could be incorrect given that the origin of most pathogens has not been established experimentally. Relatively large numbers of foliage pathogens occur on exotic plantation trees such as *Eucalyptus* and they are assumed to have been introduced into the new areas on contaminated seed. Many are relatively unimportant and have been afforded little attention.

Most of the more serious diseases of exotic plantation trees are caused by introduced pathogens. Some have been present in exotic plantations for many years and others have appeared relatively recently. New introductions continue to occur regularly and this is a trend that is not likely to change. The following examples have been selected based on relative importance and to reflect differences in infection strategy and host range.

Diplodia canker and dieback of pines In most countries where species of *Pinus* have been established as exotics in plantations, *Diplodia* canker and dieback caused by *Diplodia pinea* (also known as *Sphaeropsis sapinea*) was the first disease to be recorded. This is apparently due to the fact that the fungus is seed-borne and was, therefore, introduced into new areas probably close to the time of plantation establishment. The fungus is found in every country where pines are grown as exotics. Contemporary studies have shown that those countries that have restricted the importation of seed have populations of the pathogen with lower levels of genetic diversity than those where more regular seed introductions have been made.

For many years, *D. pinea* was thought to be a secondary, wound-infecting fungus. In contrast, recent research has shown that the fungus is a common latent pathogen in asymptomatic pine tissue. Onset of disease is closely linked to environmental stress such as drought, cold, poor site-species matching, and hail damage. The fungus is perhaps best known in South Africa where the highly susceptible *Pinus patula* is widely planted and commonly damaged by hail storms. A combination of latent infections by the pathogen, together with the susceptible species and hail damage, can lead to the death of very large areas of trees.

Dothistroma needle blight In exotic plantation forestry, *Dothistroma* needle blight caused by *Dothistroma septospora* is perhaps the best-known disease. This is due to the tremendous damage that it has caused to *P. radiata* plantations in Africa, South America, Australia, and New Zealand, particularly during the 1960s and 1970s. Many plantation programs based on this tree species were abandoned, especially those in Africa where the climate was highly conducive to infection by *D. septospora*.

Dothistroma septospora is native to the northern hemisphere where it is well known and occurs in both its sexual and asexual forms. In many areas, the fungus is relatively unimportant but there are examples of severe damage to plantations and ornamental *P. ponderosa* in the USA and *P. nigra* where it is grown as an exotic in the USA and plantations in some parts of Europe. The fungus was first discovered in exotic *P. radiata* plantations in Africa in 1957 and it rapidly spread to other areas such as Australia, New Zealand, and Chile, where *P. radiata* was being intensively propagated. The disease remains important in these areas and wide-scale aerial spraying continues to be used to reduce the impact of the disease.

Mycosphaerella leaf blotch on Eucalyptus Many species of *Mycosphaerella* infect the leaves and green branches of *Eucalyptus* spp. In exotic plantations, these fungi have been amongst the first to be recorded associated with disease. Although there is no experimental evidence to substantiate this, observations regarding disease occurrence suggest that these fungi are seed-borne and that they have been widely distributed together with seed used for plantation establishment.

Most *Mycosphaerella* spp. on *Eucalyptus* appear to be relatively unimportant. However, some species, such as *Mycosphaerella nubilosa*, have caused serious defoliation of juvenile leaves of *E. globulus* in South Africa and West Australia. *Eucalytpus nitens* is also severely damaged by this fungus in South Africa. *Mycosphaerella nubilosa* is well-known on native *Eucalyptus* in Australia and this is certainly the origin of the fungus. In contrast, *Phaeophloespora destructans*, which phylogenetically is an asexual state of a *Mycosphaerella* species, is of unknown origin and causes serious shoot and leaf blight on various *Eucalyptus* spp. including *E. grandis*, *E. urophylla*, and *E. camaldulensis* in Indonesia, Thailand, and Vietnam. This fungus was first found in Sumatra and it has gradually spread southwards. It was possibly introduced into the area from Australia or other parts of Indonesia where *E. urophylla* is native, or it has moved on to *Eucalyptus* from some other host. Irrespective of its origin, *P. destructans* has become one of the most important pathogens of *Eucalyptus* and it now threatens plantation programs elsewhere in the world.

Pitch canker Pitch canker has become one of the most important diseases threatening exotic pines in plantations. The disease (*see* **Pathology**: Stem Canker Diseases) is caused by *Fusarium circinatum*, which is known in its sexual state as *Gibberella circinata*. This fungus was discovered for the first time in the southeastern USA in 1945 on *P. virginiana* and it has caused occasional outbreaks of disease in that area. More recently, the fungus appeared in California where it was discovered causing branch and stem cankers on *P. radiata* planted along streets and in parks. The disease has spread rapidly to trees in natural stands where it has caused very serious damage and possibly threatens *P. radiata* in its native range.

The pitch canker fungus requires wounds to infect trees. These wounds can arise from physical damage to trees, for example, by wind and forestry operations. Insects are also associated with infection and these include cone- and shoot-infesting bark beetles (Scolytidae) and weevils (Curculionidae), as well as lepidoptera that damage shoots. When infections reach the main stems, parts of trees above the stem cankers and often whole trees will die. The name ‘pitch canker’ refers to the deep resin impregnation of the wood associated with infections.

The pitch canker fungus was first discovered in exotic pine plantations in South Africa in 1991. In this situation, it caused extensive losses to *P. patula* seedlings in a major pine production nursery. The fungus has subsequently spread to virtually all pine-producing nurseries in this country and it has also recently been associated with serious losses associated with the establishment of new lands. The pitch canker disease, typified by infections on aboveground parts of trees, has not been seen and, strictly speaking, pitch canker disease does not occur in South Africa.

A situation very similar to that in South Africa has recently been discovered in Chile. Here, *P. radiata* plants in nurseries are severely damaged by *F. circinatum*. The disease affects seedlings in containers and open-rooted nurseries, and most importantly, valuable clonal hedges used to produce clonal cuttings. Infections of established trees in plantations have not been seen in Chile. However, the presence of various primary insects, such as shoot moths known to be associated with pitch canker in the southeastern USA, suggests that it is only a matter of time before the disease appears in plantations.

An early hypothesis from the southeastern USA was that the pitch canker fungus might have originated in Haiti. Recent studies using DNA-based markers have shown that the fungus in California probably originated in the eastern USA. The fungus in South Africa most probably originated in Mexico, where the disease is now well-known on native *Pinus* spp. Pitch canker is known to occur in Japan, and has recently been found in Korea and in Spain. All indications are that *F. circinatum* is spreading around the world, presumably on seed, which is known to carry the fungus. Countries such as New Zealand and Australia, with substantial resources of susceptible *P. radiata*, have instituted rigorous legislation to prevent the introduction of the pathogen.

Phytophthora root rot Phytophthora root rot is a well-known disease of woody plants and can be caused by numerous species of *Phytophthora*. These fungi are unusual in that they belong to a group of organisms that are not strictly fungi (Kingdom: Stramenopila). They are soil-borne and produce structures enabling them to survive in the soil for extended periods of time. They also produce motile spores that are water-borne and move through the soil–water interface. Contamination of new areas can occur easily through the movement of soil or contaminated irrigation water.

Phytophthora spp. generally infect the feeder roots of plants and give rise to a slow decline as these infections move towards the root collars of trees. In exotic plantation forests, they are often moved into newly established areas with infected plants from nurseries. Trees can die during the first year after planting but more commonly die after 2 years or more. Disease distribution tends to be scattered in plantations. Where highly susceptible trees are planted in infected lands, they too become infected.

By far the best known *Phytophthora* species is *P. cinnamomi*. This fungus has a very wide host range and is thought to be native to Papua New Guinea, although the origin of the fungus has been deeply debated. It has caused serious losses in plantations and wind breaks of *P. radiata* in Australia. In South Africa, important species of *Eucalyptus* such as *E. fastigata*, *E. fraxinoides*, and *E. smithii* have been severely damaged.

Management of Diseases in Plantations

Many opportunities exist to reduce the impact of diseases in exotic plantations. Thus, quarantine measures to prevent the introduction of new pathogens are among the most important approaches to disease management. Eradication of pathogens after early detection might, in some cases, also be possible. Chemical control has been very successful in the case of some foliar diseases such as *Dothistroma* needle blight, where aerial spraying of fungicides has been used for many years.

Of all the approaches to disease control in exotic plantations, minimization through breeding and selection of pathogen-tolerant planting stock is most important and widely used. Considerable success has been achieved in reducing the impact of diseases through matching species to sites and planting species tolerant of the diseases, in areas where these diseases occur. Classical forest genetics has contributed substantially to the improvement of exotic plantation forestry as well as to disease resistance. Large industrial corporations that are involved in plantation forestry have generally invested in forest genetics programs and especially in ensuring access to a wide range of provenances of desired tree species. Breeding programs have also moved rapidly towards producing hybrids between species. They have thus been able to capitalize on hybrid vigor and to gain the advantages of a mixture of traits not available in single species. Hybrids have also been very useful in combatting various disease problems.

Contemporary trends are to produce clones of the best-performing genotypes and, after thorough testing, to deploy them on sites where they will grow best. Consequently, in some areas, plantation forestry has become technologically advanced, using techniques such as tissue culture and somatic embryogenesis to multiply clones. Management of clonal forests is complicated and, from a disease standpoint, maintaining reliable plantation records and establishing safe numbers of clones to plant is important. Thus, large corporations rely on geographic information systems to determine planting strategy and to ensure effective disease avoidance or resistance.

Genetic modification of exotic plantation trees to improve traits including disease tolerance and resistance is being actively pursued at the experimental level. Various genes associated with disease resistance are available and these have been transformed into trees such as *Eucalyptus* and *Pinus* that are widely grown as exotics in plantations. Tissue culture protocols are widely available for these trees, thus facilitating genetic modification. Clonal forestry and experience in deploying relatively small numbers of genetically identical clones for short rotations will also positively influence opportunities to deploy genetically modified trees. However, rotations longer than those associated with agronomic crops and the fact that forest trees are wind-pollinated, potentially producing clouds of genetically modified pollen, have raised concern. As soon as the potentially negative impacts of deploying genetically modified trees have been resolved, it is likely that these trees will play an important role in minimizing the impacts of disease.

Biological control of insect pests is well established in exotic plantation forestry but has not been used commercially to reduce the impact of pathogens. There is, however, considerable opportunity in this field and recent advances in the manipulation of fungal viruses for pathogen control deserve notice. Certainly, as diseases in forest exotic forest plantations become increasingly important, and together with the negative environmental impact of most chemical fungicides, it is likely that interest in biological control will increase.

Future Prospects

Plantations of exotics, particularly in the tropics and southern hemisphere, have yielded outstanding productivity during the last 100 years. Separation of the trees in these plantations from their natural enemies has been an important component of this success. However, disease and pest problems in exotic plantations have gradually increased due to the accidental introduction of new pathogens and the adaptation of native pathogens to be able to infect the exotic trees.

In the future, it is likely that increased investments will be needed in order to reduce the impact of pathogens in plantations of exotic trees. These will be essential if the impressive productivity that has been associated with these plantations is to be maintained. New technologies, including those associated with molecular genetics and computer science, are likely to become increasingly important in ensuring the long-term sustainability of exotic plantation forestry.

See also: **Entomology**: Sapsuckers. **Pathology**: Diseases of Forest Trees; Insect Associated Tree Diseases;

Phytophthora Root Rot of Forest Trees; Root and Butt Rot Diseases; Rust Diseases; Stem Canker Diseases. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

Further Reading

Burgess T and Wingfield MJ (2002) Quarantine is important in restricting the spread of exotic seed-borne tree pathogens in the southern hemisphere. *International Forestry Review* 4: 56–65.

Crous PW (1998) Mycosphaerella *spp. and their Anamorphs Associated with Leaf Spot Diseases on* Eucalyptus. Mycologia memoir no. 21. St Paul, MN: American Phytopathological Society.

Devey M, Matheson C, and Gordon T (1999) *Proceedings of the IMPACT Monterey workshop*. Monterey California. CSIRO Forestry and Forest Products technical report no. 112. Australia: CSIRO.

Gibson IAS (1975) *Diseases of Forest Trees Widely Planted as Exotics in the Tropics and Southern Hemisphere*, Part I, *Important Members of the Myrtaceae, Leguminosae, Verbenacae and Meliaceae*. Oxford: Kew, UK: Commonwealth Mycological Institute.

Gibson IAS (1979) *Diseases of Forest Trees Widely Planted as Exotics in the Tropics and Southern Hemisphere*, Part II, *The genus* Pinus. Oxford: Kew, UK: Commonwealth Mycological Institute.

Keane PJ, Kile GA, Podger FD, and Brown BN (eds) (2002) *Diseases and Pathogens of Eucalyptus*. Collingwood, Australia: CSIRO.

Shaw CG III and Kile GA (1991) *Armillaria Root Disease*. Agriculture Handbook No. 691. Washington, DC: United States Department of Agriculture, Forest Service.

Sinclair WA, Lyon HH, and Johnson WT (1987) *Diseases of Trees and Shrubs*. Ithaca, NY: Cornell University Press.

Tainter FH and Baker FA (1996) *Principles of Forest Pathology*. New York: John Wiley.

PLANTATION SILVICULTURE

Contents

Forest Plantations

J Evans, Imperial College London, Ascot, UK

Definition

Forest plantations embrace a range of forest types, with the common feature that the majority of the trees present were established by planting (or deliberate seeding). However, this simple statement belies the fact that when mature, many planted forests can appear similar to natural forest formations. While a geometrically shaped forest monoculture of a nonnative species is plainly artificial, many old and famous forests in Europe appear natural and reveal little of their mainly planted origin. Examples include the New Forest (UK), parts of the Black Forest (Germany), parts of the Forêt de Compiègne (France), and almost all the forests of Denmark.

There is no internationally agreed definition of a forest plantation, or 'planted forest,' the expression now widely used to embrace the continuum of forest types where forest origin is known to be by planting or direct seeding. Successive international experts meeting on The Role of Planted Forests in Sustainable Forest Management in Chile (1999) and New Zealand (2003) have recommended that the question of definition be considered. This is because the boundary between planted and natural forests is often indistinct and, among countries, there are different degrees of management, and different objectives for planted forests and a complementarity between natural and planted forests.

International agreement on a definition is not finalized, but harmonization of definitions is led by the United Nations Food and Agriculture Organization (FAO) in collaboration with several other bodies. Here discussion is confined to the more obvious types of forest plantations over which few will argue, where use of formerly nonforest land, or regularity of shape, or choice of species, or intensity of management, readily points to their artificial origin. This will include afforestation, which is the act or process of creating forest land by planting trees where forest historically did not exist such as grasslands, or to stabilize sand dunes, and reforestation, where the act or process of changing previously deforested lands back to forest land is mainly by planting trees. This commonly occurs where forest is logged or clear-felled and the next crop, of the same or a different species, is established by planting.

History

Planting trees has a long history and is recorded from ancient civilizations, e.g., the Old Testament portion of the Bible. But planting trees as a way of regenerating forests used, for example, for timber production and as a means of afforestation, is more recent. In the UK significant planting dates from the sixteenth century, and the practice only became commonplace across Europe by the eighteenth century. The nineteenth century saw plantation establishment as one means of 'modern' organized forestry and in Germany it became fashionable as an efficient way of growing a uniform crop of trees. The twentieth century saw major plantation establishment, initially in temperate and Mediterranean climatic regions and, since the 1950s, to an increasing extent in the tropics and subtropics.

Tree introductions have facilitated plantation development. Many successful plantations were built on experience gained from arboreta and trials of exotic (introduced) species. Both in temperate and tropical environments, this approach yielded species that have proved amongst the most successful of all plantation species, outstanding examples of which are conifers from the Pacific Northwest of America into western Europe, *Pinus radiata* from California into southern-hemisphere countries such as Australia, Chile, New Zealand, and South Africa, teak (*Tectona grandis*) from India, Myanmar (Burma), and Thailand into many tropical countries, and several Australian eucalypts in the tropics and subtropics. Together these trees form many millions of hectares of productive forest plantations far from their native habitats.

Today forest plantations of all types probably amount to some 187 million ha or about 6% of all closed forest in the world. Exact figures are uncertain owing to variable standards between countries of recording forest plantation statistics, including the vexed issue of definition.

Future Developments

There is already a substantial resource of planted forest, and current establishment of new plantations at an annual rate of several million hectares will soon result in such forest becoming the main source of wood products. This is predicted to occur in about 30 years' time if current rates of planting continue, and possibly a little sooner if massive afforestation arises from carbon sequestration initiatives. A total forest plantation resource of 300 million ha would satisfy the great bulk of world wood requirements for the foreseeable future.

An increasing area of planted forest is only one anticipated development. The nature of planted forests is also likely to shift in balance from: (1) domination by exotic species to greater emphasis on native ones, though exotics will always play an important role; (2) a largely industrial focus to industrial, rural development, rehabilitation, and environmental roles; and (3) a single-use to multiple-use forest.

Types of Plantation

Industrial Plantations

Industrial plantations are the arable crops of forestry; their principal objective is to grow a product, usually timber, efficiently. The main purposes include fuel production – firewood and charcoal, pulpwood for paper and cardboard, panel products, sawtimber (lumber), and sometimes veneers. Commonly one plantation supplies several of these products in the course of a rotation. Other products may also arise, whether as other round timber products, or in nontimber benefits such as amenity or even biodiversity enhancement where a plantation is growing on an impoverished site. But the dominant objective is to grow a commercial product.

While most industrial plantations are successful they have largely failed in one area: the growing of high-grade cabinet timbers for furniture and similar quality uses. In temperate countries this arises from the very long rotations required and in the tropics from silvicultural difficulties with growing mahoganies and related species of Meliaceae, because of shoot borers, and the complexity of domesticating dipterocarps, merantis, and rosewoods.

Some industrial plantations of trees are grown for nontimber forest products (NTFPs) used in naval stores, gums, and resins. Although extensive, rubber plantations (*Hevea brasiliensis*) have not generally been considered as plantation forestry since their main product is rubber latex. Today such plantations are now also exploited for their wood, which is finding a ready market in the manufacture of less bulky furniture.

Industrial purpose dominates management in terms of species choice (usually only one), stocking density, thinning prescriptions, rotation length to maximize financial returns or grow crops to a particular market specification, and clearcutting silvicultural systems for efficiency of harvest.

Social and Community Plantations and Woodlots

Planting trees is one way of compensating for loss of natural forests as a means of providing domestic products such as building poles, fencing materials, firewood, and even fodder for livestock. It was widely promoted in the 1970s and 1980s in countries of the African Sahel, in India and elsewhere usually in the drier tropics, but was not always successful. Sometimes choice of species was poor, sometimes tenure and ownership of land or even of the planted trees were unclear, but commonly the problems lay in a failure to involve the local community or villagers adequately in the decision-making process.

Today tree planting for social and community needs is embraced as part of rural development forestry and is subject to participatory processes to place it firmly in local people's control. In India these are sometimes termed 'communities of protection' or community-based forest management (CBFM) in the Philippines, while in Ethiopia many planting projects begun as food-for-work initiatives during the 1980s' famine have become a village resource. Collectively these kinds of plantation projects now often form part of joint forest management (JFM) initiatives.

Social and community plantations possess many of the same features as industrial crops: they are often, but not exclusively, single species and they tend to be block plantings, though size may be as little as 0.01 ha. As well as supplying one or more products they may confer benefits of shade and shelter, amenity, and even soil erosion control.

Environmental Planting and Buffer Zones

Some plantations have been established to harness their protective functions. While it is almost always better to conserve natural woodland cover for purposes of erosion control and catchment management, where little or no forest exists tree planting can be a useful complement to the other activities, such as terracing and check dams. This can generate conflict over water use – trees generally consume more water than other land uses, and exceptionally plantations have even been used to dry swampy areas as a way of reducing stagnant water in which malaria-carrying mosquitoes breed so prodigiously.

Not all plantation species are suitable for environmental planting. For example, plantations of teak and some eucalypts develop a thin or no litter layer, are prone to ground fires, and suppress understory vegetation, all of which makes them ill-suited for soil erosion control.

Buffer zone planting is where trees are deliberately planted to take pressure away from natural forest. Trees are established in the zone around natural forest to provide an alternative source of forest products, both woody and NTFPs. In this way pressure on natural forest is eased. Also this zone assists wildlife conservation by enlarging the area of woody cover and generally discouraging people from encroaching into natural forest. It is important that such buffer zone plantings are properly managed and, for example, include fruit trees to benefit local people.

Substantial development of plantations has also taken place to combat desertification, to stabilize dunes, to act as shelterbelts and windbreaks, and related benefits.

Rehabilitating Degraded Land and Restoring Natural Forest

Since about 1990 a number of cases have demonstrated that, under certain conditions, the recreation of a woodland environment by planting trees can act as a precursor for recovery, restoration, or regeneration of natural forest formations. Plantations suppress vigorous weeds, especially grasses; internally they bring a more equable microclimate; and generally they provide conditions often more conducive to regeneration of trees. In this sense plantations are an intermediate stage between (say) farmland and natural forest and help the process of forest restoration. The importance of such restoration often makes it eligible for funding from the Global Environment Facility (GEF).

A prominent example are the thousands of hectares of *Cordia alliodora* plantations in Ecuador which have led to successful natural regeneration in the understory of native rainforest hardwoods of *Virola* and *Brosimum* spp. In Ethiopia plantings of exotic pepper trees (*Schinus molle*) eucalypts (mainly *E. camaldulensis*) and silky oak (*Grevillea robusta*) on a woodland scale have led to rapid recolonization and recovery of native acacia (*Acacia abyssinica* and *A. tortilis*) and *Erythrina variegata* within the plantation area.

Enrichment Planting

Degraded natural forest is sometimes enriched by planting desirable tree species. Where the proportion of planted trees constitutes less than 50% of the forest, it is not considered to be a plantation. As a silvicultural system it is less common today than 30 years ago owing to expense in maintaining planted trees and, generally, indifferent success.

Carbon Sequestration

To date few plantations have been deliberately established to store carbon as one means of mitigating the rise in atmospheric carbon dioxide, which is partly responsible for global climate change. It is likely that carbon trading and financing under clean development mechanism (CDM) schemes will emerge and lead to increased investment in afforestation and reforestation. Should such plantations be established, and predictions are as high as 100 million ha worldwide in the next 50 years, the object of management will be to maximize carbon sequestration. Such plantations could potentially supply wood products, and possibly other benefits as well, but will inevitably have substantial land-use and people-related impacts.

Amenity Planting

Some tree planting has the principal objective of providing esthetic and recreational values to the urban and periurban environment. Such plantations may also provide some timber products and, where the previous land was impoverished, will enrich wildlife values too.

Plantation Silviculture

Characteristics

A feature of almost all forest plantations is that, at least for the first rotation, they are established in even-aged blocks usually of one species (monoculture). While there are many exceptions, these features of even age and single species simplify management but may increase the risks of damage from biotic and abiotic sources.

Plantations also tend to be regular in shape, with boundaries commonly following the artificial and often straight legal boundary to a property or area of land.

Species Choice

The first consideration is the objective of the plantation and what the main purpose of tree planting is. This, along with issues such as intensity of management, will largely determine what species are selected.

Much care is taken to match tree species with plantation site conditions. Commonly introduced (exotic) species are used when they offer greater productivity than the native alternatives. Many examples were cited earlier. It is clear that choice of species alone is insufficient to achieve optimum productivity, and seed origins and provenances from across the range of a potentially suitable species, as well as the fruits of selection and breeding programs, require investigation.

Understanding site is equally important and sophisticated analytical tools now exist, such as climatic mapping and environmental analysis, to characterize site and its potential for tree growth.

Establishment, Management, and Protection

Forest nurseries Almost all planted forests, as the name implies, are established by planting trees. These are young trees, usually grown in a forest nursery for 6 months to 3 years, depending on species and locality, to produce a plant typically 15–50 cm tall which is hardened off and taken to the planting site, which is often many kilometers from the nursery (**Figure 1**). This contrasts with most arable farming where seeds are sown where the plant is to grow.

Forest nurseries raise plants using one of two main methods: (1) either beds are prepared in the ground in which seed is sown into finely cultivated soil, and the seedlings are cared for, conditioned, and lifted to produce bare-root plants, sometimes called 'transplants'; or (2) seeds are sown individually into containers filled with a special soil-mix in which

Figure 1 Extensive plantations of spruce, mainly *Picea sitchensis* in Northern England 50 years after afforestation began. © J. Evans, 2004.

the young plants grow and are subsequently taken to the planting site still with a small root ball attached. Plants grown in containers have many names, usually depending on the kind of container system used: 'containerized plants' is sometimes used as the generic term. Typically bare-root methods are cheaper per plant, but containerized plants are more robust, surviving better in adverse conditions such as drought experienced at the time of planting.

A few plantations, such as poplar and quite often teak, are planted by inserting hardwood cuttings called 'sets' or 'stump plants.' Woody material of these species readily roots, thus allowing this form of vegetation propagation to be used.

Site preparation Sites for planting are usually degraded land or poor-quality pasture unfit for agriculture and of little conservation or other importance. Clearing existing natural forest simply to provide a site for tree planting is today strongly deprecated and is contrary to certification schemes, e.g., Forest Stewardship Council (FSC) principles governing plantation development. Of course, reforestation is a different case.

The planting site itself may need one or more of the following operations – vegetation clearance, cultivation, tillage, bedding, drainage, fertilizing, and fencing – before planting can begin. Assessment of such needs depends on local experience and evidence from research trials and is frequently one of the largest expenses in establishing a plantation. Prescriptions cannot be laid down, but the aim of such work is to undertake the minimum preparation and protection necessary to secure high tree survival and vigorous growth over a whole rotation.

Tree planting Planting is not a difficult operation, but must be done with care to insert roots into mineral soil. In most situations containerized seedlings or transplants should be inserted to root collar depth, but occasionally where water stress is a problem, deeper planting may be done to ensure root contact with moist soil. It is important that all trees are planted vertically and not left leaning at an angle. Planting takes place at the start of the wet season in the tropics and subtropics or in the fall or spring in temperate latitudes prior to leaf flush. Typically, 1000–4000 trees are planted per hectare depending on the object of the plantation.

Newly planted trees must be protected from browsing damage and from vigorous weed competition to allow trees to become well established. Weed control may be required from 1 to 5 years. Some plantations may need a single application of fertilizer to aid growth or correct a nutrient deficiency but the practice is not required on many sites. Phosphorus is the most commonly limiting nutrient for satisfactory tree growth and on many tropical sites a small quantity of the micronutrient boron is required. Application of pesticides at the time of planting is, unlike farming, the exception rather than the rule when tree plantations are planted on formerly nonforested sites. Pesticide use is sometimes required when replanting a former forest site, such as a second rotation crop, to control insects such as weevils, and in the tropics, termites and leaf-cutting ants.

If more than 20% of newly planted trees die, additional trees may be planted, a process with many names, including 'infilling,' 'blanking' and 'beating-up.' It is not worth doing more than once since delayed plantings invariably fail to catch up with the original trees and are destined to become suppressed.

Once plantations are established and are no longer suffering weed competition or damage from browsing animals, the next operation is frequently cleaning, i.e., the removal of unwanted woody growth.

Thinning and pruning Once the canopy has closed, plantations may be subject to regular thinning until the trees have reached desired final crop size. Thinning aims to remove poor trees to favor the best remaining ones and normally begins once a stand has reached 8–10 m height. Each thinning removes one-quarter to one-third of trees present at intervals of 3–10 years, depending on age and vigor of the stand, until rotation age is reached.

Pruning of side-branches may be done on the lower bole, up to 6–8 m, to produce high-grade knot-free timber. It is carried out in stages at around the time of first and second thinning.

Rotations and Regeneration

Plantations are grown for a purpose, and it is this purpose that determines rotation length. Some plantations may be managed to maximize their economic return, but more commonly trees are grown until they reach a size that is optimum for the intended market. Clearly, firewood plantations will be grown on a shorter rotation than trees grown for sawtimber (lumber) or veneer when large trees are required. Also, in plantation management, a few trees may be left much longer than the usual rotation for reasons of amenity or wildlife benefit.

In the tropics rotations can be as short as 2–3 years for small-sized products, 5–20 years for industrial products such as woodpulp, and 10–40 years for lumber-sized material. In temperate conditions rotation lengths are commonly two to five times as long.

Most plantations are clear-felled and sites replanted, the latter operation taking advantage of any genetically improved stock or even a change of species since the previous crop was established. Some plantations are regenerated naturally using seed from the preceding final crop trees or, where the species is suitable and small-sized products sought, from coppicing, i.e., forming the new crop from stump shoots (sprouts) of the felled trees. Coppicing is common for firewood and pole crops such as many eucalypt plantations in the tropics.

Plantation Yields and Productivity

Growth Rates and Yields

Because a suitable species is carefully matched with the planting site and because trees are spaced evenly to occupy the site and all are harvested, plantation productivities are usually considerably greater than that of natural forest (**Figure 2**). The typical range of yields is: 3–20 $m^3 ha^{-1} year^{-1}$ in temperate plantations, 5–35 $m^3 ha^{-1} year^{-1}$ in Mediterranean climates, and 5–50 + $m^3 ha^{-1} year^{-1}$ in the tropics and subtropics.

The main factors causing the above wide variation in plantation growth rates are tree species, fertility and exposure of site, and length of growing season, namely adequate summer warmth in high latitudes or sufficient moisture in Mediterranean and tropical regions where severity (length) of dry season is critical. Within these general climatic parameters moisture (rainfall amounts) often determines good and poor years for tree growth.

Maximum productivity from a site is also affected by stocking and for how long trees are grown. Long rotations to achieve large tree sizes for specified markets may diminish site productivity potential since older trees, while not overmature biologically, slowly decline in growth rate.

Figure 2 Plantation of native *Cordia alliodora* on abandoned ranch land in Lcuador which has led to good regeneration of other native hardwoods. © J. Evans, 2004.

In the future yields can be expected to increase owing to genetic improvement ranging from simply choosing a better provenance to possible use of genetic modification technology.

Problems with Plantations

Monoculture and Risk of Pests, Diseases and Other Threats

The uniform conditions of growing one tree species in large even-aged blocks may expose plantations to greater risk of damage from pests and diseases. Ecologically the potentially large food resource, the close proximity of trees to pass on infection, and even direct root contact beneath ground all suggest greater risk and potentially rapid build-up of a threatening pathogen or pest. Where an exotic (introduced) species is used, some freedom from damage is often observed in the first rotation, but this is often transitory. For example, extensive plantations of lodgepole pines (*Pinus contorta*) in Scotland (UK) grew well on very inhospitable sites throughout the 1950s and 1960s but in 1977 began to be devastated by a hitherto benign insect species associated with native Scots pine (*Pinus sylvestris*), *Panolis flammea*. The severity of damage was so great that lodgepole pine is no longer planted.

Other well-known examples include defoliation by the psyllid *Heteropsylla cubana* of the once widely planted multipurpose tree species *Leucanea leucocephala*, and *Sirex* wood wasp infestation of *Pinus radiata* plantations in Australia and recently in South America. Fungal pathogens causing serious damage such as defoliation, wood decay, or root mortality are the blights on poplar, fomes (*Heterobasidion* spp.) damage to many conifers, and *Phytophthora* spp.

All these and many other threats place plantations at considerable risk. However, experience teaches that most are containable provided that good silviculture limits risk of stress to trees through careful matching of species with site and related operations, and provided that adequate research can inform integrated pest/pathogen management programs and strategies. Only occasionally has a species been precluded owing to the threat of a devastating pest or disease, e.g., *Dothistroma* damage to *Pinus radiata* planted in the tropical highlands, and psyllid damage to *L. leucocephala*.

Abiotic Damage

The uniformity of plantation conditions can render them particularly vulnerable to fires, storms, frosts, droughts, and related events. In the late 1990s one-sixth of the entire Usutu Forest in Swaziland in southern Africa, a plantation of some 72 000 ha, was destroyed by either fires or hail damage, necessitating massive replanting programs. In the UK the threat of windthrow in forest plantations determines rotation length on many more exposed sites, with the aim of cutting trees just prior to the time they are predicted to blow down.

Sustainability of Yields Over Time

With significantly greater productivity than most natural forest, the question of sustainability of plantation yields becomes important. Could the more intensive silviculture lead to declining yields in the long term? It is difficult to answer this question categorically, and the situation will vary with site, because few plantations have been grown successively for more than two rotations and almost none for more than three rotations. However, what evidence does exist suggests that productivity is unlikely to decline; indeed, it may increase with improvements in genetic stock of plants. In one of the most intensively studied examples in Swaziland there is no evidence of yield decline after three whole rotations of pines grown for pulpwood, and even some signs of improving productivity.

There are some well-publicized exceptions to the above, namely plantations of *P. radiata* in South Australia, *Cunninghamia* in subtropical China, and *Picea abies* in Germany. In each case research has either demonstrated or at least pointed to causal factors that explain the yield decline. Such factors include excessive compaction of soil when harvesting trees, failure to conserve organic matter, and inadequate attention to invasive weeds, especially grasses. On no site does the growing of a single tree species in monoculture itself appear to be a primary cause of the problem. Indeed, in the case of South Australia, current growth rates of pine plantations now greatly exceed that of the previous rotations.

Outlook

As noted, there is already a substantial resource of planted forest which continues to expand and is destined to become the main source of wood products. What must be hoped is that this will include not only industrial grades of lumber but also high-quality timbers to replace diminishing supplies from natural forest. What must also be hoped is that much of future planting in developing countries will be fully integrated into rural development and local people's aspirations to contribute in the many ways plantations can to sustainable livelihoods.

Other emerging trends include increased planting of trees outside the forest, such as in agroforestry, partnerships between corporate enterprises and smallholders, rehabilitation of degraded land, and environmental protection roles.

Plantations as a way of growing trees efficiently appear sustainable. They will fully come to play the enormous role they can only if environmental, political, and social imperatives are addressed alongside those of sound silviculture.

Acknowledgement

This chapter is adapted from Evans J (2003), Forest Plantations, *Encyclopedia of Life Support Systems*, with permission from Eloss Publishers.

See also: **Afforestation**: Ground Preparation; Species Choice; Stand Establishment, Treatment and Promotion - European Experience. **Operations**: Nursery Operations. **Plantation Silviculture**: Rotations; Short Rotation Forestry for Biomass Production; Stand Density and Stocking in Plantations; Sustainability of Forest Plantations; Tending. **Silviculture**: Managing for Tropical Non-timber Forest Products. **Social and Collaborative Forestry**: Joint and Collaborative Forest Management.

Further Reading

Anonymous (1999) *International Experts Meeting on the Role of Planted Forests in Sustainable Forest Management*, 6–10 April 1999, Santiago. Chile: Conaf, Ministerio di Agricultura.

Anonymous (2003) UNFF *Intersessional Experts' Meeting on the Role of Planted Forests in Sustainable Forest Management*, 24–27 April 2003, Wellington, New Zealand.

Booth TH, Jovanovic T, and New M (2002) A new world climatic program to assist species selection. *Forest Ecology and Management* 163: 111–117.

Carle J, Vuorinen P, and Del Lungo A (2002) Status and trends in global forest plantation development. *Forest Products Journal* 52(7/8): 12–23.

Evans J and Turnbull JW (2004) *Plantation Forestry in the Tropics*, 3rd edn. Oxford, UK: Oxford University Press.

Evans J (1999) *Sustainability of Forest Plantations: The Evidence*. Issues paper. London: UK Department for International Development (DFID).

FAO (1967) Actual and potential role of man-made forests in the changing world patter of wood product consumption. Secretariat note. In *Proceedings of the World Symposium on Man-Made Forests and the Industrial Importance*, pp 1–50. Rome: Food and Agriculture Organization.

FAO (2001) *Forest Plantations Thematic Papers*. Working paper FP 1–15. Rome: Food and Agriculture Organization.

Savill PS, Evans J, Auclair D, and Falck J (1997) *Plantation Silviculture in Europe*. Oxford, UK: Oxford University Press.

Stand Density and Stocking in Plantations

K Theron and B V Bredenkamp, Department of Forest Science, University of Stellenbosch, South Africa

Introduction

In the third volume of the classical work *Schlich's Manual of Forestry* (1925), it is stated:

> To every method of treatment, as determined by the objects of management, corresponds a normal density of the growing stock. The degree of density may be defined as overcrowded, crowded, open, very open, interrupted, irregular, etc. Such terms are indefinite and subject to different interpretations.

Over 75 years later the terms describing the degree of site occupancy by trees are still being misinterpreted, essentially because many foresters use 'stocking' when referring to 'stand density.' These terms are not synonymous and are well defined. Stand density is an absolute measure that quantitatively expresses the number or count of trees on a unit of land, for example x stems per acre (spa) or y stems per hectare (s ha^{-1}). If trees are well spaced so that death from competition mortality is precluded, then stand density will remain constant over fairly long periods of time.

Stocking, on the other hand, is a relative measure of the degree of site occupancy with due regard to the objectives of management, and it is often expressed as a percentage of full site occupancy. At a certain stage of its development a stand may be well stocked for the production of sawtimber. In other words, that particular stand density is well suited to meet the objective of growing timber with dimensions to meet the needs of the sawmiller. That very stand will at the same time be understocked for the production of pulpwood and overstocked for the production of veneer logs. Further, because trees are continually increasing in size, stocking changes over time while stand density in terms of stems per unit area is held constant.

Basal area per unit area of land is commonly used as a quantitative measure of stocking.

The control of stand density through planting at the required spacing and spatial arrangement, suppression of ingrowth, and thinning to allow room for growth is a primary tool of forest management to achieve optimal stocking for a particular crop of trees. A collection of stands that are fully stocked is a prerequisite for the concept of a normal forest.

Determination of Optimal Stand Density

The effects of stand density on growth parameters of trees and stands of trees have been studied intensively. Much of the initial work in this field was based on an extravagant set of 27 installations of field experiments in South Africa, established mainly in the late 1930s, and known as the correlated curve trend (CCT) experiments. The results quantified many of the effects of stand density for the first time and provide an excellent example to illustrate many of the points below. The aim of the CCT experiments was a replicated installation of the experiment on each of a good, an average, and a poor site for 10 tree species grown commercially in each region where that particular species was grown in that country, in order to consolidate all spacing and thinning research. The aims were not fully met in terms of replication but an ambitious research program ensued.

At each installation large plots were established at between eight and 12 different spacings applied at random and a further eight or 10 plots were grown according to a strictly specified thinning regime. To avoid complications induced by seedling mortality and competition from weeds, the different spacings were achieved by planting at a uniform (high) stand density followed by frequent thinnings in advance of the onset of competition. This practice proved to be contentious and the current generation of spacing experiments, known as the standardized sample size (SSS) CCT experiments, does not employ it.

The premise behind the CCT experiments was that, apart from accident and disease and factors such as grass competition and differences in exposure, the following hold true:

1. In any given locality the size attained by a tree of a given age must be related to the growing space previously at its disposal; all other factors influencing its size are fixed by the locality.
2. Trees planted at a given (stand density) will, until they start competing with each other, exhibit the absolute or normal standard of growth for the species and locality. (In the original publication the term stocking was incorrectly used to denote stand density and in this section it is replaced by stand density within parentheses.)
3. Trees planted at a given (stand density) and left to grow unthinned will exhibit the absolute or normal standard of growth for the species, locality and the particular density of stock in question.

The first results from the CCT experiments in five pine species, based on observations when the oldest trees were 9 years old, were published in 1947. These early results were 'remarkable and, in a sense, unexpected.' The conclusions drawn were:

1. The age at which competition commences for a stand of given (stand density) is independent of species, site, or climate.
2. The degree of competition (using diameter at breast height (dbh) increment as index) is the same for a given age and (stand density) irrespective of species and site.
3. As (stand density) decreases, dbh and mean height increase; total volume at first increases and then decreases.

The experiments referred to in these conclusions were established under widely different climatic and site conditions by different people. Data were collected by nine research officers independently of each other (due to staff changes during World War II) and yet final thinnings in advance of competition were completed in all experiments within a few months of each other.

With hindsight, it is apparent that some licence was taken. The conclusions applied to five particular pine species as originally no other genera were tested. What was considered to be a poor site in the 1930s would be viewed differently today. Afforestation has spread into marginal areas where the sites are poorer and certainly drier and modern site amelioration techniques make afforestation of sites originally classified as 'poor' quite 'average.' The conclusions being considered 'independent of species, site or climate' thus applied to a fairly narrow range of conditions.

In the CCT experiments all treatments were allocated to plots at random with some restrictions in order to group plots of similar size.

Stand density has also been studied with systematic designs. The circular (wagonwheel) designs known as Nelder experiments (**Figures 1–3**) address either changes in growing space or changes in the shape of the growing space available to the tree in separate installations. In the former case trees are planted progressively further apart along the 'spokes' of an imaginary wheel, with the result that each position further from the hub of the wheel outwards represents a lower stand density while the shape of the growing space is maintained as essentially square. In the second case the trees are planted progressively closer together along the spoke, resulting in growing spaces that vary from square near the hub to spaces with increasing rectangularity the further the location is from the hub.

The 'Scotch plaid' experimental design is based on a rectangular grid and incorporates both increasing growing space and increasing rectangularity of growing space in each installation (**Figure 4**).

Many other experimental designs have been used around the world.

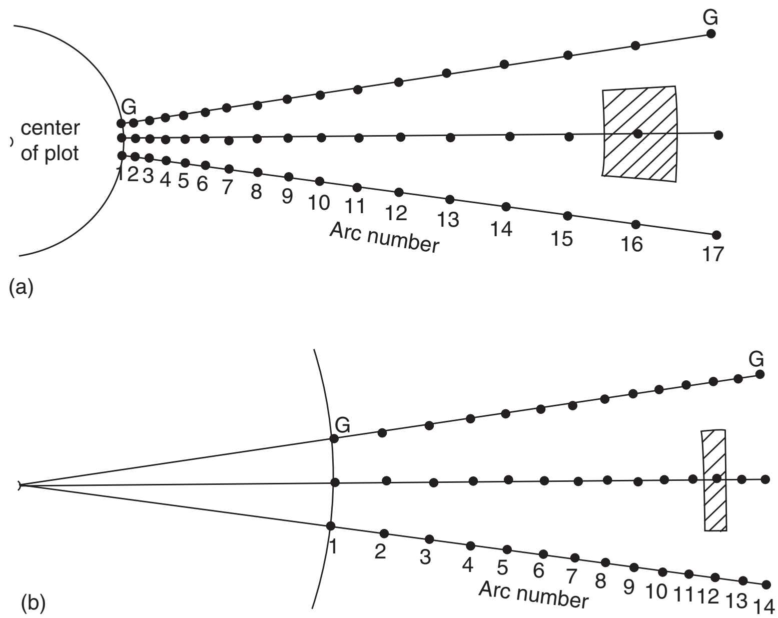


Figure 1 Nelder experiments: effects of design on shape of growing space: (a) square spacing and (b) rectangular spacing. Cross-hatched areas show the nominal growing space available to the tree. Source Reukema DL and Smith JHG (1987) Development over 25 years of Douglas Fir, western hemlock and western red cedar planted at various spacings on a very good site in British Columbia. *USDA Forestry Services Research Paper* PNW-RP-381.

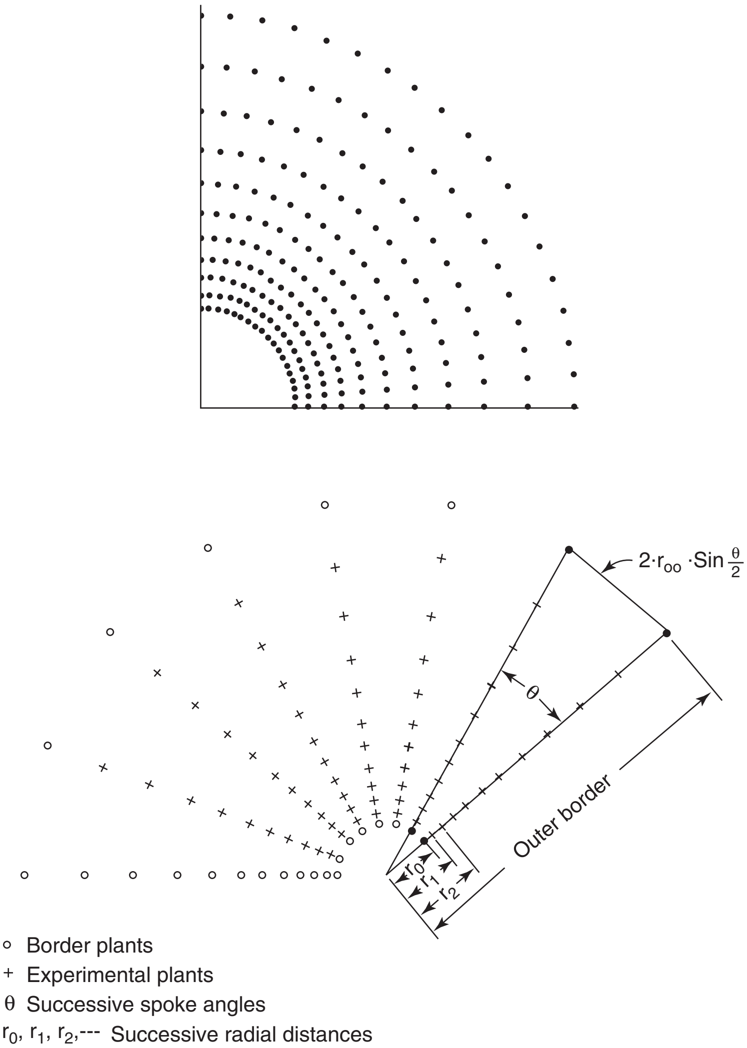


Figure 2 Nelder experiments: segments of variable-density plots (design 1a). Source: Nelder JA (1962) New kinds of systematic designs for spacing experiments. *Biomerics* **18**: 283–307 (top) and Namkoong G (1966) Applications of Nelder's designs in tree improvement research. In: *Proc. 8th Southern Conf. on Tree Improvement*, pp. 24–27. June 16–17 1965. Savannah, Georgia (bottom).

The Effects of Changing Growing Space on Trees

An increase in growing space results in an increase in dbh. Even if trees were grown at a high stand density that resulted in a reduced dbh, a thinning will result in an increase in dbh increment. The rate of that increase depends on the degree of suppression prior to the release (**Figure 5**). This effect is also observed in stands where stand density was reduced by competition-induced mortality.

The height of an individual tree is less affected by stand density than it is by site quality. However, tree height is not unaffected by stand density, and across a range of stand densities there is one that will be optimum for height growth of a particular species. Stand density that is too high or too low will impact negatively on height growth but within the limits of stand density used in plantation forestry there is essentially no effect on top or mean height.

Because stand density has a marked influence on dbh and a minimal influence on height, it has a marked influence on stem taper. The higher the stand density, the less the taper will be.

Increasing stand density results in a decrease in the diameter and length of branches and in some species there is also a decrease in the number of branches per unit length of the tree bole.

The higher the stand density, the poorer stem form will be. Trees grown under conditions of suppression tend to be more crooked than those that are free-growing and there is some evidence that the proportion of trees that are forked will also increase with increasing stand density. However, some species, such

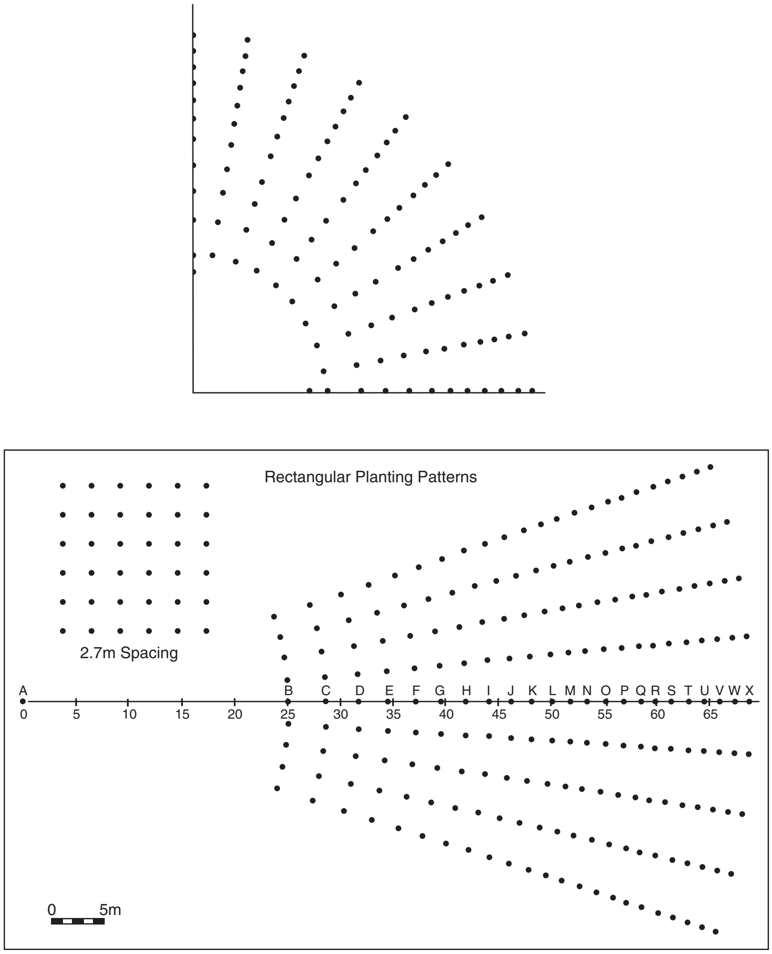


Figure 3 Nelder experiments: segments of variable-density plots (design 1b). Source Nelder JA (1962) New kinds of systematic designs for spacing experiments. *Biometrics* **18**: 283–307 (top) and Bredenkamp BV (1982) Rectangular espacement does not cause stem ellipticity in *Eucalyptus grandis*. *South African Forestry Journal* **120**: 7–10 (bottom).

as *Acacia melanoxylon* and *A. auriculiformis*, must be grown at high stand densities to avoid crook.

As a reduction in stand density increases diameter growth, the proportion of early or spring wood is increased, resulting in a reduction in timber density. There is little evidence to support the popular belief that this results in a reduction in timber strength or quality. Attempts of foresters to reduce the size of the juvenile core through reduced planting spacing and delayed first thinning generally fail to reach their objective. However, in the case of *Pinus patula* where the juvenile core may consist of as many as 20 annual rings, delayed thinnings can restrict the size of the juvenile core.

The Effects of Changing Growing Space on Stands of Trees

As stand density has such a marked impact on the dbh of the individual tree it also has a major impact on stand mean dbh. Mean dbh is controlled almost exclusively by stand density.

High stand density results in an increase in the variation of dbh. Dbh distributions are most uniform when stand density is low and most heterogeneous under conditions of suppression.

If mean height of a stand is defined as the height of the tree with average dbh (mean cross-sectional area), then mean height is affected by stand density because of the influence on dbh. Top height, which can be defined in many ways, is less affected. Top height is sometimes considered to be unaffected by stand density and is thus used to express site quality as the top height of a stand at a given index age; however, at extremes of stand density, top height is also affected.

As stand density controls dbh and affects height, the most important variables determining tree volume, stand density has a major effect on stand volume. If the object of management is merely the production of fiber, then the optimum stand density

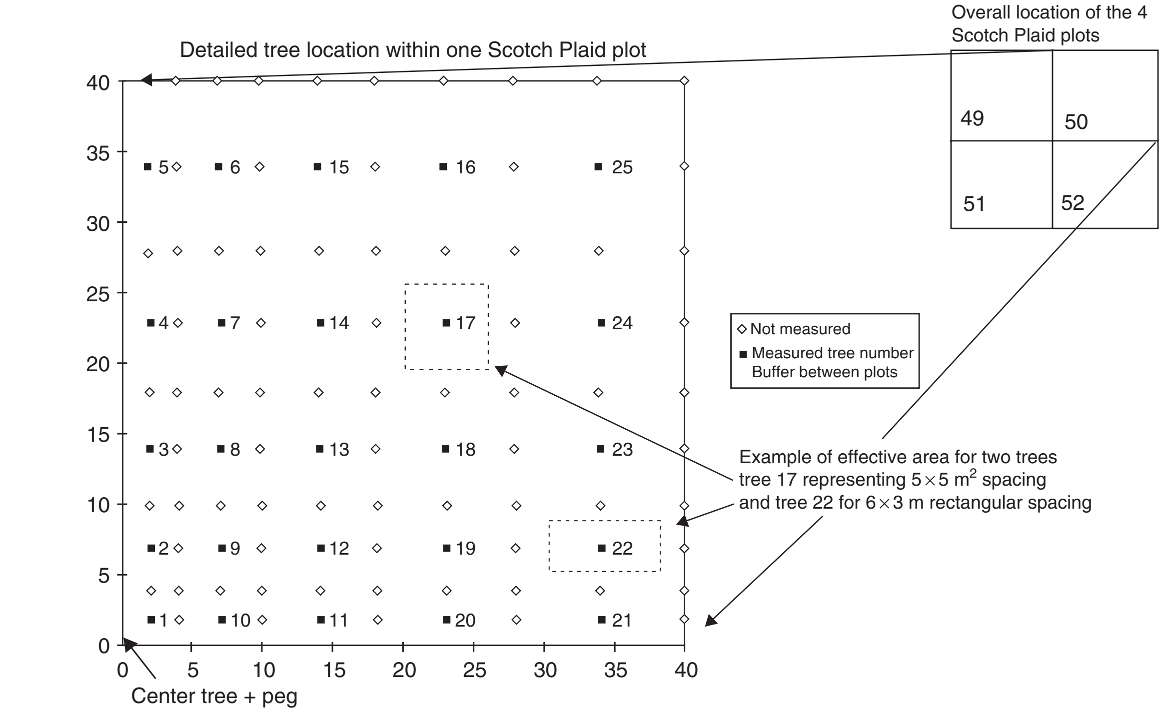


Figure 4 Layout of the 'Scotch plaid' design spacing plots. Reproduced with permission from Gerrand AM and Neilson WA (2000) Comparing square and rectangular spacings in *Eucalyptus nitens* using a Scotch Plaid design. *Forestry Ecology and Management* **129**: 1–6.

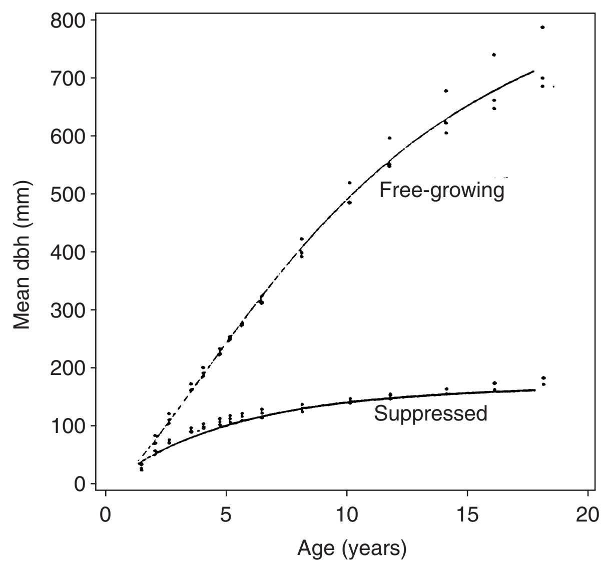


Figure 5 Diameter development of free-growing and suppressed stands of *Eucalyptus grandis* in Zululand. Note the second inflection in the trend amongst the suppressed trees. Source: Bredenkamp BV and Burkhart HE (1990) Diameter growth of *Eucalyptus grandis* under conditions of extreme suppression. *New Zealand Jourrnal of Forestry Science* 20(2): 162–167.

is the highest stand density the site can support without inducing mortality due to competition. However, if a specific crop is being cultivated, there will be an optimum stand density for that crop and that optimum will be at a much lower level than in the case with production of fiber.

The Effects of Rectangularity of Growing Space

The effects of rectangularity of the growing space, measured as the ratio of the distance between rows to the distance between the trees within the rows, on the volume production of trees and stands is negligible, if any. Between-row spacing of as much as six times the within-row spacing has been shown to have essentially no effect on the growth or the shape of the cross-section of the bole. There are however effects on branching. In general, branches oriented with the row curve away from competing branches from adjacent trees and grow towards clear space between the rows. No influence of rectangularity of growing space on the number of branches has been reported.

Spacing and Stocking Practices Around the World

Initial stand densities have been markedly reduced since the 1970s. The wider initial spacings are mainly due to increasing availability of genetically improved planting stock; better site preparation, planting, and tending; improved forest protection, and the advantage of enabling shorter rotations.

Practices differ very widely among countries. In some cold temperate countries trees are planted at 10 000–18 000 trees ha^{-1}. In the UK most conifers are now planted at densities of 2500 stems ha^{-1} whereas in the 1930s about 4500 stems ha^{-1} were planted. In southern-hemisphere countries it is now normal to plant between 600 and 1100 stems ha^{-1} where high-quality sawn timber is produced. Where pulpwood, poles, firewood, or mining timber are required, stand densities are up to 2000 stems ha^{-1}. *Populus deltoides* grown for matches is often established at 400 stems ha^{-1}. Initial stand densities of less than 400 stems ha^{-1} are mainly found in agroforestry situations.

When Very Close and Very Wide Spacings Are Used

The general goal of initial spacing is to provide sufficient trees from which eventually to select a final crop of evenly spaced and acceptably formed trees, within the restraints of site and other factors. For a given spacing, growth responses are heavily dependent on species and site factors.

Appropriate initial spacings and thinnings enable foresters to achieve the end-use objective. For the production of small-sized timber such as pulpwood, poles, and mining timber, volume production in a stand must be maximized, i.e., initial spacing is relatively close and no thinnings, or only light thinnings, are required. For the production of sawtimber and veneer, initial spacings are wider and heavy thinnings are required to produce final crop trees with big diameters in a relatively short time.

Initial spacings are generally relatively wide for fast-growing species of good tree form, where tree establishment costs are high. In the case of *P. deltoides* grown for matchwood, where minimum sizes for peeling preclude the use of timber for thinnings, initial spacings are even up to 5×5 m. Other factors to consider are mechanization, water run-off required by downstream users, and susceptibility to diseases and pests that increase with an increase in stress on trees.

Improved genetics and good silvicultural practices have reduced the need for high initial stand densities. However, where young trees are exposed to severe winds, wide spacings increase the incidence of wind damage. New Zealand evidence suggests that initial stand density of *Pinus radiata* should not be less than 600 stems ha^{-1} to ensure adequate mutual protection.

The appropriate stand density after a thinning depends largely on the amount of foliage a given species can support on a given site. The residual basal area may vary from 9 to 40 $m^2\,ha^{-1}$ with higher stand densities with evergreens, shade-tolerant species, and good sites. On sites that are so poor that the root systems compete severely but crowns cannot close, stand densities should be exceptionally low.

Effects of Spacing on Site Capture

When trees are free-growing and not competing with each other, diameter growth is less than the maximum possible. As basal area increases, competition sets in amongst trees, but total growth per hectare continues to increase, although at a decreasing rate until the maximum growth is reached, i.e., the site is fully utilized. With further increases in stand density, the stand increment remains similar over a wide range of stand densities. Therefore, individual trees grow slower in diameter as stand density increases. When competition is so severe that trees lose vigor and become more prone to disease and insect attack, increment becomes less than the maximum.

During the first year or more after establishment of a plantation, when the trees are small, the site is not fully utilized. Only later do roots and crowns spread sufficiently to compete with neighboring trees for light, moisture, and nutrients.

In even-aged monocultures a site can support only a certain number of trees of a given species and size. The maximum number of trees that can be carried decreases with age as the trees grow larger, rapidly at first but slowly towards the end of the rotation. On dry and infertile sites, competition amongst trees will occur before their crowns start to compete for light. Where soil moisture and nutrients are in abundance, competition for light may set in before the roots are in severe competition.

The most vigorous trees are most likely to survive the competition, i.e., the tallest are generally the largest in all dimensions. The weaker trees become increasingly suppressed and eventually die. This process is called natural thinning. In very dense stands, competition is so severe that dominant trees also grow slower. This can be avoided by timely thinnings.

The trees of monoculture plantations are generally uniform in spacing and size and therefore also in vigor. Either their crowns or roots will start to compete rather suddenly and then or soon afterwards will be the ideal time for the first thinning. The initial spacing should preferably be wide enough so that the trees to be thinned will have grown to merchantable size.

The earliest a plantation can be thinned without loss of increment varies with the rate of growth, which is determined by site quality, initial spacing, genetics, and intensity of silvicultural practices. It can be as early as age 2 years for *Tectona grandis* planted at 2 × 2 m in the tropics. In the UK it varies from 20 to 35 years for most conifers, but can be more than 50 years in colder climates.

If the thinning cycle is very long, thinnings are generally heavy and the site may not be fully utilized for some years after a thinning.

Thinning weight, i.e., the number of stems, or basal area, or volume per ha removed during a thinning, expressed as a percentage of the main crop before thinning, is generally between 20% and 60%. Lighter thinnings are regarded as uneconomical. Heavier thinnings leave stands more prone to wind damage and unacceptable increment due to incomplete site utilization.

The most beneficial silvicultural regime for a stand would include frequent light thinnings. These are economically not justifiable. The frequency and intensity of thinnings are thus driven more by economics than good silviculture. However, end-use potential and wood quality also play a role.

Spacing in Agroforestry, Tanbark and Biomass Plantings and Other Unconventional Stands

Spacing is manipulated to produce material which will best meet the market demands and also yield optimal profits. In all forestry stands, including agroforestry, crops are usually thinned or clearfelled before competition becomes so severe that mortality sets in.

In agroforestry, tree seedlings are often planted at the same time as food crops. Spacing between tree rows is often wider than in monoculture plantations to delay the shading of the food crop or forage grown for grazing by the trees. Trees may also be thinned and pruned so that food cropping can continue beyond the tree establishment stage.

In some agroforestry systems trees are planted in strips to provide shade or shelter to the agricultural crops or animals grazing among the trees. Such plantings may occupy less than 5% of scarce farmland.

In alley cropping, nitrogen-fixing shrubs and trees are grown in wide rows to allow cultivation of four to six rows of food crops in between. Spacing between trees varies from less than 2 m to as wide as 5 m.

In semiarid areas as few as 20 trees ha^{-1} are planted where annual crops are grown. Partial shade conditions are sometimes also created in moist areas where perennial agricultural crops, e.g., tea and coffee, are grown, by planting 50–200 trees ha^{-1}.

For woodlots, initial spacing between trees is normally closer than for commercial plantations. On good sites, trees grown for firewood may be planted as close as 1 × 1 m and if grown for poles at 2 × 2 m, to maximize yields. Rotations are typically only 3–6 years.

Acacia mearnsii plantations grown for the production of tanbark are planted at 2200 trees ha^{-1}. When established by means of direct sowing or natural regeneration, many thousands of seedlings ha^{-1} must be removed in one to three successive thinnings to retain 1200–1600 stems ha^{-1} until clearfelling at ages 8–12 years.

In recreational areas, soils are often compacted by the many visitors, thus placing stress on the trees. Therefore, spacing between trees should be wide to minimize competition amongst them.

How Spacing Interacts with other Establishment Practices (e.g., Plowing, Drainage)

The spacing at which trees are planted in plantations is usually determined accurately. For practical reasons, e.g., mechanized operations, locating young trees when weeding, and for line thinning, rows should be straight. Likewise, when natural regeneration is used, respacing or precommercial thinning should be done so that the remaining trees are in rows. Where plantations are established on level, stone-free ground, straight lines can often be seen in a number of directions. However, on many sites it is difficult to achieve precision because of steep slopes, rocks, and old stumps.

Costs of some forestry operations, e.g., weeding and extraction of thinnings, can be reduced by using tractor-mounted equipment and other big machinery. It is therefore sometimes desirable to have rectangular spacings that allow enough space between rows to accommodate such machines. For example, instead of planting approximately 1200 trees ha^{-1} at a spacing of 2.9 × 2.9 m, the distance between the rows can be increased to 3.5 m and the distance between trees in the row reduced to 2.4 m to maintain the same number of trees per hectare.

Weeds are likely to be suppressed more rapidly in closely spaced stands because of quicker canopy closure. However, this should not be the major objective of close initial spacings because the additional costs of establishing more trees usually far exceed the savings incurred on weeding operations.

After a number of coppice regenerations in *Eucalyptus* plantations for example, reestablishment with nursery-raised plants is usually necessary. It is then preferable to plant in the rows of the killed stumps rather than between the rows, to enable easy future access, e.g., for firefighting.

Use of Thinnings to Manipulate Stand Density and Achieve Optimal Stocking

Artificial thinning is the removal of a proportion of individual trees from a stand before clearfelling. It is generally understood to take place after the onset of competition. However, precommercial thinnings may take place before trees start to compete with each other. Thinnings are mostly prescribed as stems ha^{-1} or basal area to remain at a given age.

In stands that are to be thinned, more trees are established than the required final crop, mainly to ensure sufficient trees from which the final crop can be selected, but also to utilize the site better.

The main objectives of thinnings are to:

- provide the remaining trees more space for crown and root development to encourage stem diameter increment and thus reach the desired size sooner
- remove trees of poor form so that final crop trees are of good quality
- manage relatively uniform growth in order to enhance wood quality and sound end-use potential
- prevent severe stress that may induce pests, disease, and stand instability
- provide an intermediate financial return from sales of thinnings.

Thinning schedules are therefore based on both biological and economic considerations. Skillful thinning can increase economic yields although the site is not fully utilized throughout the entire rotation, because veneer and sawlog prices generally increase significantly with increased log diameters.

An infinite number of combinations is possible between initial spacing, timing and intensity of thinning, final density, and rotation length. A unique thinning regime is therefore possible to fit every case of management and market circumstances.

See also: **Afforestation**: Stand Establishment, Treatment and Promotion - European Experience. **Inventory**: Stand Inventories. **Plantation Silviculture**: Short Rotation Forestry for Biomass Production. **Silviculture**: Coppice Silviculture Practiced in Temperate Regions; Unevenaged Silviculture.

Further Reading

Avery TE and Burkhart HE (1994) *Forest measurements*, pp. 287–296. New York: McGraw-Hill.

Bredenkamp BV (1982) Rectangular espacement does not cause stem ellipticity in *Eucalyptus grandis*. *South African Forestry Journal* 120: 7–10.

Bredenkamp BV (1984) The CCT concept in spacing research. In: Grey DC, Schönau APG, and Schutz CJ (eds) *Proceedings of the IUFRO Symposium on Site and Productivity of Fast Growing Plantations*., vol. 1, pp. 313–332. Pretoria and Pietermaritzburg, South Africa: Stellenbosch University Press.

Bredenkamp BV (1990) The Triple-S CCT design. In: Von Gadow K and Bredenkamp BV (eds) *Management of* Eucalyptus grandis *in South Africa*, pp. 198–206. Stellenbosch, South Africa: Forest Mensuration and Modelling Working Group.

Bredenkamp BV and Burkhart HE (1990) Diameter growth of *Eucalyptus grandis* under conditions of extreme suppression. *New Zealand Journal of Forestry Science* 20(2): 162–167.

Clutter JL, Fortson JC, Pienaar LV, Brister GH, and Bailey RL (1983) *Timber Management; A Quantitative Approach*, pp. 64–65, 68–83. New York: John Wiley.

Evans J (1992) *Plantation Forestry in the Tropics*, pp. 38–46, 217–266, 285–303. Oxford: Clarendon Press.

Gerrand AM and Neilson WA (2000) Comparing square and rectangular spacings in *Eucalyptus nitens* using a scotch plaid design. *Forestry Ecology and Management* 129: 1–6.

Hammond D (1995) *Forestry Handbook*, pp. 83–89. Christchurch, New Zealand: New Zealand Institute of Forestry.

Lewis NB and Ferguson IS (1993) *Management of Radiata Pine*, pp. 201–240. Melbourne: Inkata Press.

Namkoong G (1966) Applications of Nelder's designs in tree improvement research. In: *Proc. 8th Southern Conf. on Tree Improvement*, pp. 24–27. June 16–17 1965. Savannah, Georgia.

Nelder JA (1962) New kinds of systematic designs for spacing experiments. *Biometrics* 18: 283–307.

Reukema DL and Smith JHG (1987) Development over 25 years of Douglas Fir, western hemlock and western red cedar planted at various spacings on a very good site in British Columbia. *USDA Forestry Services Research Paper* PNW-RP-381.

Savill P, Evans J, Auclair D, and Falck J (1997) *Plantation Silviculture in Europe*, pp. 139–161. Oxford: Oxford University Press.

Shepherd KR (1986) *Plantation Silviculture*, pp. 236–262. Dordrecht: Martinus Nijhoff.

Smith DM, Larson BC, Kelty MJ, and Ashton PMS (1997) *The Practice of Silviculture: Applied Forest Ecology*, pp. 69–130. New York: John Wiley.

Van Laar A and Akca A (1997) *Forest Mensuration*, pp. 165–173. Göttingen: Cuvillier Verlag.

Tending

G Kerr, Forestry Commission Research Agency, Farnham, UK

Published by Elsevier Ltd., 2004

Introduction

Tending generally aims to improve the composition, structure, condition, health, and growth of forests, in both single cohort and multicohort stands, to achieve management objectives. The scientific basis of a range of tending operations is described with reference to stands arising from artificial regeneration (planting (*see* **Afforestation**: Stand Establishment, Treatment and Promotion - European Experience) or direct seeding), natural regeneration (natural seeding (*see* **Silviculture**: Natural Stand Regeneration) or coppicing (*see* **Silviculture**: Coppice Silviculture Practiced in Temperate Regions)), or a mixture of both approaches. As with any silvicultural treatment, tending must be conducted with a clear understanding of the way in which the vegetation and site will develop after treatment. If the work is conducted with little foresight costs can be incurred with few, or possibly negative, effects on the development of the stand.

Tending Operations

The nomenclature of tending is an area of silviculture where terminology can be parochial and confusing. For example, the term 'singling' has many different meanings and 'formative pruning' can be translated into French in a number of different ways. For clarity, the terminology used here follows *The Dictionary of Forestry* (see Further Reading). The range of operations considered is illustrated in **Figure 1** and described below.

Brashing

Brashing is the removal of live or dead branches on a tree stem from ground level up to a height of about 2.5 m. It is usually applied to planted single cohort stands at or just after the time of crown closure. The direct effects of brashing on a stand of trees are insignificant in terms of growth and timber quality. However, there can be indirect effects: increased access aids early identification of damage or health problems, and facilitates subsequent intermediate treatments.

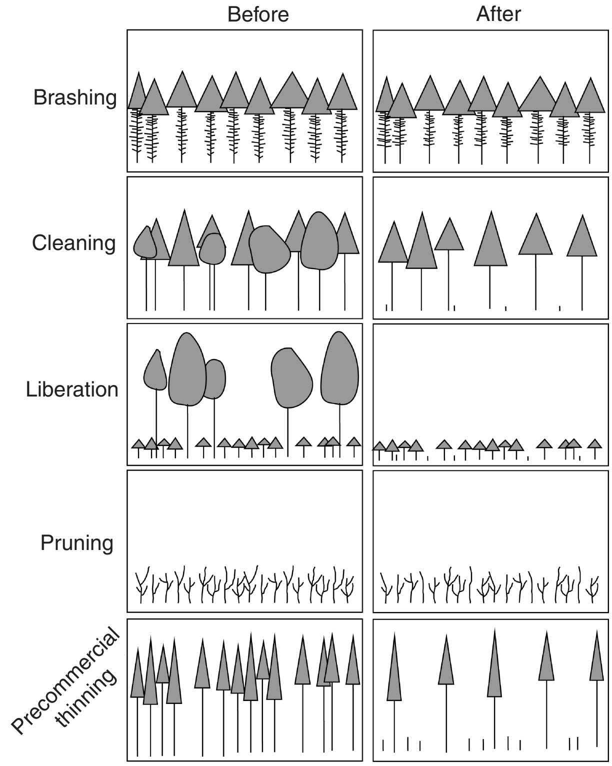


Figure 1 Diagrammatic representation of the effects of tending operations on forest stands.

Cleaning

Cleaning is a release treatment made to free selected trees from less desirable individuals that overtop them or are likely to do so (**Figure 2**). Cleaning has significant direct effects on the growth rate of selected trees because it increases access to resources. The main limiting resource is often assumed to be light in single cohort stands because cleaning has obvious effects on the canopy. However, on many sites greater access to light, water, and nutrients will all be important even though on some sites a single factor can be limiting, for example on dry sites greater access to moisture may be most critical. The main indirect effect of cleaning is the removal of 'undesirable' species and this may reduce the biodiversity of the stand. This is an important consideration if social or environmental management objectives are a priority, and in such woodlands there is no need for the undesirable species to be eliminated.

Liberation

Liberation is a release treatment to free a young cohort from competition with much larger sized trees. In many circumstances a liberation cutting corrects a problem not addressed by earlier silviculture. For example, the larger trees may be of species

Figure 2 Cleaning would now be desirable in this stand of northern hardwoods where pin cherry (*Prunus pennsylvanica*) is now dominant.

Figure 3 Pruning *Pinus radiata* to produce knot-free timber.

and sizes that could not be utilized from a previous felling and were left to reduce harvesting costs. The influence of these trees on the cohort of younger trees will depend on their number, basal area, and distribution. The presence of such trees is not always negative and they can increase species richness, improve vertical structure, and provide shelter for the younger trees; they could be girdled to increase standing deadwood.

Pruning

Pruning is the removal, close to the branch collar, of side branches and multiple leaders from a standing tree (*see* **Plantation Silviculture**: High Pruning). It is widely practiced to simulate natural branch mortality and increase the timber quality of selected trees. A secondary function of pruning is to act as a semipermanent way of marking tree selections to guide future thinning decisions. In general it is only used on 'young' trees where some degree of genetic improvement has been possible (**Figure 3**), otherwise it is really a remedial treatment for stands where production of quality timber is an important objective but establishment has not provided enough trees to achieve this.

Precommercial Thinning

Precommercial thinning is the removal of trees not for immediate financial return but to reduce stocking and concentrate growth on the more desirable trees. The effects are similar to cleaning except that, because the trees are generally older, they are dominating the site to a greater extent and the risk of losing control of the vegetation, to coppice regrowth or regeneration of pioneers, is much less. In addition, although precommercial thinning can remove less desirable species, with consequent effects on stand diversity, it is usually associated with removal of poorer phenotypes of the more desirable species.

Weeding

Weeding is a release treatment that eliminates or suppresses undesirable vegetation. The most likely need is in the period between establishment and first thinning to remove climbers such as *Clematis* spp., *Lonicera* spp., and kudzu (*Pueraria lobata*).

General Points

When tending operations are being considered the trees are established and safe from the normal adverse influences common to the site. However, trees will still need to be protected from a range of biotic and abiotic factors. A special case of this is the grey squirrel (*Sciurus carolinensis*) in the UK and Ireland. Grey squirrels can cause significant damage to a range of broadleaved species and trees are most vulnerable to damage when they are 10–40 years old (**Figure 4**). It is interesting to note that this behavior of the grey squirrel is very different to that in its native North America.

The future changes in appearance, species composition, productivity, and structure of a stand are largely governed by the spatial arrangement and height distribution of trees in the phase of growth between establishment and first thinning. Tending operations are an initial opportunity to influence this development. However, the costs of the operations can be high and, relative to decisions concerning establishment and thinnings, the long-term effects of some tending operations are uncertain. Hence, when forestry practice is subject to economic scrutiny tending operations are vulnerable. For example, in traditional French silviculture regenerating oak (*Quercus robur* and *Q. petraea*) has traditionally used a series of weeding and cleaning operations, but recently there has been much pressure for rationalization and the number of operations carried out has been significantly reduced. Similarly when regenerating northern hardwoods on the Allegheny plateau in northwest Pennsylvania, USA, almost no tending operations are carried out (**Figure 5**).

Figure 4 Grey squirrel (*Sciurus carolinensis*) damage to *Fagus sylvatica* in the UK.

Stand Development

There are several classification schemes to describe stand development. A convenient one to set tending operations in context is shown in **Figure 6**. The model describes how the stand structure of a forest changes following disturbance (*see* **Silviculture:** Forest Dynamics).

After harvest or disturbance young trees regenerate on the site and this is classified as the stand initiation phase. As the young trees grow they form a dense canopy which eliminates further regeneration and

Figure 5 Naturally regenerated northern hardwoods (mainly *Prunus serotina*); little tending will take place before the first thinning.

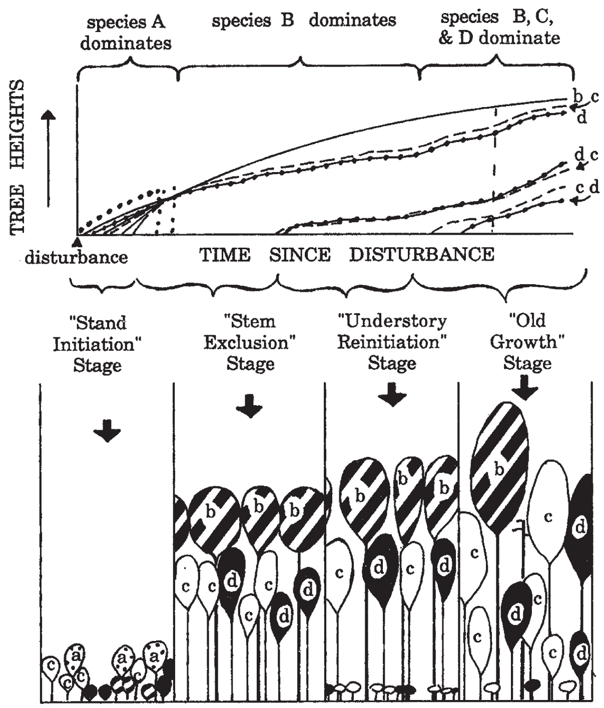


Figure 6 Schematic stages of stand development after disturbance. All trees forming the forest regenerate soon after the disturbance; however, the dominant tree type changes as stem number decreases and vertical stratification of species progresses. The height attained and the time lapsed during each stage vary with species, disturbance, and site. Reprinted from Oliver CD and Larson BC, *Forest Stand Dynamics*, update edn, Copyright © 1996 John Wiley & Sons, Inc. Reprinted by permission of John Wiley & Sons Inc.

existing stems start to die; the stand is in the stem exclusion stage. When openings form in the canopy as a result of a reduction in canopy competition, conditions for regeneration of the understory improve during the understory reinitiation phase. Eventually large trees in the main canopy die, younger trees in the lower canopy are released, and the stand develops into the old growth phase that has an all-aged structure with an irregular canopy. In single cohort stands, tending operations take place in the latter stages of the stand initiation phase and the beginning of the stem exclusion stage. Stocking is one of the primary factors that influences the development of stands moving from the stand initiation phase to the stem exclusion phase (*see* **Plantation Silviculture**: Stand Density and Stocking in Plantations). Hence the changes described below will occur sooner in an area with dense stocking, from successful direct sowing or natural seeding, compared with a planted area where costs usually prohibit stocking levels that will induce mortality quickly.

During the stand initiation phase tree crowns will not be in contact and, although the trees will be in competition for light, water, and nutrients, they can physically expand their crowns. At the point of crown closure, or soon after, the leaf area index reaches a maximum and the trees totally dominate the area. After crown closure, which is the start of the stem exclusion phase, trees begin to alter their shapes in response to the competitive environment. Foliage in the lower crown dies; as a result branch mortality commences and the growth rate of each tree decreases and the stem shape becomes less tapered. During this period of intense competition between trees (i.e., involving intimate physical crown contact) the stand is in the plastic phase as stem shape changes (**Figure** 7). During this phase the future crown classes of individual trees as dominants, codominants, intermediates, emergents, or suppressed is governed by a complex interaction of factors.

As the stand continues to develop the foliage area of the crowns remains constant but it moves further from the forest floor. At a point where the trees are fully utilizing site resources, or a where there is a constraining factor (e.g., water on a dry site), volume growth will slow dramatically, trees will become unstable due to high height : diameter ratios, height growth will stop, and possibly ‘stagnation’ will result. Stagnated stands contain trees that are very stressed and which therefore can be much more vulnerable to a range of biotic and abiotic damaging agents.

As mentioned above, the time taken for a single species, single cohort stand to stagnate is influenced mainly by stocking. This is illustrated in **Figure** 8a; stand A is initially dense but is cleaned at age x and has a precommercial thinning at age y to ensure that it does not enter the zone of stagnation. Stand B has a much lower density of trees at the end of establishment phase and this means that it will not stagnate in the period when tending operations are being considered. **Figure** 8a is a theoretical consideration and the zone of stagnation is narrow and well defined. However, in reality other factors in addition to stocking determine when, or even if, a stand stagnates; these include the inherent variability of the site, variation in age of regenerated trees, and genetics. This is illustrated in **Figure** 8b where the zone of stagnation is wider and entry into it is later compared with theory. If the stand is also multispecies a further significant factor is added that will delay the onset of stagnation, particularly if the tolerances of shade of the various species are different. In summary, and reality, although theoretically many stands with no intervention will develop towards a stagnant state there are many factors that slow this process.

In multicohort stands there are, by definition, two or more sizes of trees present and at some point in the development of the stand one of the cohorts will be

Figure 7 Dense oak stand (*Quercus robur* and *Q. petraea*) in the plastic phase of growth.

in the phase where tending operations may be required (**Figure 9**). Most growth per tree and usually per hectare occurs in the tallest cohort and manipulation of this will have the most direct effect on yield (*see* **Silviculture**: Unevenaged Silviculture). The taller cohort will also have a high degree of control over site resources: light, water, and nutrients. The lower cohort(s) can therefore reach a stage where a resource limits growth quite quickly. This is illustrated in **Figure** 8c where the zone of stagnation is less well defined and much wider, and trees can enter into it at much younger ages compared with single cohort stands. Hence, a primary concern in the management of multicohort stands is to ensure that younger trees do not lose vigor because of the ability of taller trees to dominate competition for site resources.

One area where understanding of stand development is lacking is in the ability of trees to recover from stagnation caused by periods of competition well beyond the normal intervention cycle (tending or thinning). For example, a common observation is that European ash (*Fraxinus excelsior*) will stagnate relatively quickly and generally does not recover. In contrast, European silver fir (*Abies alba*) takes much longer to stagnate and, after release many years later, can quickly resume a height growth trajectory determined by the site rather than its past competitive position. This is illustrated in **Figure 10**: at age *x* species A responds quickly to release but species B is slower. Later, at age *y*, both species respond to intervention less well although the decline in species B is much more marked than with species A. At present, understanding of these growth patterns is confined to general descriptions at the species level without much knowledge of the mechanisms involved.

Application of Operations to Guide Stand Development

The main guiding principles in the application of tending operations are:

1. To avoid conditions where the stand may stagnate.
2. To steer the stand towards the structure and composition that will achieve management objectives.
3. To achieve cost effectiveness.

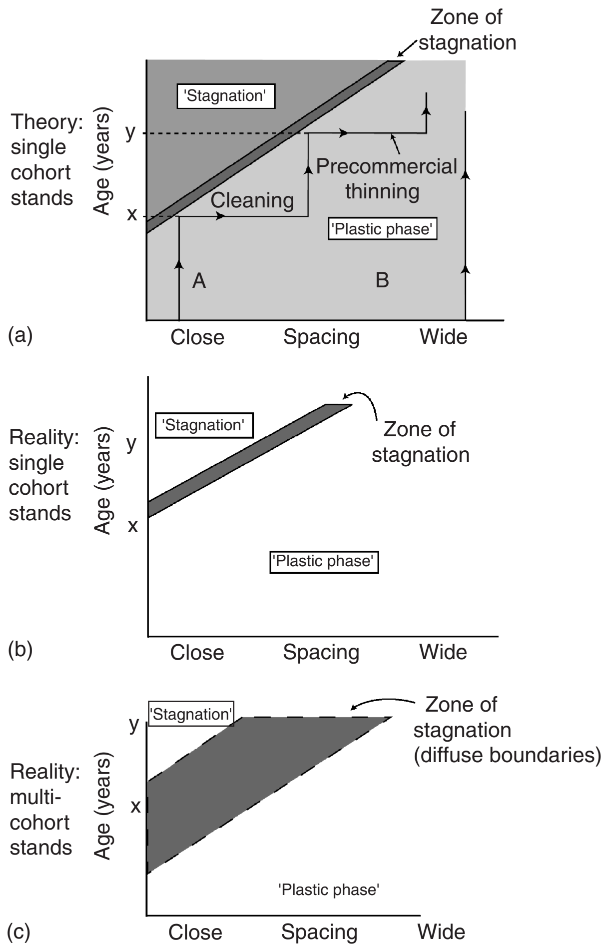


Figure 8 Relationship between tending regimes, stand development, and the zone of stagnation.

Different tending operations can influence stand development to a lesser or greater extent. Brashing and pruning can achieve specific objectives but, as discussed earlier, their influence on stand development is limited. However, cleaning, liberation, and precommercial thinning can have a significant effect on stand development.

The following points should be considered with respect to guiding stand development using tending operations:

1. How did the stand develop into its present condition?
2. What would be an appropriate operation now?
3. How will the stand develop after tending?

How Did the Stand Develop into its Present Condition?

No tending operation should be undertaken without some understanding of how the stand developed into the situation where intervention was required. For example, if drastic early cleaning is required this may reflect ecological conditions suboptimal for the selected trees or some other failure of establishment. In these situations the most important question to answer is: can the situation be remedied at acceptable cost? If not, the forest manager may have to adjust plans to take account of these changed circumstances rather than spending large sums of money fighting the natural processes that are operating on the site.

Specifying an Appropriate Operation

The structure and stage of development of the forest stand generally dictates whether the operation should be a cleaning, liberation, or precommercial thinning. However, the timing of the operation is less clear-cut and often the decision involves consideration of a number of factors such as labor and logistics, in addition to biological criteria. An example where an understanding of stand development is important for deciding the timing of a tending operation is with cleaning, where the species being removed can coppice. If the operation is carried out too early and the coppice is not killed using herbicides, there is a danger that the coppice shoots will grow into the canopy and have deleterious effects on the selected trees. In these situations it is invaluable to have some knowledge concerning the implications of delaying operations, if only to ensure that the products removed from the stand could be marketed in some way to offset the cost of the operations.

Another example of where knowledge of the effects of varying the timing of an operation is important is in cleaning hardwoods out of conifer natural regeneration. An interesting case study of this has been documented on a young stand of longleaf pine (*Pinus palustris*). In the trial the treatments were to remove the hardwoods when the pine was aged 1, 2, 3, 4, or 8 years and a control (untreated); the density of the pine was equalized in all treatments at age 4. By age 30, pine density ranged from 1482 to 1976 ha^{-1} in released plots and there were few differences in terms of diameter, height, and volume due to the different timings of the operation. However, there were significant differences with the untreated plots; competition had reduced the number of pines to 632 ha^{-1}, and the trees were smaller, with 8–10 times less utilizable volume. In conclusion, release was necessary, but delaying it at least for a few years did not diminish long-term volume production.

In most cases where a liberation cutting is required the trees to be cut will have little timber value,

Figure 9 Tending of groups of young trees in multicohort stands can be important if they are very dense.

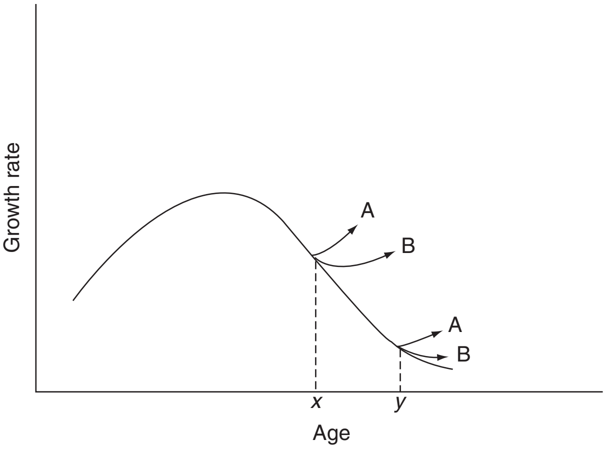


Figure 10 Changes in the responsiveness of two species to tending at different ages.

especially if they have been left with a lot of growing space so that they develop wide, spreading crowns and have all the characteristics of a 'wolf tree'. The main factor influencing when they can be removed is the physical impact of felling and extraction on the younger ones. The effects on the younger trees and the cost of the operation can be minimized by killing the trees with safe and judicious use of herbicides. This can have a positive affect of creating (or increasing) a resource of standing deadwood but this must be balanced against any possible risk to people using the forest, especially if they have been invited or encouraged into the forest for recreation. If the liberation is by cutting this will have most benefit and damage the younger trees least if it is done when the younger trees are small (less than knee high) and when the weather is not cold and frosty, to reduce the possibility of young trees snapping.

The question of how to remove the competitive effect of trees is perhaps more straightforward compared with the timing of the operation. The competitive effects of trees can be removed by cutting or killing using herbicides, or a mixture of both. If trees are to be cut a major consideration is the limitations of the equipment available; this can also influence when the operation is carried out. Herbicides can be used to kill trees by spraying foliage or by applying the herbicide to a cut in the stem. There are many factors to consider with the safe and judicious use of herbicides. A combination of cutting and herbicides can also be used, for example, to prevent coppice regrowth after cleaning.

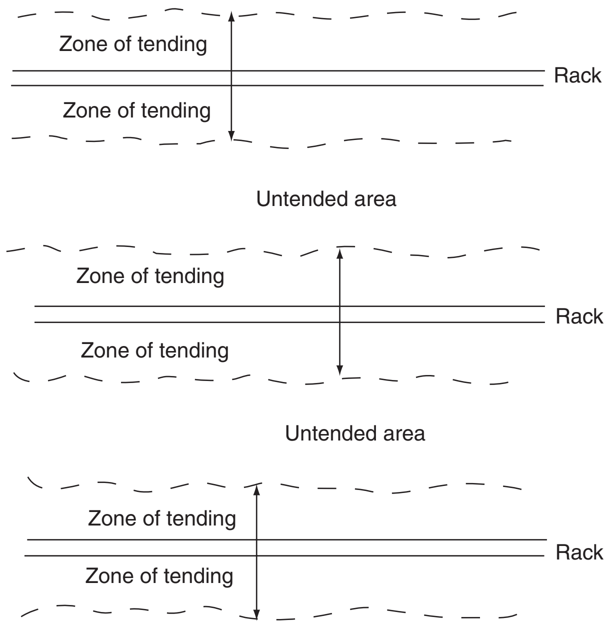


Figure 11 Rack cutting in young naturally regenerated stands to reduce costs.

If a decision has been taken that in order to fulfil management objectives a stand must be cleaned or have a precommercial thinning this will usually apply to the whole stand. However, if as with most tending operations, this is done at a cost to the landowner, treating a proportion of the stand is one way of reducing costs. Two examples of how this can be done are rack cutting and selective release.

Rack cutting This is commonly used in Denmark, France, and Germany. Parallel racks, 1 m wide, are cut every 12–16 m (*n*) through natural regeneration at an early age. Cleaning and respacing is then carried out 3–4 m (1/4*n*) on both sides of the rack, so that roughly only 50% of the crop is treated (**Figures 11** and **12**). The racks improve access and so reduce the cost of respacing, while dividing the stand for management purposes.

Selective release One method of achieving this is the cleaning and releasing of two stems (about 2 m apart), at intervals of approximately 7–8 m through the stand so that they can develop to pole size. Each favored tree is cleared to a distance of 1.2–1.5 m radius and the intervening matrix is untouched.

Prediction of How the Stand will Develop After Tending

The most likely source of information on how any one stand will react to the tending operation is by accumulated experience of treating similar stands on equivalent sites. There are a few models that can be used by the forest manager to help decision making; perhaps the best-known are those for *Pinus radiata* grown as plantations in New Zealand (**Figure 3**).

Figure 12 Cleaning oak (*Quercus robur*) in France showing racks (see also **Figure 11**).

Conclusion

Tending is the application of intermediate treatments after establishment but before the first thinning. The main guiding principles in the application of these operations are: (1) to avoid conditions where the stand may stagnate; (2) to steer the stand towards the structure and composition that will achieve management objectives; and (3) to achieve cost effectiveness. Factors influencing decisions concerning tending in single cohort and multicohort stands are different because in the latter large trees significantly influence the availability of light, water and nutrients to younger trees.

Tending operations can significantly improve stand productivity; but as they are labor intensive they may not always be cost effective and are therefore under pressure in forest management systems.

See also: **Afforestation**: Stand Establishment, Treatment and Promotion - European Experience. **Plantation Silviculture**: High Pruning; Stand Density and Stocking in Plantations. **Silviculture**: Coppice Silviculture Practiced in Temperate Regions; Forest Dynamics; Natural Stand Regeneration; Unevenaged Silviculture

Further Reading

Boyer WD (1985) Timing of longleaf pine seedling release from overtopping hardwood: a look 30 years later. *Southern Journal of Applied Forestry* 9(2): 114–116.

Evans J (1982) Silviculture of oak and beech in northern France: observations and current trends. *Quarterly Journal of Forestry* 76(2): 75–82.

Evans J and Turnbull JW (1984) *Plantation Forestry in the Tropics*, 3rd edn. Oxford: Oxford University Press.

Harper JL (1977) *Population Biology of Plants*. London: Academic Press.

Helms J (1998) *The Dictionary of Forestry*. Wallingford, UK: CAB International.

Matthews JD (1989) *Silvicultural Systems*. Oxford: Oxford University Press.

Nyland RD (1996) *Silviculture: Concepts and Applications*. New York: McGraw-Hill.

Oliver CD and Larson BC (1996) *Forest Stand Dynamics*, update edn. New York: John Wiley.

Smith DM, Larson BC, Kelty MJ, and Ashton PMS (1997) *The Practice of Silviculture: Applied Forest Ecology*, 9th edn. New York: John Wiley.

White J (1980) Demographic factors in populations of plants. In: Solbrig OT (ed.) *Demography and Evolution in Plant Populations*, pp. 21–48. Oxford: Blackwell Scientific Publications.

Yoda K, Kira T, Ogawa H, and Hozumi K (1963) Self thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology (Osaka City University)* 14: 107–129.

Thinning

P Savill, University of Oxford, Oxford, UK
J Evans, Imperial College London, Ascot, UK

Introduction

Thinning is an operation that artificially reduces the number of trees growing in a stand with the aim of hastening the development of the remainder. It is normally carried out several times and starts a few years after the canopy closes. The trees removed are usually the same species as the trees favored. In many situations in forestry about 3000 trees ha^{-1} may be planted, or when natural regeneration is relied upon, the number may be 250 000 or more. The mature stand contains no more than 300 trees ha^{-1}, and with some broadleaved species fewer than 100. Thus, a minimum of around 90% of all trees established at the start of a rotation are removed before the end in thinnings.

Competition can be manipulated by foresters either by the spacings used at establishment (in planted forests), or by thinning after the trees have grown for some years, or both. Thinning is carried out for a number of reasons:

1. To reduce stand density and hence to reduce competition, leaving the remaining trees more space for crown and root development. This promotes stem diameter growth and usable sizes are reached more quickly.
2. To remove dead, dying, and diseased trees, or any others that may cause damage to the remaining healthy ones.
3. To remove trees of poor form: crooked, forked, or coarse trees, so that future growth is concentrated only on the best trees.
4. To provide the owner with some revenue though, if this is not possible, as in some early thinnings, in the expectation of greater returns later in the rotation.
5. More occasional reasons include maintaining light beneath the canopy to encourage grass growth for grazing, for providing poles for building, or for amenity, recreational, or ecological reasons.

Responses of Crops to Thinning

Thinning a stand reduces the number of trees competing for light, soil moisture, and nutrients. This has a number of effects on the remaining trees:

1. Natural mortality (or self-thinning) is reduced because the remaining trees have better access to the resources needed for growth.
2. The lower branches of the crowns receive more light, and so remain alive for longer, hence the trees have deeper crowns than in unthinned stands.
3. The increased space round a tree after thinning promotes the growth of shoots, foliage, and roots. The crown expands outwards to occupy the gap left in the canopy where the neighboring tree was felled. The resulting greater photosynthetic area increases growth.
4. Diameter growth increases significantly. Height growth is little affected.
5. Because thinning mainly affects diameter growth, the stems in thinned stands taper more rapidly than in otherwise similar unthinned stands.

6. Provided a reasonably intact canopy is maintained, total cumulative production per unit area does not vary very much within a wide range of thinning treatments. Production is spread over fewer crop trees where thinning is frequent and heavy, meaning that they grow faster than where the same increment per unit area has to be spread over many more trees.
7. The removal of suppressed trees, which may often be on the verge of death, has a negligible effect on volume growth but if a proportion of the most vigorous trees are felled, there is an immediate reduction in growth because the remaining trees are not able to make full use of the resources of the site. However, over a range of treatments, there is no permanent loss of increment. The stand not only recovers its normal level of growth, but also, over time, makes good the production lost when the increment was below normal immediately after thinning. The length of the recovery cycle is proportional to the volume removed in thinning; the heavier the thinning, the longer the period of recovery.
8. If there is a large standing volume of timber and live branches, as in a stand which has not been thinned, it will consume more assimilated carbon for respiration than where lower volumes are maintained through thinning, hence cumulative net production will be reduced in dense stands. The reduction will become more marked as the volume of standing timber increases.
9. There are two ways in which thinning practices can significantly reduce total cumulative production. The first is by consistently removing the most successful trees in the stand, the dominants, which are those most able to respond, and leaving the less efficient, smaller trees to grow. The second occurs if the intensity of thinning is so great that the site is not being efficiently used. There may often be sound economic reasons for carrying out both these practices.
10. Other responses to thinning include delayed natural pruning, since the extra light allows lower branches to survive for longer. The branches grow thicker and, unless pruned, result in larger knots in the wood.

Time of First Thinning

First thinnings should be carried out before live crowns become too small. They should normally occupy 30–40% of the stem height of broadleaved species, and 40–50% for conifers. If thinning is delayed, as is often the case, because it is more profitable to fell larger trees, the future development of a stand can be impaired.

The earliest a stand can be thinned without a loss of potential production varies according to the rate of growth in fully stocked stands. It can be as early as age 12 years for Maritime pine (*Pinus pinaster*) in southwest France, and 15 for Douglas-fir (*Pseudotsuga menziesii*) in the Massif Central. In Britain, it varies between ages 20 to 35 for most conifers, and can be up to 50 years or more in the much harsher climate of Sweden. At this time in most regions the total standing volume per hectare varies between about 70 $m^3 ha^{-1}$ for light-demanding species, such as larch (*Larix*), to about 100 $m^3 ha^{-1}$ for more shade-tolerant ones.

Thinning Intensity and Thinning Cycle

In an analysis of British thinning experiments it has been shown that the proportion of growing stock that can safely be removed annually without decreasing future production is close to 70% of the maximum mean annual increment over what is termed the 'normal thinning period.' This period occurs during the time when current annual increment is at its highest and ends shortly before the age of maximum mean annual increment. Annual thinning yields before and after the normal thinning period are lower. An example for a Norway spruce (*Picea abies*) stand with a maximum mean annual increment of 20 $m^3 ha^{-1} year^{-1}$ is shown in **Figure 1**. Here it is possible to remove 14 $m^3 ha^{-1} year^{-1}$ (i.e., 70% of 20) between the ages of 25 and 55 years without prejudicing future production. If a stand is thinned at this 'marginal intensity,' by the end of the rotation about half the total cumulative production will have been removed in thinnings and the other half remains for the final harvest (**Figure 2**). By contrast, in an unthinned stand of the same species, age, and growth rate, the standing volume will be about 10% less than this cumulative total because competition will have caused some of the trees to die and hence some potentially useful production to be lost, as well as losses through increased respiration. In terms of basal area, 25% or more must be removed per hectare before any substantial increases in diameter will occur to the remaining trees. In practice, there may be good economic or other reasons for thinning more heavily or more lightly than the marginal intensity (**Figure 3**).

Thinning can vary in intensity: it can be light or heavy, or not carried out at all, but commonly, something close to the marginal thinning intensity is adopted in most places. The thinning intensity has three related aspects: (1) the time of first thinning

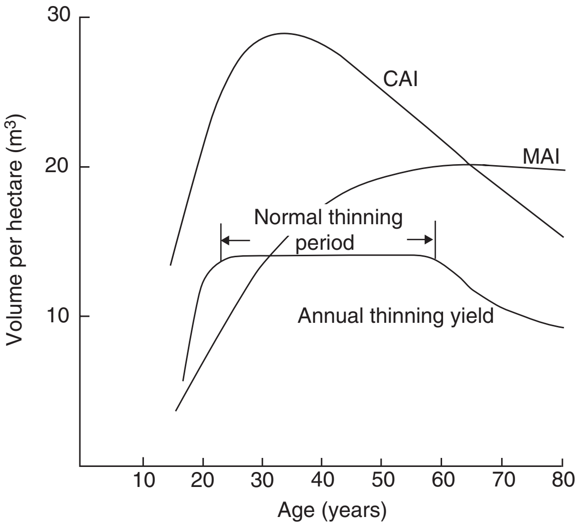


Figure 1 Relationships between age, and mean annual increment (MAI), current annual increment (CAI), and annual thinning yields for yield class 20 $m^3 ha^{-1} year^{-1}$ Norway spruce (*Picea abies*) thinned at the marginal intensity. Reprinted from Savill P, Evans J, Auclair D, and Falck J (1997) *Plantation Silviculture in Europe.* With permission from Oxford University Press.

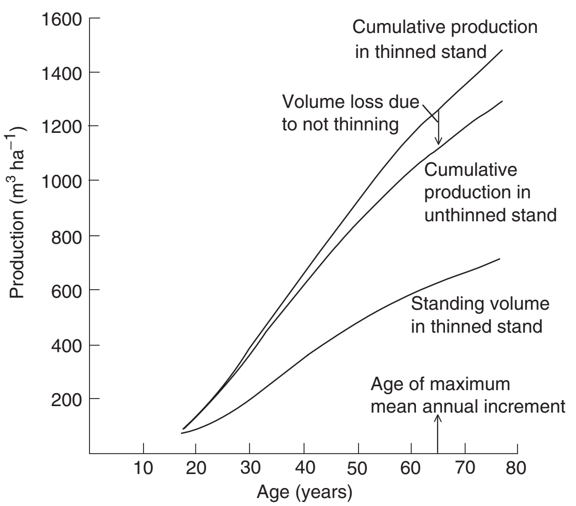


Figure 2 Cumulative production in thinned and unthinned Norway spruce (*Picea abies*) of yield class 20 $m^3 ha^{-1} year^{-1}$ and planted at 2500 stems ha^{-1}. Reprinted from Savill P, Evans J, Auclair D, and Falck J (1997) *Plantation Silviculture in Europe.* With permission from Oxford University Press.

(see above); (2) the standing volume removed in a single thinning (the thinning weight), and (3) the frequency of thinning (the cycle). The thinning weight and cycle are not independent in relation to intensity. For example, if a regime stipulates that 60 $m^3 ha^{-1}$ (weight) should be thinned every 3 years (cycle), then the average annual rate of removal is

Figure 3 Fourth thinning of Mexican cypress (*Cupressus lusitanica*) in a well-grown plantation in Kenya. © J. Evans, 2004.

20 $m^3 ha^{-1}$. However, this rate of removal (intensity) could also be achieved by felling 100 $m^3 ha^{-1}$ on a longer cycle of 5 years. In each case the thinning intensity is the same.

A stand could be thinned every year but it is normally more profitable to obtain the benefits of scale, by thinning occasionally and heavily rather than frequently and lightly. Cycles are commonly adjusted to remove 40–60 $m^3 ha^{-1}$ in a single operation or between one-fourth and one-third of the trees each time. Long cycles are associated with slow-growing stands and short ones with more productive crops.

Type of Thinning

A certain intensity or weight of thinning can be achieved in many different ways regarding the kinds of trees that are removed. A useful indicator of the size of tree removed, and hence for describing the thinning type, is the ratio of the mean volume of thinnings (v) to the mean volume of the stand before thinning (V). The types of thinnings normally carried out may broadly be classified as follows:

1. Systematic methods

   line and strip thinnings – v/V ratio 1.0

2. Selective methods:

   low thinning – v/V ratio about 0.6

   intermediate thinning – v/V ratio about 0.8

   crown or high thinning – v/V ratio about 1.2

3. Combinations of 1 and 2

   e.g., Queensland selection thinning – v/V ratio variable.

Systematic or Neutral Methods

Systematic thinning entails the removal of trees in a predetermined way, regardless of their individual size or quality. Complete lines of trees are usually removed, though other systematic patterns are possible. Systematic methods are neutral in terms of the size of trees removed. On average they will be the same as the average in the stand as a whole, hence $v/V = 1$.

Systematic methods are now very commonly employed as first thinnings which, because of the small average tree size, usually yield little income. Neither brashing (low pruning) nor selective marking of trees is necessary so costs are low. Also, extraction routes for the first and subsequent thinnings are created.

The disadvantages are that defective trees are not deliberately removed, and the removal of a complete range of tree sizes, including some dominants, results in a small loss of total cumulative production. Even a single-line thinning can lead to the development, through larger branches, of some undesirable reaction wood on the exposed trees along the edges of lines. It may also expose a stand to serious risks of windthrow.

Selective Thinning Methods

Low thinning is a selective thinning that particularly favors the dominants by removing trees progressively from the lower to the upper canopy classes. The first trees to be marked for removal are suppressed trees, then subdominants ($v/V = 0.6$); in heavy, low thinnings some of the dominants may then have to be felled to achieve the desired volume. At the other extreme, crown thinning favors the most promising stems which are usually dominants (**Figure 4**). Most commonly, poorer quality dominants and codominants are removed and these have higher average volumes than in other types of thinning ($v/V =$ about 1.2).

Figure 4 Early thinning of ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus*) to secure high-quality broadleaved woodland. © J. Evans, 2004.

The commonest type of selective thinning is intermediate between low and crown thinning ($v/V = 0.8$), but in all selective thinnings defective trees, especially defective dominants, are also removed.

Included among numerous variations to these methods is the early selection of final crop trees in broadleaved stands. The best trees are marked when they are young and favored in subsequent thinnings. Because some inevitably become damaged or do not grow as well as expected, it is necessary to mark, at the outset, two or three times the number that will actually form the final crop.

The effects of some of the various types and intensities of thinning on productivity have been illustrated in the context of a classic British trial, the Bowmont Thinning Experiment of *Picea abies* in Scotland. In it, four thinning intensities were applied, described as:

- B grade: mainly dead and dying trees were removed, an extreme form of low thinning.
- C grade: a moderate low thinning, intermediate between B and D.
- D grade: a heavy low thinning in which only the best trees, mainly dominants, were left and given space for full crown development. It was somewhat heavier than the marginal thinning intensity.
- LC grade: a moderate crown thinning, resembling D except that suppressed and subdominant trees were left to fill spaces between the best dominants. Defective dominants were removed.

The results (**Table 1**), 64 years after planting, confirm the expected trends of larger individual trees being found in the heavier thinning treatments, but with little overall difference in total production except in the largely unthinned treatment B.

Combinations of Systematic and Selective Thinning Methods

Where circumstances permit, there are attractions in combining some of the cost savings of purely systematic thinning with the ability to select for vigor and good growth form. The Queensland selection method is a combined method and was developed for treating hoop pine (*Araucaria cunninghamii*) plantations in Queensland and has a wider potential for use in tropical and temperate forests.

Table 1 Some results of the Bowmont Thinning Experiment (in Norway spruce) 64 years after planting

Treatment[a]	*Stems ha^{-1} (number)*	*Top height (m)*	*Mean tree dimensions*		*Volume ha^{-1} standing (m^3)*	*Cumulative crop yield to date*	
			dbh[b] *(cm)*	*Volume (m^3)*		*Basal area ha^{-1} (m^2)*	*Volume ha^{-1} (m^3)*
B	2204	19.6	21.7	0.333	733	109	861
C	1062	20.2	27.8	0.569	605	123	965
D	327	21.6	42.5	1.387	453	127	953
LC	691	20.9	30.2	0.641	443	128	924

[a] For explanation see text.
[b] dbh, diameter at breast height.
Reproduced with permission from Hamilton GJ (1976) The Bowmont Norway spruce thinning experiment 1930–1974. *Forestry* 49: 109–119.

Table 2 An example of the selection of trees in Queensland high pruning

Selected	S				S	S	S				S	
Tree number	1	2	3	4	5	6	7	8	9	10	11	12

It involves selecting dominant trees along rows for retention and marking them in an obvious way, in Queensland by high pruning. The trees are selected by considering running groups of four trees (counting blanks as trees) on a row-by-row basis as, for example, in **Table 2**. Thus, the first group comprises tree numbers 1, 2, 3, and 4. Of these, 1 is the best stem and is selected (S) and pruned. The next group is tree numbers 2, 3, 4, and 5, and of these 5 is selected. In the next group, 3, 4, 5, and 6, tree 6 is better than 5 and therefore the best in the group and is selected. In the next group, 4, 5, 6, and 7, tree 6 remains the best of this new group, so no additional tree is selected, and so on.

Selection can be done quickly by unskilled workers and results in about 40% of the stems originally planted being selected, though the percentage can be varied by altering the size of the group. Thinning rules can be applied equally simply in relation to the selected trees. For example, all trees which are equal in height to or taller than the selected trees and adjacent to them may be removed in the first thinning.

Thinning and Wood Quality

The faster diameter growth in thinned stands can cause an increase in the size of the core of juvenile wood which is undesirable for many end uses. This is particularly so if the thinning is done early, before the lower branches have died naturally. In thinned stands, branches and hence knots are bigger and may be associated with more reaction wood. Among many conifers, a high wood density is desirable if strength is required. The faster growth following heavy thinnings results in lower density because the wide annual growth rings contain relatively wide bands of low-density earlywood. These alternate with narrow bands of higher-density latewood. The resulting uneven texture is also undesirable. Ideally timber should have as consistent a texture as possible, and this is produced by regular, moderate thinnings. Infrequent, very heavy thinnings lead to much more varied wood properties. Thinning also increases taper, and slightly reduces the amount of the log that can be used.

On the positive side, the removal of leaning and misshapen trees, and ones with crooked stems and basal sweep, reduces the amount of reaction wood and spiral grain remaining in the stand, and the trees left to grow on will have a higher percentage utilization. Also, because the remaining trees are encouraged to grow large, their sawlog and veneering potential is improved since more of the log is used.

Thinning Policy

The purpose of most commercial forestry has been described as ‘the production of neither the greatest volume, nor the largest sizes in a given time, but the production of material which will most suitably fit the demands of the market, yielding, at the same time, the greatest revenue.’

Unfortunately, this is much more easily said than done. Many forest owners have a general idea of what they are trying to achieve but no one can know precisely what market demands will be decades ahead.

The regimes that achieve the best results consequently differ widely, according to the economic and other conditions in a country and region, and often according to the particular circumstances of individual owners.

See also: **Afforestation**: Stand Establishment, Treatment and Promotion - European Experience. **Harvesting**: Harvesting of Thinnings. **Mensuration**: Growth and Yield. **Plantation Silviculture**: Forest Plantations; Stand Density and Stocking in Plantations; Tending. **Wood Formation and Properties**: Wood Quality.

Further Reading

Assmann E (1970) *The Principles of Forest Yield Study*. Oxford, UK: Pergamon Press.

Evans J and Turnbull JW (2004) *Plantation Forestry in the Tropics*, 3rd edn. Oxford, UK: Clarendon Press.

Hamilton GJ (1976) The Bowmont Norway spruce thinning experiment 1930–1974. *Forestry* 49: 109–119.

Hamilton GJ (ed.) (1976) Effects of line thinning on increment. In *Aspects of Thinning*, Forestry Commission Bulletin no. 55, pp. 37–45. London: HMSO.

Kilpatrick DJ, Sanderson JM, and Savill PS (1981) The influence of five early respacing treatments on the growth of Sitka spruce. *Forestry* 54: 17–29.

Leban JM, Houllier F, Goy B, and Colin F (1991) La qualité du bois d'Épicéa commun en liason avec les conditions de croissance. *Forêt Entreprise* 80: 11–27.

Savill P, Evans J, Auclair D, and Falck J (1997) *Plantation Silviculture in Europe*. Oxford, UK: Clarendon Press.

Slodicak M and Novak J (2003) Thinning experiments in Norway spruce stands after 40 years of investigation: 1st series. *Journal of Forest Science* 49: 45–73.

Yoda K, Kira T, Ogawa H, and Hozumi J (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology Osaka City University* 14: 107–129.

High Pruning

R James, Australian National University, Canberra, Australia

Introduction

Pruning is a technique usually employed with the aim of enhancing the quality of solidwood products derived from the butt log of trees in forest plantations. The aim of the technique is to remove knots from the outer wood of such logs but it may also result in loss of growth when living foliage is removed or may introduce rot into the wood, especially in hardwood species. While pruning has been known for many years it is not commonly applied except where trees grow fast enough to provide returns that satisfy economic criteria. It is most common in New Zealand where most stands of radiata pine (*Pinus radiata*) are pruned and where a price premium for pruned logs has been established.

Pruning Defined

Pruning can be defined in straightforward terms as the removal, close to the stem, of living or dead branches from standing trees. The process of pruning is closely allied to that of 'brashing' which refers to the removal, by beating, of branches on a tree stem from ground level to a height of about 2 m. In some countries (e.g., the UK) the term 'high pruning' may be used to refer to pruning above the height where branches have been removed by brashing.

The definition clearly refers to the deliberate action of removing branches using tools designed for the purpose. Sometimes this is called 'artificial pruning' to distinguish it from the practice of natural branch shed which occurs in many species, particularly within natural stands over an extended period of time. Pruning has been known to and used by foresters for some time. It was mentioned by John Evelyn in 1664, in his book *Sylva*, in which he referred to pruning as having been practiced by the 'ancients.' It has been applied as a scientifically based technique for many decades and examples appear in modern literature from at least 1935. Despite its history, pruning is not a general practice in all parts of the world and although statistics are poorly recorded it seems to be mainly carried out in plantations of countries in the southern hemisphere such as Argentina, Australia, Chile, the Republic of South Africa, New Zealand, and Uruguay. These countries can obtain the fast individual tree growth necessary to provide a yield of improved timber within an economic time frame. In New Zealand, where pruning has been a prominent feature of plantation silviculture since the 1970s, over 1 million ha or two-thirds of the area of radiata pine plantation forest has received pruning treatment. As a consequence, the technology associated with pruning pine has been well developed in that country and much of the information presented here has come from New Zealand sources, including recent research papers.

Rationale for Pruning

Doubts about the economics of pruning usually preclude its use in natural forests although it is a frequent practice in urban forests where the main objective is improved access, increased visibility, and enhanced appearance. In plantations, branches are usually removed to a height of about 6 m and pruning may be carried out in a number of stages or 'lifts' to a specified height or diameter up the stem. Except for brashing where a club may be used, branches are usually severed by shears or saws. Even in plantations pruning may not be regarded as an essential operation. Where it is applied as part of stand silviculture it may be carried out for a number of objectives such as: a precaution against the spread of fire into the upper crown, to provide stand access, to reduce timber degrade, and finally as a planned series of operations aimed at eliminating or reducing the effect of knots as a source of degrade in sawn and sliced or peeled wood. (Additional, minor, but locally important objectives may include the use of the branches themselves as stock food, fuelwood or to obtain essential oils. Other special products can include cricket bats made from pruned willow and matchsticks from veneer peeled from pruned poplar.) Eliminating degrade and provision of high-quality wood are similar but the impetus to carry out pruning to reduce degrade implies that some features of the stand or its silviculture will cause the wood to be degraded by exceptionally large knots should pruning not be applied. An example is the pruning of 'stand edge' trees in South Australian plantations of radiata pine where the extra growing space resulting from roads, fire-breaks or other clear space adjacent to the stand may result in branch sizes much larger than those within the stand which are controlled by normal silviculture.

Application of Pruning Techniques

Pruning as a method of preventing the spread of fires, to provide access within the stand or obtain fodder or fuel does not require strict timing. However when the provision of clear, knot-free timber is the aim, then the pruning should be carefully programmed and carried out at times in the life of the stand which will result in the maximum size of a clearwood zone outside the 'defect core' of knotty wood.

The process by which clear, knot-free timber is produced by pruning is illustrated in **Figure 1**. When trees are young and stem diameter is small, branches are removed and, after a process of occlusion (or covering of the branch stub by continuing growth), normal stem growth continues with the new wood being free of knot defect. Since trees taper, pruning is usually carried out in lifts (generally two to four) to avoid enlarged cores at the base of the tree. Pruning should be scheduled to minimize the size of the defect core within the pruned zone yet retain sufficient foliage to permit the tree to continue with adequate growth. Sawn timber or veneer recovery will also be enhanced if the maximum diameter of the defect core is the same for each lift. Since sawing and peeling are carried out effectively in straight lines, boards cut from the outside of the log will be knot-free until the saw encounters the limits of the defect core. Because sawn pieces are usually graded on the basis of the worst defect, the value of some boards would be reduced if they contained isolated defects caused by a diameter over pruned stubs which was larger than the others in the same pruning series. Thus an important component of efficient pruning technique is to time operations so that the maximum DOS is the same for all lifts. Models to predict maximum DOS have been developed and these are used for scheduling operations in plantations of radiata pine in New Zealand and Australia. These models are driven by the expected diameter of the tree at the base of each pruning lift or stage. This can be related to the tree or stand mean diameter at breast height, a parameter which is commonly measured or predicted during the course of forest management.

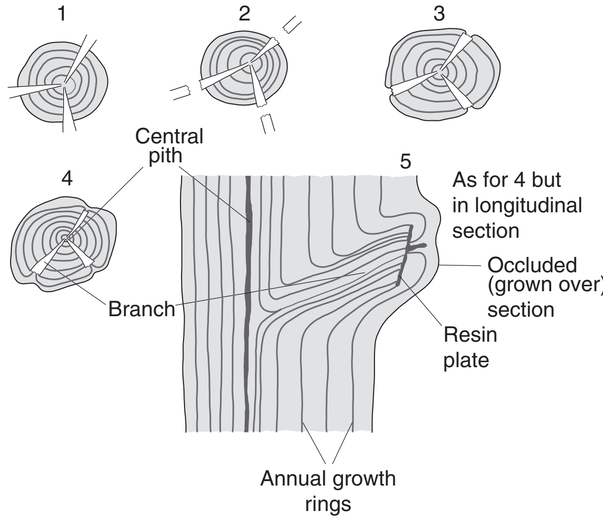


Figure 1 Production of knot-free 'clearwood' using pruning.

A pruning schedule which could be used for stands of radiata pine grown in eastern Australia is given in **Table 1**. The schedule is designed to result in a maximum diameter over pruned stubs of 18 cm for all three lifts. The stand is assumed to have been planted at 1000 stems ha^{-1} for a final crop of 200 stems ha^{-1}. Three thinnings are scheduled, two without yield and one, to 200 stems ha^{-1}, with yield in year 20.

The efficient production of knot-free wood can be achieved only if pruning is accompanied by rapid individual tree growth. This is achieved by thinning (or removing) all unpruned stems. As pruning is usually carried out when the trees are young and

Table 1 Schedule of silvicultural operations for radiata pine (*Pinus radiata*) in eastern Australia, featuring pruning to improve wood quality in the butt log

Age (years)	*Silvicultural operation*
0	Plant 1000 stems ha^{-1}
5.8	Prune 350 stems ha^{-1} to 2.2 m
5.8	Thin to 500 stems ha^{-1} residual stocking, without yield
6.7	Prune 275 stems ha^{-1} to 4.0 m
7.6	Prune 200 stems ha^{-1} to 5.8 m
7.6	Thin to 350 stems ha^{-1} residual stocking, without yield
20	Thin to 200 stems ha^{-1} residual stocking, with yield
30–35	Clearfell

DOS is small, the thinned trees may also be too small in diameter to provide a useful product and the thinning will be without yield (or 'to waste'). The example of a pruning regime given in **Table 1** has two such thinnings scheduled to occur at the same time as the first and third pruning lifts with the objective of reallocating stand growth to the pruned crop trees.

The total diameter of the defect core is however larger than just the DOS. It will be enlarged by any inclusion of resin or bark which is incorporated at time of occlusion and any exaggeration from stem crookedness. In the case of peeled veneer logs the defect core will also be exaggerated by noncentral pith. In conifers the presence of resin pockets within the clearwood zone may eliminate any improvement arising from pruning. Resin pockets (or streaks) are often typical of a particular location and may occur locally in excess; an effect seen in plantations of radiata pine and slash pine (*P. elliotii*). Pruning should not be applied on such sites.

The correct selection of crop trees, particularly of the straightness and most vigorous, and the combination of pruning with other silvicultural operations such as thinning so that growth is enhanced, is necessary to ensure that the benefits of pruning are maximized. When pruning is applied to improve wood quality, it should be applied over a complete commercial log length (with appropriate allowance for stump height and any applicable cutting allowance) to obtain full financial benefit. Pruning above the first or butt log is rare but has been carried out in countries where labor costs are low.

Effect of Pruning on Tree Health

In conifers the severed stub usually becomes coated with a layer of exuded resin which is generally sufficient to prevent fungal infection. This protective mechanism is not present in hardwoods and for some (e.g., the eucalypts, *Eucalyptus* spp.) the chance of rot occurring as a result of the pruning operation is quite high.

To avoid the formation of internal rot, it is necessary to adopt a quite different method of scheduling pruning of eucalypts. Eucalypts shed their branches under natural conditions and during the long rotations applied in extensively managed natural forests this is sufficient to provide defect-free timber. The process of natural branch shedding is well known. The branch dies and an abscission zone develops close to the trunk in which the xylem of the branch becomes blocked and subsequently brittle. With the growth of the stem, the branch becomes more horizontal in orientation and pressure from the continued growth of the trunk together with the weight of the dead branch eventually results in its ejection from the growing stem with a part of the branch occlusion zone remaining within the trunk. When pruning removes a dead branch there is no residual weight to ensure ejection and the short stub remaining outside the abscission point may be 'caught' by the enlarging stem wood and dragged outwards with continuing growth, leaving a kino-filled trace behind. This effect has been observed in both *Eucalyptus nitens*, a temperate eucalypt, and the tropical eucalypt *E. grandis*, although the rate of occurrence has not been established. While this effect negates the objective of pruning it can be counteracted by pruning only green (living) branches. When this is done the occlusion process is similar to that of conifers (**Figure 2**). The scheduling of pruning in eucalypts therefore involves 'chasing the green crown' or pruning before the natural death of branches occurs in the lower crown. Models of the change in height of the base of the green crown can be used to schedule pruning so that branches are pruned while they are alive.

However green pruning disrupts the natural protection from rot formation which, is afforded by the abscission zone in the natural branch shedding process. Research in both New Zealand and Australia has found decay associated with pruning especially the pruning of large (>2 cm) branches; although rot is mainly restricted to the defect core. Results from one study (in *E. nitens*) found that about half of the pruned trees will contain stem rot associated with at least one pruned branch. For some species pruning in the correct season may confer some protection from infection, e.g., *Prunus avium* is reported to suffer bacterial canker when pruned in winter or spring and should be pruned at other times. However results from surveys of eucalypts are conflicting on this aspect and a seasonal effect is yet to be established.

The effect of pruning on stability during windstorms is not clear. If there is an effect, it is probably

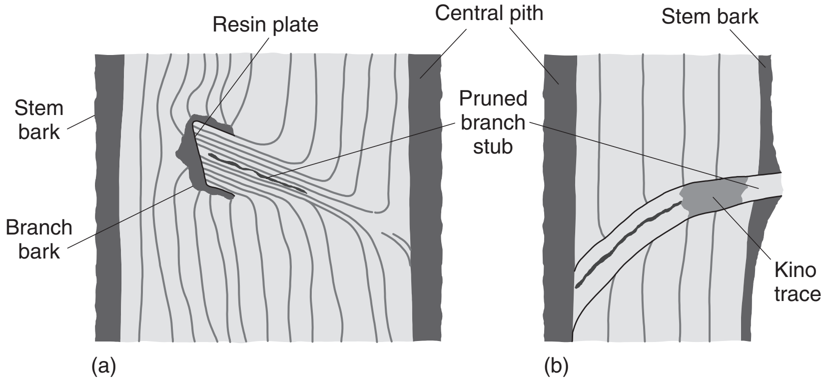


Figure 2 Detail of occlusion over pruned branch stubs in (a) *Pinus radiata*, (b) *Eucalyptus nitens*. (a) Shows normal conifer occlusion over a dead branch, (b) illustrates a frequent result when dead branches of a eucalypt are pruned. Redrawn with permission from Gerrand AW, Neilsen WA, and Medhurst JL (1997) Thinning and pruning eucalypt plantations for sawlog production in Tasmania. *Tasforests* 9: 15–34.

only found in young stands where the length of pruned stems represents at least one-quarter of total tree height. For older trees, especially where the lower branches of unpruned trees would be dead and leafless, there is probably no difference in susceptibility to storm damage between pruned and unpruned trees. In young trees pruning could:

- reduce the crown surface area and hence the area on which the wind could exert pressure
- allow greater air movement through the lower stand in the pruned zone
- lessen the energy-absorbing effect of tree to tree canopy contact
- elevate the center of gravity and center of bending moment and thus alter the natural sway of the tree.

The net effect of these theoretical possibilities is unclear as observers have found both greater and lesser damage amongst pruned trees within stands that have suffered damage from windstorms.

Pruning Tools and Methods

The tools used for pruning are mostly simple hand-operated tools such as shears or saws. The shears may be of the double-fulcrum type and either one or two cutting blades may be used. If saws are used they may be self-supporting blades with a short or long handle and commonly with back-raked teeth (which cut on the pull stroke). Alternatively they may be of the frame and tensioned blade type. Ladders are used to support the operator when branches are pruned above 2 m. This is more efficient than using saws mounted on poles (*see* **Operations**: Ergonomics). In the past a number of striking tools such as axes or modified slashers have been used. The use of these has largely been discontinued because of the damage caused to the stem, the irregular surface of the cut branch, and the danger to the operator.

There have been a number of attempts to mechanize the operation of pruning, but with little success. The necessity for repeat visits to carry out each lift, lack of easy access to trees under forest conditions, and the difficulty of building a power unit without the disadvantages of weight, noise, vibration, air pollution, and the danger inherent in motorized cutting tools have precluded mechanization on an operational scale. Although lightweight chainsaws are sometimes used for the first, ground-based, lift, especially where branches are large, the inherent danger of this operation and the restrictions imposed by safety regulations mean that it is not a widely applied method. Recent developments in electronics have led to one method of power-assisted pruning that is currently used in Argentina and Chile. Power is supplied by a set of lightweight (about 3 kg) rechargeable batteries which is carried on a waist-band and shoulder harness and which powers shears similar to those used by some types of hand shear. Studies carried out in Argentina have shown that while productivity increases are marginal, the workers are less fatigued and achieve target rates more easily, and the workforce need not be restricted to the 'fit young male' category. The forestry version of this tool is a modification of equipment developed in France for vineyard pruning and used for that purpose in many other countries.

Effect of Pruning on Tree Growth

When living branches are severed in pruning there will inevitably be a reduction in tree foliage. Although this lower foliage may be less photosynthetically active than that of the upper crown, there may be some loss of increment as a result. This effect has been well established for many species (both hardwoods and softwoods) throughout the world. Some experimental results suggest that almost any level of foliage removal will result in at least some reduction in tree growth. However other results suggest that removal of inefficient lower foliage may result in some increase in tree growth. The necessity of obtaining a small defect core will usually require that some of the 'green crown' (or living foliage) be removed even if this results in some growth loss. For pines, regimes are often designed to ensure that a 4-m length of green crown is left after pruning. For eucalypts, where the mechanism for scheduling is focused more on the height of the base of the living crown than diameter over pruned stubs, removal of 40–50% of the length of the green crown has been identified as an acceptable compromise. Physiological changes within the remaining foliage have been noted probably leading to increased photosynthetic efficiency in the residual crown. In any case, where reduction of growth has been observed, the effect has been temporary. Of more concern than this temporary reduction in growth is the permanent loss of tree stem dominance status. That is, when trees that were selected for pruning because of their dominance are left to compete with unpruned trees, they are liable to lose dominance because the loss of foliage has slowed their growth and reduced their ability to compete with the unpruned stand component.

Removal of living foliage may stimulate the growth of epicormic branches within the pruned zone. In pines these arise from stem-borne needle fascicles and in hardwoods from dormant buds beneath the bark. It is common practice to use a knife to remove needle fascicles from pine stems when pruning branches and for both pines and hardwoods to remove epicormic branches that have formed since the last pruning lift.

Growth is derived from the foliage of the crown, and crown length per hectare has been found to be correlated, on a stand basis, with growth for young stands of New Zealand grown radiata pine. Although the relationship is not a simple one it has been used as the basis for models which can be used to predict the early growth of stands and particularly the effect of early pruning and thinning on subsequent growth.

The Economics of Pruning

The decision whether or not to incorporate pruning into a silvicultural regime will depend on an assessment of the financial benefits, including the improvement in returns from pruned compared to unpruned logs. A study which investigated the effects of various parameters on estimates of pruning profitability (plantation grown radiata pine in New Zealand) using a silvicultural modeling system found that profitability was not particularly sensitive to total pruned height or diameter over pruned stubs but in both cases the volume yield of clear grades was sensitive to these effects. The lesser effect on financial estimates was probably a result of trade-offs between costs and production effects. Price assumptions and interest rate markedly affected estimated profitability.

As there are few firmly established premiums for pruned logs estimates of future prices are usually regarded as a matter of informed conjecture. Since pruning involves considerable investment and results will not be obtained for some years, the decision to prune involves some risk. One source of price information is the New Zealand Ministry of Agriculture and Forestry which publishes averaged prices received for New Zealand grown radiata pine, on a quarterly basis. Based on data as at June 2002, there was a premium of about \$US50 m^{-3} (Japanese Agricultural Scale, free on board) for pruned export logs and \$US36 $tonne^{-1}$ (mill door) for pruned domestic logs.

While premiums have been established for some markets, it is a matter of judgment whether they will be available more generally or whether they will be sufficient to compensate for the cost of the investment in pruning. Some utilization companies are using technology instead of pruning to improve the appearance of sawn wood. This can include cutting out knots and finger-jointing the shortened lengths into boards, covering boards with a plastic sheet on which has been printed a photographic image of knot-free wood and extruding defect-free components from wood pulp. Some would regard such solutions as less aesthetically pleasing than wood from pruned trees.

Even when margins for pruned logs have been established, pruned log quality must be determined before the margin is realized. This may be achieved from presentation of silvicultural records. The Pruned Log Certification Scheme which has been established in New Zealand is a record system that allows evaluation at time of sale. For the certification scheme, parameters that would indicate the quality of pruning (such as the average diameter over pruned branch stubs) are assessed immediately after pruning has taken place and records are held by authorities independent from the forest owner. Prospective purchasers can use these records and the size of the trees at time of felling to estimate the yields of high-quality timber. Assessment at time of sale varies from simple pragmatic rules-of-thumb, to sawing of samples, to detailed measurement of the internal and external properties of sample logs. An example of pragmatic assessment is the acceptance of pruned logs where growth since pruning has eliminated all appearance of nodal swelling, such logs being regarded as having increased their diameter sufficiently for knot-free timber to be recoverable. An example of detailed assessment is the Pruned Log Index used in New Zealand. This is derived from measurements of log size, log shape, and defect core size and relates directly to, but remains independent of, grade and value recovery by any sawmill. Application of this measure of pruned log quality resulted in mill door prices for pruned logs which ranged from \$NZ140–215 m^{-3} (approx. \$US75–115) during 2002.

See also: **Harvesting**: Harvesting of Thinnings. **Operations**: Ergonomics. **Plantation Silviculture**: Forest Plantations. **Plantation Silviculture**: Rotations; Stand Density and Stocking in Plantations; Tending. **Tree Physiology**: Physiology and Silviculture.

Further Reading

Evans J and Turnbull JW (2004) *Plantation Forestry in the Tropics*, 3rd edn. Oxford, UK: Oxford University Press.
Florence RG (1996) *Ecology and Silviculture of Eucalypt Forests*. Melbourne, Australia: CSIRO Publishing.
Helms JAI (1998) *The Dictionary of Forestry*. Bethesda, MD: Society of American Foresters.
James RN and Tarlton GL (eds) (1990) *New Approaches in Spacing and Thinning in Plantation Forestry*, Proceedings of an IUFRO Symposium. Rotorua, New Zealand: New Zealand Forest Research Institute.
Lewis NB and Ferguson IS (1993) *Management of Radiata Pine*. Melbourne, Australia: Inkata Press.
Montagu KD, Kearney DE, and Smith RGB (2002) The biology and silviculture of pruning planted eucalypts for clear wood production: a review. *Forest Ecology and Management* 6174: 1–13.
Savill PS and Evans J (1986) *Plantation Silviculture in Temperate Regions*. Oxford, UK: Clarendon Press.
Shepherd KR (1986) *Plantation Silviculture*. Dordrecht, The Netherlands: Martinus Nijhoff.
Smith DM (1962) *The Practice of Silviculture*. New York: John Wiley.

Rotations

P Maclaren, Piers Maclaren & Associates, Rangiora, New Zealand

Introduction

When should a tree be harvested? At 'maturity'? Unlike animals, trees do not reach a maximum size and then stop growing, so the definition of 'maturity' is not clear. A tree can be harvested at any age that the owners consider desirable. The question of rotation age (also called rotation length) is very relevant for foresters and indeed has long been one of the main decisions that foresters are trained to make.

Because forests usually contain a mixture of species and age classes, they are more complicated than stands which can consist of even-aged trees growing from bare ground – like a crop of wheat. Starting with the simplest situation, a planted or naturally regenerated tree in an even-aged stand, there are several phases in the growth cycle.

Stages of Tree Growth

The first phase is site capture. Of the thousands, or tens of thousands, of seedlings per hectare, few trees can survive the initial years. The tree uses energy to put down roots, build up a green crown, and outcompete weeds. Access to water and nutrients is vital, but light is often not so limiting. Wood production is not of major survival benefit, and in any case the plant does not yet have the resources to generate high amounts of photosynthate. The tree expands until it encounters the influence of neighboring trees, at which point the rate of growth slows, for both the roots and crown. Weeds become suppressed and cease to be a major problem.

In phase 2, the tree can progress in only two ways: by competing with, and taking over the space of the neighbors, or by extending upwards. The tree's survival is guaranteed only if it can maintain access to light, water, nutrients, carbon dioxide, and space. For most species, light becomes critical, because a well-lit tree can acquire the energy to obtain the other resources. On the other hand, overtopping by neighbors will suppress and kill a tree. That is the main reason trees produce wood – survival advantage is ensured by gaining height and securing the light.

As the tree's height increases, the lower branches become shaded and die. A steady state is reached where growth at the top of the tree is matched by death at the bottom of the green crown. Nutrients are translocated upwards from branches as they become moribund. The important point for foresters is that trees in phase 2 require low inputs of minerals – most nutrients are used in the formation of the green crown, and little extra is required for either the maintenance of the crown, or for the production of wood. Wood is a carbohydrate, comprising overwhelmingly carbon, hydrogen, and oxygen and little else. Once the 'factory' has been constructed, good growth can be expected wherever there is adequate temperature, water, and sunlight.

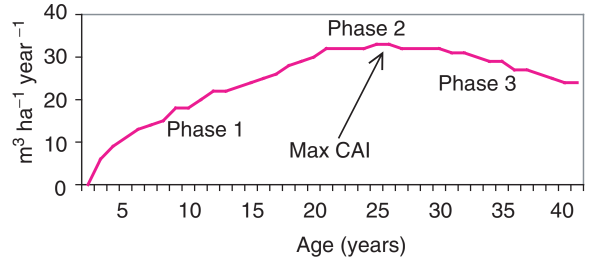


Figure 1 Annual stemwood growth (net current annual increment (CAI) and volume). Adapted from the New Zealand National Exotic Forest Description 1995. Although indicative of the weighted-average growth for radiata pine in New Zealand, the line has been smoothed for the sake of clarity.

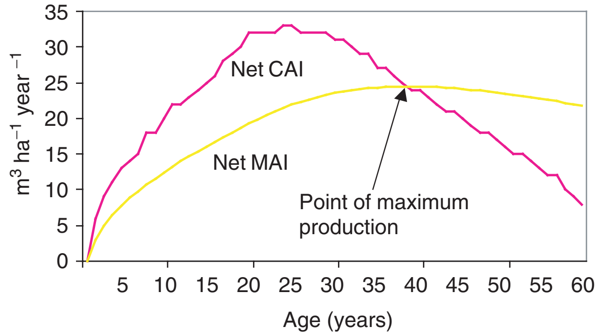


Figure 2 Rotation age to maximize production. CAI, current annual increment; MAI, mean annual increment. Adapted from New Zealand National Exotic Forest Description (1995). For the sake of clarity, the data have been smoothed and extrapolated past age 40.

But eventually the tree's increasing size and age come at an energy cost: water must be pumped from the root tips to the topmost foliage, and starch must be translocated the same distance in reverse. The tree's size makes it vulnerable to the effects of wind, and the wounds it has developed over its long life make it susceptible to attack by insects and disease. Its productivity drops off and it becomes senescent (phase 3). Thus there is a point in the life of an individual tree or stand where it is the most productive at growing stemwood (**Figure 1**).

Gross and Net Increment

The volume increment of the stand is measured per unit area (i.e., per hectare or per acre). Gross increment is the wood produced each year, and net increment is the same, less the quantity lost through death and decay. While individual trees may still be actively growing, other trees are dying, and the forester must consider the stand as a whole. The current annual increment (CAI) is the wood produced in the most recent year. The mean annual increment (MAI) at a given age is the CAI averaged up to that age. It is usually expressed in net terms, but can include the wood harvested from extraction thinnings. Such thinnings are a way of using, and preventing, loss from natural mortality.

Rotation Age for Maximum Volume

As the stand progresses from phase 1 to phase 2, and more resources are channeled into wood production, the CAI increases. As long as this is greater than the MAI, the MAI will continue to improve. At the point where the CAI has declined to equal the MAI, the MAI will have attained its maximum level (**Figure 2**). The point of maximum MAI is of great significance to foresters, because if all stands were harvested at this age then the forest would be producing the maximum sustainable volume.

For hundreds of years the main job of foresters in both Europe and China was to 'conserve the maturity' of the forest resource – to prevent trees being felled before they had reached their maximum potential. It is always tempting to overcut, i.e., cut more wood than the allowable volume that has been calculated by estimating the yield of a theoretical forest where the stands were harvested at their maximum MAI.

A healthy mixed-aged forest can sustain a certain level of production indefinitely, but assume that a greedy government or population cuts more wood than this figure. What effect does this have? The average harvest age is reduced, the productivity of the forest is diminished, and it will require greater and greater numbers of younger and younger trees to meet the same demand. If overcutting is allowed to continue, eventually trees only a few years old will be harvested. These will not provide nearly the same quality or quantity of wood as the original 'mature' forest.

At the other end of the spectrum, an overmature forest is also not productive. This means that it contains a high proportion of trees that are senescent or at risk from storm or insect damage. Overcutting this forest will, if done carefully, restore the forest's vigor, by returning the average rotation age to its peak value of MAI.

In practice it is difficult to calculate the age and amount of maximum MAI for any tree species. A huge database is needed, as growth rates vary with species, soils, climate, management regime, and genotype. Some of these are constantly changing. It is also difficult to quantify mortality. Some death and decay are inevitable, as a result of trees becoming more crowded. Trees naturally thin themselves out as they take up more space, and this can be predicted with a reasonable degree of accuracy. Such tree loss is called attritional mortality. Tree death also commonly occurs from storm events, from fire, drought, frost, and epidemics of disease and pests. If large numbers of trees die, this is called catastrophic mortality. The distinction between the two types is vague, and in any case the two types influence each other. The significance of the latter is that it is inherently unpredictable and cannot easily be built into models.

Even if the forester overcomes these difficulties, the job is not complete. It is not sufficient to determine the rotation age that will provide the greatest quantity of wood from a given area of forest in perpetuity. Wood quality must also be considered. Revenue at harvest is a combination of both quantity and quality.

Rotation Age for Maximum Harvest Revenue

Generally speaking, the older the tree, the better the quality of wood, unless the tree has started decaying. Wood density is an important attribute, being a determinant of strength, stiffness, and hardness. It increases with tree age: the outer growth rings are denser than the inner rings. The proportion of heartwood also increases with tree age. Heartwood is noteworthy because it imparts durability and color, depending on species. Heartwood can be yellow, brown, black, red, or combinations of these. This contrasts with sapwood, which is generally a bland white and is nondurable. In addition to these well-known qualities, a number of other characteristics, such as moisture content, spiral grain, and distortion in processing, become less problematic with maturity. Most importantly, the lower branches of very old trees die and fall off, with subsequent wood being knot-free (‘clearwood’).

Wood is sold in distinct grades, with log specifications that relate to straightness, number of growth rings, heartwood content, branch presence and size, and small-end diameter, among other considerations. Often there are substantial price differences between successive log grades, which may correspond to different end-uses. The stumpage revenue at clear-felling therefore does not increase smoothly with age: it may remain fairly flat over several years and then rise sharply when a critical threshold of wood quality is attained.

Near the time of harvest, the value and value increment of a stand need not be predicted from generalized silvicultural models – it can be obtained more directly from inventory models. Individual trees often display features that are inherently unpredictable, so generalized models have limited utility. For example, a tree may have a predictable height and diameter at breast height, with an excellent butt-log up to a certain height, but upper logs are downgraded by lack of straightness, woodpecker holes, or other stem damage. Average branch size may be predictable, but individual large branches or forking (possibly induced by a storm event affecting most trees in the stand at a certain height) are not so amenable to mathematical modeling. Good inventory models will optimize the value of individual trees when cut into logs. Although these models may amalgamate data to describe the whole stand, they will simulate future growth without losing the detail obtained from an inventory of individual, idiosyncratic trees.

The output of intensive measurement and modeling for mature stands is an accurate assessment of standing value, currently and for a decade into the future. While the volumes by log grade are predictable by this process, any projection of prices is fraught with difficulty. One can use current prices, or prices averaged over the last (say) 12 quarters, or prices obtained from a trendline, or prices estimated from anticipated market conditions.

Rotation Age for Maximum Profitability

An astute forester will take all these things into consideration when determining rotation age, but the task is still not complete. The combination of quantity and quality of wood provides the revenue at harvest for a range of ages, but it is necessary also to consider cost, risk, and the time interval between costs and returns.

Maintaining a forest is not usually free of costs. Imagine a forest where stands are harvested at 60 years of age. The forester calculates that the revenue will improve if stands are harvested at age 80. But to do this each stand has to undergo 20 years of extra fire protection, land taxes, and supervision. The investment carries an extra 20 years of risk: the older stands could be susceptible to disease or storm damage. Most critically of all, the revenue will need to be deferred for 20 years, and time is money. This difficult concept needs some explanation.

Faced with an offer of $1000 today or a promise of $1000 in 1 year’s time, most people would take the former. The money can be used right now for paying off debt, for investing in another project, or obtaining interest via somebody else’s investment. In the jargon, people have a time preference for early returns. A rational time preference can be calculated by examining the compound interest on alternative investments. This is called the cost of capital. In addition to the cost of capital, risk is sometimes included in the figure. For example, the $1000 today is certain, whereas the $1000 next year is only a promise. For all these reasons, future returns are heavily discounted, and the greater the investment interval, the higher the discount factor. It is important to understand that this is the major reason why rotation lengths in commercial forests are less than the point where revenue is maximized. The optimum rotation age financially is less than the optimum rotation age physically.

The Opportunity Cost of Capital

To illustrate this concept, let's consider the financial growth of a tree crop grown as an even-aged stand. As the crop grows, it becomes more valuable. The return on capital is the current value increment of the crop divided by its standing value. The current value increment increases, but eventually cannot keep pace with the gain in value of the stand. The ratio of increment to standing value increases to a maximum and then declines. The possibility of selling the asset and investing the money elsewhere becomes ever more tempting. This occurs well before the stand has reached its maximum MAI for value or even for volume. The complaint is often heard that a stand is being felled 'just when it is starting to show substantial annual gains in value,' and long before it has achieved its maximum average volume production. True, but is it gaining in value relative to the considerable – and increasing – value of the asset?

To reinforce this point, let's consider two mixed-age forests of the same species and growth potential. Forest A is grown on a rotation of 80 years, whereas forest B has a 40-year rotation. They are both managed sustainably, with a constant proportion harvested and replanted every year. Forest A has a greater proportion of older trees and has a standing value twice as high as forest B.

An accountant standing at the gates of the forests observes that daily inputs (i.e., costs) to each forest are the same, but the daily outputs are substantially different. The older forest is producing more wood every day, because the rotation age is closer to the peak of MAI.

Simple accounting would suggest that forest A is more profitable (revenue minus costs), but this is not necessarily the case. More capital is tied up in forest A. If this forest were liquidated (i.e., cut down and sold) it would sell at twice the price of forest B. It would be possible to use the money to buy two forests exactly like forest B. Thus it is not only important to maximize the output of the forest relative to daily costs, it is also important to minimize the capital tied up in the forest. The easiest way to do this is by maintaining a relatively low rotation age.

Foresters who calculate the internal rate of return (IRR) for a crop of trees at every rotation age often experience a sense of shock: the maximum IRR is found at very young ages – far lower than conventional wisdom would suggest. Rapid turnover of capital is of crucial importance in any calculation involving IRR: it is important to keep costs down, to delay costs, and to obtain revenue at the earliest opportunity.

An alternative approach is to use net present value (NPV), where the discount rate is specified. Discount rates used in forestry are commonly 6%, but can be 10% or more. The discount rate represents the real (i.e., inflation-adjusted) rate of return that foresters expect to get from alternative investments, plus a factor for risk. Rates of this magnitude may be reasonable for short-term investments, but the awesome exponential power of compound interest over the time spans implicated in forestry suggest that such rates are unreasonable for forestry and unsustainable for the general global economy. Be that as it may, the effect of using high discount rates is exactly the same as that of using IRR. It emphasizes the value of money upfront, and downplays the benefits of distant rewards.

Because many foresters throughout the world have used IRR or NPV at a high discount rate to determine their regimes, trees harvested from plantation forests are usually very young. This means they have a small diameter and are inferior for either structural or appearance uses. They are inferior in terms of strength, stiffness, and hardness because of their low wood density, among other characteristics. They are inferior for appearance purposes because they contain very little heartwood and very little knot-free wood (unless pruned). Short-rotation regimes can be justified as long as there is a good market for pulpwood and chip-and-saw grades, or as long as reconstituted wood can satisfactorily and cost-effectively substitute for the natural product, but it is conceivable that the predominance of short-rotation regimes could lower the price of this material and result in a premium for older and larger trees. It is also possible that there could be a swing away from the use of high discount rates in forestry.

Forests Versus Stands

One final point must be made regarding rotation age. A forest is more complicated than a stand, and the optimum solution for a forest may not coincide with the optimum solution for the stands within it. This is because there may be supply commitments, or there may be bottlenecks of labor or machinery. Even if there were no such restrictions, it makes sense to sell wood when the price is high and to minimize harvesting when the price is low. In other words, some stands may be felled long before their optimum rotation and others may be felled a lot later. A specialist branch of forestry is concerned with estate modeling, which varies the rotation length of individual stands to ensure both continuity of supply for the whole forest and responsiveness to market signals.

Consider a processing plant that handles large, old logs (perhaps it requires clearwood with a high proportion of heart). It pays a very high price for the wood, and is a dominant customer of the forest. It requires a regular, predictable supply of this type of wood.

The resource forester examines the inventory records of the whole forest and observes that there is an impending gap in the supply of this log grade, followed soon after by a glut. This is because no real forest exists where there is a perfectly balanced mixture of age classes. Disruptions such as planting booms, wars, depressions, storms, or fires always mean that there is a higher proportion of certain age classes, and gaps where there are no trees of optimum age. What to do? The answer may be to overcut the oldest age classes, followed by undercutting the next oldest. In other words, in order to satisfy the major customer and fill the gap in supply, some age classes will cut well before their optimum rotation age and others many years afterwards.

The forester's decision has long-lasting consequences. Not only does it greatly influence the asset value, the cash flow, and the profitability of the existing resource, but it also has a major bearing on the next generation of trees. This is because a planting boom immediately follows a harvesting boom, because land cannot be left idle for long without weed encroachment. The existing age class structure of the forest is creating headaches for planners, but it behoves them also to consider the effect of their actions on their successors.

Summary

The issue of rotation age is a good example of the complexity of forest science. To the uninitiated, forestry may seem like a simple business ('you plant a tree and you cut it down') but a deeper examination reveals the difficulties of determining and imposing rational solutions on long-lived biological systems. The measurements, calculations, and models in forestry can be highly complex but can never reach the degree of precision that could be attained in purely physical systems. Also, the payback periods envisaged by the forester are significantly longer than almost any other human endeavor. What factory, what engineering structure, what work of art, would take three decades or more to commission?

See also: **Afforestation**: Stand Establishment, Treatment and Promotion - European Experience. **Ecology**: Reproductive Ecology of Forest Trees. **Plantation Silviculture**: Short Rotation Forestry for Biomass Production; Sustainability of Forest Plantations. **Silviculture**: Unevenaged Silviculture.

Further Reading

Evans J and Turnbull JW (2004) *Plantation Forestry in the Tropics*. Oxford (3rd edition) [Chapter 18].
Matthews JD (1989) *Silviculture Systems*, Oxford.
Savill PS, Evans J, Auclair P, and Falck J (1997) *Plantation Silviculture in Europe*. Oxford. [Chapter 10]
Smith DM (1986) The Practice of Silviculture. Wiley (8th edition).

Multiple-use Silviculture in Temperate Plantation Forestry

W L Mason, Northern Research Station, Roslin, UK

Published by Elsevier Ltd., 2004

Introduction

Silviculture can be defined as the growing and tending of forest stands to meet management objectives. One of the characteristics of forests is that they can be managed to meet a wide range of objectives, from timber production to provision of recreation opportunities, from conservation of rare species to sheltering farm animals during harsh weather. In recent decades, a common tendency has been to try and zone forests into areas of 'dominant use' where a particular objective would take precedence over all the others. Thus recreation might be the most important objective close to a forest visitor center whereas the emphasis would be on timber production in areas with little public access and low visibility. Management for these contrasting objectives might foster stands that would vary appreciably between zones. Thus stands in the first zone might be very variable over a short distance with a range of tree species of different sizes, whereas the second would have much less spatial variation with more regular stand structures composed of one to two species. This approach may be termed 'single' or 'dominant use' silviculture where the aim is to maximize the yield of a particular output (visitor days or volumes of timber) subject to providing minimum levels of any other outputs. However, it is often possible and desirable to manage stands for several objectives at the same time, for instance by providing a habitat with an attractive landscape that accommodates game shooting and where regular harvests of timber provide income for the owners. This alternative strategy is called 'multiple-use' silviculture because managers explicitly seek to develop stands that will provide for a range of uses at the one time. The purpose of this short review is to explain some of the increasing interest in 'multiple-use' silviculture and outline some of the challenges to its wider adoption. The emphasis is upon experience in the British Isles, but the principles should be applicable in other countries and forest types.

Plantation Forests: An Example of Dominant Use Silviculture

A frequent legacy of national forestry policies during the nineteenth and twentieth centuries is extensive areas of conifer plantations that were established in many parts of the north temperate zone to provide a wood supply for local industries. Examples of such plantations can be found in Britain, Ireland, The Netherlands, Belgium, Germany, New Zealand, Chile, South Africa, and many other countries (**Figures 1** and **2**). The plantations created during this era of forest expansion have often developed into homogeneous stands of trees of similar ages ('even-aged') of one or two species. The main silvicultural system used in their management has been clear-felling. Under this system all the trees on a given area (coupe) are felled and removed from site when they have reached the desired size for processing. The average coupe size can vary from less than 1 ha to up to 50 ha or more, depending upon location and visibility. The felled area is generally reforested by planting young seedlings that have been raised elsewhere in a forest nursery. However, if the chosen tree species produces regular supplies of seed, and if the site is of low fertility so that weed competition is not serious, then reforestation may be achieved through natural regeneration. In either case, the aim is to ensure rapid growth of the young trees so that a full canopy cover is restored. Any competing vegetation or unwanted tree species are normally removed during the establishment phase. In a similar way, any trees of poorer quality of lesser vigor are gradually thinned out after canopy closure so that by the time of clear-felling, the stand is composed only of the better-quality stems. The age at which clear-felling occurs (rotation age) varies with species and site but in the north temperate zone is generally between 40 and 120 years.

Figure 1 Cawdor. An internal view of a 100-year-old Scots pine plantation in north-east Scotland managed under a group shelterwood system. The mixture of mature trees and clumps of regeneration of pine and other species provides a varied woodland which is both attractive to the local community for recreation and a source of valuable timber for the landowner. Courtesy of the Forestry Commission.

Recent changes in forest policy in many countries have given much greater emphasis to the sustainable management of existing forests for multiple benefits, including maintenance and enhancement of biodiversity, provision of recreational opportunities, and increased visual diversity, as well as timber production. There has been ongoing criticism that the limited number of tree species and the lack of structural diversity within the stands of plantation forests is not compatible with management for multiple objectives. A particular concern has been that the relatively short rotations employed have resulted in a lack of older stands and the rich habitats

Figure 2 Glenbranter. An 80-year-old Sitka spruce stand in western Scotland which is starting to develop some of the features of the later phases of stand development. Note the large trees, the regeneration in the background, the fallen deadwood, and the developing ground flora which all combine to provide some of the features aspired to in multiple use silviculture. Courtesy of the Forestry Commission.

associated with features such as large trees, abundant deadwood, and an open stand structure. Such criticisms have been particularly strong in countries where plantation forests are a major part of the forest area as in Great Britain and Ireland, or where the natural forest stands have been gradually simplified towards a structure similar to a planted forest (e.g., Scandinavia, parts of Central Europe). As a result, there has been a growing perception that conventional plantation silviculture based upon clear-felling may not be the most effective way of delivering multiple benefits, particularly in forests with high landscape, recreation, or conservation values. This has led to increasing interest in the use of a range of alternative silvicultural systems to clear-felling such as shelterwood and selection systems, all of which involve retaining some mature trees on the site during the regeneration phase. This approach has been given a variety of names such as 'continuous cover forestry,' 'close-to-nature forestry.' and 'ecological silviculture,' to name but a few.

Stand Dynamics and Multiple-Use Silviculture

A better understanding of these issues is gained by considering the development of a forest stand over time, otherwise termed stand dynamics. While this is a complex process with appreciable variation between both forest types and regions of the world, a comparatively simple conceptual model in widespread use separates the development into four distinct phases. These are generally known as stand initiation, stem exclusion, understory reinitiation, and old-growth with the first being the youngest and the last the oldest stage in the process. It is not inevitable that a stand has to develop through all four phases since damage caused by a major disturbance (e.g., the wind storms of 1987 in southern England and of 1999 in France and Germany) will destroy so much of the overstory that a stand reverts back to the initiation phase.

Table 1 gives more details of these phases using a Scottish Scots pine (*Pinus sylvestris*) stand as an example. A point to notice is that a forest will generally contain stands at different stages of this development process, depending upon the history of harvesting or natural disturbance due to fire, wind, snow, or disease. The frequency of such disturbances can affect the relative area of stands in the different phases. Thus an area with frequent severe disturbances from wind or fire will have comparatively few stands in the old-growth phase and more in the younger phases than would be the case where such events are less frequent.

The traditional practice in timber management of harvesting a stand at or close to the age of maximum mean annual volume increment tends to occur towards the end of the stem exclusion phase. Management would also seek to maximize the return on investment by reducing the length of the stand initiation phase. The impact of this silvicultural approach can be examined by looking at the way a range of timber and other benefits change with different stand development phases (**Figure 3**).

In this figure, the variation of an illustrative range of market and nonmarket benefits is presented in relation to these four phases for Sitka spruce (*Picea sitchensis*) plantation forests in northern Britain. The benefits are not quantified, but the relative values are supported by findings from studies on public preference and biodiversity carried out in Great Britain and elsewhere in the last decade. For example, timber value peaks in the stem exclusion and early understory reinitiation phases but declines towards old-growth. By contrast public preference is lowest in the

Table 1 An outline of the four phases of stand development using a Scots pine (*Pinus sylvestris*) stand in northern Scotland as an example. Reproduced with permission from Mason WL (2002) Silviculture and stand dynamics in scots pine forests in Great Britain: Implications for biodiversity. *Investigacíon Agroria; Sistemas y Recursos Forestales* Fuera de serie no. pp 175–198

Phase	*Approximate tree age (years)*	*Approximate height of dominant trees (m)*	*Comments*
Stand initiation	0–20 (40)	0–5	The period during which the trees are becoming established on the site, but a closed canopy has not yet been formed. The longer period refers to what happens when natural regeneration is being used and/or the trees are being affected by browsing.
Stem exclusion	20–80	5–20	The trees form a closed canopy over the site. No shrub or tree understory is present. Tree death will occur as a result of competition unless this is reduced by thinning.
Understory reinitiation	80–150	20–25	Gaps start to occur in the canopy as a result of disease or disturbance. Regeneration of pine and other tree species can occur. Height growth has slowed down but diameter growth continues.
Old growth	150–350 (or more)	25 or more	The survivors of the original trees begin to die out. The stand becomes a mosaic of groups of trees each of different ages. Comparatively low stocking compared to the previous two phases. Increasing abundance of standing and fallen deadwood.

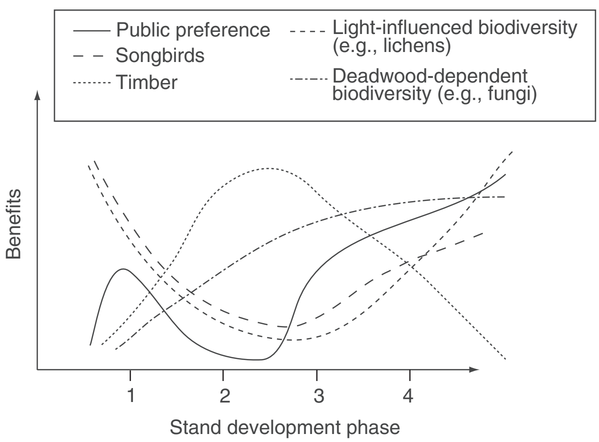


Figure 3 The changes in relative magnitude of selected benefits with different stand development phases in Sitka spruce (Picea sitchensis) plantations in Scotland. Phase 1, stand initiation; 2, stem exclusion; 3, understory reinitiation; 4, old growth. See text for further details.

stem exclusion phase and highest in the stand initiation and old-growth phases. Deadwood-dependent biodiversity is highest in the old-growth phase.

These relationships also suggest that management regimes that produce forests dominated by stands of a particular phase will not produce as wide a range of benefits as could be achieved if all the development phases were represented. This has particular implications when alternative silvicultural systems to clear-felling are being evaluated for possible use in forest management.

Silvicultural Systems and Multiple-Use Silviculture

As noted earlier, there is a range of silvicultural systems that can be used to manipulate stand structure to meet objectives. For the purpose of this discussion, three main systems can be distinguished although there are many local and regional variants, and one type can often intergrade into another. These are:

1. The clear-felling system where a particular area of a forest is cleared in a single operation and is generally followed by replanting.
2. The shelterwood systems where again a particular area of forest is cleared, but in this case the process involves a number of regeneration fellings designed to promote natural regeneration.
3. The selection systems where selective felling of trees is being carried out and natural regeneration is being fostered over the whole forest area.

In general terms, these systems provide different proportions of the various stand phases and therefore different flows of benefits. Thus, a clear-felling system provides a forest with stands that are predominantly moving from the stand initiation to the stem exclusion phase and back again. Stands in the later phases can be provided if stands are retained beyond normal rotation age, but once they are felled they return to the stand initiation phase. By contrast, a shelterwood system, with regeneration occurring either under the canopy of the mature trees or in gaps adjacent to these trees, provides some characteristics of the understory reinitiation phase. Once the regeneration is established, the overstory trees are generally removed so that the stand reverts to a stem exclusion phase. Depending upon the extent of the regeneration fellings and the amount of the overstory that is retained, the area in the stand initiation phase can be appreciably reduced compared to that found under a clear-felling regime. A selection system differs again since one essential aim is to foster and develop regeneration in small gaps so that the whole stand is predominantly in the understory reinitiation phase. Finally, in a broadleaved plantation, one also has the option of introducing a coppice system where the combination of mature trees and different sizes of underwood can provide features of all stand development phases except old growth.

Therefore, if one is seeking to introduce multiple-use silviculture to a forest previously managed for timber production using a clear-felling system, introduction of one of the alternative systems on a percentage of the area will change the proportion of the various stand phases in that forest. This is generally likely to increase the range and spread of benefits being obtained. For example, the recent colonization of many plantation forests in upland Britain by the goshawk (*Accipter gentilis*) is associated with the retention of more stands into the early understory reinitiation phase. By contrast, uncritical adoption of an alternative system can imperil species dependent upon particular habitats. In pine forests in lowland Britain, populations of the rare wood lark (*Lullula arborea*) require the bare ground conditions associated with stand initiation following clear-felling. Greater use of shelterwood or selection systems would limit the amount of such open habitat and could reduce the population.

The various silvicultural systems produce stand structures which show different horizontal and vertical distributions of features such as foliage, branches, open space, and stand microclimate. All of these can influence factors like the growth of a tree, the habitat available for a given organism, or the spiritual enjoyment of the forest. The clear-felling system will produce stands that are more homogeneous than those produced by the other main systems. Thus, in a 50-year-old Sitka spruce plantation nearing felling age which has been managed for timber production with regular thinning, the spacing between trees will be uniform, and there will be relatively little variation in tree height or diameter. The tree crowns will intercept about 90% of incident light so that there is little vegetation growth on the forest floor and there will be no other tree species present in the canopy. By contrast, in a stand of the same species being managed on a selection system to produce large dimension timber (i.e., 60 cm diameter at breast height), there will be a wider range of diameters and heights associated with trees of different ages, and the light climate may vary considerably where overstory trees have been harvested and regeneration is developing.

A point that emerges from this discussion is that none of the systems as traditionally formulated is designed to provide the old-growth phase and associated deadwood habitat which is increasingly recognized as lacking in many forests that have been intensively managed for timber production. This is not to say that the systems cannot be adapted for this purpose, but rather that one needs to understand the range of stand structures that can be produced by each system and that mix of structures which is appropriate to provide a sustained flow of market and nonmarket benefits.

Site Classification, Mixtures, Native Species, and Multiple-Use Silviculture

Since the interest in adopting multiple-use silviculture often occurs in response to reactions against plantation forest management for timber production, this is often accompanied by attempts to increase the species diversity of such forests. A common aspiration is to convert single-species stands into mixtures and to increase the percentage of native species in such forests.

However, the success of such aspirations is critically influenced by the availability of a site classification methodology that adequately reflects the ecological factors affecting tree growth in different regions and on varying soils. Without such knowledge, it is difficult to decide which species can be appropriate for use in mixture and at which stage in a stand development life cycle it is most effective to introduce them. For example, in northern Britain there has been increasing interest in the potential of introducing birches (both *Betula pendula* and *B. pubescens*) into Sitka spruce plantations to increase visual amenity and species diversity. These species are broadly compatible with Sitka spruce in terms of site fertility but are less tolerant of wind exposure. Both birches can be found colonizing clear-felled sites in the stand reinitiation phase and can persist into the early stem exclusion phase in areas that have been replanted with Sitka spruce. However, examination of height growth curves for these species shows that they are unlikely to compete with Sitka spruce in the long term and that intimately mixed species stands of birch and spruce are unsustainable in the stem exclusion phase. Therefore, it appears that a strategy for increasing the percentage of birch in spruce forests would need to be based around the creation of pure stands of birch within a spruce matrix. Such stands would need to be large enough to provide for the development of mature trees to ensure a seed source whenever nearby harvesting or wind disturbance created an area for potential regeneration.

An understanding of the limiting factors on a site is essential if species diversification is to be successful as part of multiple-use silviculture. An example can again be drawn from the birch–Sitka spruce case in northern Britain. There have been a number of instances where spruce plantations were established on exposed sites with difficult access and the prospects for commercial timber production have proved limited. In such circumstances, conversion of the spruce plantation to a native birch forest should provide a better flow of benefits over time. However, clear-felling of the spruce and replanting with birch has been problematic, largely because the removal of the spruce has resulted in a loss of stand microclimate and the birches have suffered from the wind exposure. Site assessments indicate that a more certain, if longer-term approach would be to establish birch within gaps developed within the spruce plantation and progressively remove the conifer matrix, possibly over 10–20 years.

A further point that is raised by these examples is that the introduction of multiple-use silviculture into plantation forests requires an ability to consider what the 'future-natural' state of the stands is likely to be, particularly if it is anticipated that such forests will continue to be managed with timber production as one of the objectives. In countries where the plantations are dominated by nonnative species and/or little natural forest remains, then it may not be obvious what are the appropriate species to introduce into the plantations, let alone what pattern of mixture or silvicultural system should be employed. In such situations, a site classification which can provide objective guidance on species suitability will prove an invaluable aid.

Challenges to Greater Use of Multiple-Use Silviculture

As outlined in the previous sections, successful adoption of multiple-use silviculture requires a grasp of the stand dynamics of the particular forest type(s), an appreciation of how different benefits are affected by silvicultural system and stand development phase, and an understanding of how silvicultural options are limited by site conditions. However, even where these prerequisites have been achieved, there are still a number of serious challenges to be considered. These are:

1. The need to relate the desired structures at a stand level to the wider pattern that is appropriate for a whole forest or catchment. As shown in **Figure 1**, the various phases of stand development each provide a different mix of benefits and it is generally unrealistic to expect a single stand or small forest area to provide the whole range of potential benefits. Therefore, some thought has to be given to the various benefits that are to be provided at a whole landscape level and how the flow of benefits is to be sustained over time. Such an approach can be difficult enough when the landscape unit is managed by a single landowner, but it becomes very complex when there are a number of owners with contrasting objectives.
2. An assumption underpinning the link between the landscape and stand levels is that it is possible to agree what should be an acceptable mix of stands in the different phases and how these might be distributed over a forested landscape. Reference is often made to using natural disturbance regimes for a given region (e.g., the return periods for damaging winds) as a means of calculating the proportion of stands in different phases. Unfortunately, this approach requires good knowledge on disturbance history which is often lacking or can be an artifact of past forest management. Examples of the latter include a reduction in fire frequency because of fire suppression policies or an increase in wind damage because of delayed thinning.
3. Forest management in the last century tended to simplify stand structures in many forest types in the interests of increased timber production as has been shown by numerous studies in Scandinavia and North America. Therefore a major silvicultural challenge is to identify and foster stands that can eventually provide the structures characteristic of the understory reinitiation and old-growth phases. In particular, there is a lack of guidance on the potential structural and spatial features of old-growth stands in areas where plantation forests have been created. It is unclear whether the development of such features can be accelerated through stand manipulation practices such as thinning to produce a variable spatial distribution of trees (variable density thinning). The best location for and the appropriate size of such stands in a forested area also requires to be considered.
4. Successful application of multiple-use silviculture will require better understanding of the way key outputs from the forest are influenced by silvicultural practices. For example, adoption of continuous cover forestry systems may seem desirable to avoid the visual impacts associated with clear-felling, but dense natural regeneration within such stands might produce a closed and less attractive internal forestscape for walkers. The complex

interactions between stand structures and desired outputs mean that managers will need to be certain which are the key species, values, and products which their forests are to provide. They can then propose how such outputs will be affected by changes in stand structure achieved through silviculture, decide which mix of interventions is most appropriate, carry these out, and monitor the results after a suitable time interval. The silvicultural prescriptions may then be changed as a result of the information provided by the monitoring.

5. This highlights the need for decision support tools that are capable of simulating the development of stands under contrasting management regimes and that can be linked via a geographic information system (GIS) to show the flow of benefits over space and time from particular strategies. For instance, widespread adoption of a selection system might produce stands that were very heterogeneous at a small scale, but a landscape that was monotonous and where species dependent upon the stand initiation phase were underrepresented. Better understanding of how different benefits are influenced by stand structure is important here since silvicultural interventions seek to provide those structures that are thought to fulfill management objectives. Criteria for success in even-aged plantation management are well researched and described for many forest types in the world, but equivalent aids for multiple-use silviculture are rare.

In the last analysis, successful implementation of multiple-use silviculture requires the development of a shared future vision for a forest that can be used to inspire the public, employees, and various stakeholders. In areas such as the British Isles where the area of native woodland is small and fragmented, it is unrealistic to expect the native woods to provide the social and environmental benefits while the considerably more extensive area of plantation forests is managed largely as a wood factory. Instead, the plantation forests have to be diversified through multiple-use silviculture to provide the mix of benefits required by commitments to sustainable forest management. The challenge for foresters in such situations is not whether to adopt multiple-use silviculture, but rather how to do it and where best to begin the process.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Natural Disturbance in Forest Environments; Plant-Animal Interactions in Forest Ecosystems; Reproductive Ecology of Forest Trees. **Genetics and Genetic Resources**: Forest Management for Conservation. **Landscape and Planning**: Forest Amenity Planning Approaches; Landscape Ecology, Use and Application in Forestry. **Recreation**: User Needs and Preferences. **Silviculture**: Natural Stand Regeneration. **Social and Collaborative Forestry**: Social Values of Forests.

Further Reading

Bell S (2003) *The Potential of Applied Landscape Ecology to Forest Design Planning*. Edinburgh, UK: Forestry Commission.

Humphrey JW, Holl K, and Broome A (1998) *Birch in Spruce Plantations: Management for Biodiversity*. Forestry Commission Technical Paper no. 26. Edinburgh, UK: Forestry Commission.

Hunter ML (1999) *Maintaining Biodiversity in Forest Ecosystems*. Cambridge, UK: Cambridge University Press.

Kelty MJ, Larson BC, and Oliver CD (1992) *The Ecology and Silviculture of Mixed Species Forests*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Kimmins H (1992) *Balancing Act: Environmental Issues in Forestry*. Vancouver, Canada: University of British Columbia Press.

Kohm KA and Franklin JF (1997) *Creating a Forestry for the Twenty-First Century*. Washington, DC: Island Press.

Matthews JD (1989) *Silvicultural Systems*. Oxford, UK: Oxford University Press.

Nyland RD (1996) *Silviculture: Concepts and Applications*. New York: McGraw-Hill.

Oliver CD and Larson BC (1996) *Forest Stand Dynamics*. New York: John Wiley.

Peterken GF (1996) *Natural Woodland: Ecology and Conservation in Northern Temperate Regions*. Cambridge, UK: Cambridge University Press.

Schütz J-P (1997) *Sylviculture 2: La Gestion des Forêts Irrégulières et Mélangées*. Lausanne, Switzerland: Presses Polytechniques et Universitaires Romandes.

Sustainability of Forest Plantations

J Evans, Imperial College London, Ascot, UK

Introduction

Plantation Forests

The present extent of planted forests worldwide probably exceeds 180 million ha. New planting in both tropical and temperate regions is leading to a significant net increase of forest plantation each year. It is predicted that in time a greater proportion of industrial wood will be sourced from plantations than from exploiting natural forests, and that this trend towards increasing reliance on planted forest for wood production will continue. Thus forest plantations appear set to become a major, even dominant, form of forest development. But as a way of growing trees, is it sustainable?

Sustainability

The concept of sustainability in plantation forestry may be considered to have two components. There are the general or broad issues of sustainability – so clearly articulated and placed on the international agenda in the 1980s by the Brundtland commission – of whether, in the case of tree plantations, using land and devoting resources to them is a sustainable activity from the economic, from the environmental, or from the social sense. Is such development unsustainable because it is economically questionable, or environmentally damaging, or a threat rather than a help to people's livelihoods and way of life and lead to alienation? The same questions may be increasingly asked about sustainable agriculture. Each of these, and related issues, are important in their own right and fundamentally depend on national policies governing plantation development, understanding their impacts, and ensuring full public participation in the process. They concern the concept of 'sustainable livelihoods' as a crucial dimension of the grand aim to eliminate world poverty by 2030.

An example in the case of plantations and sustainable environmental impacts is that it is generally accepted that plantations should not be established on land obtained simply by clearing natural forest formations. There is plenty of already degraded land resulting from past clearance or poor farming practices and which is of no importance for conservation, but will grow trees well: indeed, plantations can help restore degraded land. Thus plantations should not conflict with natural forest but be complementary to them. These and other issues relate to what can be labeled 'broad-sense' sustainability.

The second issue to do with sustainability concerns the practice of plantation silviculture itself. Is growing trees in plantations a technology that can work in the long term? Is such silviculture ecologically sound or are there inherent flaws which will eventually lead to declining growth rates as plantation crop succeeds plantation crop? This is what is meant by 'narrow-sense' sustainability and is the subject of this article.

'Narrow-Sense' Sustainability

The question raised is: can tree plantations be grown indefinitely for rotation after rotation on the same site without serious risk to their health and rate of growth? More specifically, can their long-term productivity be assured, or will it eventually decline over time? Are some sites or forest crops more at risk than others and is this influenced by how they are managed? These questions are pertinent, owing to the increasing reliance on planted forests, but are also scientifically challenging since in previous centuries trees and woodlands were seen as soil improvers and not impoverishers. Are today's silvicultural and management practices more damaging because of greater intensity, such as clonal plantations, optimizing stocking levels, and harvesting on short rotations, which lead to high timber yields typically two to five times that of natural forest increment? Furthermore, are the use of tree-breeding programs, refined fertilizer treatment, more sophisticated manipulation of stand density and so on likely to lead to even more productive forest crops with time, or could they mask evidence of genuine site degrade or increasing risk of damaging pests and diseases?

Figure 1 Litter raking beneath *Pinus caribaea* in southern China. This regular removal of needles, twigs, and branches intempts the nutrient cycle.

Understanding sustainability also applies to nonindustrial uses. Sustaining the numerous benefits people derive from plantations should be a top priority and arise out of good management. Does the perpetual gathering and removal of leaves, twigs, and litter from beneath tree stands, so widespread in India and China, for example (**Figure 1**), simply loot the site of nutrients? And what of the flow of nontimber products, often of more value than wood, and perhaps less directly damaging to sites when harvested? These are relevant to plantation forestry, even if it is not always possible to answer such questions adequately.

Evidence of Productivity Change

Productivity Change in Successive Forest Rotations

Problems with data For forest stands (crops) firm evidence of productivity change over successive rotations is meager with few reliable data. Compared with agriculture, the long cycles in forestry make data collection difficult. Records have rarely been maintained from one rotation to the next or have simply been lost; funding for such long-term monitoring is often a low research priority; measurement conventions and even practices change which confound ready comparison; detection of small changes is difficult; and often the exact location of sample plots is inadequately recorded. In addition, because few forest plantations are second-rotation, and even fewer third- or later-rotation, even the opportunity to collect data has been limited. Unfortunately without data it is difficult to demonstrate whether plantation silviculture is robust and so refute (or otherwise) claims that successive rotations of fast-growing trees inevitably lead, for example, to soil deterioration.

Review of Evidence Comparing Yields in Successive Rotations

Over the last 100 years there have been six main reports that have thrown into question the sustainability of plantations over successive rotations. They are grouped here by region.

Spruce in Saxony and other European evidence In the 1920s reports began to emerge suggesting that significant areas of second- and third-rotation spruce (*Picea abies*) in lower Saxony (Germany) were growing poorly and showed symptoms of ill-health. There was a fall of two quality classes in second- and third-rotation stands, but this was only recorded over 8% of the plantation area. This became a much researched decline and was attributed to insect defoliation, air pollution, the effects of monoculture, drought, and simply the intensive forms of forestry practiced. It is now clear that much of the problem arose from planting spruce on sites to which it was ill-suited, to litter raking that depleted soil of nutrients, and planting on degraded agricultural land. Later studies, that included other sites, showed that growth of spruce was unchanged from rotation to rotation or even increased. Today young stands of pure spruce in Saxony and Thuringia appear to be growing more vigorously than equivalent stands 50 or 100 years ago.

Elsewhere in Europe reports of productivity comparing first and second rotation are limited. In Denmark no great change has been observed for Norway spruce crops but for beech (*Fagus sylvatica*) second-rotation productivity is reported as significantly better. In the Netherlands growth of second-rotation forest is generally 30% faster than the first where it has been assessed. Similarly, in Sweden second-rotation Norway spruce shows superior growth. In France some decline was reported from successive rotations of *Pinus pinaster* in the Landes, though this is not attributed to site deterioration. In the UK most second-rotation crops are equal to or better than the previous rotation and, in the case of restocking of Sitka spruce (*Picea sitchensis*), there is no requirement to reapply phosphate fertilizer which had been essential for establishing the original crop.

***Pinus radiata* in Australia and New Zealand** Reports of significant yield decline in second-rotation *Pinus radiata* emerged in South Australia in the early 1960s and by the end of that decade fall-off in productivity of about 30% affected most pine plantations in the state. These reports were alarming and generated a great deal of research into possible causes. By 1990 it had become clear for South Australia that harvesting and site preparation practices which failed to conserve organic matter, and an influx of weeds in the second rotation, especially massive growth of grasses, were the main culprits. With more sensitive treatment of a site, conservation of organic matter, and good weed control the decline problem was eliminated. With the additional use of genetically superior stock, growth of second- and third-rotation pine became substantially superior to the first crop, a situation which now prevails throughout the state. Indeed, a substantial proportion of the second and third rotation has been upgraded from low site qualities (mean annual increments (MAIs) 13–18 $m^3 ha^{-1} year^{-1}$) to high (MAIs 25–33 $m^3 ha^{-1} year^{-1}$).

In the state of Victoria the yield of second-rotation *P. radiata* is equal or superior to that of the first rotation and in New South Wales basal area and volume per hectare increases of 13 and 18% respectively are reported in the second rotation. In Queensland a careful study of first- and second-rotation *P. elliottii* of the same seed origin shows no evidence of yield decline, but a 17% increase in volume per hectare at 9 years where organic matter was left undisturbed.

In parts of New Zealand, on a few impoverished ridge sites in the Nelson area, there were signs in the 1960s and 1970s, albeit transitory, of yield decline. Today, as with plantations in Australia, holistic management and genetic improvement lead to yield gains from one rotation to the next.

Pines in Swaziland and South Africa Long-term productivity research by the writer in the extensive industrial pine plantations of the Usutu forest, Swaziland, began in 1968 as a direct consequence of the reports from South Australia about second-rotation decline. For 35 years measurements have been made over four successive rotations of *P. patula*, grown for pulpwood, from a forest-wide network of long-term productivity plots (**Figure 2**). Plots have not received favored treatment, but subject to normal forest operations, and tree growth simply measured and recorded during each successive crop.

Over most of the forest, where granite-derived soils occur, third-rotation height growth is significantly superior to second and volume per hectare almost so. There had been little difference between the first and second rotations. On a small part of the forest (about 13% of area), on phosphate-poor soils derived from very slow-weathering gabbro, a significant decline had occurred between first and second rotation, but this has not continued into the third rotation, where there is no significant difference between rotations. Fourth-rotation measurements are currently ongoing and initial results suggest it is growing better than all previous rotations: there is certainly no evidence of decline.

The importance of the Swaziland data, apart from the long-term nature of the research, is that no fertilizer addition or other ameliorative treatment has been applied to any long-term productivity plot from one rotation to the next. Although some third-rotation *P. patula* is probably genetically superior to the second rotation, this effect is small and more than compensated for by the severe drought in the period 1989–1992 which will have adversely impacted third-rotation growth. These data are also of interest because plantation silviculture practiced in the Usutu forest over some 72 000 ha is intensive, with pine grown in monoculture at stockings of 1100–1500 stems per hectare, never thinned, and on a rotation of 15–17 years, which is close to the age of maximum MAI. The limited genetic improvement of some of the third rotation could have disguised a small decline, but evidence is weak since breeding generally improves net primary productivity (NPP), which cannot be realized if one or more nutrients is deficient. Also, it can be strongly argued that without the severe and abnormal drought, growth would have been even better than it is. The current indications of improved fourth-rotation growth probably reflect the impact of genetic improvement. Overall, the Swaziland evidence suggests no serious concern over narrow-sense sustainability.

Figure 2 Signs of three rotations in the Usutu forest, Swaziland, photographed in 1986. Old first-rotation stump (indicated), second-rotation stump cut 6 years ago, and third-rotation stand in background. This site now supports a fourth-rotation stand of pine which is growing better than the three previous rotations.

In South Africa there is no evidence of productivity decline over successive rotations other than localized small-scale examples arising from compacted soil. Excessive accumulation of undecomposed litter in some high-altitude stands of *P. patula* does give rise to concern over increasing soil acidity and nutrient immobilization. In wattle (*Acacia mearnsii*) crops grown intensively for their bark for tannin production, there is no evidence of yield decline with successive rotations.

Chinese fir in subtropical China About 6 million hectares of plantations of Chinese fir (*Cunninghamia lanceolata*) have been established in subtropical China. Most are monocultures and are worked on short rotations to produce small poles. Foliage, bark, and sometimes roots are all harvested for local use. Reports of significant yield decline have a long history. Typically there is a drop in productivity between first and second rotation of about 10% and between second and third rotation of up to a further 40%. Chinese forest scientists attach much importance to the problem and pursue research into monoculture, allelopathy, and detailed study of soil changes. However, it is clear that the widespread practices of whole-tree harvesting, total removal of all organic matter from a site, and intensive soil cultivation that favors bamboo and grass invasion all contribute substantially to the problem.

Teak in India and Java In the 1930s some evidence suggested that replanted teak (*Tectona grandis*) crops (second rotation) were not growing well in India and Java. Although significant soil erosion is widespread under teak and organic matter is frequently lost as leaves are burnt, research into the 'pure teak problem,' as it was called, did not generally confirm a second-rotation problem. Site deterioration under teak does often occur with yields from plantations not coming up to expectation but causes are mainly management-related, namely poor supervision of plantation establishment, overintensive taungya (intercropping) cultivation, delayed planting, and poor aftercare. There are few data from successive rotations – the ideal way of evaluating changes in productivity – since teak rotations are long, typically 50–80 years.

Southern pines in the USA Plantations of slash (*P. elliottii*) and loblolly (*P. taeda*) pines are extensive in the southern states. Significant planting began in the mid-1930s as natural stands were logged out .With rotations usually about 30 years, restocking first began in the 1970s. The growth of this second rotation appears variable, with reports of both better and poorer growth. Changes between rotation are attributed to differences in site preparation and to competition from understory shrubs and weeds. Where weeds are well controlled and appropriate site preparation used, such as a bedding plough, growth is often superior. Genetically improved stock and use of fertilizers are expected to bring further increases.

Within-Rotation Yield Class/Site Quality Drift

The recently observed phenomenon of yield class or site quality change with time has two aspects – change between predicted and actual yield over time, and correlation of site quality (yield class) with date of planting rather than just site fertility.

Inaccuracy in predicted yield For long-rotation (>20 years) crops it is usual to estimate yield potential from an interim assessment of growth rate early in life and then to allocate a stand to a site quality or yield class. This is a good way of forecasting likely yields overall, though imprecise for estimating actual final timber outturn from individual stands. A change from predicted to final yield can readily occur where a crop has suffered check or other damage in establishment that delays its development and thus distorts early estimates of site potential based on growth-to-age relationships. Similarly, fertilizer application which corrects a specific deficiency may also have this impact. However, there is some evidence for very-long-rotation (>40 years) crops in temperate countries that initial prediction of yield or quality class underestimates final outturn, i.e., the crops grow better in later life than expected. Either the models derived from data of 40 or more years ago were wrong, or they are now inappropriate to present conditions, or growing conditions are improving in the sense of favoring tree growth. Across Europe, research by the European Forest Institute shows this to be happening and it is attributed to rises in atmospheric CO_2 and nitrogen input in rainfall, better planting stock, and cessation of harmful practices such as litter raking.

However, as noted earlier, the opposite may occur with teak. High initial site quality estimates do not yield the expected outturn and figures are revised downward as the crops get older. Plantation teak does suffer soil erosion in established stands, development of understories is rare, and burning of debris, especially the large dry leaves, is commonplace. Like litter raking, these practices may contribute to loss of nutrients from a site.

Relation of quality (yield) class with time of planting Closely related to the phenomenon of changing yield potential as a crop grows is the observation that date of planting is often positively related to productivity, i.e., more recent crops are more productive than older ones, regardless of inherent site fertility. This shift is measurable and can be dramatic and is well seen for *P. radiata* in Australia and New Zealand, where the more recent the planting, the more productive the stand. And in the UK, attempts to model productivity on the basis of site factors have often been forced to include planting date as a variable. Maximum mean annual growth of Sitka spruce increases by about $1\,m^3\,ha^{-1}\,year^{-1}$ for each succeeding decade up to the present. This phenomenon seems common and suggests that some process favors present growing conditions for trees over those in the past, such as the impact of genetic and silvicultural improvements – and cessation of harmful ones – and possibly the 'signature' of atmospheric changes.

Interventions to Sustain Yield

Genetic Improvement

Change in species, seed origin, use of new clones, use of genetically improved seed and, in the future, genetically modified trees all offer the prospect of better yields in later rotations.

Species change There are surprisingly few examples of wholesale species change from one rotation to the next, which suggests that in most cases foresters have been good silviculturists, drawing on trials and long experience with a species before commencing large-scale plantations. It is also worth noting that, where a successful exotic species is replaced by a native one in the second rotation for reasons of conservation or public preference, productivity may diminish.

Better seed origins, provenances, and land races The impact of these genetic improvements are well known and reported elsewhere (*see* **Tree Breeding, Practices**: Genetics and Improvement of Wood Properties). It is important to cover the range of site conditions where a species is believed to have potential owing to site – genotype interaction. The best seed origin in one location may not be the best in another. This refinement in understanding offers the prospect of further yield improvement.

Clonal plantations Some of the world's most productive tree plantations, including both eucalypts and poplars, use clonal material. Both the potential productivity and uniformity of product make this form of silviculture attractive and it is likely to expand in the future. Although clonal forestry has a narrow genetic base, careful management of clone numbers and the way they are interplanted can minimize pest and disease problems. Use of 30–40 unrelated clones per stand is usually considered to provide security against catastrophic failure in most circumstances.

Tree breeding Genetic tree improvement offers by far the greatest assurance of sustained and improved yields from plantations in the medium and long term. Improvements of 20–50% are reportedly relatively easy to achieve. A compilation of estimated percentage gains from genetic and silvicultural interventions in plantation forestry is now incorporated into the Food and Agricultural Organization's global fiber supply model.

Genetically modified trees There are presently no significant plantations of genetically modified trees, except possibly in China. The expectation is that genetic engineering may be used to develop disease resistance, modified wood properties, or cold or drought tolerance. Research in progress includes modified lignin content of eucalypts and poplars and insertion of disease-resistant genes in elms (*Ulmus* spp.).

Subject to their public acceptance, these powerful genetic tools will become increasingly cheap and hence accessible to forestry use and offer an important aid to intensification of production.

Role of Different Silvicultures

Silvicultural knowledge continues to increase through research and field trials, often focused by greater understanding of tree and stand physiology. While large yield improvements appear unlikely, several incremental gains can be expected. Examples include the following:

1. Manipulation of stocking levels to increase output of total fiber or a particular product such as high-quality sawlogs. The object will be fuller site occupancy, less mortality, and greater control of individual tree growth.
2. Matching rotation length to optimize yield – the rotation of maximum mean annual increment – offers worthwhile yield gain in many cases. Of course, other factors frequently prevail, leading to rotation lengths other than this one.
3. In some localities, such as the British Isles, prolonging the life of a stand of trees subject to windthrow will increase yield over time, since most threatened stands are felled or windblown long before maturity. Research to predict damaging storm impacts and silvicultural research which increases crop stability and stem strength assist increase in yield.
4. Use of mixed crops may help in tree stability, may possibly lower pest and disease threats, but is unlikely to offer a yield gain over growing the most productive tree species the site can support.
5. Moves to silvicultural systems that maintain forest cover at all times – continuous-cover forestry practices – such as shelterwood and selection systems are likely to be neutral to slightly negative in production terms while yielding gains in tree quality, aesthetics, and probably biodiversity value.
6. Crop rotation, as practiced in farming, appears unlikely as a feature in plantation forestry, although there are examples of tree plantations benefiting from a previous crop of nitrogen-fixing legumes such as *Acacia mearnsii*. Industry is likely to require a similar, not widely differing, species when replanting.

Traditionally, use of exotics carefully matched to site has often offered a yield gain over native species, even where suitable native species are available, owing to relative freedom from pest and diseases. This advantage cannot be expected to last indefinitely and there are already examples of increasing susceptibility of exotics to local pests and diseases.

Fertilizing

Regular and automatic application of mineral fertilizer as in much of farming practice is not presently a feature of plantation forestry, with the exception of some tropical eucalypt plantations. Most forest use of fertilizer is to correct known deficiencies, e.g., micronutrients such as boron in much of the tropics and zinc in Australia, macronutrients such as phosphorus on impoverished sites in many parts of the world, and nitrogen in some locations such as the Pacific Northwest of the USA. In most instances, fertilizer addition has only been required once in a rotation to obtain satisfactory establishment and growth.

Spectacular yields have been achieved on some sites by frequent or even annual fertilizer addition as part of intensive management that includes full weed control and optimal spacing. Examples include the British Forest Research experiment Wareham 156, the trials by Torsten Ingestad in Sweden, and the biology of forest growth experiment carried out by the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Australia. These trials are experimental and serve more to elucidate principles of stand physiology, applied nutrition, and maximum growth potential rather than to offer practical and economically worthwhile operational prescriptions, since wood is a low-value product. In some situations irrigation offers similarly dramatic increases in growth.

Monitoring of nutrient levels in foliar analysis or fertilizer trials has a role mainly as an aid to good overall silviculture, although increasingly foliar analysis is used in intensively managed plantations as a diagnostic growth promotion tool to inform fertilizer prescriptions. Fertilizing is likely to be the principal means of compensating for nutrient losses on those sites where plantation forestry practice does cause net nutrient export to the detriment of plant growth.

Site Preparation Establishment Practices

Ground preparation to establish the first plantation crop will normally have introduced sufficient site modification for good tree growth. Cultivation loosens soil, improves rooting, encourages drainage, limits initial weed growth, improves water percolation, may reduce frost risk and, perhaps importantly for the long-term health of the forest, brings relatively unweathered soil minerals nearer to the surface and into the main feeding zone of tree roots. Substantial new investment in site manipulation is unlikely in second and subsequent crops owing to the cost of handling stumps and the implied failure first time round. Exceptions are alleviation of soil compaction after harvesting, and measures to reduce infections and pest problems. For example, in the UK destumping and windrowing of debris on some alkaline sites helps avoid fomes infection (*Heterobasidion annosum*).

Weed control strategies may change from one rotation to the next, owing to differing weed spectrum and whether weeds are more or less competitive to planted trees. The issue is crucial to sustainability since all the main examples of yield decline problems cited earlier reflect worsening weed environments, especially worsening competition from monocotyledons such as grasses and bamboos.

Changes between rotations in treatment of felling debris and organic matter may occur, such as cessation of burning, use of windrowing, or removal from site in whole-tree harvesting. It is clear that the felling, harvesting, and reestablishment phase is crucial to sustainable practice and needs to be viewed as a whole to minimize impacts from compaction along extraction routes, from loss of organic matter, and from soil erosion.

Organic Matter Conservation

Treatment of organic matter both over the rotation and during felling and replanting is as critical to sustainability as coping with the weed environment. While avoidance of whole-tree harvesting is probably desirable on nutrition grounds, both prevention of systematic litter gathering during the rotation and careful handling of accumulated organic matter at harvesting are essential to minimize disturbance and help aeration of soil and accelerate decomposition. Many authors attribute poor tree growth of the past and evidence of increasing yields in many plantations today to better conservation and handling of organic matter.

Holistic Management

Where all the above silvicultural features are brought together, a rising trend in productivity can be expected. If any one is neglected, it is likely that the whole will suffer disproportionally. For example, operations should not exclusively minimize harvesting costs, but rather those of harvesting, reestablishment and initial weeding should be taken as holistic activity, and without impairing tree vigor.

Holistic management also embraces active monitoring of pest and disease levels, and researching pest and disease biology and impacts will aid appropriate responses such as altering practices, e.g., delayed replanting to allow weevil numbers to fall. Careful reuse of extraction routes to minimize compaction and erosion is a further example.

Conclusions

Three main conclusions may be drawn from this review of yield assessments made over long periods, and often more than one rotation, and the summary of interventions to sustain yields.

1. Measurements of yield in successive rotations of trees suggest that there is no significant or widespread evidence that plantation forestry is unsustainable in the narrow sense. Where yield decline has been reported, poor silvicultural practices and operations appear to be largely responsible.
2. Evidence in several countries suggests that current rates of tree growth, including in forest plantations, exceed those of 50 or 100 years ago owing to changes in the environment, especially atmospheric composition, and improvements in silviculture.
3. There are several interventions in plantation silviculture which point to increasing productivity in the future, providing management is holistic and good standards are maintained. Genetic improvement in particular offers the prospect of substantial and long-term gains in yield over several rotations.

See also: **Afforestation**: Species Choice; Stand Establishment, Treatment and Promotion - European Experience. **Inventory**: Stand Inventories. **Plantation Silviculture**: Forest Plantations; Rotations; Stand Density and Stocking in Plantations; Tending. **Resource Assessment**: Forest Resources. **Silviculture**: Natural Stand Regeneration. **Sustainable Forest Management**: Certification; Overview. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance; Genetics and Improvement of Wood Properties. **Tree Breeding, Principles**: Conifer Breeding Principles and Processes.

Further Reading

Boardman R (1988) Living on the edge – the development of silviculture in South Australian pine plantations. *Australian Forestry* 51: 135–156.

Chacko KC (1995) Silvicultural problems in management of teak plantations. In: *Proceedings of the 2nd Regional Seminar on Teak*: '*Teak for the Future*,' May 1995, pp. 91–98. Yangon, Myanmar, Bangkok: FAO.

Davidson J (1996) Off site and out of sight! How bad cultural practices are offsetting genetic gains in forestry. In: Dieters MJ, Matheson AC, Nikles DG, Harwood CE, and Walker SM (eds). *Tree Improvement for Sustainable Tropical Forestry*, pp. 288–294. *Proceedings of QFRI-IUFRO Conference*, Caloundra, Queensland, Australia.

Evans J (1984) Measurement and prediction of changes in site productivity. In: Grey DC, Schonau APG, Schutz CJ, and van Laar A (eds) *IUFRO Symposium on Site and Productivity of Fast Growing Plantations*, April 1984. vol. 1, pp. 441–456, Pretoria, South Africa.

Evans J (1999) *Sustainability of Forest Plantations: The Evidence*. Issues paper. London, UK: Department for International Development.

FAO (1992) *Mixed and Pure Forest Plantations in the Tropics and Sub-tropics*. FAO Forestry paper no. 103. Rome: Food and Agriculture Organization.

Haywood JD (1994) Early growth reductions in short rotation loblolly and slash pine in central Louisiana. *Southern Journal of Applied Forestry* 18: 35–39.

Kanowski PJ (1997) Afforestation and plantation forestry: plantation forestry in the 21st Century. In: *Proceedings of the 11th World Forestry Congress*, October 1997, *Antalya*, vol. 3, pp. 23–34.

Keeves A (1966) Some evidence of loss of productivity with successive rotations of *Pinus radiata* in the south east of S. Australia. *Australian Forestry* 30: 51–63.

Libby WJ (2002) *Forest Plantation Productivity*. A FAO working paper FP/3, prepared in association with Palmberg-Lerche C, February 2002. Rome, Italy: Food and Agriculture Organization of the United Nations (available electronically).

Nambiar SEK (1996) Sustained productivity of forests is a continuing challenge to soil science. *Journal of Soil Science Society of America* 60: 1629–1642.

Spiecker H, Meilikaainen K, Kohl M, and Skovsgaard JP (eds.) (1996) *Growth Trends in European Forests*. European Forest Institute Research report no. 5. Berlin: Springer-Verlag.

Weidemann E (1923) *Zuwachsruckgang und Wuchstockungen der Fichte in den mittleren und den unteren Hohenlagen der Saschsichen Staatsforsten*. Tharandt. Translation no. 302, by Blumenthal CP, Washington, DC: USDA 1936.

Woods RV (1990) Second rotation decline in *P. radiata* plantations in South Australia has been corrected. *Water, Air and Soil Pollution* 54: 607–619.

Short Rotation Forestry for Biomass Production

M G R Cannell, Centre for Ecology and Hydrology, Penicuik, Scotland, UK

Introduction

Some hardwood species have very rapid juvenile growth and also coppice readily. They are often natural pioneers. High yields can be sustained over many coppice rotations as short as 3–15 years. These properties can be exploited to produce large quantities of woody biomass, which can be used for pulp or to produce energy.

Recent ideas on short-rotation forestry developed during the 1960s with discussions on silage sycamore in the USA. The initial attraction was the prospect of obtaining both high yields and early returns on investment. There was also the added advantage of producing a uniform product by using clones and of rapidly selecting and deploying improved genetic material.

The notion of growing species such as willows, poplars, and eucalypts over short coppice rotations gained momentum as agricultural surpluses in Europe and North America offered the possibility of large areas of fertile land becoming available. At the same time, there was increased interest in biomass as a renewable energy source, while, in the tropics, short rotations enabled exceptionally high yields of wood pulp to be produced, with high financial returns.

This article outlines the extent to which short-rotation forestry is being practiced, the yields being obtained, some aspects of the silviculture, pest and disease problems, the utilization of short-rotation biomass, and environmental impacts.

Short-Rotation Forestry Around the World

Globally, *Eucalyptus* is probably the most widely planted genus. About 10 million ha have been planted worldwide, notably in China, India, Brazil, South Africa, Chile, and Portugal. Much of this area is managed on short rotations, virtually all for pulp. Over recent decades there has been a large increase in international trade in pulp from *Eucalyptus* and other fast-growing plantations.

Aracruz Celulose began growing *Eucalyptus* in Brazil in 1967. It is now one of the world's leading suppliers of bleached eucalypt pulp. Most of the pulp is exported. The plant produces about 1 million tonnes of pulp per year and is supplied by plantations covering about 150 000 ha. Aracruz has not only been commercially successful; it has also pioneered the development of new genetic stock, nursery methods, and clonal propagation.

Elsewhere in the tropics and subtropics, a wide range of species is grown on 10–15-year rotations for pulp and other products, including *Terminalia* spp., *Acacia* spp., *Casuarina* spp., *Virola koschnyi*, *Jacaranda copaia*, and many other species. Mention should also be made of the many woody species used in tropical agroforestry systems, yielding fuelwood, wood products, and green manure. Species such as *Sesbania sesban* have rapid juvenile growth, coppice rapidly, and fix nitrogen.

In North America, there are not many examples of short-rotation forestry being practiced commercially, but there are vigorous research and development programs. In Canada, attention has focused on poplars in Ontario province, grown on rotations of about 10 years, harvested with feller/bunchers. In the USA, the Short Rotation Woody Crops Program and the Biofuels Feedstock Development Program have examined the potential of growing fast-growing hardwoods on suitable agricultural land. Extensive trials involving about 150 species have been conducted since 1978. Databases exist on species yields in different regions, effects of varying spacings, fertilizer responses, pesticide prescriptions, and harvesting methods. The most productive species, besides *Eucalyptus* in Florida and Hawaii, have been *Populus* clones, *Liquidambar styraciflua*, *Acer saccarum*, *Platanus occidentalis*, and *Robinia pseudoacacia*.

In Europe, extensive short-rotation *Eucalyptus* plantations are grown for pulp along the Atlantic seaboard in Portugal and Spain. Elsewhere, Sweden pioneered the growth of willow and poplar as biofuels in the Swedish Energy Forestry Project, launched in 1976. Currently, 15% of Sweden's energy is supplied from biomass. Commonly, willow is grown over 6-year rotations on abandoned farmland, yielding biomass for small combined heat and power plants. New clones have been selected, cultural prescriptions defined, and harvesting machinery developed. Elsewhere in Europe, short-rotation forestry is practiced in most countries, but on a relatively small scale. However, the ambition of the European Commission to meet 12% of the European Union's primary energy demand from renewable sources by 2010 might require up to 10 million ha of energy crops, much of which would be short-rotation coppice.

Considerable research on short-rotation biomass plantations has been coordinated by the International Energy Agency (Bioenergy) since 1974, particularly within the task group Short Rotation Crops for Bioenergy Systems. The country partners are Sweden, Norway, Netherlands, Denmark, UK, Croatia, USA, Canada, Australia, and New Zealand.

Biomass Yields

Yields of *Eucalyptus* at Aracruz reach 40–50 $m^3\,ha^{-1}\,year^{-1}$, in excess of 30 $t\,ha^{-1}\,year^{-1}$ dry matter, over 7-year rotations. Similar extraordinarily high yields can be achieved over 4–8-year rotations by *Eucalyptus* in New Zealand and *Leucaena leucocephala* in Florida and other subtropical regions. Record yields approach 100 $m^3\,ha^{-1}\,year^{-1}$.

During the 1970s, some exaggerated claims were made for the potential yields of poplar and willow in temperate regions. Claims were based on yields in small plots, with large edge effects, which can give yields four to seven times greater than those in extensive commercial plantations. Also, breeding is unlikely to increase biomass yields as much as has occurred in agricultural crops, where yield has been increased largely by increasing the fraction harvested (the harvest ratio) rather than total biomass.

In Sweden, dry biomass yields of coppice willow from well-designed trials average about 8–9 t ha^{-1} $year^{-1}$ in the north-east, 9–10 t ha^{-1} $year^{-1}$ in the east, 11–12 t ha^{-1} $year^{-1}$ in the far south, and peak at 16–17 t ha^{-1} $year^{-1}$ along the west coast. In England, dense plantings of the erect willow clone 'Jorunn' have produced 11–12 t ha^{-1} $year^{-1}$ on 3-year rotations, while hybrid poplar clones have produced 12–14 t ha^{-1} $year^{-1}$ on 4-year rotations on wet sites. Overall, biomass yields of well-tended short-rotation poplar and willow growing on fertile sites in central and northern Europe are likely to be 8–12 t ha^{-1} $year^{-1}$. However, when in extensive cultivation on less-than-ideal sites, yields are lower, often in the range 4–8 t ha^{-1} $year^{-1}$.

Clones of willow, poplar, and other species differ severalfold in yield. Analyses suggest that these yield differences are mainly due to differences in the amount of light intercepted during the growing season, because clones differ in times of leaf emergence, leaf-fall and canopy structure. Early spring foliation is particularly important. Clones differ less in the amount of biomass produced per unit of light intercepted, commonly around 0.8–1.5 g MJ^{-1}, similar to agricultural crops with the same photosynthetic mechanism.

Profitability

Short-rotation pulp production using *Eucalyptus* in tropical and subtropical regions is clearly highly profitable in some locations and has attracted substantial venture capital. The same is true for the short-rotation pulp plantations in countries like Chile, China, India, and Portugal.

The uptake of short-rotation forestry in North America and most of Europe has been more constrained. In England, the only significant power plant to be fueled by willow coppice (ARBRE in Yorkshire) has ceased operation. The obstacles to short-rotation forestry are primarily: (1) the relatively low cost of electricity generated from fossil fuels; (2) the high cost of agricultural land, often inflated by agricultural subsidies; and (3) the lack of an industry infrastructure for handing biomass. The technologies for cultivation, harvesting, and conversion do not seem to be the main constraints, although advances can be made.

Research in many countries has quantified the costs of cultivation, storage, transport, and conversion to electrical energy. Profitability is normally very sensitive to energy prices and coppice yields, provided transport distances do not exceed about 100 km. However, there appears to be a 'catch-22' of investors reluctant to finance tree planting without guaranteed markets or conversion plants without guaranteed feedstock supplies. Some market intervention is required to develop both a level playing field with other land uses and energy sources and to establish industries with a critical mass.

Silviculture

Species and Breeding

As indicated above, a variety of species are used for short-rotation biomass production, the only condition being that they have rapid juvenile growth and coppice readily. The same selection strategies are used as in conventional tree-breeding programs, except the vegetative propagation is normally much easier, so that clones and multiclone mixtures can be selected. Most countries have lists of approved and recommended clones, based on screening for yield and pest and disease resistance.

In Europe and many other regions, *Eucalyptus globulus* is the preferred eucalypt species for short-rotation pulp production.

Poplars are the most universally grown species in temperate regions, being hugely diverse and tolerant of a wide range of conditions. Poplars of the *Aigeiros* and *Tacamahaca* sections respond to nutrient-rich, well-watered conditions and are easily propagated by cuttings, whereas species of aspen belonging to the *Leuce* section root less easily but are tolerant of a wide range of site conditions.

The *Salix* genus is hugely variable and is characterized, like poplar, by hybridization and the selection of clones, several hundred of which have been screened for their potential to produce biomass.

Site Conditions

The idea of short-rotation forestry is to obtain high yields over short periods of time, capitalizing on rapid juvenile growth. That rapid growth will only occur on fertile soils, rich in nutrients and with adequate water. A ready supply of both nutrients and water is required for rapid canopy development and photosynthesis. Former agricultural land, able to sustain arable crops, is ideal, but less fertile grassland can be used with fertilization. The rootable depth should be at least 1 m and, to allow mechanization, there should not be more than 6% side-slope and 10% in-row slope.

Forests, including coppices, use more water than short vegetation because they intercept 10–30% of rainfall, which evaporates from leaf surfaces without reaching the ground. Thus, short-rotation forests have similar effects on local hydrology to high forests, potentially decreasing groundwater and river flows. In Sweden, it has been estimated that the evaporation of intercepted rain accounts for 11% of total annual evaporation. Also, rapid photosynthesis by fast-growing species is always accompanied by high transpiration of water. Poplar and willow coppice transpire about 1 kg water for every 3.5 g of stem-wood produced, so $10\,\mathrm{t\,ha^{-1}\,year^{-1}}$ is equivalent to 286 mm rainfall — allowing for no groundwater recharge. Thus, an adequate water supply is crucial, and areas with summer droughts, or where groundwater supplies need to be sustained, may not be suitable.

Cultivation

The International Energy Agency (Bioenergy) has produced a Production Systems Handbook for Seven European countries and the USA. It provides a decision support system on species, spacing, cultivation, harvesting, and production costs.

It is normally assumed that sites need to be deep-ploughed. As mentioned, the sites need to be fertile enough to support fast-growing broad-leaved species. Willow and poplar grow best on mildly acidic soils with pH 6.0–7.0. Fertilizers are generally required to make good the nutrient losses from harvesting. High nutrition speeds canopy development, maintains a high leaf area index, a low root-to-shoot ratio and high light conversion efficiency. Herbicides are normally needed to suppress ground vegetation and temporary fencing may be needed to protect trees from browsing.

Spacing has little effect on biomass yield, provided a full canopy cover is established rapidly, but it obviously has a large effect on average stem size. A rule-of-thumb is that the optimum spacing is that required to reach the point of self-thinning by the end of the rotation. However, the market determines the type of biomass required and hence the spacing and harvest machinery. For poplar and willow grown for bioenergy in Europe, planting 5000–10 000 cuttings per hectare is recommended, with a rotation of 4–6 years. Rotations of 6–10 years are favored in parts of the USA, with 1000–2500 cuttings per hectare. Very short rotations of 1–3 years are rarely economic because of high establishment costs, weakened stools, and difficulty in handling small stems.

Harvesting

Mechanization is essential and is part of the attraction of short-rotation forestry. Commercial short-rotation forestry harvesting machines are available using single pass cut and chip and whole stem systems. The latter are used to harvest larger stems produced over longer rotations. Harvesting accounts for over half the costs of production, so considerable research has been done to produce dedicated machines. Clearly, harvesters can compact the soil when wet and harvesting is best done in winter when the ground is frozen.

Pests and Diseases

Warnings that clonal plantations of fast-growing species would be vulnerable to outbreaks of pests and diseases have proved to be justified. Pests and diseases have become serious issues in most places where large areas of poplars and willows have been grown in trial plantations. There are around 130 known pest species on poplar and willow and many fungal pathogens. It is uneconomic to apply pesticides or fungicides. However, there are resistant types. For instance, poplar susceptibility to defoliation is roughly in the order *Populus nigra* < *P. trichocarpa* < *P. deltoides* × *nigra* < *P. trichocarpa* × *deltoides* and resistant clones can be found.

In Sweden, gall midge (*Rhabdophaga terminalis*) became a serious pest on *Salix alba*, with the result that this species was rejected from the bioenergy program.

In the UK, willow beetle (*Phratora vulgatissima*) affected over half of the willow bioenergy trials, with very heavy infestations on young trees. Research has identified volatile organic production by the leaves as being related to beetle resistance and semiresistant clones have been selected. Also, it has been shown that mixtures of five or more clones, including resistant clones, slow the build-up of beetle populations.

Fungal pathogens are also a serious problem. Rust (*Melampsora epitea*) is probably the most important factor limiting willow yields in the UK. It is also a serious pathogen on poplar. The fungus expresses great variation in virulence types and specificity to clones, and alternates (spends half its life cycle) on *Larix* (also *Ribes*, *Allium*, and *Saxifraga*). It is therefore wise to locate willow or poplar plantations distant from these alternate hosts. Again, mixed clonal stands delay the onset and progress of the disease and can provide an effective means of control.

Coppicing exposes the stools to infection and particular care has to be taken to treat stumps to inhibit rot fungi.

Utilization

At present, short-rotation forestry can compete, in some instances, with traditional forestry in the production of pulp, especially in the tropics and warm temperate countries. There are also limited markets for poles and stakes, and in the future there may be demand for biomass as a chemical feedstock.

As mentioned, the economics of growing biomass for energy (other than traditional fuelwood in the tropics) is currently uncertain. In most regions, biomass energy is competitive at current fuel prices only if: (1) yields are high; (2) plantations are close to conversion plants; (3) residues and waste materials are used as well as newly grown biomass; and (4) there are, preferably, saleable products from the biomass plantations in addition to bioenergy. It is, of course, possible to establish short-rotation forestry enterprises that produce pulp in the first instance and then make the transition to supply energy at a later date.

Nevertheless, concerns about carbon emissions and future energy security have stimulated considerable research on the potential to produce renewable energy from biomass. The energy content of dry woody biomass is about 18.5 MJ kg^{-1}, regardless of species. Clearly, energy is used to cultivate, harvest, dry, and transport biomass to electricity-generating plants, but this is commonly only about one-twentieth of the energy contained in the biomass delivered to the plant. One tonne of dry biomass contains about 0.5 t of carbon and has about the same amount of chemical energy as 0.5 t of coal (which is carbonized biomass) or 0.44 t of oil or 0.28 t of methane gas. Globally, if 200–400 million hectares of high-quality land were used to grow biomass (14–28% of the current cropland area), with an average yield of 10 t ha^{-1} year^{-1}, it could, theoretically, generate 37–74 EJ year^{-1} (9–18% of current global energy production from fossil fuels), offsetting 15–30% of global carbon emissions. A more conservative estimate of the likely contribution of biomass to global energy supplies by 2050–2100 is 9–37 EJ year^{-1}, requiring 50–200 million hectares. As mentioned, European renewable energy ambitions might require 10 million ha of biomass energy crops by 2010, and there is the potential to increase this 10-fold during this century.

Environmental Impacts

When compared with natural forests, short-rotation biomass plantations are at odds with the paradigm of an environmentally desirable land use. They are even-aged, regularly clear-felled, have no large dead trees and woody debris, and have little recreational value and a limited range of habitats for wildlife.

However, when compared with agricultural land, short-rotation forests offer some benefits and few disadvantages. Increased litter fall can improve soil conditions after some years. Land in the USA, which lost 18 t ha^{-1} year^{-1} of soil by erosion under arable cropping, lost only 2 t ha^{-1} year^{-1} when converted to short-rotation forestry. Compared with arable agriculture, nitrogen leaching to groundwater may be decreased, with less nitrous oxide emission. Short-rotation forests can, in fact, be used for sewage sludge disposal, and as wastewater filters to purify municipal wastewater, landfill leachate, and sewage. In Sweden, wastewater with 160–190 kg N ha^{-1} year^{-1} has been applied to fast-growing willow coppice without substantial nitrate leaching and, in some instances, the trees have taken up heavy metals, reducing levels in soils.

Short-rotation forests can sustain levels of biodiversity that are equal to, although different from, those on farmland. Arthropods are abundant on willows and poplars (sometimes as pests), which support a high bird population. The bird populations in hybrid poplar plantations in the USA are higher than those in crop fields. Short-rotation forests can also be used as cover for game.

See also: **Environment**: Carbon Cycle. **Hydrology**: Impacts of Forest Plantations on Streamflow. **Non-wood Products**: Energy from Wood. **Pathology**: Diseases affecting Exotic Plantation Species; Rust Diseases. **Plantation Silviculture**: Forest Plantations. **Silviculture**: Coppice Silviculture Practiced in Temperate Regions. **Temperate Ecosystems**: Poplars. **Tree Breeding, Practices**: Genetic Improvement of Eucalypts. **Tropical Ecosystems**: Eucalypts.

Further Reading

Bullard MJ, Mustill SJ, McMillan SD, *et al.* (2002) Yield improvements through modification of planting density and harvest frequency in short rotation coppice *Salix* spp. – 1. Yield response in two morphologically diverse varieties. *Biomass and Bioenergy* 22: 15–25.

Bullard MJ, Mustill SJ, Carver P, and Nixon PMI (2002) Yield improvements through modification of planting density and harvest frequency in short rotation coppice *Salix* spp. 2. Resource capture and use in two morphologically diverse varieties. *Biomass and Bioenergy* 22: 27–39.

Cannell MGR (2003) Carbon sequestration and biomass energy offset: theoretical, potential and achievable capacities globally, in Europe and the UK. *Biomass and Bioenergy* 24: 97–116.
Dubuisson X and Sintzoff I (1998) Energy and CO_2 balances in different power generation routes using wood fuel from short rotation coppice. *Biomass and Bioenergy* 15: 379–390.
Geyer WA (1989) Biomass yield potential of short-rotation hardwoods in the Great Plains. *Biomass* 20: 167–175.
Hohenstein WG and Wright LL (1994) Biomass energy production in the United States: an overview. *Biomass and Bioenergy* 6: 161–173.
Hummel FC, Palz W, Grass IG (eds) (1988) *Biomass Forestry in Europe: A Strategy for the Future*. London: Elsevier Applied Science.
Makeschin F (1999) Short rotation forestry in Central and Northern Europe – introduction and conclusions. *Forest Ecology and Management (special issue)* 121: 1–7.
Mitchell CP (1994) Developments in the production and supply of wood for energy. *Renewable Energy* 5: 754–761.
Stjernquist I (1994) An integrated environmental analysis of short-rotation forests as a biomass resource. *Biomass and Bioenergy* 6: 3–10.

Propagation *see* **Genetics and Genetic Resources**: Propagation Technology for Forest Trees. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Current and Future Signposts; Forest Genetics and Tree Breeding. **Tree Physiology**: Physiology of Vegetative Reproduction; Tropical Tree Seed Physiology.

Protection *see* **Health and Protection**: Biochemical and Physiological Aspects; Diagnosis, Monitoring and Evaluation; Forest Fires (Prediction, Prevention, Preparedness and Suppression); Integrated Pest Management Practices; Integrated Pest Management Principles. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance.

PULPING

Contents

Fiber Resources

P J Ince, USDA Forest Service, Madison, WI, USA

Published by Elsevier Ltd., 2004

Introduction

In economics, primary inputs or factors of production define the term 'resources.' Resources include land resources (plants, animals, and minerals), labor, capital, and entrepreneurship. Almost all pulp and paper fiber resources are plant materials obtained from trees or agricultural crops. These resources encompass plant materials harvested directly from the land (wood, straw, bamboo, etc.), plant material byproducts or residuals from other manufacturing processes (wood chips from sawmills, bagasse fiber from sugarcane processing, cotton linter, etc.), and fibers recovered from recycled paper or paperboard.

Some relatively expensive nonplant fibers derived from mineral resources are also used in papermaking (e.g., synthetic plastic fibers) but very small quantities and only in some specialized paper or paperboard products.

Resources derive value from their utility in producing goods or services, but utility varies among different fiber resources and utility varies as technology and product demands shift over time. Different plant fibers have different physical properties that influence their utility in pulping and papermaking. Utility of industrial resources also depends on profitability, or availability of resources at competitive market prices. Market demands for fiber products and supplies of fiber resources vary over time, and thus the market value and utility of fiber resources are variable over time. Some resources have competing multiple uses and alternative values in society. Forest resources have value in producing a range of different wood products, not just pulp and paper products. Forest resources also have alternative values in society because they produce other important services such as recreational, spiritual, environmental, or aesthetic services.

For example, selected species of trees grown in monoculture (single-species) plantations may have high intrinsic value in pulping or papermaking because of uniformity in fiber quality or desirable fiber characteristics, but cultivating trees in plantations can be more expensive than relying on natural regeneration of trees in a forest. The typically more heterogeneous mixture of tree species found in a naturally regenerated forest may have less intrinsic value in pulping or papermaking because of less uniformity or less desirable fiber characteristics, but may have utility in any case because of lower cost. However, a natural forest will likely have high value to society in terms of ecological or aesthetic amenities. Also, advances in plantation systems or biotechnology can yield faster-growing trees or more desirable trees for pulping, which can affect the market value of fiber resources. The actual market values of wood and fiber resources are determined by shifting patterns of resource abundance and overall demand. This article describes various categories of fiber resources used for pulp and paper products, factors influencing their utility and relative market values, and trends in fiber resource supply and demand.

Pulping Processes

Understanding the utility and value of pulp and paper fiber resources begins with an understanding of how fiber resources are converted into products of value to society through modern pulping and papermaking processes. Pulping generally refers to various industrial processes used to convert raw plant materials or recycled paper into a fibrous raw material known as pulp, which is used primarily to make paper or paperboard products (and, to a smaller extent, other products derived from cellulose such as synthetic rayon). Plant materials such as wood, straw, or bamboo generally contain cellulose fibers together with lignin, a natural binding material that holds together cellulose fibers in wood or in the stalks of plants.

Although pulping and papermaking are ancient technologies, commercial pulping and papermaking processes have advanced significantly since the eighteenth century, toward more capital-intensive and increasingly large-scale automated production processes, with continued emphasis on improvement in product uniformity and quality as well as production efficiency. Modern society places considerable value on uniformity of quality and efficiency in production of pulp, paper, and paperboard products. At the present time, most pulp produced worldwide is wood pulp (pulp made from wood that is either harvested from trees or obtained as wood residues or byproducts from other wood-manufacturing processes).

Wood pulps are categorized by pulping process, with two major categories known as chemical and mechanical. Actually both types of processes typically use a combination of chemical and mechanical means to reduce wood into pulp. Chemical pulping relies mainly on chemical reactants and heat energy to soften and dissolve lignin in wood chips, followed by mechanical refining to separate the fibers. Mechanical pulping often involves some pretreatment of wood with steam heat and/or weak chemical solution, but relies primarily on mechanical equipment to reduce wood into fibrous material by abrasive refining or grinding.

The chemical pulping processes involve reaction or 'cooking' of wood chips with a solution of chemicals in a heated digester vessel for an extended period (up to several hours or more) followed by mechanical refining. Principal chemical pulping processes include the alkaline sulfate (or kraft) pulping process, acid sulfite, and semichemical pulping. Mechanical pulping processes include thermomechanical pulping (TMP), chemimechanical (CMP), chemithermomechancial pulping (CTMP), and groundwood pulping. The TMP, CMP, and CTMP processes involve reduction of wood chips into pulp in mechanical disk refiners, usually after pretreatment of chips with steam and/or weak chemical solutions. The older groundwood process involves grinding of wood bolts (small logs) into pulp against a grindstone.

Mechanical and semichemical pulps typically have much higher yield than kraft or sulfite pulps, as measured by weight of pulp produced per weight of wood input (over 90% yield for mechanical pulps and over 80% for semichemical pulp, versus 50% or less for kraft or sulfite pulps). However, kraft and sulfite pulps usually have higher market value because they have higher costs of production and because their fiber quality is usually better and more uniform, with generally less lignin or other wood constituents and proportionately more cellulose fiber and more intact fibers. Kraft and sulfite pulps can be more readily bleached to yield high brightness or whiteness that is desirable in many paper products, and kraft pulp typically produces a stronger sheet of paper or paperboard.

After wood pulp, the second largest and growing share of pulp produced worldwide is pulp made from recycled paper or paperboard. In the recycling process, recycled paper or paperboard is rewetted and reduced to pulp principally by mechanical means, followed by separation and removal of inks, adhesives, and other contaminants, through chemical deinking and mechanical means. Because the fibers in recycled paper and paperboard have been fully dried and then rewetted, they generally have different physical properties than virgin wood pulp fibers (for example, microfibrils on the surface of recycled fibers tend to be collapsed), and a portion of the fibers tends to be broken or damaged because of recycling. Without further processing, these differences in fiber properties would contribute to lower product quality (e.g., weaker interfiber bonding and hence lower strength in recycled paper or paperboard products), while contaminants contribute to lower and less uniform product quality (lower brightness, sheet defects, etc.).

To a large extent modern processing technology can compensate for inherent disadvantages of recycled fiber, but additional processing results in additional costs. Modern mechanical refining is used, for example, to resurrect surface fibrils, and modern papermaking machines and coatings can enhance sheet strength and surface properties, while the efficiency of contaminant removal has been improved by modern deinking systems. The market value of recycled fiber is influenced by intrinsic challenges associated with producing uniform product quality (contaminant removal and differences in fiber surface properties), challenges that can be overcome, but at a cost.

A smaller but still substantial volume of pulp is made from non-wood plant fibers, including agricultural fibers such as straw and other plant fibers such as bamboo, bagasse (residual of sugarcane refining), and annual fiber crops such as kenaf. In general, non-wood plant fibers are more costly to collect and process than wood fiber in regions of the world where wood supplies are adequate, and thus pulp is produced almost exclusively from wood fiber in most regions of the world. However, substantial quantities of non-wood pulp are produced in regions of Asia and Africa where wood fiber is relatively less abundant and non-wood fibers are available. **Table 1** summarizes estimated global pulp production in the year 1999 by principal category, and by major region.

The estimated 1999 worldwide total pulp production was 304 million metric tons (including pulp from recycled fiber). This compares to worldwide paper and paperboard output of 315 million metric tons in 1999. There is a difference between the output tonnages because many paper products contain the added weight of coatings, additives, or fillers, such as clay coatings on coated printing papers. In addition, there are some minor losses of pulp in conversion into paper or paperboard, and also a small fraction of pulp production (around 1%) goes to products other than paper or paperboard

Table 1 Global pulp production by category and region, 1999, in million metric tonnes

Region	*Chemical wood pulp*[a]	*Mechanical wood pulp*[b]	*Recycled pulp*[c]	*Nonwood pulp*[d]	*Totals*
Europe[e]	28.3	14.6	36.3	0.5	79.7
North America	66.1	16.3	35.7	0.2	118.3
Asia[e]	17.8	2.3	44.9	15.2	80.2
Australia and New Zealand	1.0	1.2	1.7	0.0	3.9
Latin America	9.9	0.4	6.9	1.1	18.3
Africa	1.7	0.3	1.3	0.7	4.0
World totals	124.8	35.1	126.9	17.7	304.4

[a] Chemical pulp includes sulfate (kraft), sulfite, and semichemical pulp.
[b] Mechanical includes thermomechanical, chemithermomechanical, and groundwood pulp.
[c] Recycled inferred from paper consumed for recycling, adjusted for yield estimate (~88%).
[d] Nonwood includes pulp from straw, bamboo, and various agricultural plant fibers.
[e] Data for Europe include all of Russia; data for Asia include all of Turkey.
Source: International Fact & Price Book (2001) Brussels, Belgium: Pulp & Paper International (PPI)/Paperloop.

(such as dissolving pulp used to produce rayon or other cellulose synthetics).

Papermaking

The utility and value to society of paper or paperboard products depend on their physical properties, such as the strength of paperboard used in corrugated containers, the softness and absorbency of tissue paper, or the smoothness and printability of paper used for printing or writing. Papermaking, the process of making paper or paperboard products from pulp, has been described classically as a felting process, in which a mat of randomly distributed pulp fibers is formed and then pressed into a sheet and dried. Variation in modern methods of sheet forming, intensity of pressure and energy applied in sheet pressing, and other process variables strongly influence physical properties of the finished sheet, which can range from the soft and absorbent properties of modern facial tissue to the rigid strength properties of modern containerboard.

Products of a felting process derive strength, integrity, and other physical properties differently than other common fiber-based products, such as woven products (e.g., textiles) where intertwining of fibers into threads and weaving of threads into fabric provide strength and integrity, or composite fiber products (e.g., fiberglass) where an adhesive or bonding agent combines with fibers to provide strength and integrity. The strength and integrity of finished paper or paperboard products depend on random interlacing and weak (nonchemical) bonding among fibers, and this is influenced by the papermaking process and by the inherent properties of individual pulp fibers, such as fiber length, flexibility, and fiber surface properties. Other paper properties such as sheet smoothness and printability are also influenced by fiber properties, such as the length and stiffness of individual fibers.

There is substantial variation in fiber properties among different plant species, and different types of pulp fibers have distinctly different physical characteristics, which influence the quality and utility of fiber resources in papermaking. For example, wood fibers from softwood (coniferous) trees are generally longer and more flexible while wood fibers from hardwood (deciduous) trees are generally shorter and more rigid, properties that tend to give quality advantages of sheet tensile strength to softwood fibers but sheet smoothness and printability to hardwood fibers. Chemical pulps generally afford stronger and more uniform sheet properties than mechanical pulps, and chemical pulps are more easily bleached to a high degree of whiteness or brightness, but chemical pulps generally have lower yield and are more costly to produce. Pulps made from recycled paper are generally associated with some degradation of fiber properties or more fiber breakage relative to virgin fibers, and use of recycled materials also introduces contaminants (inks, adhesives, etc.). Variations in quality and characteristics of fiber resources can thus substantially influence the market value of various fiber resources.

Paper and paperboard products serve several primary categories of end uses, each of which subtends a fairly unique range of functions and product requirements. Primary end uses for paper and paperboard include: (1) printing and communication, with requirements for sheet smoothness, brightness, and printability; (2) packaging and wrapping, with requirements for strength and protection at the most affordable cost; and (3) sanitary products with requirements for absorbency, bulk, and softness. Although these product characteristics depend directly on properties of individual fibers and the source of fiber raw material, they also depend on characteristics of the papermaking process.

The physical properties and hence the utility and value of paper or paperboard products can be greatly enhanced or influenced by the papermaking process, or by subsequent processes of sheet coating or finishing. In some cases this can partially or wholly overcome inherent limitations of certain fiber resources or pulp categories. The techniques used in sheet forming, pressing, and drying can influence properties such as sheet strength and smoothness. For example, softwood fiber was historically preferred in products where sheet strength was highly valued, such as in linerboard (paperboard used in corrugated boxes) because the longer and more flexible softwood fibers inherently provided more interfiber bonding and sheet strength. However, advances in sheet pressing and drying technology (higher-intensity pressing, extended presses, and multilayer forming) have significantly improved interfiber bonding and thus advanced the strength properties of linerboard made from recycled fiber and even hardwood fiber.

Other advances in sheet forming, pressing, and drying have enhanced physical properties such as softness and absorbency in tissue paper products, while the smoothness of printing paper has been improved by additional press finishing or supercalendering. Likewise, applications of coatings, pigments, and fillers have enhanced the quality and economy of printing, publishing, and packaging paper products. With advances in papermaking technology, improvements in product quality and uniformity have been achieved while expanding the use of lower-valued fiber resources.

Fiber Markets

Demands for pulp and paper fiber resources are derived from society's dependence on paper, paperboard, and related products for human welfare and prosperity. Society has come to depend on paper and paperboard products for many purposes integral to human welfare and prosperity, including education, information storage, and product advertising (in pages of books, magazines, catalogs, newspapers, and countless other forms of printed media or written communication), protection, transportation and security of goods in transit and in storage (in corrugated boxes and shipping containers, food packaging, and an enormous variety of other packaging and industrial applications), and protection of human health and sanitation (via tissue and sanitary paper products).

Although there is a direct correspondence between demands for pulp and paper fiber resources and the demands for paper and paperboard, there is not such a direct correspondence between trends in value or prices of fiber resources and trends in paper or paperboard commodity prices. **Figure 1** illustrates, for example, historical trends in the US average real price indexes for pulpwood, recovered paper (wastepaper recovered for recycling), and paper and paperboard commodities.

As shown in **Figure 1**, the real price index for paperboard commodities increased in the 20-year period from 1982 to 2002, ending the period up by about 25%. Likewise, the real price index for paper commodities increased over the same period, ending the period up by about 10%. The real price index for recovered paper (wastepaper recovered for recycling) was much more volatile (plotted against the right axis in **Figure 1**), although trends in the price index for recovered paper generally followed the trends for paper and paperboard over the same period, and also ended the period up by more than 40%. The real price index for pulpwood exhibited considerably different behavior over the same period, and by the end of the period had declined by more than 40%. The variation in price behavior among these different indexes reflects the role of different market forces influencing market prices.

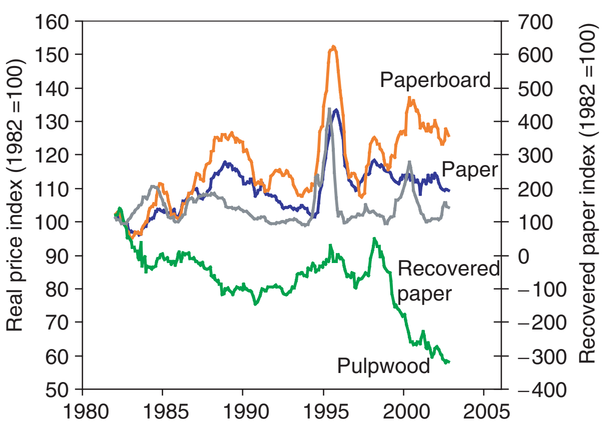


Figure 1 US real price indexes for pulpwood, paper, and paperboard, 1982–2002. Paper, paperboard, and pulpwood indexes plotted on left axis, recovered paper index plotted on right axis.

The variable price history of paper and paperboard commodities is primarily a function of variation in product demands in relation to available production capacity (the output capacity of paper and paperboard mills). To some extent there is a reflection of trends in fiber resource prices in the trends of paper and paperboard prices (**Figure 1**), but the variation in paper and paperboard prices is more strongly influenced by variation in demands for paper and paperboard commodities and by capacity utilization. Paper and paperboard commodities are used widely throughout society in virtually all sectors of the economy – domestic, institutional, commercial and industrial. Thus the trend in overall demand for paper and paperboard tends to be correlated with cyclical trends in broad indicators of economic activity, such as overall industrial production and per capita gross domestic product (GDP). The production capacity of mills that produce pulp, paper, and paperboard commodities establishes the short-run supply potential, with actual production varying in response to market demand. The ratio of actual production to available capacity (capacity utilization ratio) is a key determinant of product prices, with prices tending to be high when capacity utilization is high and low when capacity utilization is low.

The market value or price of fiber resources also tends to be influenced by the demand and price situation for paper and paperboard, and this has been particularly true for recovered paper prices (**Figure 1**). However, there are other important market forces that influence the supply of fiber resources, and thus the trends in market value for fiber resource do not precisely follow the trends in paper and paperboard prices. Indeed, for pulpwood in the USA (and in some other regions) the price trend has been opposite to the trend for paper and paperboard prices (i.e., downward as opposed to upward, as shown in **Figure 1**). Fiber resource supply tends to influence the market value of fiber resources as much as fiber resource demand, and fiber resource supply varies over time depending on such factors as the periodic volume of timber growth and availability for harvest, the area of forests or plantations managed for pulpwood production, and trends in recovery of wastepaper for recycling.

In the USA, for example, in the period between 1982 and 2002 there was a significant increase in the recovery of wastepaper for recycling, particularly during the period from the late 1980s to the early 1990s, reflected in a period of relatively depressed real prices for recovered paper (**Figure 1**). By the mid-1990s, however, the utilization of recovered paper had increased substantially, both in domestic paper and paperboard mills and in foreign mills that were increasingly importing recovered paper from the USA. Thus, in the mid-1990s the increased demands for recovered paper (domestic and export) helped to stimulate a significant spike in recovered paper prices. However, with the rapid escalation in US recovered paper prices, export demands subsided and prices rapidly declined. The mid-1990s' price spike in recovered paper markets also coincided with a price spike for paper and paperboard commodities, induced in part by speculative purchasing of market pulp and by relatively strong demands for paper and paperboard during the mid-1990s. Pulpwood prices also showed some firmness in the early to mid-1990s, but pulpwood prices in the USA were eventually dominated by expanding supplies of timber with expansion and maturation of pulpwood plantations, particularly pine plantations in the South USA, where millions of additional hectares of pine plantations were established in the 1980s and 1990s. In addition, the increased use of recycled fiber (which more than doubled in the USA during that period) also tended to offset growth in pulpwood demand and dampened the trend in real pulpwood prices.

Trends in Fiber Resource Supply and Sustainability

Although global demands for pulp and paper fiber resources have been increasing and are expected to continue increasing in the future, the available supply of fiber resources has likewise been increasing, and both supply and demand appear increasingly sustainable into the foreseeable future. In part this is because consumption of paper and paperboard products is not rising exponentially in developed countries such as the USA, but rather consumption is decelerating (continuing to grow but at a slower pace over time) with declining consumption per unit of GDP. Also, there remains vast potential to increase output from fiber plantations worldwide, and there is potential to increase paper and paperboard recovery for recycling. Indeed, in recent years (since the mid-1990s) pulpwood and recovered paper prices have been subsiding globally.

In the USA, which produces and consumes more pulpwood by far than any other country, wood pulp production declined by 12% while consumption of pulpwood at wood pulp mills declined by approximately 15% from the mid-1990s to 2001. Real prices of softwood pulpwood in the USA also declined in recent years, with prices in the South USA (the principal production region) declining to the lowest recorded levels in modern history (several decades over which pulpwood prices have been surveyed and reported). Pine plantations in the South have the potential to supply significantly greater volumes of fiber in the future, although expansion of supply may be inhibited by low prices and limited growth in demand.

Although paper and paperboard production and demands for fiber resources are going up in other developing regions of the world, such as in Asia and Latin America, global development of fiber resources is keeping pace with capacity expansion. China, for example, is experiencing fairly rapid economic growth, with expanding production capacity in modern papermaking facilities, but mills in China are able to rely in the near term on expanded wood pulp production in East Asia (in countries such as Indonesia) as well as global supplies of market pulp and recovered paper. For the future China can also rely on indigenous sources of fiber supply, having established a larger area of tree plantations than any other country.

Globally, wood fiber supply has expanded with the expansion of fast-growing plantations of species such as pines, eucalyptus, and acacia. Although plantations have in some areas displaced native forests, managed plantations account for only a small fraction of forested land area (e.g., only 6% in the USA, for example). Plantations generally have a potential to supply a much greater volume of wood fiber per unit of land area than unmanaged or native forests, and thus the use of a small fraction of land area for plantations can offset the harvest of pulpwood on large areas of forest. Environmental certification of forests and forest plantations has expanded globally over the past decade and is now common in many areas of the world, with increased emphasis on preventing illegal logging and encouraging sustainable forestry practices. Managed plantations are an integral part of ensuring the sustainability of forest resources in the future. Globally, plantations are expected to increase their share of total wood production from around 20% to upwards of 50% by 2050.

The recovery and use of paper for recycling have been on the increase, as the proportion of fiber obtained by recycling has been increasing. Globally, recycled fiber accounts for well over 40% of pulp fiber (**Table 1**), and some countries have achieved much higher rates (over 50% in Japan and around 60% in Germany). Although product needs and capacity growth may constrain the use of recycled fiber in some cases, there is still the potential to expand its recovery and use in the future.

See also: **Papermaking**: Overview; The History of Paper and Papermaking; World Paper Industry Overview. **Pulping**: Environmental Control.

Chip Preparation

W S Fuller, FRM Consulting, Federal Way, WA, USA

Introduction

Wood chips used in pulp mills are small, engineered pieces of wood cut from logs and wood pieces left over from the manufacture of solidwood products such as lumber and plywood. The target dimensions of a chip are usually 4–6 mm thick, 15–20 mm in length and width (**Figure 1**). This is the size range that will allow most batch and continuous chemical and mechanical pulping systems to reduce the wood uniformly to individual fibers and fiber bundles. There is no 'perfect chip' since wood variability does not allow consistently making the same chip over and over. There is an ideal chip size distribution that matches the needs of the mill's digester(s). This article will describe the process of making chips that meets the specifications of pulp mills. The basic chip production processes are:

Figure 1 Typical pulp chips sampled after going through the chip screen system.

- debarking of logs increases pulp yield and cleanliness
- chipping of logs and wood products residuals makes small particles (called chips) in as uniform size distribution as possible
- chip screening removes fines and oversize chips to improve pulping uniformity
- prevention of contamination of chip flows with metal, rocks and especially, plastic
- chip transportation and storage systems receive, store, convey, and meter chips without damaging them
- quality control programs monitor chip production and deliveries.

Mill Layout

The area in the mill that logs and chips are received, stored and processed is called the woodyard. The building or structure that contains debarking, chipping, and screening equipment is the woodroom. In cold climates, almost all the functions are contained in heated buildings to prevent freezing of equipment and people. In more temperate zones, only a sheltering roof is used to protect the chipper and screen from rain.

The goals of the woodyard and woodroom organizations are to:

- produce chips that are not only the right size for the mill's digesters, but also have very low short-term variability (i.e., hourly and daily)
- deliver chips to the pulp mill that have little or no contamination and a bark content that is below the mill's tolerance level
- manage the inventory of logs and chips at target levels that do not create a loss in chip value from deterioration in storage
- monitor the quality of chips received at the mill, made in the wood room and delivered to the digester with sampling and testing frequency consistent with the use of the data for decision-making.

Debarking

Bark is essential for a tree's growth and health. It is a protective layer around the wood that resists drying, attack by molds, wood staining and rotting fungi,

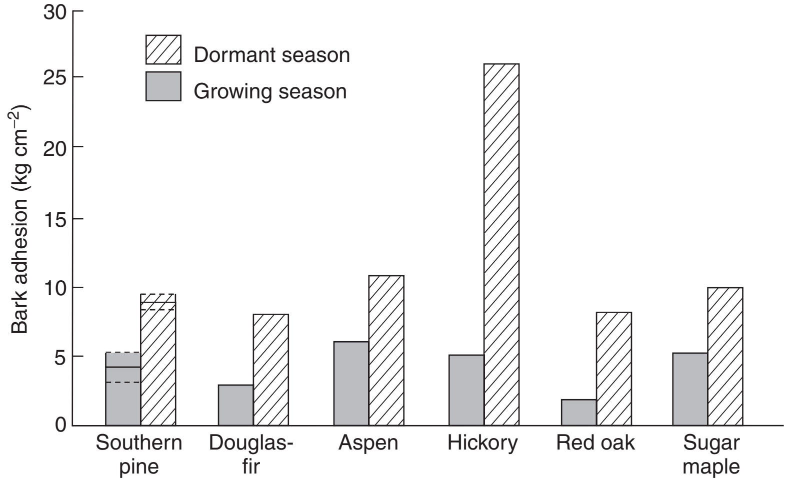


Figure 2 Comparison of bark adhesion for several common North American pulpwoods showing the difference between the tensile force required to remove the bark in dormant and growing seasons.

and most insects. Between the wood and the bark there is a single growth layer called cambium. This single cell layer is where tree growth occurs. Bark is formed toward the outside of the tree and wood to the inside. During the growing season, this layer breaks easily and bark is removed with little force. However, during the dormant, winter season, the bark and the wood are tightly bonded together by the inactive cambium layer and more force is needed.

The mechanism of bark removal is applying enough force to break the bond between the bark and the wood. The amount of force has been quantified for the most common North American wood species for both dormant and growing season conditions. **Figure 2** shows that bark adhesion approximately doubles in the winter for most wood species. In the industry, it is well known that debarking hickory (*Carya* spp.) is almost impossible in the winter and the data shows its high bark adhesion. At the other extreme, the bark of some hardwoods, like poplar (*Populus* spp.), is so loosely attached in the spring that it easily falls off in big sheets that are difficult to convey and process into wood waste fuel.

Other factors also influence the ability to remove bark. Thick bark absorbs energy and requires more time or force to remove it. Logs dry out after long storage times and the bark bonds to the wood more tightly.

There are two primary types of equipment to apply the force needed to remove bark from logs. In sawmills and plywood plants, mechanical ring debarkers are most common. **Figure 3** shows how debarking tools surround and rotate around each log. The tools are sharp and press against the log. The bark is peeled off the log and drops down to a

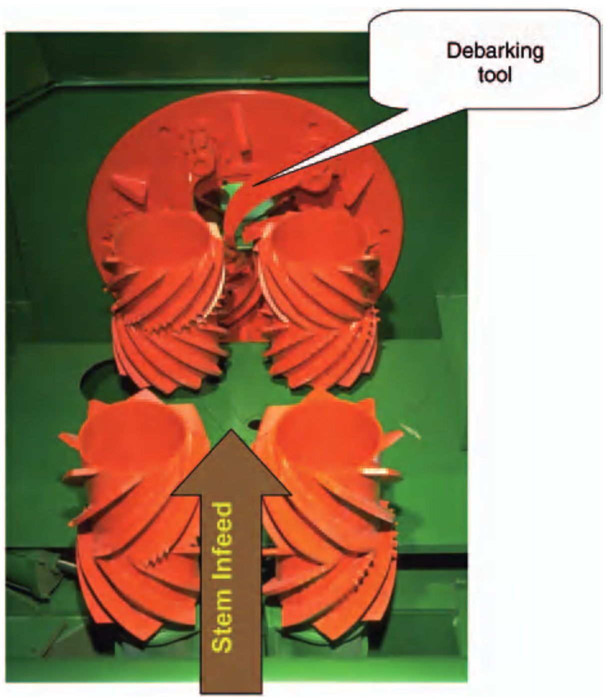


Figure 3 Mechanical 'ring' debarker. The debarking tool pressure on the log surface is adjusted for the diameter, storage time, and season.

refuse conveyor going to the wood waste fuel or bark products processing systems. While the linear speeds of the debarkers now reach 150 or more meters min^{-1}, this type of debarker can economically prepare logs for sawing or peeling.

In pulp mill woodyards, large drum debarkers ranging from 4 to 8 m in diameter and over 60 m long can debark up to 100 to 250 cm^3 of logs h^{-1} (**Figure 4**). Wood comes to pulp mills in two forms, shortwood and longwood. Shortwood tumbles

Figure 4 Long-log drum debarkers in an area with cold climate where equipment must be enclosed for winter operation.

randomly and longwood rolls in parallel against each other as the drum turns. The drums rotate at 6–10 rev min^{-1}, adjustable in more modern installations. Logs are fed into the open infeed end of the drum and the level is optimally about 50% full. Since the drum outlet is about 1 to 2 degrees lower than the infeed, the logs move down the drum. An adjustable vertical, horizontal, or elliptical discharge gate controls the rate of debarking. Operators control the residence time in the drum by adjusting the feed rate and the gate position. The tightness of the bark determines how long the wood must stay in the drum to keep the bark levels below the mill's tolerance levels. During the spring and early summer, it typically takes half an hour or less to reduce bark levels to well below 1%, depending on log size and species. In autumn and winter, the residence time may need to be as long as 1 hour to achieve the same low bark levels. However, long residence times will cause excessive wood loss as the logs hit each other and the walls of the drum. A balance must be achieved so that wood loss is controlled and bark levels are near the tolerance limit. The bark tolerance level varies between mills depending on the wood species, bleach sequences used, and customer demands for clean pulp and paper. In a survey of North American mills, a bark tolerance level in the range of 0.5–2% was typical. High debarking efficiency with low wood loss will achieve one of the primary objectives of the woodyard in reducing the bark content below the tolerance limit of the mill.

Chipping

Pulp mill chips are produced either in a pulp mill woodroom at a wood products mill, and most commonly, at both. The basic chipping mechanism is the same for each, but the difference in the wood sizes and shapes requires different sizes and types of chipper systems. Sawmill waste chipping is more challenging since the infeed material varies widely in size and shape (**Figure 5**). In general, woodroom chippers will be larger in diameter (1.8–3.1 m) than sawmill chippers (1.2–1.8 m). The life expectancy of a woodroom chipper is 30 years or more, while sawmill chippers are lighter duty construction and have a 10–15-year life.

Figure 5 Sawmill chipper infeed. Vibratory conveyors are commonly used to convey sawmill waste to chippers. The size and shape of sawmill by-products varies widely. Some flows are relatively uniform (a) while others contain long slabs, trim blocks, and chip screen oversize (b). uniform sawmill chipper feed material produces more uniform chips.

The basic chipping mechanism is a sharp knife passing through the wood, cutting across the grain (**Figure 6**). There is first a cutting action and as the knife continues to move into the wood a shearing action that pops off chips. This continues until the knife has cut completely through the log or piece of wood when the next knife begins its cut. Chippers have multiple knives mounted on a disk or a drum. The disk chipper is the most common (**Figure 7**). A slot is cut radially through the disk so that the chips will exit from the back of the disk after being cut. The knives are mounted at each of these slots with a clamp mounting or a face mounting (**Figure 8**).

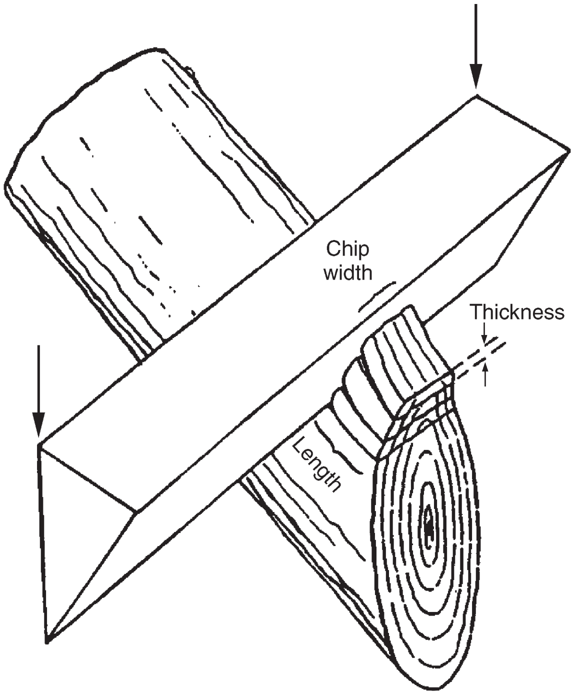


Figure 6 Chip cutting action. Only the chipper knife and log are shown in this drawing of how chips are formed as the knife passes through a log. The knife cuts the wood off at the desired length. As the knife continues into the log, it creates shear forces that pop off a chip at the designed thickness. As chip length increases, chip thickness also increases.

A woodroom chipper infeed system has these basic parts: (1) an infeed conveyor moves the logs from debarking to the chipper; it is usually a heavy link chain, heavy-duty rubber belt conveyors or a combination of the two; (2) the infeed chute guides the wood from the conveyor to (3) the chipper spout at the disk face. The chute is commonly at a 38-degree angle to the disk. The chute can be oriented to feed the wood by gravity or pulled in horizontally by the knives (**Figure 9**).

A disk chipper has 4–12 clamp-mounted knives positioned radially along slots that pass through the chipper disk. The chips will go through the disk after the knife cuts them off the log. Mounted on the back of the chipper disk are fanlike blades that catch the chips and blow them out of the top of the chipper hood. Without these blades, the chips fall onto a conveyor below the chipper. This is a bottom discharge compared to the overhead or blown discharge. The blades often have protrusions that break up the ribbon or card of chips that pass through the disk.

The layout of sawmill residual chippers is quite similar to a woodroom except that the material chipped is much smaller and has a wide variety of sizes (**Figure 5**). Sawmill chipper infeeds can be at either a right angle to the chipper shaft or as in some newer sawmill systems, the disk is tilted over the infeed chute, exerting more pull-in and hold-down forces on sawmill residuals or small logs.

Chipper maintenance is critical in producing an optimum chip size distribution. Maintaining the designed wood to knife interface requires daily, weekly, monthly, and yearly inspections and replacement of parts when the wear limits are exceeded. Most wear points can be checked during knife changes. Chipper knives can wear quickly depending on the tonnage being chipped, the wood species, the moisture content of the wood, and the amount of rock and metal contaminants that reach the chipper. Simple wear only requires grinding, but grinding done carefully so that correct knife angles are restored and metallurgy not altered by overheating. Other key wear areas are the anvils, bed knives, and face plates. Deciding the timing for knife changes depends on the rate of wear, the chip quality needs, and the times the mill making chips or the woodroom is down for enough time to change knives and inspect the chipper without losing production time. Shift changes and meal breaks are such times. The best way to decide when knife changes are needed is by tracking the chip quality. There is a gradual increase in pin chips and fines after a knife change. Depending on the mill tolerance for small particles and screen capacity, a tonnage or time for knife changes is decided based on chip quality and normal downtime schedules.

A 'disposable chipper knife' has become popular in the last 10 years. These knives have two chipping edges, are in segments about 40–60 cm long and are turned around and relocated on the disk in a pattern that takes advantage of the fact that some zones get more chipping action than others. **Figure 10** shows a cross-section of a disposable knife, knife holder and method of mounting the knife.

Chip Screening and Cleaning

Each pulping system operates best with a specific chip size distribution. Finding that distribution is

Figure 7 (a) Horizontal feed disk chipper and approx. 50 cm diameter fiber log; (b) gravity feed disk chipper and 15–20 cm diameter shortwood; (c) horizontal feed disk chipper and approximately 30 cm diameter fiber logs; (d) drive side view of a horizontal feed disk chipper; note the straight line design from the drum to the feed that eliminates log transfers and plug-ups; (e) chipper operator changing chipper knives; required safety equipment is being worn and a holding device has been made to reduce the risk of cuts while handling the newly sharpened knife; (f) the back side of a chipper with card breakers during a knife change; note that the chipper slots have been lined with a wear plate to prevent disk damage over time.


(a)
(b)
(c)
(d)
(e)
(f)

Figure 8 Woodroom chipper with hood raised for knife changing. The knife slots and knives reach from the hub to the edge of the chipper.

done with well-planned mill trials, pilot scale trials at a screen manufacturer's facility, applying information reported at a conference, literature searches or simply by observing how the day-to-day operations fluctuate as chip quality changes. These are listed in the order of likely success. Given an optimum size distribution, a chip screening system can be designed that meets the mill's needs. The size fractions most commonly removed from a chip flow are over length, over thick, pin chips, and fines (as defined by a Chipclass classifier in **Figure 11**). A well-designed screen system will remove a target size at high efficiency with low loss of good fiber.

The goal of a pulping system is to make pulp at the highest yield possible, with low variability the pulp properties that meet the customer needs. One of the most important contributions a woodroom can make to pulp mill operations is narrowing the chip size distribution after everything has been done to make optimum chips in the woodroom, sawmills, satellite chip mills, and plywood plants. Pulp chip screening equipment is designed specifically to remove and often reprocess the extremely large and small chip sizes.

There are several classes of chip screening equipment:

1. Rotary or gyratory screens. Although the first type of chip screens to be used in woodrooms, these screens are still used alone in sawmills or in combination with some of the more recent screening concepts in woodrooms (**Figure 12**). This type of screen segregates chips on the basis of length or width using flat punched steel plate or woven wire mesh stacked up to three or more decks. The circular or elliptical motion of the screen is in the horizontal plane of the plates. The top deck has the largest square, circular, oval, or rectangular openings 40–60 mm in diameter, length, or diagonally. Oversize chips are rechipped in a small drum or disc chipper. To remove the smaller fractions, plates or steel mesh with 4–6 mm round or square openings are placed in the bottom deck of the screen. The screening efficiency of this type of screen is relatively low. Typically, the small fraction removal efficiency is

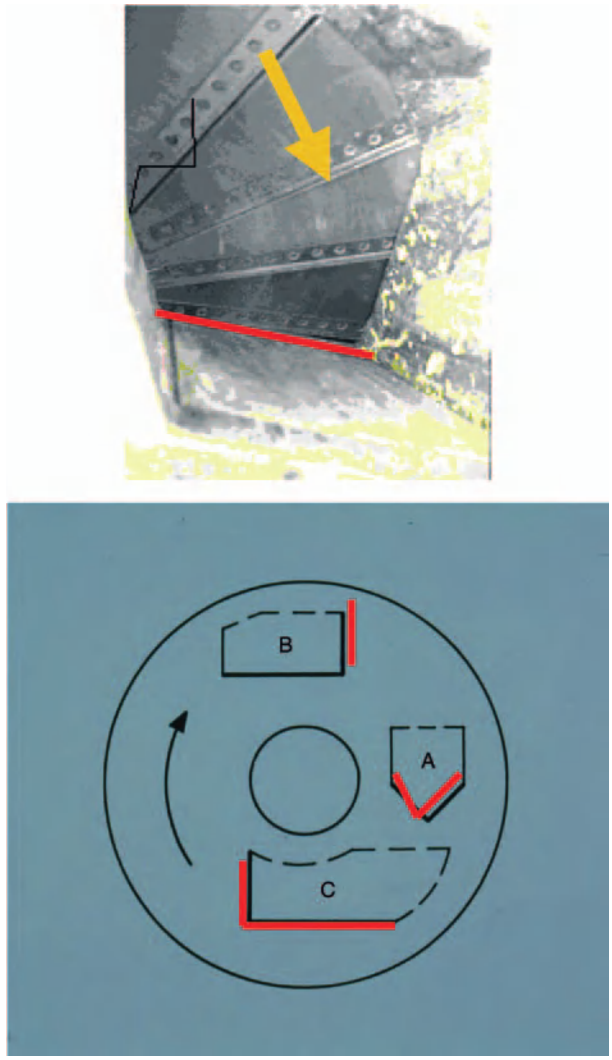


Figure 9 Spout location is a key part of chipper design. The picture shows a chipper spout with the direction of rotation marked with an arrow. The anvil location is marked with a red line. This design keeps wood in the lower right corner for uniform chipping. The sketch shows typical anvil locations of other designs: (A) a gravity feed with anvils at both of the bottom edges, (B) a horizontal spout overshaft with a vertical anvil, and (C) a spout undershaft horizontal feed with bottom and side anvils. Design (B) is not recommended for roundwood applications since the wood is lifted up against the force of gravity and wood (logs or sawmill residuals) do not remain stable.

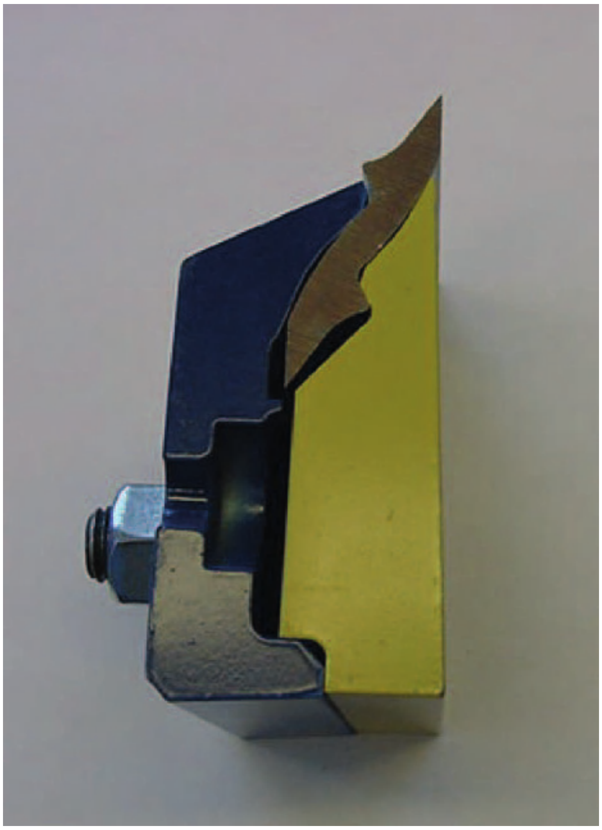


Figure 10 A cut-away section of a disposable chipper knife clamped into a knife holder that is then bolted into the knife pocket. Note the two chipping surfaces that allow the knife to be turned over when one side becomes dull.

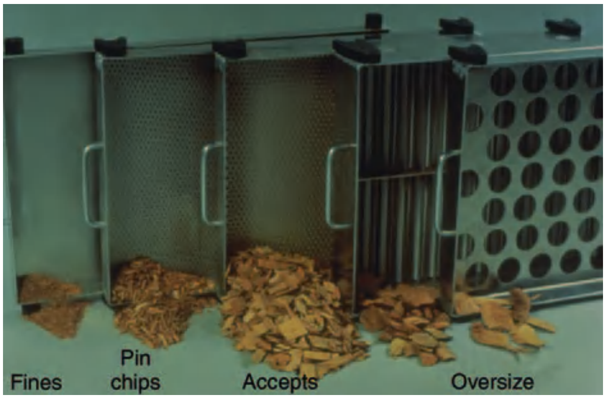


Figure 11 Chip classifier tray series that relates to pulping and chip handling operations. Oversize undercook, causing high dirt levels due to uncooked wood in the center. Feeders and chip chutes can plug due to long oversize. Pin chips can impede digester liquor circulation in high or highly variable amounts. Fines contain fibers that are too small to make good paper and contain high amounts of dirt and bark contaminants.

no more than 50–65%. A rotary/gyratory screen is usually a component of a multiscreen woodroom screen house and due to its simplicity, is used in sawmill and veneer plants.

Figure 12 A typical gyratory screen. Note that the round holes are larger in the feed end of the screen and smaller at the discharge end. This has been used to increase screen capacity, but actually reduces removal efficiency.

2. Disk screens. In the 1970s the industry became increasingly aware that chip thickness was as or more important than chip length. The disk screen is designed to remove over thick chips. A series of parallel shafts at a 90 degree angle to the chip flow have thin disks spaced uniformly and rotate in the same direction. The disks alternate and overlap so that the interface opening between opposing disks is in the range of 6 to 10 mm (**Figure 13**). Unscreened chips are evenly fed across the first rows of disks and the rotating motion moves a mat of chips down the screen with the help of undulations or serrations on the disk edges. The thinner, acceptable chips and small particles fall between the disks while the over thick and over length ones drop off the end of the screen. High screening efficiency always translates to some near-size acceptable chips staying with the rejects. During the process of treating the rejected oversize and carry-over of unacceptable chips, some of the fiber loss will be recovered. Disk wear is a significant issue for disk screens. Periodically, the interface openings should be checked with calipers and chip samples taken to determine the overall system efficiency. In areas where sand contaminants are found, the interface opening is increased in as little as 18–24 months. Some early attempts to screen out small particles with disk screens were commercially unsuccessful due to plugging, sensitivity to chip moisture content, and wear.
3. Roll screens. The development of roll screens to segregate both large and small particles has provided greater flexibility in screen system design and operation. The rolls are arranged with their shaft at a right angle to the chip flow. The roll surface is machined to form a pattern of diamond

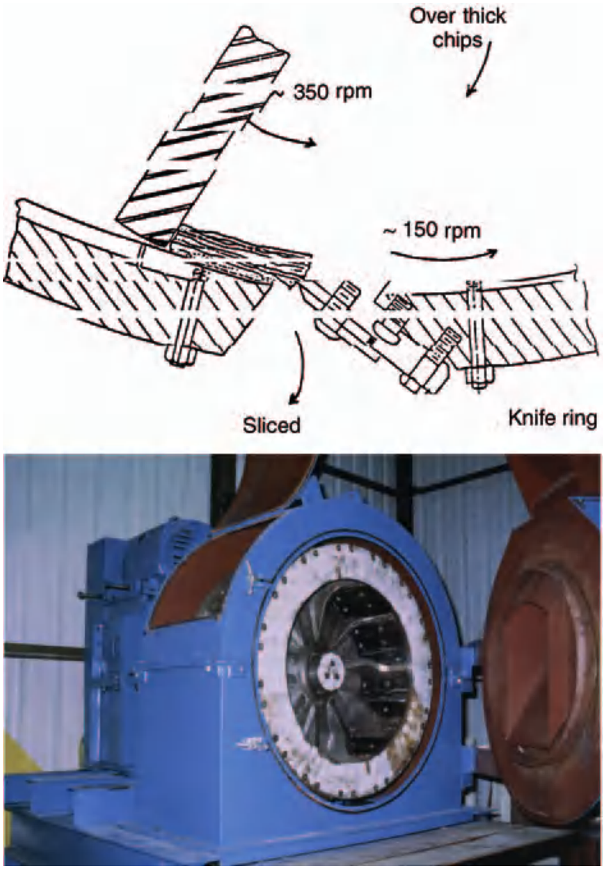


Figure 13 Chip slicing. The two rings in the slicer rotate in the same direction, but the inside ring brings the chips to the knife at a faster speed than the knife ring is rotating.

shaped peaks and valleys (**Figure 14**). The inter-roll opening is adjustable from 1.5 to 8 mm. Thickness screening is possible using the inter-roll opening to reject over thick and over length chips. The application of roll screens to fines screening and pin chip recovery provides the ability to tune the system by adjusting both the roll speed and the spacing. This is particularly important in responding to the higher pin chip and fines content produced by chippers in the winter months. Over time, the mix of sawmill chip supplying a mill will change and with it the average size distribution. The adjustability of roll screens provides the unique opportunity to respond to change without the high cost of system rebuild.

4. Bar and blade screens. Another way to provide an interface opening through which oversize chips cannot pass is the arrangement of segments of bars or thin blades that oscillate the length of the screen to move the chips down the screen and separate the over length and over thick chips. Wear is much slower in the bar screen than any other.

Over length, over thick, and accept chips rejected by thickness screens need treatment before they can be put back into the chip stream. The composition of the over length and over thick chips is dominated by wood knots and the distorted wood around branches. A few wood and pulping experts contend that the wood in these oversize categories is very high in compression wood and therefore should be diverted into the mill fuel system. Very few mills have analyzed this option and most mills continue to reprocess the oversize material to make it pulpable. The options available for rechipping and oversize treatment include:

1. Rechippers. Both disk and drum versions of rechippers are available. Disk rechippers are 1–1.5 m in diameter. Both horizontal and gravity feed are common. Tests have shown that it may take as many as three to five passes before a rechipper will reduce some oversize pieces to a size that will be accepted in rescreening. Fines production is increased by rechipping from random cutting and repeated recycling. The inadequacies of a rechipper has encouraged the development of better options, particularly since thickness screening implementation began in the 1970s.
2. Chip slicer. A machine that normally makes flakes for the production of flakeboard has been adapted to slice over length and over thick chips to a thickness that will pulp more easily (**Figure 13**). Oversize and carried-over accept chips are fed into the center of a drum surrounded by two concentric rings. Slicer knives are mounted on the inside of the outer (knife) ring that turns at about 150 rpm and in the same direction as the inner or anvil ring. At about 350 rpm, the inner ring anvils sweep the oversize material into the slower moving knives. A slice is taken at the target chip thickness (6–8 mm). As long as a rock or metal contaminant does not damage the knives, slicers have operated for 6 to 8 weeks before a knife change was needed. Four weeks is about average.
3. Chip crackers or conditioners. The poor pulpability of oversize material is due to the inability of pulping liquor to penetrate the chip. In laboratory studies, it has been observed that large chips that have partially separated during chipping will pulp almost as well as accept chips. It follows that if fissures can be created in oversize chips, liquor penetration should be sufficient to achieve pulping. This has been commercialized in chip crushers or conditioners (**Figure 14**). The oversize chips drop through the nip between two large rolls turning toward each other. There is pressure applied to prevent the nip from opening

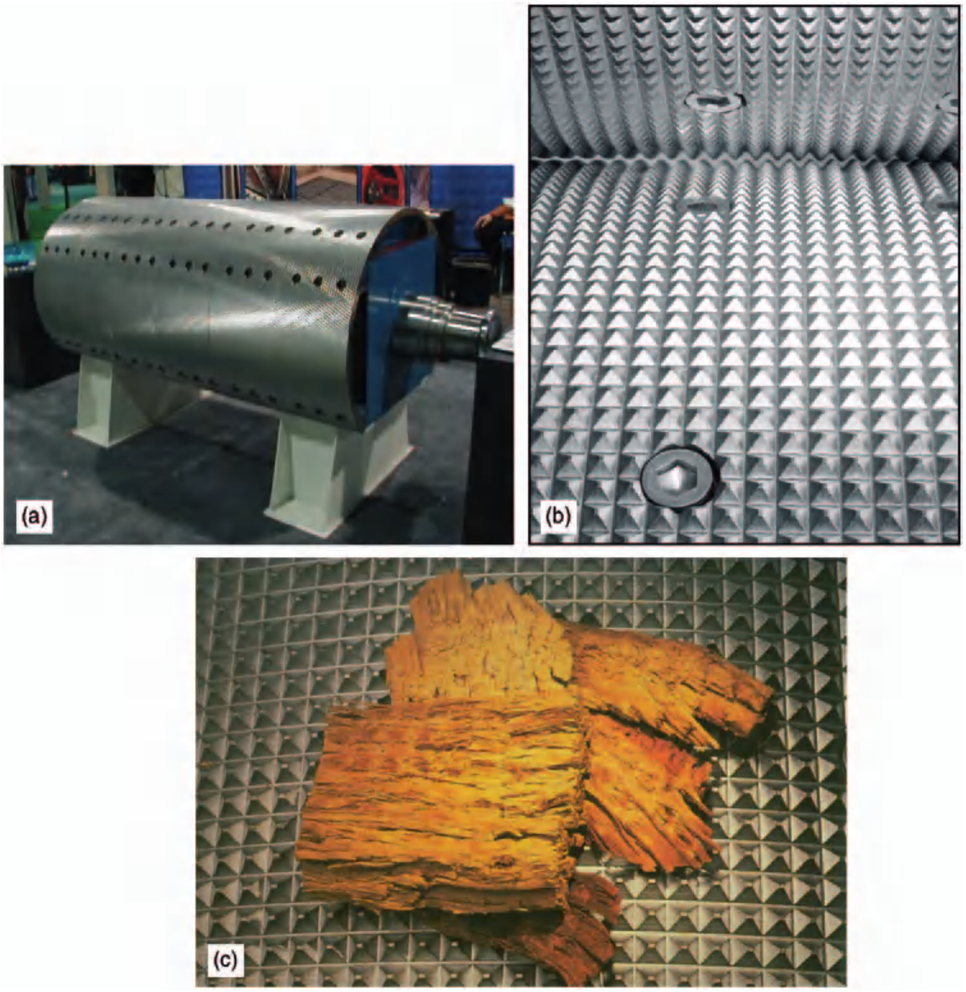


Figure 14 Chip cracker or chip conditioner. (a) One of the pair of rolls in the system; (b) close-up of the inter-roll opening; (c) examples of oversize after going through the roll opening. Note how the large chips are fissured by the crushing force and the roll surface.

when several chips go through at the same time. There is less maintenance since there are no knives to sharpen. The roll surface metallurgy resists abrasion and the occasional wrench. As with chippers and slicers, there needs to be protection from the occasional tramp metal and rocks that find their way into chip supplies.

Wear and equipment damage is a major problem in rechipping, slicing, and crushing oversize chips. Rocks and metal debris are particularly troublesome. Since both of these materials sink in water, running the oversize through a chip washer or settling basin will eliminate this problem. Sand and grit can be removed in a chip washer in much the same way as rocks. Mechanical pulping systems almost always have chip washers to reduce wear in the primary refiners.

In regions where freezing conditions preclude the use of water as a separation medium, air density separators have been highly successful. The oversize chips are fed into a vertical pipe that contains upward flowing air from a blower system. By adjusting the air flow, denser rock and metal debris will fall out of the oversize chip flow onto a conveyor belt below while the less dense wood will rise and be caught in a cyclone feeding a slicer, chip conditioner, or cracker.

There are other types of contaminants that must be controlled in the mill area to prevent paper downgrade due to spots and holes in the pulp sheet. Grease, oil, char, paint, rubber, and plastic are some of the most common contaminants. The most difficult of these is plastic contamination. Once plastic is in the pulp, there are very few methods of removing it economically. Plastic is introduced into chip flows primarily by people who do not understand the consequences of disposing of things like a sandwich bag, ear plugs, a candy wrapper, and other debris into a chip truck or onto a conveyor. After

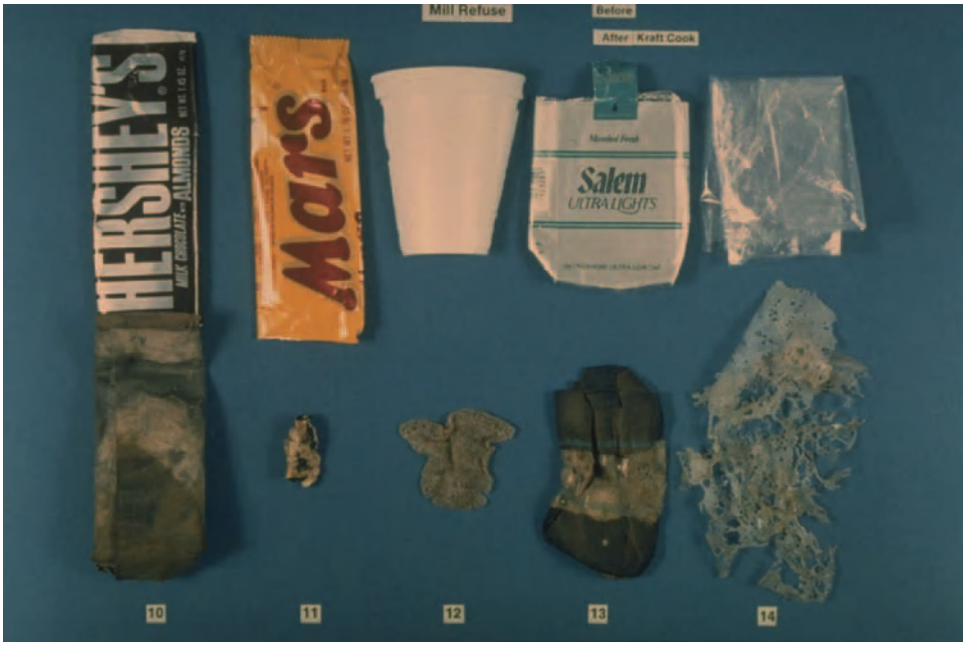


Figure 15 Common plastic items shown before and after kraft pulping. The wrapper on the far left is made of paper and will become part of the fiber furnish. The plastic bag at the far right has become a brittle lattice that will break easily in pulp handling and contaminate several hundred tons of pulp.

spare parts have been installed, the plastic packaging is often left to blow onto chip piles. It is commonly dropped onto the conveyor that is near something being repaired. **Figure 15** shows the results of a laboratory pulping study to determine how plastic reacts in pulping. Plastic will not dissolve in the kraft pulping process. Rather, the heat causes it to shrink, become filamentous, or form a hard tacky glob. The most reliable method of controlling plastic contamination is education of everyone from the point of chip production to the digester. The education must be continuous and effective.

Several types of screen combinations are available to design a screen room system. Sawmills and plywood plants install systems that are simple to operate and have relatively low capital cost. **Figure 16** shows this type of system and the more complex systems used in pulp mill woodrooms. Pulp mills can justify more complex systems based on the improvements a narrower size distribution and reduced oversize and fines can bring to mill operations. For example, the oversize chips in **Figure 17** have been pulped with no slicing or crushing treatment. Kraft pulping liquor could not penetrate more than 2 mm into the over thick chip. The distorted grain of surrounding a wood knot also shows a lack of penetration. One of the first observations a pulp mill makes after a screen room start-up is the dramatic drop in these partially pulped chips and fewer shives, small undercooked slivers of wood that break off of partially cooked chips.

Chip Storage and Handling

Chip storage would not be needed if on-site chipping and chip deliveries from off-site chip sources were precisely timed with the digester(s) demand for chips. A few mills are able to achieve as little as 3 days of inventory. This is the exception. If a mill buys chips from several sawmills, their delivery rate varies widely due to such things as shift scheduling, market conditions, equipment breakdowns, and availability of trucks. Chip mill production varies primarily with availability of logs, weather, soil conditions, and log availability. The amount of chips a mill stores depends on the level of risk the chip buyer and the pulp mill manager are willing to share. If a mill manager wants to have no risk of running out of chips, the chip buyer will maintain a large inventory taking into account the reliability of chip suppliers to fulfill the contracted deliveries. An impending wood products market decline would cause the chip buyer to increase inventory just in case the market slump lasted longer than expected. If the decline does not happen or is shorter than expected, the mill has an even larger inventory. It would seem logical to curtail deliveries, but sawmills and chip mills have no or limited chip storage capacity. This is an expensive approach to inventory management. The money invested in chips could be earning a return in other investments; the high inventory will deteriorate faster than normal and the properties of the chips going to the digester will be more variable. A better strategy is

Figure 16 The sawmill or satellite woodyard screen system (a) with only a gyratory screen is much less complex than a thickness screening system installed in most woodyards (b). Note the aerodynamic separator up-draft tubes can be seen on the closest side of the system.

to agree on a level of inventory that the pile should never go below (called a critical level). An estimate of the reliability of sources to deliver is made. Also, how quickly inventory could be replaced if a large supplier(s) could not deliver at all (after a fire, for example). This would establish a target chip inventory and a lower inventory level that if reached would trigger purchase options to be sure the inventory stayed above the critical level. A mill that routinely stored about 175 000 tonnes could comfortably operate at an inventory around 45 000 tonnes. **Figure 18** shows modern circular and linear chip storage systems.

Excessive inventory, long storage times, and physical damage when moving chips around result in two types of losses: physical loss and biochemical loss.

The physical deterioration is primarily fines generation. This occurs in blowlines as the chips impact the walls of the blowline at repeated bends and sharp corners. Fines are also created when chip dozers move chips from unloading systems onto the pile and later, back to the reclaim pit (**Figure 19**). Because chip dozers are so heavy, breakage extends down into

Figure 17 Oversize chips after kraft pulping. (1) Overthick chip with partial impregnation and a woody center; (2) overlength and over thick chip with only the first few millimeters on the outside that are pulped; (3) the distorted grain and compression wood near a branch created an oversize that has only surface pulping; (4) an over thick chip with a woody center; (5) knotwood creates a badly formed chip that only pulps on the surface.

Figure 18 State-of-the-art chip storage systems. Automated outstocking and reclaim is used to maintain a first-in/first-out pile rotation. The arrangement is either circular (a) or linear (b).

the pile half a meter or so. In all cases, acceptable chips break into pin chips and fines. Several studies have measured pin chips and fines generation in full-scale, commercial piles. **Table 1** reports data for a blow line test only. An adequate rule of thumb is that a doubling of fines and a 50% increase in pin chips can be attributed to the combination of tractor activity and pneumatic handling.

Biochemical deterioration is caused by a series of biological events that can heat the pile to a temperature that begins destructive chemical reactions.

Figure 19 Sources of fines generation. (a) Blowlines allow chips to be conveyed around existing equipment but the number and severe angles will break chips up; (b) wear plate or flat-backs should be replaced when worn rather than mended; (c) rubber-tired chip dozers cause less damage per pass than tracked dozers (d). However, high traffic in an area will degrade chip sizes for either type.

Table 1 Southern pine roundwood and residual chips transported through a 250-m blowline with six turns (sum of angles = 280 degrees)

Sample point	*Chip size classes*				
	+45 mm rh over length (%)	*+8 mm bar over thick (%)*	*+7 mm rh accepts (%)*	*+3 mm rh pin chips (%)*	*Passes 3 mm rh fines (%)*
Into the blowline	0.2	2.2	81.6	14.5	1.5
Out of the blowline	None	1.0	73.6	21.8	3.6

rh, round hole (the shape of the classifier tray openings).

Hardwoods deteriorate at least twice as fast as softwoods. This text refers to softwood chips only. Internal pile temperatures are hard to measure without laying wires in the pile as it is built. This is not feasible in normal mill operations, but useful in smaller-scale study piles. A dial thermometer with an extended stem (up to 75 cm) will allow grids of surface temperature to be established and monitored periodically. More simply, an experienced dozer operator knows when areas are heating up faster than normal and can take temperature readings. From studies, the internal temperature is 15–20°C hotter than the surface readings. Following the heating curves in **Figure 20**, the initial heating to about 40–50°C in the first 2 weeks is caused by the growth of bacteria, mold, and the respiration of living sapwood cells in the fresh chips. Further heating is determined by the pile height and the degree of compaction. If the pile height remains at about 15 m and tractor activity is kept to a minimum, the pile temperatures remain at or below 50°C. At 50°C, few molds, wood staining, and wood rotting fungi can survive. However, at this temperature, the acetyl group on cellulose molecules is cleaved off, freeing acetic and formic acid and heat. If the heat cannot escape because the pile is being compacted by dozer activity or more chips being added to the pile, pile temperature will move higher. The higher temperature and acid conditions make the acid forming reactions go faster. If the pile height is increased to 45–50 m and compaction increases with more spreading of new chips on the pile, the temperatures will reach 60–70°C. Further height and consequent compaction increases will bring the temperature to 70–80°C. As cellulose and lignin begin to acid hydrolyze, an autoxidation cycle is begun. At this point, further heating will be determined by the amount of compaction. If heat cannot escape due to the combined actions of tractor activity and increased pile height, the pile will be out of control. There is a high risk that an internal fire will be ignited as temperatures rise above 80°C.

Chips that have been degraded in pile storage by heat have lower pulp yield and strength. The degree of loss depends on the length of time the chips were exposed to temperatures over 65°C. Since mills rarely, if ever, track temperatures in enough detail to develop a time–temperature relationship, the results of samples taken as a degraded pile was dismantled might be useful. The first pulp property that falls off is tear: 10% loss of tear is common in piles stored for 4–6 months at 65–70°C. In those same conditions, burst and breaking length losses will be 1–3%. Pulp yield loss is from 1 to 5 percentage points (e.g., going from 54% to 49%). Badly deteriorated chips with a pH below 3 and a buffering capacity over 100 ml g^{-1} produce pulps at a 30–35% yield and with at least 50% strength loss.

Chip pile measurements Attempting to get the book and physical chip inventory values to agree is very difficult, if not impossible. The values that go into the equation vary quite a lot:

$$\text{Book inventory} = \text{physical inventory} + \text{physical losses} + \text{biochemical losses}$$

Below are the ranges of error in data that go into the equation from a number of studies and mill practice:

- Belt scale weights: 0.5–1% (with good design and maintenance)
- Truck scale weights: 1–2% (in the USA, there is a requirement for calibration and periodic, unannounced, spot checks to confirm accuracy)
- Surveyed pile volume (ground or aerial): 1–3%
- Bulk density (kg of wood per cubic meter of pile volume): as high as 25%
- Moisture content (sample and dry): 2–7%
- Moisture content (meter): 1–2%
- Losses (mechanical and biochemical): 25–50%.

Only a few of the measurements have low error ranges. The best numbers are the green weights from truck scales, moisture content, and the pile volumes from aerial or ground surveys. The errors are cumulative and usually result in unreliable estimates. Using these data results in periodic corrections when a pile is completely reclaimed. The adjustments can be positive or negative.

Better estimates of inventory can be obtained by investing in belt scales before and after chip pile storage.

Chip Quality Control

An important principle in establishing a quality control program is that if the data are not going to be used to make meaningful decisions, there is no reason to do the test at all. A corollary to this is: a testing program will produce meaningless data if samples are taken at the wrong location using incorrect methods.

Sampling tools need to be more than just a shovel gathering a bucket of chips anywhere you can easily get to the flow. The scoop should be large enough to allow oversize chips to be caught. The size of the sample should be only enough chips to do the testing required. This avoids the need to split the sample, a

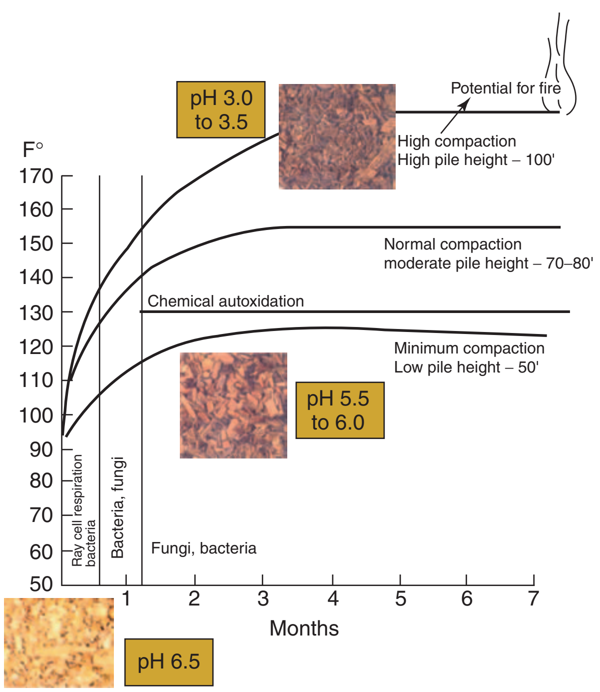


Figure 20 Conifer chip pile temperature profile. The rate of heating and the maximum temperature are primarily determined by pile height and compaction after the first 1–2 months. Initial heating is the result of rapid bacteria growth and respiration of the remaining living cells in the wood. Note the change in pH and color as the chips degrade from exposure to high temperature. The chips in the top photo easily break up into small particles.

process that introduces as much or more error as incorrect sampling. If special testing will require more than the normal scoop full, it is better to collect two scoop fulls and composite them for testing. If a barrel of chips is needed to send to a research laboratory, it should be gathered over a full day to avoid the risk of getting chips from one supplier or type of chip that is only a part of the total chip consumption.

After deciding what chip flows need to be sampled, sampling points must be located where they are safe to access, easy to get to, and allow a sample scoop to be inserted and so that chips can be gathered that represent the entire cross-section of the flow. Belt conveyor transfer points are an ideal place to do this. In most cases, there is access to the entire flow as it falls from one conveyor to the next. If not, a door can be cut in the hood. Access is preferable with the flow of chip coming toward the sampling point. The scoop is inserted upside-down, pushed all the way through the flow, turned over and quickly drawn out to take the sample from the entire depth of chip flow. A permanently mounted tube sampler replicates this sampling process. **Figure 21** shows several standard and tube sampling applications. There are other types of samplers that allow representative sampling of truck deliveries. Since installing samplers is almost always an add-on to existing systems, there are few that are alike. There are commercial samplers available that can be adapted to many situations.

A sample taken from the top of a moving belt or the top of a delivery truck or rail car will always contain fewer fines than a representative sample. As soon as chips are moved along a belt, in a rail car or truck bed, fines immediately begin to percolate downward. Similarly, a sample removed from the lower part of a rail car or chip trailer will be biased with more fines that have moved down the chip bed. Sometimes, a sample taken correctly at a transfer point is not representative. The likely cause is several types of chip flows joining together and one of them being loaded toward one side of the conveyor. The addition of cracked or conditioned oversize back into the accept flow often comes down a chute, depositing to one side of the belt.

The most widely used test methods to track woodroom and supplier quality performance are:

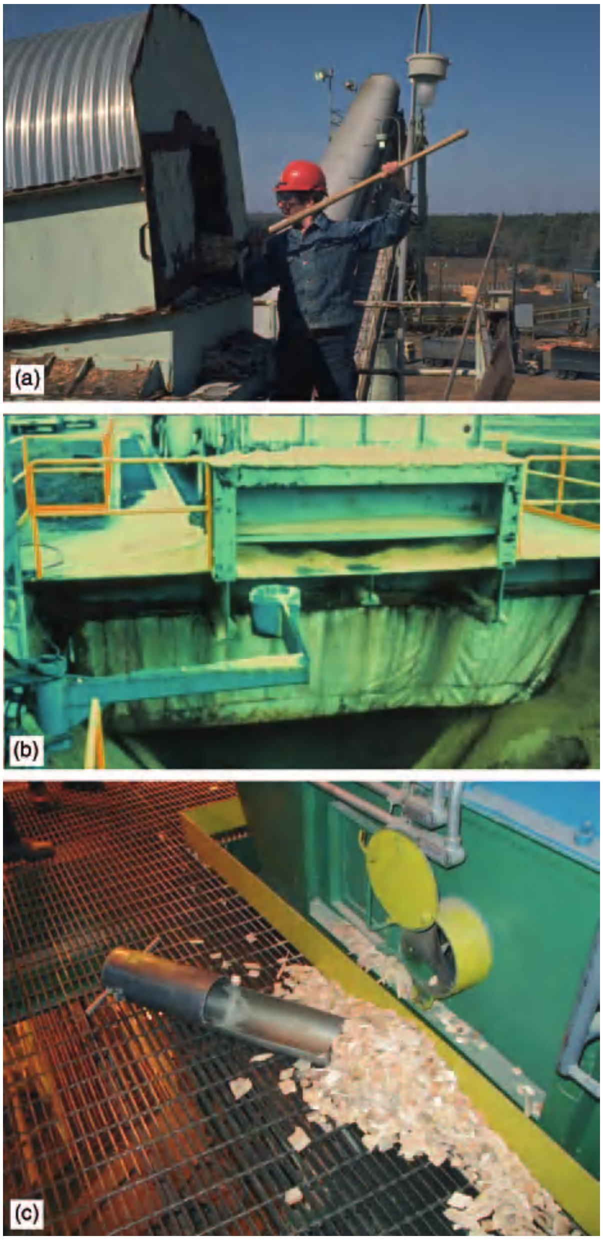


Figure 21 Options for chip sampling. (a) Manual sampling at a belt transfer point using a scoop sized to collect enough chips for the tests being done; (b) an automatic sampler using a bucket mounted on a swinging arm for truck dump sampling; (c) a tube sampler and sample port at a chip screen system to remove chips after screening.

1. Moisture content or %OD (percentage of oven-dry solids) solids. This is used to convert the green weight of chip deliveries to a dry weight. Moisture contents of sawmill and plywood plant residuals, woodroom production, and wood chipped thinnings can differ by as much as 15–20% points. Depending on the mix of wood being used, a pulp mill may be buying a lot of water at chip prices. Factors that influence the reliability of this test were listed earlier.
2. Bark content. The test is a tedious separation of all bark and wood. Optical methods of testing bark have not been successful. To speed the test up, some mills only measure bark in the accepts fraction. This underestimates the actual bark content since up to half of the bark breaks down into small pieces. The need for precise estimates is

diminishing as pulp bleaching technology has made headway in controlling pulp dirt associated with bark that was not removed in sawmill or woodroom debarking. A survey of mills confirmed that the specification for bark has been increasing in recent years from less than 0.5% to 1–2%.

3. Size distribution. There is no agreement on which testing machine and method should be used to describe the size variation in chips. There are two systems that are the most popular. One is currently sold under the trade name Chip Class. It was conceived as part of the Swedish pulping work that demonstrated the importance of thickness in kraft pulping. As shown in **Figure 22**, a series of trays are stacked on a table with linear motion. Each of the fractions has a different importance to the pulping process:

- Over length (retained on a 45 mm hole)
- Over thick (retained on bars spaced 8 mm apart)
- Accepts (retained on a 7 mm round hole)
- Pin chips (retained on a 3 mm round hole)
- Pan (passed through the 3 mm round hole)

An automated version of the Chip Class mounts the classifier trays in a hexagonal drum. The small fractions come out first and weights are accumulated and delivered in a final report by the system PC.

The Rader CC2000 classifier is based on thickness with the ability to separate pin chips and fines (**Figure 23**). Chips are fed into a rotating drum of movable bars. At the beginning of the test, the bars are 2 mm apart and thin chips are extracted. Automated balances weigh the amount of material leaving the drum as the space between the bars is increased in 2 mm increments up to 12 mm. A PC controls the cycles and calculates the percentage in each size classification. Several companies have adopted one or the other as standard size classification methods for their mills.

Figure 22 Chip Class classifier. The classifier next to the Chip Class is the Williams Classifier. It is the earliest classifier that the industry adopted as a standard. It is based on round holes only.

The most critical element of a chip quality control program is the technical staff. Training in test methods should go back to the written method rather than word-of-mouth training. In addition to doing the tests correctly, there must be training to recognize visually what chips should look like, and also to be able to see a problem before the test values are available. It is better to have this person out of the normal progression ladder because experience is vital to the success of a long-term testing program. The testing facilities should be designed specifically for chip testing with good light, heating control, office area for meetings and paperwork, room for all equipment, open area to lay out samples on the floor in sorting and displaying them, and located near the

Figure 23 Rader CC2000 classifier. (a) Two systems allow much more productivity from the chip testing laboratory; (b) like all instruments, it must be periodically cleaned and carefully calibrated.

Figure 24 Chip quality education tool. A display of chip quality definitions, impact on the mill, and real examples of each material type will help suppliers, truck drivers, and others who work with chips to understand the importance of chip quality. Customers of the pulp and paper products will appreciate this example of making chip quality a high priority. The one category missing in this display is emphasis on the requirement to eliminate contamination of chips with metal, plastic, dirt, and rocks.

woodroom. The chip testing position should never be near entry level and the lead tester should be part of the woodroom operating team.

A chip quality report should be more than a stack of computer printouts. In order to be able to see trends and changes, key data should be presented in graphs that are easily interpreted. The graphical reports should be made visible to everyone working in the woodyard and woodroom and discussed with suppliers. With the available spreadsheet graphics programs available, graphing of data should be standard practice. Visual displays focusing on aspects of quality should be developed so that those who deliver chips can know what they should look like, too (**Figure 24**).

Woodyard and Woodroom Safety

Woodyard safety is a critical function for every woodyard employee. Whenever in the operating area, personal protective equipment must be consistently used to reduce the risk of injury. The noise levels around operating debarking, chipping, and screening systems is well above the level that causes permanent hearing loss. Safety glasses with side shields are always needed to prevent wood dust and debris and flying objects from damaging eyes. Hard hats prevent injury from falling objects or head injury in areas with low headroom. When cleaning up dusty areas, respiratory masks will prevent inhalation of small wood particles that can accumulate in the lungs and cause long-term health problems. Some people are sensitive to the molds that grow in enclosed and damp areas such as conveyor tunnels. These people should not be assigned work in the contaminated areas. Equipment that is subject to high stress and impact loads need to be examined periodically. A logjam in the chipper infeed must be cleared to resume production. It is essential that no person place himself or herself at risk of falling into an operating chipper infeed at any time and particularly in this situation. Mechanical systems such as the one shown in **Figure 25** are invaluable in this instance. The rams are pushed in and out to dislodge the jammed logs. If no such device is installed on a chipper, the chipper must be stopped with the use of a disk brake and locked out and tagged out to prevent starting when workers are clearing the chute. Only then should woodroom operators get near the logs in the infeed to attach grapples attached to overhead winches. Log tongs should be attached with both a shackle and a restraining chain in the event the shackle breaks. Normal required lock-out and tag-out procedures are followed to return the chipper to service. Chipper knives are very sharp and should be handled with steel reinforced gloves.

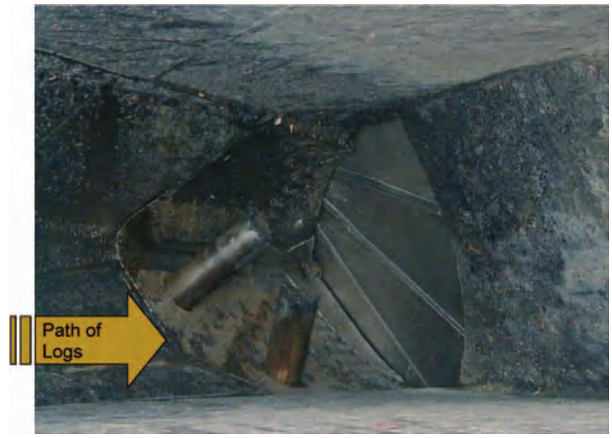


Figure 25 Rams that can be pushed into the chipper infeed to dislodge logs that sometimes frequently plug the spout. This is much safer than trying to break up the jam with pike poles or log tongs and takes less time.

Large mobile equipment and trucks used to transport, store, and reclaim logs and chips have limited visibility and even less in bad weather and at dawn and dusk. If two-way radio communication is possible in the mill, it is good to carry one while working in such hazardous areas. Sign-in and sign-out log sheets are also used to keep track of visitors and workers from other parts of the mill. A short, 10 to 15 minute, safety meeting of woodyard and woodroom operators at the beginning of the work period allows everyone on the crew to hear about special situations, like digging of a large ditch across a woodyard road, and identify and remedy hazards that were observed the day before. With everyone participating, prevention is a lot easier than the consequences of a serious accident.

See also: **Harvesting**: Wood Delivery. **Operations**: Logistics in Forest Operations. **Papermaking**: Overview. **Pulping**: Bleaching of Pulp; Environmental Control.

Further Reading

Fuller WS (1985) Chip pile storage – a review of practices to avoid deterioration and economic losses. *TAPPI Journal* 68(8).

Hartler N (1996) Achievement and significance of optimal chip quality. *TAPPI Journal* 79(2).

Hatton JV (1984) Quantitative evaluation of pulpwood chip quality. *TAPPI Journal* 60(4).

Isenberg IH (1980) *Pulpwoods of the United States and Canada*, 3rd edn. Volumes 1 – Conifers and Volume 2 – Hardwoods. Appleton, WI: Institute of Paper Chemistry.

Piggott RR and Thompson RA (1987) Drum debarking: key factors for design and performance. *TAPPI Journal* 70(8).

Mechanical Pulping

J H Cameron, Western Michigan University, Kalamazoo, MI, USA

Introduction

When mechanical action is the principal means for separating fibers from wood, the pulping processes are known as mechanical pulping, and the resulting pulps are mechanical pulps. This section contains descriptions of mechanical pulping processes, products, applications, limitations, and future prospects for mechanical pulps.

Mechanical pulping includes a large number of processes involving mechanical action or a combination of mechanical action and chemical pretreatments that separate fibers from the wood matrix. The main difference between mechanical pulping and chemical pulping is that, in mechanical pulping, the fibers are separated without removing the lignin, whereas in chemical pulping, the lignin is dissolved from the wood using chemicals. Mechanical pulps are characterized by high yield, high lignin content, and relatively stiff fibers that can be bleached to high brightness levels but that will photoyellow (darken) on exposure to light. The yield from the mechanical pulping processes ranges from as high as 98% for some groundwood pulps to about 85% for some of the chemimechanical pulps. In refiner mechanical pulping, the woodchips may be pretreated with chemicals either to reduce refiner energy usage or to help separate the fibers. Compared to chemical processes, the chemimechanical pulping processes remove only a small amount of the lignin in the wood. Since mechanical fibers are stiff and contain large amounts of lignin, these fibers form poor fiber-to-fiber bonds, which decreases sheet strength, but increases sheet opacity and bulk. Because of their high yield and low chemical consumption, these pulps are less expensive to produce and have less impact on the environment than do chemical pulps. The production of mechanical pulps worldwide is about 30% of the total virgin pulp production and is increasing because of its higher yield, lower cost, and less complex environmental concerns. On a per-country basis, the percentage of mechanical pulps ranges from 9.2% of virgin pulp in the USA to 45% in Canada and 62% in Germany.

Usage

The major use of mechanical pulps is in nonpermanent (grades that do not require permanent lightfastness) printing grades. Mechanical pulps are historically used in the following grades: newsprint (newspapers, paperbacked books, magazines), supercalendered magazine (catalogs), and coated mechanical and coated fine paper (commercial printing grades). Depending on the strength properties of the mechanical pulp, newsprint usually contains from 80% to 100% mechanical pulp, with the remainder being chemical pulp added to increase sheet strength. In addition to the nonpermanent printing grades, mechanical pulps are also used in a wide variety of other paper products, including board and tissue/towels. A short description of the major applications for mechanical pulp is presented here.

Newsprint

The quality parameters for newsprint are runnability (low frequency of breaks during printing) and printability (smoothness, opacity, brightness, ink pickup, and strikethrough). Traditionally, newsprint furnishes consist of 80–85% stone groundwood with the remaining fiber being lightly bleached kraft. The groundwood provides high bulk, high opacity, and good ink receptivity, while the kraft provides resistance to cross-machine tear.

Supercalendered Magazine

This grade is usually manufactured with mechanical pulp (typically 70% of the fiber), chemical pulp (30% of the fiber), and a high level of filler, typically 20–30%. These papers are printed using gravure and offset printing processes, which require good smoothness, ink receptivity, and high opacity, all provided by the mechanical pulp. The high level of filler reduces sheet strength, requiring a relatively high level of long fibers, usually softwood kraft.

Coated Papers

One of the most important coated grades is lightweight coated (LWC), used in gravure and offset printing. This grade normally contains 50–70% mechanical pulp with the remaining fiber being chemical pulp and up to 17% filler. These papers have low basis weights (less than $40\,g\,m^{-2}$ for the base sheet), which require a relatively high level of chemical pulp.

Other Products

Fine printing and writing papers are normally classified as wood-free (free of mechanical pulp), but will tolerate as much as 10% mechanical pulp. The mechanical pulp increases opacity, bulk, and printability. Since mechanical pulps are stiff, they are added to the middle layers of multiple-layer board grades. Because of their high bulk, resiliency, and low cost, mechanical pulps are also added to tissue and towel furnishes.

Historical Background

Before 1800, books were printed on handmade paper produced from many different fibers, principally flax before the invention of the cotton gin. With the invention of the cotton gin by Eli Whitney in 1793, cotton gradually replaced flax as the principal papermaking fiber. The first successful use of wood fiber as a paper stock was groundwood in the early 1840s. Fredrich Keller of Hainchen, Saxony and Charles Fenerty of Springfield, Nova Scotia are independently credited with the invention of groundwood pulping. Fredrich Keller, a bookbinder, apparently started experimenting with pressing wood against a grinding wheel with running water after reading about the shortage of rag fibers. By the mid-1840s, he had developed his groundwood process such that newspapers were printed using groundwood. In 1846, Keller sold his invention to JM Voith of Heidenheim, Germany and the first commercial grinders were installed in a mill in 1852. Fenerty, the credited co-inventor, operated a sawmill in Nova Scotia, and pursued groundwood experiments by pressing wood against a grinding wheel. However, after writing to the Halifax newspaper describing his invention, Fenerty did not further pursue the concept.

Mechanical Pulping Processes

From the starting point of pressing wood against a grinding stone with running water, a large number of mechanical pulping processes have been developed. The more important of these are listed here:

- Groundwood (GW): produced by pressing wood against a wet grinding surface.
- Pressurized groundwood (PGW): similar to groundwood but at a temperature of 100°C, which generates steam pressure.
- Refiner mechanical pulp (RMP): plate refining of wood at atmospheric pressure and no chemical treatment.
- Thermorefiner mechanical pulp (TRMP): the wood chips are heated with steam before refining at atmospheric pressure.
- Thermomechanical pulp (TMP): the wood chips are presteamed and fiberized at temperatures above 100°C. After fiberizing at high temperature, the fibers are often further treated by refining at atmospheric pressure.
- Pressure thermomechanical pulp (PTMP): like TMP, but with both refining stages being pressurized.
- Chemical mechanical pulping (CMP): the chips are treated with chemicals before refining at atmospheric pressure.
- Chemithermomechanical pulp (CTMP): chemicals are added prior to fiberizing at temperatures above 100°C.

Mechanical Pulp Properties

Mechanical pulps are produced from many different tree species using several different mechanical pulping processes. These pulps are incorporated into a large number of furnishes for use in a variety of paper products. The characteristics of the pulps depend on the tree species, the mechanical separation process, and the treatment steps following mechanical pulping. The papermaker incorporates specific mechanical pulps into paper furnishes to produce the desired characteristics. In general, mechanical pulps provide good sheet formation, increase sheet bulk, increase sheet absorption, increase sheet opacity, and increase sheet resiliency, but reduce sheet strength. Many of these properties, such as resiliency and bulk, are important for the impact printing processes. The lower strength results from the high lignin content of these pulps, which reduces the surface area available for bonding and reduces the fiber flexibility, thus decreasing the relative bonded area. A major reason why mechanical pulps are not used in permanent grades is that they photoyellow (darken) on exposure to light. One needs to recognize that mechanical pulps differ greatly in their characteristics, and they must be used with knowledge of how the various types will affect the furnish and product properties.

General Process Objectives

Groundwood and Pressurized Groundwood

GW is produced by pressing bolts (debarked short-logs) against large rotating grindstones. Today, the grindstones are artificial stones made from silicon carbide or aluminum oxide abrasives with a fused bonding agent. They are typically 1.5 m in diameter and driven by 2000–4000-kW motors. The grit on the stone surface rapidly becomes rounded and the fibers are separated through a series of compression–decompression pressure pulses. **Figure 1** illustrates a representative grinder and shows the key grinder elements. The bolts are fed in a pressurized magazine to the grinding stone. Since the stone gradually wears, an online lathe is periodically used to sharpen the stone. The separated fibers are washed from the stone into the pit with grates controlling the size of the fiber bundles allowed to pass out of the wood magazine.

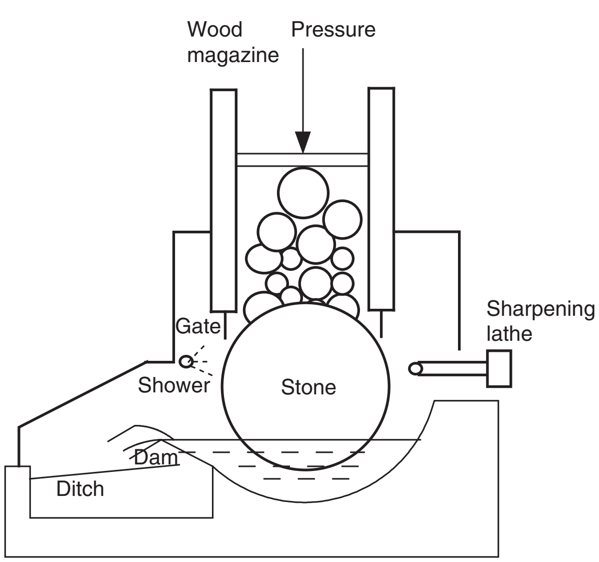


Figure 1 Representative grinder for groundwood production.

Low-density woods, because of their thin fiber wall and relatively large lumens, are good candidates for GW processes. These low-density species tend to be northern species because of the greater predominance of springwood with its thinner fiber walls. The flexing of the fiber walls allows the wood to absorb the compression–decompression, which results in fiber separation. With high-density woods, such as southern pines, the compression–decompression forces are not absorbed by the flexing of the fiber walls, and the fibers are cut rather then separated, resulting in poor pulp quality. Water washes the pulp from the grindstone and keeps the grindstone clean.

Having low density and relatively white color, spruce and fir are commonly used for pulp in newsprint, and in nonpermanent printing grades, while aspen is used in the base sheet of coated mechanical grades. Since these species are found at northern latitudes, Canada produces a high percentage of the GW pulps.

In PGW, the pressure is controlled using compressed air, enabling temperatures as high as 140°C to be reached. This increased temperature softens the lignin between the individual fibers, resulting in better fiber separation and improved strength properties. At high temperatures (typically above 160°C), there is a risk that lignin will become fluid and coat the fibers, which reduces fiber bonding and sheet strength.

Refiner Mechanical Pulp, Thermomechanical Pulp, Pressure Thermomechanical Pulp Processes

Refiner pulping uses two disks marked with bars radiating outward: usually one disk rotates (rotator) and one remains stationary (stator). Before refining, the wood is debarked and chipped. The wood chips enter at the center of the disk and are forced toward the perimeter of the refiner. The disk rotates at high speeds, typically 1500–2000 rpm, exposing the wood chips to a series of compression and decompression stages as the chips are forced from the center to the perimeter of the disks. Normally two refining stages are employed. The first stage operates at a consistency of about 30% and separates the fibers from the wood (fiberizing); the second stage operates at a consistency of about 10% and improves the paper-making properties of the fibers (refining).

TRMP and TMP are modifications of RMP, with TMP being the dominant RMP process. With thermorefiner pulping, the wood chips are heated with steam but are refined at atmospheric pressure. With TMP, the chips are presteamed at atmospheric pressure and then screw-fed to pressurized refiners. Both refining stages are usually pressurized and operate at pressures from 3 to 5 bars and temperatures from 140 to 160°C. The higher temperatures provide easier fiber separation and result in an increase of about 50% in paper strength at the same freeness and same total refiner energy relative to RMP.

RMP processes offer several advantages over GW and PGW processes. These include the ability to refine wood residues, including sawdust, less staffing requirements, and the ability to use lower-quality woods.

Chemical Mechanical Pulping and Chemithermomechanical Pulping

In these processes, the wood chips are treated with chemicals before the fibers are mechanically separated in the refiner. Compared to chemical pulping, the chemical treatment in these processes is very light, and the yield typically ranges from 80% to 95% compared to the yield of 45–50% in the chemical pulping processes. The objective of the chemical pretreatment is not to remove the lignin, as would be the case in chemical pulping, but to aid in the mechanical separation of the fibers in the refiner. Among the benefits of the chemical pretreatment are improved fiber properties, whose properties are between those of RMP and chemical pulping, and reduced refiner energy. Although the major reason for the chemical pretreatment is improved fiber properties, it is common to treat the wood chips simply to reduce the required refiner energy.

CMP consists of treating the wood chips with sodium sulfite (2–4% on oven-dried wood basis) in the case of softwoods and sodium sulfite (0–4%) plus sodium hydroxide (1–7%) in the case of hardwoods. Few hardwoods, the exceptions being aspen and popular, can be mechanically refined without the addition of chemicals. Sodium peroxide, which bleaches the pulp and allows higher hydroxide levels to be used, can be added in combination with the sodium hydroxide and sodium sulfite. The cold process, used for some of the denser hardwoods, employs sodium hydroxide without sodium sulfite. The wood chips are refined at atmospheric pressure, and the temperature is held relatively low (70–80°C), with higher temperatures resulting in darker wood.

In chemithermomechanical refining, the wood chips are presteamed with chemicals at temperatures above 100°C, followed by first-stage refining above 100°C and atmospheric second-stage refining. CTMP and TMP are the most widely used mechanical refining processes.

Postprocessing of Mechanical Pulps

Refining of Fiber Rejects

Since only part of the wood is separated into fibers during the first mechanical pulping stage, the fiber bundles must be separated from the fibers and further refined. The separation process consists of a series of screens and centrifugal cleaners. In addition to separating the fiber bundles (sieves), course fiber, sand, and other inorganic materials are removed at this stage. The screens and cleaners are arranged in cascade sequence, such that the amount of material to be disposed is minimized. The fiber rejects from the screens and cleaners consists of fiber bundles and course undeveloped fibers; these are further refined at either low consistency (3–5%) or at high consistency (30–50%) in a single-disk refiner. High consistency increases the refining intensity and normally produces superior fiber properties.

Bleaching of Mechanical Pulps

While increasing brightness is the bleaching objective for both mechanical and chemical pulps, the means through which this is accomplished are significantly different. With chemical pulps, bleaching is accomplished by removing the lignin remaining in the pulp after chemical pulping and brightening the other pulp constituents. This is often referred to as true bleaching. With mechanical pulps, bleaching is accomplished by brightening the color-containing compounds (chromophores), which are primarily lignin structures.

Pulp brightness is dependent on wood species, wood storage, the pulping process, and the bleaching process. There are considerable color differences between wood species and between sapwood and heartwood. For example, loblolly pine (*Pinus taeda)* has a typical brightness of 50%, while black spruce *(Picea mariana)* has a typical brightness of 67%. The cellulose and hemicelluloses are almost colorless and contribute little to mechanical pulp's color. While the extractives are yellow and reduce brightness, they are present at relatively low levels. Since lignin is present at high levels and is dark in color, it is the primary compound responsible for the darker color of mechanical pulps.

Wood will darken during storage, with unbarked logs darkening more than debarked logs. Although some of this darkening can be removed by bleaching, the final pulp will almost always be darker in color. To preserve brightness, unbarked logs have been stored underwater. Another reason for darkening of mechanical pulp is the condensation of colorless phenolic groups that form color compounds when they condense, a development that is accelerated at the high temperatures used in some of the mechanical pulping processes.

Some of the mechanical pulps, such as those produced from black spruce, have a high enough initial brightness for use in some applications, such as newsprint, without brightening. Other mechanical pulps need to be bleached because the processes and species used for their production result in low brightness levels, or because the product requires a higher brightness level.

Both reductive and oxidative bleaching are used with mechanical pulps. The objective of bleaching mechanical pulps is to convert the chromophores nonlight-absorbing compounds – to brighten the pulp. In addition to brightening the pulp, bleaching also reduces the extractive content of the pulps. The reductive agents include sodium dithionite–sodium hydrosulfite ($Na_2S_2O_4$), sodium bisulfite ($NaHSO_3$), formamidine sulfininc acid (FAS HO_2S-CNH-NH_2), and borohydride; and the oxidative agents include hydrogen peroxide (H_2O_2), sodium hypochlorite (NaOCl), and ozone (O_3). Of these bleaching agents, the most common are sodium dithionite and hydrogen peroxide.

Peroxide Bleaching

Both high pulp consistency and high pH increase the brightness levels that can be achieved with peroxide bleaching. Therefore the consistency is normally adjusted to 15–20% and the pH to about 11.5. There is an increase in brightness with increasing peroxide dosage up to a peroxide dosage level of about 4% based on (OD, % oven dried, ISO 287) pulp. Brightness increases of about 15 points, (% ISO), can be achieved with 4% addition of hydrogen peroxide.

Dithionite Bleaching

Sodium dithionite bleaching is usually performed at a pH of 6.0–6.5 and at 8–12% consistency. The normal dosage levels are from 0.5–1.0% and result in a four- to eight-point increase in brightness. An addition level of 2.0% sodium dithionite on OD pulp increases the brightness by about 10 points, % ISO.

Two-Stage Bleaching

The bleaching effects of peroxide and dithionite tend to be additive and two-stage processes are in operation. These consist of a medium peroxide stage followed by sulfur dioxide or sodium bisulfite acidification of the pulp to destroy the residual peroxide, thickening to high consistency and dithionite bleaching. Brightness gains from 15 to 20 points are achieved with two-stage processes.

Transitional Metal Ion Removal

A key variable in mechanical pulp bleaching is the presence of transitional metal ions, such as iron or magnesium. These ions catalyze the decomposition of both hydrogen peroxide and sodium dithionite. In addition to decomposing the bleaching agents, they also accelerate color reversion of the bleached pulp. Transitional elements need be avoided by using evaporator condensate in the bleaching plant or by the use of chelating agent, the most common being either ethylenediaminetetraacetic acid (EDTA) or diethylenetetraminepentaacetic acid (DTPA).

Color Reversion of Mechanical Pulps

Color reversion, either photoyellowing or thermal darkening, is the most significant hindrance for further acceptance of mechanical pulps. The optical and strength properties of CTMPs are sufficient for use in most printing paper grades. Unfortunately, CTMP darkens during storage or on exposure to light (photoyellowing). Photoyellowing of lignin-containing paper can lead to a brightness decrease of more than 30 points in a short time (6–8 months) compared to only a 3-point decrease with kraft pulp. Although wood pulps may be bleached to various brightness levels, all pulps diminish in brightness with age. Brightness reversion has been studied with various high-yield pulps, such as GW, TMPs, and CTMP. Progress on extending the brightness of high-yield, lignin-containing pulps has come slowly. Although many techniques for reducing color, including free radical scavengers (such as ascorbic acid), ultraviolet absorbers or chemical modification of the chromophores have been proposed, there is no accepted commercial process for eliminating or reducing color reversion of mechanical pulp.

Mechanical Pulp Properties

Fiber properties depend on the pulping process and type of wood, and are influenced by the species, percentage of juvenile wood, and the earlywood (springwood) to latewood (summerwood) ratio. The fiber properties that are considered the most important in determining paper properties are fiber length, cell wall thickness, and juvenile wood percentage. In comparing mechanical pulps to chemical pulps, mechanical pulp fibers are stiffer, shorter, and contain a higher level of lignin than do chemical pulps. In comparing the different mechanical pulping processes, CTMP and TMP bond better than do GW or RMP. Therefore, less chemical reinforcing pulp is required with TMP and/or CTMP than is required with GW. Conversely, the incorporation of GW would increase light scattering more than TMP or CTMP.

The Future

Mechanical pulp usage is expected to increase by about 4% per year. The current trend of decreasing fine paper basis weight is expected to continue, leading to increased use of mechanical pulps for their high opacity and bulking attributes. These changes will likely increase the need for strength and brightness of mechanical pulps. This, together with the need to decrease the electrical refining energy, will result in more complex mechanical pulping processes with new pretreatments to decrease energy usage and improve the fiber properties. The strength properties of mechanical pulps will continue to improve, decreasing the need for chemical pulps in nonpermanent printing grades. Recycled fiber, which can be produced with less energy than mechanical pulps and can replace mechanical pulps in many of the current grades, is the principal competition to mechanical pulping. The continual growth of recycled fiber may constrain the growth of mechanical pulps.

See also: **Packaging, Recycling and Printing**: Packaging Grades. **Papermaking**: Overview; Paper Grades; Paperboard Grades; The History of Paper and Papermaking; World Paper Industry Overview. **Pulping**: Fiber Resources.

Further Reading

General Paper Manufacture – Mechanical Pulps

Casey JP (1980) *Pulp and Paper Chemistry and Chemical Technology*. Chapter 4 – Pulping. New York: John Wiley.
International Mechanical Pulping Conference Proceedings. (1985, 1987, 1991, 1993, 1995, 1997, 1999). Atlanta, GA: TAPPI.
Kappel J (1999) *Mechanical Pulps: From Wood to Bleached Pulp*. Atlanta, GA: TAPPI Press.
Leask RA and Kocurek MJ (1987) *Pulp and Paper Manufacture*, vol. 2. *Mechanical Pulping*, Atlanta, GA: TAPPI Press.
Peel JD (1999) *Paper Science and Manufacture*. Vancouver, BC, Canada: Angus Wilde.
Sundholm J (1999) *Papermaking Science and Technology*, vol. 5. *Mechanical Pulping*. Helsinki, Finland: Finnish Paper Engineers' Association and TAPPI.

Color Reversion of Mechanical Pulps

Dence CW and Reeve DW (1996) *Pulp Bleaching – Principles and Practice*. Section III: The chemistry of bleaching and brightness reversion. Atlanta, GA: TAPPI.
Heitner C and Schmidt J (1991) *Light-Induced Yellowing of Wood-Containing Papers – A Review of Fifty Years of Research*. *Proceedings of the 6th International Symposium on Wood and Pulping Chemistry* vol. 1, pp. 131–149. Melbourne, Australia.

Bleaching of Mechanical Pulp

Dence CW and Reeve DW (1996) *Pulp Bleaching – Principles and Practice*. Section V: The technology of mechanical pulp bleaching. Atlanta, GA: TAPPI.

Chemical Pulping

R G Aravamuthan, Western Michigan University, Kalamazoo, MI, USA

Introduction

Pulping processes reduce wood or any other fibrous raw material to a fibrous mass. Chemical pulping essentially dissolves the noncellulosic components in wood, mainly lignin, and thereby liberates the fibers. This process, also known as 'delignification,' centers around the removal of ligneous binding material, but, in the process, certain hemicellulosic as well as cellulosic components are dissolved. Once the pulping process becomes less selective (in the removal of lignin as compared to cellulose and hemicellulose), the process is stopped; further processing of pulp proceeds via extended delignification and bleaching processes. Although the bleaching process is intended to bleach the 'brown' unbleached pulp into bright white pulp, the initial stages in a multistage bleaching process are more aptly called delignification since they essentially contribute to additional and preferential lignin dissolution.

In a chemical pulping process, upwards of 80% of wood lignin is removed with some concomitant carbohydrate (mainly hemicellulose and some cellulose) dissolution. The overall yield of pulp in this stage can be expected to be around 50% of the original wood. Further delignification cannot be effectively carried out by conventional pulping chemicals and is hence left to bleaching chemicals.

Two major chemical pulping processes are sulfite pulping and kraft pulping. Sulfite pulping can be carried out at different pH levels with different bases – calcium at low pH (1–2), magnesium (3–5), and ammonium and sodium over the entire range of pH. The pH levels used in sulfite pulping cover the entire range of 1–13 (1–2, acid sulfite; 3–5, bisulfite; 5–7 neutral sulfite (semichemical) – NSSC; 9–13, alkaline sulfite). On the other hand, kraft pulping is a distinctly alkaline process and works in the range of pH 11–14, using the cooking chemicals of sodium hydroxide and sodium sulfide (the reactive species being the hydroxide and hydrosulfide ions).

History

The first commercial sulfite pulp was used in 1874, while the kraft process was commercially used almost a decade later (1885). However, the superior strength properties obtained by kraft pulp came to be recognized early in its development and many soda mills (using only sodium hydroxide) converted to the kraft process to compete with the sulfite mills. Around 1930, with the introduction of the Tomlinson recovery furnace, the kraft process gained favor over the sulfite pulp mills. The one major disadvantage of the alkaline processes (kraft or soda) was overcome with the use of powerful bleaching agents like chlorine, chlorine dioxide, and other chlorine compounds.

Sulfite pulp mills, until 1951, were mainly using calcium base without any efficient chemical recovery system. Sulfite mills, not to be left behind, began to use more powerful bases such as magnesium, sodium, and ammonium that could be used under less acid cooking conditions and were amenable to efficient recovery systems. With the advent of chlorine dioxide as a pulp bleaching agent in the 1950s, the last advantage of sulfite pulps over kraft pulps – specifically, higher brightness and/or better bleachability – was overcome by kraft pulps.

By 1990, the world annual pulp production from sulfite mills was only about 8% and the kraft pulping process had become the leading chemical pulping process. Recent investments in sulfite pulp mills have come in the form of the development of alkaline sulfite processes and the introduction of pulping additives such as anthraquinone, which has been very successfully applied earlier in the alkaline processes – kraft and soda.

On the other hand, in the kraft pulping process, current modifications center on continuous process improvements to improve the yield and selectivity of delignification in the final stages, alleviating the environmental impact of the process, and designing a better recovery system.

Sulfite Pulping

The sulfite pulping liquid is prepared by absorbing sulfur dioxide (prepared by burning sulfur with a controlled excess of oxygen and quickly cooling the product gas to around 200°C to prevent further oxidation to sulfur trioxide) into different bases. The reactions are:

$$SO_2+H_2O \rightarrow H_2SO_3 \quad (1)$$

$$CaCO_3+H_2SO_3 \rightarrow CaSO_3+CO_2+H_2O \quad (2)$$

$$CaSO_3+H_2SO_3 \rightarrow Ca(HSO_3)_2 \quad (3)$$

The sulfite pulping terminology can be explained by equation 3. H_2SO_3 is true free SO_2; since $Ca(HSO_3)_2$ leads to one-half $CaSO_3$ and one-half H_2SO_3, free $SO_2 = H_2SO_3 + 1/2\ HSO_3^-$ and combined $SO_2 = SO_3^{2-}$ and $1/2\ HSO_3^-$. The absorption product is later fortified by additional SO_2 absorption from digester relief gases under higher pressure. A higher percentage of free SO_2 is formed with a calcium-based liquid compound, compared to other bases. The effectiveness of sulfite pulping depends on the diffusion of SO_2 and the base ion into the wood. The diffusion process is helped by monovalent ions like Na^+ and NH_4^+ as well as higher pH. Lack of such diffusion leads to polycondensation and dark pulp ('burnt chips'). Any process that hinders such diffusion, like crushed chips from blunt chipper knives, leads to burnt cooks. The acid sulfite pulp with Ca as the base conducted under low pH is more susceptible to such problems. A slow heating period, relatively long cook time, and a low cooking temperature (130°C) are characteristic of acid sulfite cooks. In addition, the acid sulfite cooks are not amenable to woody materials with resins such as Douglas fir or pines. In the case of monovalent bases, due to more rapid penetration and lower free SO_2, faster heating times, higher temperatures, and shorter cooking times can be achieved.

Delignification is achieved by the formation of lignosulfonic acids, which become soluble in the presence of base. In addition, the lignosulfonic acid undergoes cleavage into lower-molecular-weight fragments to make them soluble. The process also leads to acid hydrolysis of hemicelluloses, which are then dissolved. This hemicellulose dissolution is sometimes taken advantage of in making hemicellulose-free pulps which are needed for dissolving grades.

To aid in more complete delignification and better hemicellulose retention and/or to increase the species-friendliness of the process, several two-stage sulfite processes have been tried with an acid pH (3–4) in the initial stage followed by neutral (6–6.5) stage (magnefite process) or alkaline pH conditions (pH 9–10 in Sivola process) in the subsequent stage. Complementary processes starting with high pH (5–6) in the initial stage followed by low pH (1.5–2 in two-stage acid and 3–4 in Stora process) in the second stage are also in vogue.

As explained earlier, the future of the sulfite process on a large scale does not seem bright, though special sulfite pulping systems like NSSC (high-yield pulp), sulfite treatment in chemithermomechanical pulping (CTMP), sulfite-AQ process or alkaline sulfite with anthraquinone and methanol (ASAM) may hold their own in specific niche markets.

Sulfite pulps find their market in bond and writing or reproducing papers that require good formation but only moderate strength and in tissues where softness, bulk, and absorbency are the main characteristics. Sulfite pulps are also used to produce grades such as greaseproof and glassine that need pulps with high hemicellulose content due to its relative ease of delignification.

Kraft pulping

The kraft process uses the cooking chemicals of NaOH and Na_2S and an excellent chemical recovery process. The make-up chemical is provided in the form of sodium sulfate (hence the name sulfate process) or salt cake. The sodium sulfate is reduced in the chemical recovery furnace to Na_2S and the other sodium components are converted to Na_2CO_3. The Na_2CO_3 is converted in the causticizing cycle to NaOH by the use of lime. The lime itself is regenerated by calcining the $CaCO_3$ formed in the causticizing reaction. The various reactions are as given below:

$$Na_2SO_4 + 4C \rightarrow Na_2S + 4CO \text{ (reduction}-\text{furnace)} \quad (4)$$

$$Na_2CO_3 + CaO + H_2O \rightarrow CaCO_3 + 2NaOH \text{ (causticizer)} \quad (5)$$

$$CaCO_3 \rightarrow CaO + CO_2 \text{ (lime kiln)} \quad (6)$$

The cooking liquid thus consists of NaOH, Na_2S, and other inerts (Na_2SO_4, Na_2SO_3, etc.) as well as unconverted Na_2CO_3. The effective cooking species is not Na_2S but NaHS, generated as follows:

$$Na_2S + H_2O \rightarrow NaHS + NaOH \quad (7)$$

Hence, in the cooking liquor, NaOH + one-half Na_2S is known as effective alkali and NaOH + Na_2S is known as active alkali. Other terms that are used in kraft cooking are causticity (NaOH/NaOH + Na_2CO_3) and sulfidity (Na_2S/Na_2S + NaOH). Sulfidity has an important role to play in kraft cooking in that HS^- helps in breaking specific lignin bonds and hence in delignification. The extent of sulfidity is also found to influence the transition point between bulk and residual phases of delignification. Higher sulfidities also help to preserve cellulose viscosity during cooking.

Process Cycles

On the whole, the kraft pulping process consists of two cycles (**Figure 1**): (1) pulping/cooking liquor cycle, and (2) causticizing and lime cycle. The pulping of wood chips is done with white liquor containing the active chemicals (NaOH and Na_2S). The residual black liquor, consisting of reaction products of lignin and solubilized carbohydrate moieties, is then evaporated and burnt in the recovery furnace. The inorganic smelt (Na_2CO_3 and Na_2S), dissolved in water or weak white liquor and called green liquor, is then causticized to convert the Na_2CO_3 to NaOH to reform the white liquor. The causticizing and lime cycle, as explained earlier, uses quick lime to convert Na_2CO_3 to NaOH, which generates calcium carbonate (lime mud). The lime mud is washed, filtered, and pressed, and then burnt in a lime kiln to regenerate CaO to be used in the causticizing cycle.

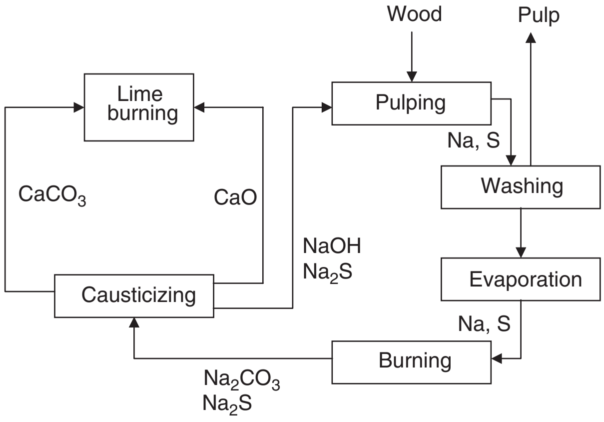


Figure 1 The kraft process.

Batch and Continuous Processes

The kraft cooking process is conducted either in batch or continuous digesters, with some small process variations. In batch cooking, the digester is packed with wood chips and liquor, and the contents are heated up according to a predetermined schedule with direct or indirect steam, usually with forced circulation through the aid of liquor circulation pumps that can turn over the liquid contents of the digester about once every 10 min. The maximum temperature in a kraft cooker is between 160 and 175°C and the cooking time is adjusted to obtain a particular yield or delignification. Cooking time is also adjusted for any variations in the actual process temperature. After cooking, the pulp is discharged into a blow tank wherefrom the blow vapors are passed on to heat recovery systems via accumulator and heat exchangers. The heating-up period in the bath digester allows for impregnation, which is aided by the alkaline nature of the cooking liquor. The capillary penetration of chemicals in a longitudinal direction is six times that of diffusion of chemicals in a radial direction (across the fiber wall).

In a continuous digester, the chips are first passed through a steaming vessel where air and other noncondensables are purged. This helps give better penetration of chemicals into chips. Hence, chip thickness is also an important variable in kraft pulping and leads to fewer screen rejects. However, it is not as critical as in sulfite pulping. The preheated chips and the liquor then enter the continuous digester where they move through different zones – impregnation, heating, cooking, and washing. Each of these zones is maintained at different temperatures and finally the pulp is discharged at the bottom of the digester at a comparatively cooler temperature of around 80°C.

The auxiliary components required for a continuous digester, although more complex than those for the batch digesters, are of lower capacity due to constant leading. The equipment itself is more compact and requires less space. Also, there is better energy recovery and reuse, leading to less steam requirement. However, one major advantage of the batch system is that it offers greater operating flexibility and ease of start-up and shutdown. Also, more efficient turpentine recovery is achieved from batch digesters due to the scheduled relief gas flows throughout the cooking cycle. Grade change or species change in a continuous digester should be planned ahead to reduce variations in product quality. Some of the recent improvements in batch digester systems, such as rapid displacement heating, lead to better heat recovery and reuse in bath systems. The computer control systems that are available for batch digesters have reduced the fluctuations in steam demand from batch units ('resource leveling').

Lignin Reactions

The chemicals that penetrate into fiber lumens and diffuse into fiber walls react with lignin through OH^- and HS^- and break major lignin bonds. The fragmented lignin is then dissolved. In the latter parts of the cooker, the lignin fragments in solution can take part in condensation reactions and be readsorbed on the fiber surfaces, resulting in dark cooks. HS^- reduces the possibility of such condensation reactions by blocking some reactive groups. Along with lignin, some of the carbohydrate is removed during the cooking process. The carbohydrates are susceptible to primary and secondary alkaline 'peeling' and alkaline hydrolysis reactions. In a typical kraft cook, about 80% of lignin, 50% of hemicelluloses, and about 10% of cellulose can be brought into solution.

The delignification reactions proceed in three distinct phases — initial, bulk, and residual. Kraft cooks are typically terminated at the end of the bulk delignification phase, since delignification slows down in the residual phase and condensation reactions increase. Also, during the residual phase, the carbohydrate reactions continue, leading to the loss of viscosity and strength in pulp. The effective result is a dark and hard-to-bleach pulp with lower strength properties. The delignification rate reactions in the three phases can be represented by the following equation:

$$-\mathrm{d}L/\mathrm{d}t = kL^a[\mathrm{OH}^-]^b[\mathrm{HS}^-]^c \qquad (8)$$

Thus, the delignification rate depends on the extent of the remaining lignin and the activities of the reactive species. The delignification kinetics is of first order with respect to lignin ($a = 1$); the values of b and c vary with the phases of delignification (**Table 1**).

Thus, the initial phase of delignification, in which there is rapid lignin removal, is independent of HS^- and OH^- and is characterized as an extraction process. This phase is diffusion-controlled with low activation energy of 40 KJ mol^{-1}. This stage removes approximately 20% of the lignin, while the bulk stage removes upwards of 60% of the lignin – mostly after major lignin bonds are broken. Delignification in the bulk stage depends on both OH^- and HS^-, while the residual-stage delignification depends only on OH^-. However, in the residual stage, OH^- is bound to be low and cooking is hence stopped at this point to avoid the effects of condensation previously mentioned.

The bulk stage of delignification has been extensively studied and it has been found that the reaction rate constant k follows the Arrhenius equation, $k = k_0 e^{-E/RT}$, where the activation energy E is about 135 kJ mol^{-1}. The kraft cooker is often controlled on the basis of H-factor, which is the relative reaction rate integrated over time. The relative reaction rate is defined as k/k_{100} and by an arbitrary assignment of a value of 1 for k_{100}. Under these conditions, the relative reaction rate is given by exp $(43.2 - 16.113/T)$ where T is the temperature in Kelvin scale. Extensive relative reaction rates have been tabulated for temperatures spanning the heating

Table 1 Values of b and c

	Initial phase	*Bulk phase*	*Residual phase*
b	0	0.7	0.7
c	0	0.4	0

and cooking range and the H-factor for any cooker is calculated on the basis of the measured temperature–time profile of a kraft cooker. The variance in relative reaction rates with temperature is a measure of relative delignification rates at a specified concentration (activity) of the reactive species.

Carbohydrate Reactions

Similar reaction rates have been determined for carbohydrate reactions in kraft cooking with two main differences: (1) activation eenergy of cellullose chain cleavage is 179 $\mathrm{kJ\,mol^{-1}}$ (42.78 $\mathrm{kcal\,mol^{-1}}$); and (2) cellulose chain cleavage in all three phases only depends on OH^-

$$-(\mathrm{d}c/\mathrm{d}t) = kc^a[\mathrm{OH}^-]^b\ c \quad \text{where } a, b = 1 \qquad (9)$$

throughout the cook. A factor similar to H-factor, defined for cellulose cleavage, is G-factor. The relative effect of temperature on the G-factor is much higher than in the case of the H-factor. That is the major reason why there is a limit on the maximum temperature of a kraft cooker. Recent modifications in kraft cooking have sought to reduce the cooking temperature as far as possible (**Table 2**).

The carbohydrates (cellulose and hemicellulose) are susceptible to peeling (removal of one end-unit at a time) and alkaline hydrolysis (a random cleavage of the polymer molecule) followed by secondary peeling. The hemicellulose content is significantly reduced by these reactions while there is relatively low loss of cellulose – about 10% – due to the low accessibility of cellulose chains by virtue of their crystallinity. The acidic products of such reactions also consume the alkali in the cooking liquor. The reactions involving carbohydrates and the neutralization of acidic components start rather early in the cooking process. To determine the extent of the loss of cooking chemicals in such reactions, online cooking liquor analysis is carried out in digester operations and the sampling point is determined on the basis of the accumulated G-factor. The cooking time is then controlled for a calculated H-factor which depends on the targeted lignin removal and the cooking liquor strength ($OH^- + HS^-$ activities). About 90% of the extractives (fatty and resin acids) are removed during the initial phase of the cook and the sodium salts can later be removed from the black liquor by acidulation in the form of 'tall oil.' Volatile turpentine is recovered from the vapor relief during cooking.

The kraft process is also characterized by redeposition of xylans from liquor on to fibers in the later stages of cooking. The kraft pulp consists of these five carbon sugars (pentosans), which are not conducive to producing dissolving grade pulp. In such a case, the kraft cooking process is preceded by an acid prehydrolysis stage in which the wood chips are exposed to direct steaming for about 2 h and the natural wood acids present are allowed to hydrolyze the hemicellulose to soluble sugars at high temperatures (170°C). This, of course, reduces the pulp yield by 5–7%, compared to normal kraft cooking.

Table 2 Ratio of temperature in cellulose and lignin

	Temperature		
	160°F	*170°C*	*Ratio*
Cellulose – G-factor	3960	9100	3.1
Lignin – H-factor	398	921	2.3
Ratio	7.4	9.9	

Extended Delignification

Extended delignification is practiced in many commercial kraft pulping operations to reduce the bleach chemical cost and bleach plant pollution loads. This seeks to fine-tune the kraft process to achieve additional delignification without the deleterious efffects of a residual delignification phase. The extended delignification involves maintaining high sulfidity, leveling out the alkali concentration profile throughout the cook, decreasing dissolved lignin concentration, cooking at a low temperature, and cold blow. This has resulted in the multistage addition of cooking liquor, removal of spent liquors at various stages, and low temperature/longer-duration cooks, and extensive equipment modifications to achieve all of the above.

The other type of extended delignification is oxygen delignification, which is compatible with the kraft process and is a subsequent process step. The oxygen-stage effluent can be added to black liquor and processed through the traditional kraft recovery cycle, thereby reducing the bleach plant pollution loads.

Pulping Additives

Another disadvantage of the kraft pulping process – the low yield from wood due to carbohydrate degradation – is overcome by using pulping additives such as polysulfide, borohydride, and anthraquinone. While all of these protect carbohydrates from the peeling reaction by oxidizing (polysulfide, anthraquinone) or reducing (borohydride) the end groups of carbohydrate chains, anthraquinone is the only reagent which has a redox cycle of its own. In the oxidation cycle, it protects the cellulose chain, and in the reduction cycle it leads to lignin fragmentation. Use of small levels of anthraquinone (about 1 $\mathrm{lb\,t^{-1}}$

of pulp) increases the yield (2–3%) and lowers the effective alkali requirement as well as increasing the delignification rate. The other two compounds have not found favor with the industry either because of the cost or because of the associated pollution problem due to sulfur compounds.

Control Parameter

A major control parameter in kraft pulp is a target kappa number (which directly relates the percentage of lignin left in pulp). Thus, a lower kappa number indicates a higher level of delignification. The higher the *H*-factor and/or active alkali, the lower will be the kappa number. The target kappa number is based on one or more of the following: (1) maximum pulp strength; (2) limitations on recovery loading; (3) maximum screened unbleached pulp yield; and (4) maximum bleached pulp yield. The cooking is essentially controlled by using the *H*-factor as a primary variable based on a desired kappa number and the cooking liquor strength from online analyzers. The desired *H*-factor is maintained in the batch digester by adjusting time and/or temperature, while in the continuous digester it is done by manipulating the temperature.

Pulp Properties

Softwood kraft pulps produce the strongest papers and are used in wrapping, sack, and liner papers. Bleached kraft pulps are used, along with high-yield pulps, in magazine-grade or newsprint furnish to provide additional strength and runnability on high-speed machines. Bleached grades are also used for toweling and boards. Unbleached grades for packaging applications are cooked to a higher kappa number to maximize the screened unbleached pulp yield while the bleached grades for writing, printing, and tissue applications are cooked to a lower kappa number.

Pulp Processing

Chemical pulps, as they come out of the blow tank, are fiberized enough to pass through knotters that can remove irregularly shaped reaction wood pieces, overthick chips, and other uncooked chips. Knots are generally defined as the pulp that is retained on 3/8 in. perforated plate. The removed knots can be recycled to a digester for recooking. The knotters can be atmospheric vibrating knotters or pressure screen knotters. The former have been superseded by the latter due to the fact that the open-type design generates foam and liquor splashing and the foam generated hinders the subsequent washing operation. The major disadvantage of the pressure knotter is that the knotter rejects should be processed through a secondary screen to recover the good fiber rejected along with the knots.

The pulp is then washed in multiple stages to remove the residual liquor from the pulp. This helps to reduce the costs of further processing and to recover the maximum amount of spent chemicals. The aim is to do so using a minimum amount of wash water, thereby reducing the dilution and consequent evaporation costs. Washing is done using any of the following: a battery of countercurrent rotary vacuum washers, rotary pressure washers, atmospheric or pressurized diffusion washers, or horizontal belt washer or dilution/extraction equipment.

Washing can be characterized either as displacement or diffusion washing. In displacement washing, a thick layer of pulp is built on a screen and wash water is applied to displace the liquor in the sheet and the displaced liquor is drained either by vacuum or forced out by pressure. Three or four stages are generally used to achieve an overall removal of about 99%, since the displacement for a single stage rarely exceeds 80% and can vary from stage to stage depending upon factors such as fiber mat drainage characteristics, air entrainment, pulp temperature, and pulp hardness and freeness.

Pulp slurry feed to a washer is prepared by mixing the filtrate of a particular stage with the exiting stock from a previous stage. In addition, the filtrate from a particular stage is also used as wash liquor in the previous stage. A countercurrent operation is maintained by balancing the liquor flows throughout the system, with fresh wash water being added to the final washer. The fresh water flow rate is controlled by monitoring the dissolved solids concentration in the exit stock from the final washer.

Diffusion washing is marked by a relatively long period of contact between the pulp and the wash liquor which allows the liquor solids to diffuse from the fiber structure. The diffusion rate depends on the temperature, concentration gradient, and fiber structure. Since the fibers are submerged, there is no air entrainment. The time of contact can vary between 10 min per stage in a multistage diffusion washer to about 2–4 h at the bottom of a Kamyr continuous digester.

Rotary pressure washers are similar to vacuum washers, but have some advantages: (1) a single washer can be operated with two or three displacement stages; (2) due to the high pressure, a high-temperature wash liquor can be used without the fear of fluffing the pulp; and (3) the closed vapor circulation system helps to prevent pollution.

The horizontal belt washer resembles a Fourdrinier paper machine in that the pulp suspension is distributed on a moving filter belt from a headbox to form a thick mat. The displaced filtrate is collected at the bottom and the filtrate from one section is used as wash liquor in the previous section in a classic countercurrent system. Unlike the rotary washer system, there is no mixing and reforming of pulp between stages.

The dilution/extraction system consists of diluting a pulp slurry with a weaker liquor and rethickening. Modern extraction presses which can thicken the pulp to a consistency of 30–40% have made such a system, operated in multistages, comparable with regular washers.

The diverse washing systems are often compared in terms of a single efficiency factor, viz., Norden efficiency factor, defined as the number of mixing stages that will give the same result as the washing equipment under consideration when operated at the same wash liquor ratio. From the computed cumulative Norden factor of the proposed equipment system and the dilution factor proposed, the anticipated washing efficiency of the system can be predicted from literature data.

The washed pulp is then screened through pressurized contrifugal screens with either centrifugal (outward) or centripetal (inward) flow or both. The screen perforations can be either taper-drilled holes or slots with relief on the accept side. Slots are oriented perpendicular to the direction of rotation so that the long dimension of the debris is presented to slot width. Slots, with their widths normally smaller than hole diameter, are more effective in removing smaller cubical debris. However, with screen open areas in the 3–7% range, compared to 10% for screens with holes, slotted screens have lower throughputs. The screen cleanliness efficiency is defined as $1-(S_a/S_i)$, where S_a and S_i are weight fractions of debris in the accepts and inlet flow, respectively. The cleanliness efficiency depends on the perforation size and type, and percentage reject rate.

The screened pulp may then be centricleaned by employing centrifugal force (density differences) and fluid shear (particle shape). The stock enters tangentially and is rotated by inlet guides. As the stock flows inward, the velocity increases, resulting in high centrifugal force near the center which carries the dense particles outwards and away from the accepted pulp. The dirt (which is heavier) held in the downward current continues toward the tip under increasing force (due to narrowing diameter). The smaller the debris size to be removed, the smaller should be the diameter of the cleaners to be employed. The contracleaning system is normally operated in three stages in a cascade sequence (with the rejects of the primary being fed to the secondary, and the secondary accept being fed to the primary, and so on) so that the overall rejected fiber is usually less than 1% while a reject rate of 10–20% is maintained in each stage to ensure good cleaning efficiency.

The cleaned pulp is then thickened using various filters (10–15% consistency), gravity thickener (4–8%), screw extractor, or various presses (>20%) before being stored in high-density chests/towers. Integrated pulp mills often store the pulp at 10–15% consistency. Nonintegrated operations can deliver pulp in wet laps (40–45%) or dry laps (80–85% oven dry) using equipment similar to the paper machine. Besides steam cylinder drying of pulp laps, pulp can be dried in air float dryers or flash-dried after prefluffing the pulp, using hot air as a drying medium.

See also: **Papermaking**: The History of Paper and Papermaking; World Paper Industry Overview. **Pulping**: Chip Preparation; Fiber Resources; Physical Properties.

Further Reading

Biermann CJ (1996) *Handbook of Pulping and Papermaking*, 2nd edn. Chapters 3 and 4. San Diego, CA: Academic Press.

Gullichsen J and Paulapuro H (2000) *Papermaking Science and Technology – Books 6A and 6B – Chemical Pulping*. Helsinki, Finland: Fapet Oy.

Kocurek JJ (1985/1989) *Pulp and Paper Manufacture*, vols 4 and 5, 3rd edn. The Joint Textbook Committee of the Paper Industry, TAPPI/CPPA.

Sjostrom E (1993) *Wood Chemistry – Fundamentals and Applications*, 2nd edn. Chapter 7. San Diego, CA: Academic Press.

Smook GA (1992) *Handbook for Pulp and Paper Technologists*, 2nd edn. Chapters 4–10. Bellingham, WA: Angul Wild.

Bleaching of Pulp

T J McDonough, Institute of Paper Science and Technology, Atlanta, GA, USA

Introduction

The term ‘bleaching,’ when used in reference to wood pulp, means chemical treatment of the pulp to increase its ability to reflect visible light or, in other words, its brightness. The color of unbleached pulp is practically all due to the lignin it contains, so bleaching necessarily implies that the lignin is either decolorized or removed. Chemical pulps contain relatively small amounts of residual lignin, so it is practical to bleach them by removing the lignin. Mechanical pulps, on the other hand, contain so much lignin that to remove it would require large amounts of bleaching chemicals and would be prohibitively expensive. Consequently, mechanical pulps are bleached by decolorizing the lignin instead of removing it. Since it is not feasible to decolorize the lignin completely, bleached mechanical pulps are generally not as bright as bleached chemical pulps. The latter are virtually free of lignin and contain only polysaccharides, which are practically colorless.

In addition to increasing brightness, bleaching simultaneously improves other desirable pulp properties by removing contaminants such as extractives and small particles of bark or incompletely pulped wood. For specialty pulps, such as dissolving pulps, the conditions of the bleaching process can be adjusted to provide for removal of undesirable hemicelluloses. In some applications these other properties are even more important than brightness and the pulp may have to be bleached to a brightness that is higher than needed, to achieve the required levels of contaminant removal.

Lignin removal is accomplished by treating the pulp alternately with oxidizing agents and alkali. Lignin is much more susceptible to oxidation than cellulose and the other polysaccharide components of the pulp, and is selectively removed. Nevertheless, the polysaccharides are not completely resistant to attack and can be damaged if the bleaching process is not carefully selected and controlled. The damage that does occur causes a small amount of the polysaccharide fraction to dissolve and is accompanied by depolymerization of the remainder. Such depolymerization, if it is sufficiently extensive, can result in a loss of pulp strength. Its extent is monitored by dissolving a sample of the pulp in a cellulose solvent and measuring the viscosity of the resulting solution. Some bleaching agents are less likely to damage cellulose than others and are said to be more selective.

Most chemical pulp bleaching sequences use chlorine dioxide to accomplish at least part of the required lignin oxidation. They generate an effluent that contains lignin degradation products and other organic materials, some of which are chlorinated. Since the effluent also contains chloride ion and other chlorine-containing ions, it cannot be recycled and burned in the mill's chemical recovery system. Consequently, pulp bleaching processes generally have the potential to affect the environment and must be selected and operated with due regard for the environment.

We can summarize the above introduction to pulp bleaching in the form of a working definition. Bleaching is the treatment of pulp to remove or decolorize its lignin component and thereby increase its brightness and other desirable properties while preserving pulp yield and strength, with due regard for potential effects on the environment.

Significance

Bleaching ranks among the most important of the processes used to manufacture pulp and paper. **Table 1** contains estimates of the amounts of the different kinds of pulp that the global pulp and paper industry produced in 2001. World production of bleached chemical pulp amounted to 78.8 million tonnes, or more than 44% of total pulp production. This figure underestimates the total amount of pulp bleached, since it does not account for the bleaching of substantial proportions of other pulp types, such as mechanical, nonwood, and deinked pulps. It would not be unreasonable to assume that nearly two-thirds of global pulp production benefits from some sort of bleaching process.

Kraft Pulp Bleaching Stages and Their Development

Hypochlorite

In the early part of the twentieth century, bleaching was a simple batch process that relied almost exclusively on calcium hypochlorite, made by bubbling chlorine gas into a lime slurry. The hypochlorite (H) stage was begun by adding the chemical to a warm suspension of unbleached pulp at low consistency. The stock was slowly agitated until the desired degree of bleaching had been achieved, after which the pulp was washed free of the spent bleach liquor and reaction products. The next step in the development of the technology was introduction of two-stage (HH) bleaching, in which only part of the hypochlorite was added and allowed to react, after

Table 1 Estimated 2001 world pulp production by type (millions of metric tons)

Pulp type	*Production*
Bleached kraft	76.3
Unbleached kraft	32.4
Bleached sulfite	2.5
Unbleached sulfite	1.1
Semichemical	7.0
Mechanical	34.7
Nonwood	14.3
Unspecified	10.0
Total	178.3

which the pulp was washed and subjected to a second stage, similar to the first. This simple modification of the process had two beneficial effects. First, the removal of dissolved but still oxidizable reaction products after the first stage reduced overall chemical consumption. Second, the reduction in the maximum and time-averaged concentrations of the oxidizing agent reduced its propensity to attack and degrade the cellulose and other polysaccharide components of the pulp. This subtle introduction of stagewise bleaching was a seminal event in the development of today's multistage bleaching sequences.

Chlorine

The commercial introduction of chlorine gas as a bleaching agent was a similarly significant milestone in the development of modern bleaching technology. The first reported commercial chlorination (C) stage was developed at the Nekoosa-Edwards Paper Co. in 1930 and 1931. It was based on the earlier observation by Cross and Bevan that lignin is rapidly chlorinated and that the chlorinated lignin is soluble in alkali and can be removed in a caustic extraction (E) stage following the C stage. Lignin removal in C and E stages allows final brightening in a subsequent H stage with a much smaller application of hypochlorite than would be necessary to achieve the same result in the single-stage process or in the two-stage HH sequence. In addition, the high selectivity of chlorine and the reduction in the amount of the relatively nonselective hypochlorite applied gave a stronger bleached pulp. Finally, it proved possible to reach higher brightness levels in the multistage CEH process. This development marked the advent of the modern multistage bleaching sequence, in which the early stages remove the bulk of the residual lignin, sometimes without significant brightness increase, and the later stages cause large gains in brightness by removing the last traces of residual lignin.

Chlorine Dioxide

The commercialization of chlorine dioxide use in the early 1940s took all of these advances one step further. WH Rapson, who was at the time an employee of Canadian International Paper Company, pioneered the use of chlorine dioxide in North America. Commercial chlorine dioxide bleaching began at that company's mill in Temiscaming, Quebec in the summer of 1946. Almost simultaneously, two Swedish mills started up similar systems. Chlorine dioxide is a powerful brightening agent and is immeasurably more selective than hypochlorite. Adding a chlorine dioxide (D) stage after the hypochlorite stage to give a CEHD sequence made it possible to achieve much higher brightness levels without compromising pulp strength. In the years following its first full-scale application, chlorine dioxide displaced more and more hypochlorite, and by the 1960s the CEDED sequence had become the standard for the industry.

As well as being an efficient brightening agent for application in the later stages of a bleaching sequence, chlorine dioxide can assume a role similar to that of chlorine, earlier in the sequence. Used in this way, chlorine dioxide oxidizes lignin while it is still present in relatively large amounts and renders it soluble in a subsequent alkali extraction stage. For many years, however, chlorine dioxide was considered too expensive to be used as a complete replacement for chlorine and its use at an early stage in the sequence was restricted to replacing only part of the chlorine in the chlorination stage. This was practiced for either of two reasons – to prevent loss of pulp strength, as indicated by excessive viscosity loss, or to improve delignification efficiency. In the former application, only small fractions of the chlorine were replaced, usually in the neighborhood of 10%. Such a small amount of chlorine dioxide, when added at the same time as the chlorine or shortly afterwards, serves to neutralize free radicals responsible for cellulose degradation during chlorination. When used to improve delignification efficiency, larger fractions of the chlorine were replaced, typically about 50%. This level of substitution results in a significant increase in apparent lignin removal, as measured after the alkali extraction stage that follows the chlorination stage. When used in this way, the chlorine dioxide is added to the pulp before the chlorine. The use of substitution levels much higher than 50% results in a loss of efficiency and 100% substitution usually requires more than the theoretical amount of chlorine dioxide.

In spite of this loss in efficiency, complete replacement of chlorine by chlorine dioxide began in the late 1980s in Sweden and has since become widespread. The practice began in response to new environmental regulations and environment-related market pressures. The potential of bleaching effluents to affect the environment is usually estimated by characterizing them in terms of the results of several different chemical test methods. One of these is a method for determining the effluent's content of adsorbable organic halide, abbreviated as AOX. In effect, AOX is an estimate of the total amount of chlorine in organic compounds found in the effluent. Some organic chlorine compounds are highly toxic, notably chlorinated dibenzodioxins (dioxins), chlorinated dibenzofurans (furans), and highly chlorinated phenolic compounds. Since it is much easier to measure AOX than to measure amounts of individual toxic compounds, most jurisdictions have adopted AOX as a basis for regulation (in spite of the fact that most of the organic chlorine compounds found in bleaching effluents are not toxic). In general, AOX limits have been set at very low levels by the environmental authorities in pulp-producing countries, effectively forcing the industry to phase out the use of molecular chlorine. Its complete replacement by chlorine dioxide gave rise to the term 'elemental chlorine-free' bleaching, or ECF bleaching. Bleaching with chlorine dioxide generates far less AOX than bleaching with the equivalent amount of chlorine. It also generates no detectable levels of dioxins or highly chlorinated phenolic compounds and usually generates no detectable levels of furans.

Hydrogen Peroxide

Hydrogen peroxide is similar to chlorine dioxide, in that it can be applied at a later stage in the bleach sequence to attain high brightness. Though not as highly selective as chlorine dioxide, a hydrogen peroxide (P) stage does not adversely affect pulp strength if the bleaching conditions are appropriately chosen. Both hydrogen peroxide and chlorine dioxide found wide application, but the generally greater cost-effectiveness and selectivity of chlorine dioxide resulted in its being more widely adopted. Although, as noted above, the CEDED sequence had become the standard for the industry by the 1960s, hybrid sequences such as CEHD and CEDP were still in common use. More recently, technologies have been developed for using peroxide to remove significant amounts of lignin earlier in the bleaching sequence while simultaneously brightening the pulp. These methods employ forcing conditions of high temperature and pressure to accelerate the normally sluggish reaction of hydrogen peroxide with lignin. The use of such forcing conditions is only feasible if the pulp is pretreated to remove traces of transition metal ions, which would otherwise catalyze decomposition of the peroxide. This is achieved by inserting a chelating agent (Q) stage ahead of the peroxide stage. A chelating agent commonly used for this purpose is diethylenetriaminepentaacetic acid (DTPA). Peroxide may also be used to enhance the effectiveness of alkali extraction stages and oxygen stages. Conversely, oxygen may be added under pressure to give a pressurized peroxide (PO) stage as part of a strategy to impose forcing conditions in the peroxide stage. The advent of this practice during the 1990s has blurred the distinction between peroxide and oxygen stages.

Oxygen

During the period of chlorine dioxide's ascent, research was being conducted on two other promising bleaching agents – oxygen and ozone. Oxygen, when applied together with alkali in an oxygen delignification (O) stage, is capable of removing much of the residual lignin in a kraft pulp, but its low solubility and its tendency to be nonselective (especially in the presence of trace amounts of one or more transition metal ions, notably iron, manganese, or copper) slowed the development of oxygen delignification processes. Ozone is even more reactive toward lignin than oxygen but its tendency to be nonselective similarly hindered its commercialization. Oxygen was the first of the two to achieve the status of a commercially viable bleaching agent, owing in part to the discovery of a cellulose 'protector' by Robert and coworkers in France in the early 1960s. They found that adding a small amount of magnesium ion to the pulp before oxygen bleaching deactivated trace metal ions and allowed about half of the residual lignin to be removed without affecting pulp strength. Soon after this, in 1970, a mill in Enstra, South Africa, started up the first commercial oxygen delignification system. The significance of this development lay in its potential for decreasing the environmental impact of the bleach plant. Unlike the effluents from C stages or stages following C stages, oxygen-stage effluents do not contain significant amounts of chloride ion, so they can be recycled to the mill's chemical recovery system and ultimately destroyed by burning in the recovery furnace. The quantities of materials discharged to the environment are roughly proportional to the amount of lignin in the pulp entering the bleach plant. Consequently, removal of, for example, 50% of the lignin in an oxygen stage before conventional bleaching (such as in an OCED sequence) can result in a roughly 50% reduction in bleach plant discharges.

In addition to being used to reduce the lignin content of the pulp entering the bleach plant, oxygen can be used in the bleach plant itself. The earliest such application appeared in about 1980 and consisted of reinforcement of the first caustic extraction stage. Oxygen is dispersed in the pulp after addition of alkali, transforming the E stage into an (EO) stage. The result is more efficient removal of lignin that has been solubilized by the preceding oxidative stage (then C, now D). The benefit can be realized either in the form of reduced cost for bleaching agents in the succeeding stages of the sequence or reduced AOX, by decreasing the application of chemical in the stage preceding the (EO) stage. Adding both oxygen and hydrogen peroxide to the extraction stage has an even greater effect than adding oxygen alone. The result is an (EPO) stage. A related but more recently developed use of oxygen in the bleach plant combines it, under pressure, with hydrogen peroxide, giving a (PO) stage.

Ozone

Ozone has even greater potential than oxygen for lessening the effects of bleaching on the environment because its greater reactivity, at least in principle, allows it to remove nearly all of the lignin in a form that is recyclable to the recovery system. That same reactivity, however, can lead to cellulose degradation and loss of pulp strength if the ozone is not applied uniformly and in controlled amounts, under appropriately selected conditions. Because of these demanding requirements, the commercial application of ozone took a long time after the initial discovery of its bleaching power. In 1992, however, Union Camp Corporation announced that it had successfully developed a viable ozone (Z) stage capable of selectively delignifying kraft pulp. That company started up a 1000-ton per day bleach plant incorporating both ozone and chlorine dioxide stages, the sequence being OZED. Since then, many other commercial ozone stages have been put into operation, though not all of them are placed in such a way that their effluents can be recycled to the recovery system.

Ozone may be used in close combination with chlorine dioxide by sequentially adding the two chemicals in the same stage. The resulting stage may be designated (DZ), (ZD), (D/Z) or (Z/D), depending on the order of addition and the time that is allowed to elapse between additions of the two chemicals.

Hemicellulose-Degrading Enzymes

In 1987, Finnish researchers proposed the idea of using hemicellulose-degrading enzymes as pulp-pretreating agents to facilitate subsequent bleaching. Although they do not themselves remove lignin from the pulp, xylanases were shown to be capable of rendering the lignin in unbleached pulp to be more readily removed by subsequent treatment with chlorine dioxide and alkali. The xylanase (X) stage typically results in reductions in chlorine dioxide requirements of approximately 5 kg per ton of pulp. The technology has been commercialized in a significant number of bleached kraft mills.

Prehydrolysis

Another significant discovery emerged from Finnish research laboratories during the 1990s. This was the finding that a significant fraction of the oxidizable material (as measured by the kappa number, a test designed to estimate the amount of residual lignin in pulp) is not lignin. This material, hexenuronic acid, is formed from xylan during kraft pulping, and consumes chlorine dioxide during bleaching. Since hexenuronic acid is also susceptible to removal by acid hydrolysis, this discovery led to the development of an acid hydrolysis (A) stage that can be used as a pretreatment to reduce the requirement for chlorine dioxide significantly during subsequent bleaching. Since hardwoods contain much more xylan than softwoods, hardwood pulps contain more hexenuronic acid than softwood pulps. The prehydrolysis process has been commercialized in hardwood pulp bleach plants at several mills.

Bleaching Sequences

Successive incremental additions of any bleaching chemical result in progressively smaller incremental effect, regardless of whether the effect in question is lignin content reduction, brightness increase, or some other property change. Furthermore, an asymptotic limit is approached that usually falls far short of the desired target level and high total chemical charges are needed to approach the limit. On the other hand, if chemical addition is stopped at some economical level and the pulp is washed before the same chemical is again incrementally added, the incremental increases in effect are initially larger than if the washing step had been omitted. To illustrate, a DD sequence requires less chlorine dioxide than a single D stage to reach a given brightness and is capable of reaching a higher brightness. Furthermore, if the bleaching chemical in question is an acidic oxidant, such as chlorine dioxide, the effect is strongly enhanced by intermediate alkali extraction. Thus, a DED sequence requires much less chemical to reach a given brightness and is capable of reaching a much higher brightness. By extension, a DEDED sequence requires still less chemical and is capable of reaching an even higher brightness.

Notation

As is already apparent from the preceding paragraphs, a system of shorthand notation has evolved for designating the individual stages that make up a bleaching sequence. The uppercase letters appearing in parentheses are used to represent the stages to which they refer. A single uppercase letter represents a bleaching stage that consists of a mixer, a retention vessel (usually a tower), and a washer. A stage to which two chemicals are added sequentially without intermediate washing is represented by an ordered combination of letters within parentheses, with or without an intermediate '/,' depending on whether the time elapsed between the two chemical additions is greater or less than 1 min. Simultaneous addition is indicated by using a '+' instead of a '/.' Examples are D, (ZD), (D/Z), and (C+D). A bleaching sequence is then represented by an ordered combination of stage designators, D(EPO)DED, for example. Numerical subscripts are sometimes used to denote the position of a stage within the sequence, for example, D_0(EPO)D_1ED_2.

Partial Bleaching Sequences

One may consider a chemical pulp bleaching sequence to be made up of two partial sequences, a delignifying partial sequence and a brightening partial sequence. The purpose of the former is primarily to remove lignin, rather than to increase brightness. The purpose of the latter is primarily to increase brightness by removing the small amount of remaining lignin and perhaps decolorizing traces of lignin that remain with the bleached pulp. **Table 2** provides lists of delignifying and brightening partial sequences. Any one of the former can be combined with any one of the latter to create a full bleaching sequence, capable of bleaching softwood kraft pulp to brightness values in the range 80–90, depending on the particular sequence. Note that the partial sequences listed in the table are only examples; many more could have been included.

Table 2 Examples of delignification and brightening partial bleach sequences

Delignification	*Brightening*
CE	H
(C+D)E	HEH
(DC)(EO)	HED
D(EPO)	D
ODE	DD
OD(EO)	DED
OXD(EPO)	DEDP
OXQP	DPD
OZ	(EPO)P
OOQP	PP
OQPZ	Q(PO)

ECF and TCF Sequences

As already noted, sequences based on the use of chlorine dioxide without any use of molecular chlorine are termed elemental chlorine-free (ECF) sequences. Sequences that use no chlorine compounds or molecular chlorine are referred to as totally chlorine-free (TCF) sequences. The latter sequences generally have higher costs and are less able to achieve high brightness and high strength simultaneously. With reference to **Table 2**, examples of ECF sequences are D(EPO)DED, OD(EO)D, and OZED. Examples of TCF sequences are OXQPPP and OQPZQ(PO).

Process Conditions

The operating state of a bleaching stage is generally characterized in terms of chemical charge, consistency, time, temperature, and terminal pH. Some bleaching stages, such as a brightening D stage, are invariably operated within a narrow range of conditions that have been determined to give near-optimum results. Others, such as the oxygen stage, exist in a variety of different forms, each with its own range of operating conditions. Thus oxygen stages may be operated at medium consistency (10–14%, MC) or high consistency (20–27%, HC) and initial chlorine dioxide (D_0) stages may be operated at low consistency (3.5–4%, LC) or MC. Typical process conditions for some bleaching stages are given in **Table 3**.

Bleaching of Mechanical and Other High-Yield Pulps

Among the principal virtues of mechanical pulps are their very high yields. Unavoidably associated with such high yields are correspondingly high lignin contents. Since the lignin content of the wood raw material may be as high as 30%, mechanical pulps may have lignin contents approaching this figure. This precludes bleaching by lignin removal, which would negate the yield benefit and consume inordinately large amounts of bleaching chemicals. Consequently, high-yield pulps are bleached with chemicals that decolorize lignin instead of removing it, sometimes referred to as lignin-preserving bleaching agents.

The two main bleaching chemicals used for this purpose are sodium dithionite (commonly known as sodium hydrosulfite) and hydrogen peroxide. Bleaching with hydrosulfite, a powerful reducing agent, is used when the required brightness increase is relatively small. The maximum brightness increase achievable depends on the wood species, but is almost never greater than 10 points. To illustrate, a mill making thermomechanical pulp as the main component of a newsprint furnish may use hydrosulfite to increase the brightness of the pulp from 55 to 60, a value typically required for newsprint. Hydrosulfite bleaching is conducted at low or, less often, at medium consistency and at the highest feasible temperature, usually 60–70°C. It is necessary to exclude air, since oxygen rapidly destroys hydrosulfite.

The ability of hydrogen peroxide to serve as a lignin-preserving bleaching agent may seem counterintuitive, given the above reference to its use as a delignifying agent for chemical pulps. It is found, however, that if the conditions are appropriately

Table 3 Typical process conditions for individual bleaching stages

Stage	*O*	*D*	*(EPO)*	*D*	*E*	*Z*	*Q*	*P*	*(PO)*	*A*
Variant	Medium consistency	Delignifying		Brightening	Second extraction	Medium consistency				
Chemical applied ($kg\,t^{-1}$)										
Oxygen	30		5			50			30	
Ozone					5	5				
Magnesium sulfate	1							1	1	
Chlorine dioxide		20		10						
Sodium hydroxide	30		25	5	5			10	30	
Hydrogen peroxide			5					15	30	
DTPA							1			
Consistency[c] (%)	12	3.5	12	12	12	12	12	12	12	12
Time (min)	60	30	60[a]	180	60	3	60	240	120	240
Temperature (°C)	90	60	70	70	70	40	70	90	110	95
Average pressure (kPa)	500		100[b]			800			500	
Terminal pH	10.5	2.5	10.5	4	10.5	3	6	10.5	10.5	3

[a] Of which 10 min is under oxygen pressure.
[b] Pressure supplied by hydrostatic head in upflow tube, decreasing from 200 to 0 kPa.
[c] Consistency is the fiber concentration, defined as (weight of dry fiber)/[(weight of dry fiber) + (weight of water)], expressed as a percentage.
DTPA, diethylenetriaminepentaacetic acid.

chosen, the action of the peroxide will be limited to destruction of chromophoric structures within the lignin without degrading it to the extent that it would dissolve and be removed. The conditions are milder than those used to delignify chemical pulp and include the use of sodium silicate and magnesium sulfate to stabilize the peroxide toward metal-catalyzed decomposition. Bleaching is usually conducted at the highest possible consistency, a temperature in the range 40–60°C, and in the presence of sufficient alkali to result in a terminal pH of about 10.5. Under favorable conditions, peroxide bleaching may be capable of raising the brightness by 20 points or more, so it is used when the brightness gain needed is greater than can be achieved with hydrosulfite alone. Still higher brightness gains can be achieved by sequential bleaching with peroxide and hydrosulfite, usually in that order, though the brightness gains are far from additive. Hydrosulfite applied after a peroxide stage may result in only 1–3 points brightness increase.

Bleaching of Recycled Fiber

Recycled fiber often contains chemical pulps mixed with mechanical pulps, chemimechanical pulps, or both. For this reason recycled pulps are usually bleached with lignin-preserving bleaching agents. Complicating factors not encountered in the bleaching of virgin pulps are incomplete ink removal, the presence of dyes, and the greater contribution of resistant chromophores to the color of the pulp, the less resistant ones having been removed during virgin fiber processing. All of these factors are obstacles to the attainment of high brightness. Hydrogen peroxide may be used during repulping or deinking, to prevent alkali-induced yellowing and perhaps achieve some degree of brightening, and may also be used in a subsequent bleaching stage. Dithionite may be used subsequently for 'color stripping' or decolorization of dyes. Another powerful reducing agent, formamidine sulfinic acid (FAS) may be used for the same purpose. FAS is more expensive than hydrosulfite, but may be cost-effective. Ozone can also be used for color-stripping. Because of the extreme variability in the characteristics of recycled fiber feedstocks, it is difficult to generalize further. Experimentation is necessary to identify appropriate bleaching processes and conditions for any given recycled fiber supply.

Bleaching Equipment

A pulp bleaching stage normally consists of a mixer, a pump, a retention tower, and a washer. Good mixing is a critical prerequisite for efficient bleaching and good bleached pulp quality. Mixing equipment found in bleach plants may be of several types: continuous stirred tanks, peg mixers, static mixers, and high-shear mixers. High-shear mixers, introduced in the early 1980s, have allowed efficient fiber-scale mixing to be achieved at medium consistency and have enabled medium-consistency applications of gaseous bleaching chemicals that were previously impossible. These include medium-consistency delignification with oxygen or ozone and oxygen-reinforced alkaline extraction. High shear is created by passing the pulp suspension through a narrow gap between two surfaces moving at a high velocity relative to one another.

Bleaching towers are vertical, cylindrical, plug-flow reactors that provide the necessary time for micro-scale chemical concentration gradients to be evened out by diffusion and for the bleaching reactions to be completed. There are three basic types: downflow, upflow, and upflow–downflow. Downflow towers are used for bleaching chemicals that are not gases under normal conditions. Upflow towers are used for stages employing gaseous bleaching chemicals. The hydrostatic head of the pulp column provides sufficient pressure to prevent loss of gas from the pulp suspension before it has had time to react. Upflow–downflow towers combine the advantages of both component types. The pulp and bleaching chemical enter at the base of the upflow tube, which provides the hydrostatic head necessary to keep gaseous bleaching chemicals in solution. It provides sufficient retention time for much of the bleaching chemical to be consumed by the pulp, thus reducing the likelihood of gas loss at the top of the tube. The pulp then falls into the downflow part of the tower, where the reaction is completed. The retention time can be controlled by controlling the depth of the pulp bed in the downflow part of the tower.

The pulp emerging from a bleaching stage is generally washed before entering the next stage. This removes organic material that would otherwise consume chemical in the next bleaching stage, as well as spent and residual bleaching chemical. The type of washer most often used is the rotary drum filter, though diffusion washers and wash presses may also be used.

Figure 1 is a schematic representation of a generic bleaching stage, showing the washer following the previous stage, a steam mixer discharging to a standpipe feeding a stock pump, a high-shear chemical mixer, an upflow–downflow tower, and the bleached pulp washer.

Novel Bleaching Systems

Most of the bleaching systems discussed above have found wide commercial application. Some newer technologies have been implemented only recently and can, at the time of writing, be found in only a few operating mills. Still others are at the research stage and may hold promise for the future.

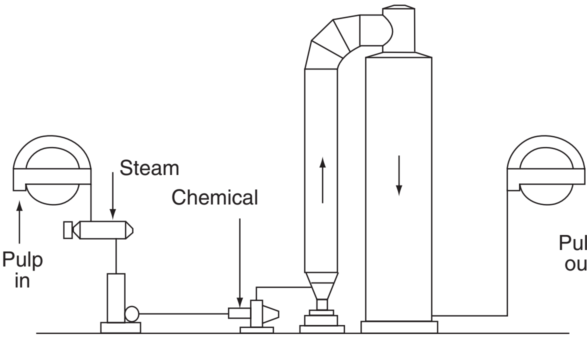


Figure 1 Schematic representation of a generic upflow–downflow bleaching stage. Reproduced with permission from Dence CW and Reeve DW (eds) (1996) *Pulp Bleaching: Principles and Practice*. Atlanta, GA: TAPPI Press.

Peracids

Peracids, more correctly called peroxyacids, are analogs of hydrogen peroxide in which one of the hydrogens is replaced by an acyl group. They can be prepared by reacting an acid with hydrogen peroxide. Acetic acid gives peracetic acid and sulfuric acid gives peroxymonosulfuric acid, also known as Caro's acid. Both of these peracids are selective pulp-delignifying and brightening agents. They are more reactive than hydrogen peroxide and therefore can be used under milder reaction conditions. Peracetic acid is currently being used for pulp bleaching in a few mills in Europe.

Dimethyldioxirane

Dimethyldioxirane is derived from acetone by inserting a peroxidic oxygen into the carbonyl group, forming a molecule with a reactive, three-membered ring. It is both reactive and selective, but would have to be generated on site because of its relative instability. In principle, its generation is straightforward, involving preparation of Caro's acid from sulfuric acid and hydrogen peroxide, followed by reaction of the Caro's acid with acetone. However, the economics of the system depend on cheap and efficient recovery of both acetone and sulfuric acid, an engineering challenge that has not yet been met.

Lignin-Degrading Enzymes

The most important member of this class is laccase. Early attempts to bleach pulp with laccase failed because the laccase molecule is too large to diffuse into the pulp fiber, where the lignin is located. This problem was partially solved in the early 1990s, when it was discovered that certain compounds can serve as 'mediators.' Such a compound diffuses into the fiber and oxidizes lignin, thereby being reversibly converted to its reduced form. The reduced mediator diffuses out of the fiber into the bulk medium, where it is reoxidized by laccase, regenerating the oxidized form, which is capable of again diffusing into the fiber and further oxidizing lignin. Furnishing oxygen to reoxidize the laccase completes the cycle. The process is not yet commercial, since the known mediators are too expensive. It is possible that further research will solve this problem.

Polyoxometalates

Another process that has not yet reached the point of commercialization employs polyoxometalates (POMs), metal oxide anions (heteropolyanions) formed from simple oxides of vanadium, molybdenum, or tungsten. They have oxidized forms that are capable of oxidizing lignin and being regenerated by oxidation with oxygen or hydrogen peroxide. Current research envisages a zero effluent concept: an aqueous solution of POM is applied to the pulp under anaerobic conditions. It oxidizes and degrades the lignin and itself becomes reduced in the process. The spent liquor containing the reduced POM and the dissolved organic material (mostly oxidized lignin) is separated from the pulp and oxidized with oxygen at high temperature. The reduced POM catalyzes the destruction of the organic material, converting it to carbon dioxide and water. At the same time, the oxidized form of the POM is regenerated and can be used again for bleaching. From an environmental standpoint, this conceptual process is extremely attractive, since it emits only carbon dioxide and water and uses no chlorine compounds. However, considerable engineering development is still needed to realize the extremely high POM recoveries that would be needed to make it economically feasible.

See also: **Packaging, Recycling and Printing**: Paper Recycling Science and Technology. **Pulping**: Chemical Additives; Chemical Pulping; Environmental Control; Mechanical Pulping; New Technology in Pulping and Bleaching.

Further Reading

Dence CW and Reeve DW (eds) (1996) *Pulp Bleaching: Principles and Practice*. Atlanta, GA: TAPPI Press.

Hatch RS (ed.) (1953) *The Bleaching of Pulp*. TAPPI monograph series no. 10. Atlanta, GA: TAPPI Press.

McDonough TJ (1986) Oxygen bleaching processes. *Tappi Journal* 69(6): 46.

McDonough TJ (1992) Bleaching agents, pulp and paper. In: Howe-Grant M (ed.) *Kirk-Othmer Encyclopedia of Chemical Technology*, 4th edn, vol. 4, pp. 301–311. New York: John Wiley.

McDonough TJ (1998) The revolution in bleached chemical pulp manufacturing technology. In: Turoski V (ed.) *Chlorine and Chlorine Compounds in the Paper Industry*, pp. 3–23. Chelsea, MI: Ann Arbor Press.

McDonough TJ (2000) Pulping and bleaching technologies for improved environmental performance. In: Springer A (ed.) *Industrial Environmental Control, Pulp and Paper Industry*, Chapter 13. Atlanta, GA: TAPPI Press.

Rapson WH (ed.) (1963) *The Bleaching of Pulp*. TAPPI monograph series no. 27. Atlanta, GA: TAPPI Press.

Rydholm SA (1965) *Pulping Processes*. New York: Interscience.

Singh RP (ed.) (1979) *The Bleaching of Pulp*. Atlanta, GA: TAPPI Press.

Tench L and Harper S (1987) Oxygen bleaching practices and benefits: an overview. *International Oxygen Delignification Conference Proceedings*, pp. 1–11. Atlanta, GA: TAPPI Press.

New Technology in Pulping and Bleaching

R H Atalla, R S Reiner and C J Houtman, USDA, Madison, WI, USA
E L Springer, University of Wisconsin, Madison, WI, USA

Published by Elsevier Ltd., 2004

Introduction

Innovation in advancing technologies for production of pulp and paper has been driven, by and large, by the needs to reduce the environmental impact of pulp mills or to enhance the yield in processes of conversion of wood to fibers. 'Fiberization' of wood chips is carried out in two categories of processes. One, chemical pulping, relies on removing the lignin that binds the cellulose fibers together by chemical delignification processes. The other is based on mechanical fiberization of the wood while retaining much of the lignin. The resulting pulps have significantly different properties. The chemical pulps are used in the manufacture of paper or packaging materials that require the fibers to have excellent mechanical properties or to have high brightness for the manufacture of fine papers. The mechanical pulps are used as fillers or in the manufacture of papers that do not require fibers of high strength. Some chemical pulps are also used as a source of high-purity cellulose for the manufacture of cellulose derivatives or for the production of regenerated cellulose fibers. We will touch upon some advances in both arenas.

Much of the chemical pulping industry is focused on use of the kraft pulping process, and efforts to make the process more efficient continue; both pulping and bleaching operations have been modified and improved.

Pulping and bleaching processes are subjects of separate articles (*see* **Pulping**: Bleaching of Pulp; Chemical Pulping; Mechanical Pulping). Since both involve delignification of wood fibers, there is some continuity in the processes and the boundary between them can occur at different levels of delignification, depending on the conditions and operational choices at each mill. It is well to consider the operational differences between them however.

The pulping process begins with wood chips and delignifies them to a point where the individual fibers that make up the chips are free to separate from each other. Pulping operations are intended to fiberize the wood by removing much of the lignin. If the pulp is to be used for the manufacture of container board, it can be used at the point where the lignin content has been reduced to between 8% and 10%. The kraft process (*see* **Pulping**: Chemical Pulping) is based on using a mix of NaOH and NaSH in the white liquor to digest the wood in an alkaline anaerobic environment. The lignin and polysaccharide degradation products solubilized in the process are then burned, after concentration of the black liquor, to recover both the energy content and the inorganic components. The inorganics are then causticized again and recycled into the digesters.

When the pulp is to be used to manufacture white papers, it is necessary to continue the delignification until the pulp has less than 1% lignin. At that point it is subjected to a bleaching process, often thought of as brightening, that removes the remaining lignin and oxidizes residual color bodies so they can be solubilized during extraction to give a white pulp of high brightness. These processes are usually based on creating an oxidizing environment that can both delignify and bleach. The transition from pulping in an anaerobic alkaline environment to bleaching in an oxidizing environment can occur at different levels of lignin content. It can be as high as 10% lignin, where the early oxidative delignification step is thought of as an extension of the pulping or a pretreatment prior to bleaching. But it can also be as low as 3% when the extended cooking of the pulp under anaerobic alkaline conditions is used to achieve the maximum delignification prior to the entry into the oxidizing environment.

The innovations to be described in this article are in processes at different points in the delignification. Some are intended to improve the efficiency and selectivity of the alkaline anaerobic pulping environment while also reducing the need to use sulfur or eliminating it entirely. Others are based on the application of oxidative environments in manners that require little or no chlorine-based bleaching agents or create a more selective environment. Selectivity is defined as the removal of lignin and its degradation byproducts, with minimal damage to cellulose and other cell wall polysaccharides.

Some important advances in the technology of mechanical pulping will also be described, as will be some innovations with respect to preparation of fibers and pretreatments applied prior to transfer to the paper machine.

Chemical Pulping

Kraft Process

As noted earlier, the kraft process is the most common chemical pulping process (*see* **Pulping**: Chemical Pulping). The chipped wood is introduced into an anaerobic alkaline environment under conditions that result in maximizing the solubilization and removal of lignin, while minimizing the degradation or removal of cell wall polysaccharides, principally cellulose. The pulping process is usually stopped at a lignin content of 4–5% because further treatment under these conditions results in unacceptable losses in cellulose or degradation of the mechanical properties of the fibers. In recent years, however, ways have been found to extend the kraft pulping process to somewhat lower lignin contents without extensive reduction in pulp strength. For continuous digesters, the system is called modified continuous cooking (MCC); for batch digesters, one version of the system is called rapid displacement heating (RDH). In these systems the alkali concentration in the digester is manipulated so as to reduce the damage to the cellulose and hemicelluloses during pulping. The guiding principle in these systems is creation of a countercurrent flow of the pulping chemicals and wood chips. Their aim is to keep the concentration of alkali lower and more uniform throughout the cooking process and also to minimize the concentration of dissolved lignin at the end of the cook. A major problem with these systems is that pulp yield can be substantially reduced. This is in contrast to oxidative delignification, where delignification to the same lignin content results in significantly higher pulp yields. The use of MCC or RDH to reduce the lignin content results in reduction of the organics in the effluent stream as much of the lignin removed in the later delignification is sent to the recovery boiler. This of course is also true of the oxidative delignification processes. Both MCC and RDH systems are employed in many mills. Others rely on oxidative delignification using either oxygen or ozone to carry out the delignification from about 5% to less than 1% before transfer to the bleach plant.

Other Alkaline Pulping Processes

While it can no longer be regarded as a recent innovation, the use of anthraquinone (AQ) as a pulping catalyst has been developed further in recent years. It is usually used to enhance the effectiveness of kraft pulping; in some instances it has also been used with soda pulping, that is, without sulfur.

Recently, it has been shown that octahydrodimethyl-anthraquinone (ODiMAQ) is a much more effective delignification catalyst than is AQ. It is thought that ODiMAQ can be produced for about the same cost per unit weight as AQ. It is anticipated that soda–ODiMAQ cooking will be more attractive economically than soda–AQ. If oxidative delignification is introduced early in the delignification process, at the level of 8–10% lignin content, it may well be that the soda–ODiMAQ treatment is more effective than soda–AQ. If followed by oxidative delignification, it may become an option for sulfur-free pulping.

Polyoxometalates in Pulping

Over the past decade a new oxidative delignification system has been developed. Although it has been developed primarily in the context of bleaching, it is likely to be useful in early delignification. Here it would be a replacement for MCC, RDH, oxygen, or ozone delignification. It is based on the use of polyoxometalates (POMs) as regenerable selective oxidants.

The POMs are designed to mimic the action of oxidative enzyme systems that can oxidize and solubilize lignin without damaging the cellulose. They are inorganic cluster anions that are similar to the structures of many minerals. Certain of these POMs in aqueous solution are very selective in oxidizing the lignin of kraft pulp under conditions that result in little damage to the cellulose and hemicelluloses. To minimize damage to the pulp, the delignification must be carried out under anaerobic conditions. After reaction with the pulp, the solution can be filtered off and regenerated. Some of the POMs that are very effective in delignification can also be readily regenerated with oxygen under relatively mild conditions. During the regeneration, these same POMs act as oxidation catalysts for the wet oxidation of the solubilized lignin and carbohydrate fragments to carbon dioxide and water. The reduced POMs are readily washed from the pulp and can be recovered for regeneration with very little loss. Thus, the overall POM delignification process is a two-stage process that selectively delignifies pulp in water using oxygen as the only consumable in the regeneration process; there are no liquid waste or toxic byproduct steams. Of the POMs studied to date, $Na_6[SiV_2W_{10}O_{40}]$ best fulfills the requirements of both the delignification stage and the regeneration and wet-oxidation stage. In multicyclic experiments, it has been found to be thermodynamically stable in both stages. Other POMs are currently being synthesized and evaluated for their effectiveness.

In studies of high-lignin pulps, it has been shown that significant increases in yield can be achieved by stopping kraft or soda–AQ cooks at relatively high lignin content (8–10%) and delignifying the pulps further to bleachable levels with aqueous solutions of a POM. POM delignified kraft pulp was found to give higher yield and stronger pulp than did POM-delignified soda–AQ pulp. It was thought that a higher level of AQ than that used (0.20%) might yield results equivalent to those of kraft pulp.

In a recent study, lodgepole pine chips were cooked to a lignin content near 9% with soda–ODiMAQ and then further delignified to a lignin content of about 4% with aqueous solutions of POM. The yield and strength results from these pulps were then compared with previous results from kraft and soda–AQ cooking of the same wood followed by delignification to the same lignin levels with the same POM. Favorable comparisons were also made with pulps produced from the same chips and delignified to about 4% lignin content by single-stage kraft, soda–AQ, and soda–ODiMAQ methods.

Although a considerable amount of work has been done on suppressing the odor emitted from the kraft process, the problem still persists. At some future date, the public is likely to demand that the kraft process be abandoned. Then the soda–ODiMAQ pulping followed by the POM delignification system is a feasible alternative. The pulp yield is significantly higher than that of the kraft process and the pulp strength, although somewhat less than that of kraft pulp, is more than adequate. Soda–AQ followed by POM delignification may also be feasible, although since AQ and ODiMAQ are equivalent in cost, based on overall yield data available at present, soda–ODiMAQ may be preferred.

Bleaching Chemical Pulps

The increased emphasis on reducing the environmental impact of pulp bleaching has led to exploration of the use of enzyme systems. In an effort to achieve this goal, research has increased toward enzymatic treatments. There are two fundamental approaches: the first is to enhance the removal of lignin by traditional bleaching chemicals. The application of xylanases in commercial systems is indicative of the promise of this approach. The second approach has been to use enzymes that act directly on lignin. The work here has focused largely on manganese peroxidase- and laccase-mediator systems. There are currently economic limitations to their commercial implementation. Additionally, POMs are being developed as inorganic analogs to enzymes in the direct oxidation of lignin.

Polyoxometalates in Bleaching

It has been shown that POMs can be used to delignify even high-lignin pulps to very low-lignin contents without excessive damage to the pulp. Only a single brightening stage would be required to attain high brightness after POM delignification. Based on present knowledge, it seems that the POM bleaching process is well adapted to facilitate the TCF kraft mill and bleach plant. Only effluent from the final brightening stage would go to the kraft recovery cycle. The POM delignification and regeneration/wet-oxidation cycle would be self-contained and would not contribute effluent to the kraft recovery cycle. This would either increase pulp mill capacity or reduce the size of the required kraft recovery furnace. POM bleaching is a novel technology that may revolutionize the bleaching of chemical pulps.

Xylanase Treatment

The application of xylanases to fibers between chemical pulping and the bleaching sequence is being rapidly implemented in mills worldwide. This has occurred for many reasons. Xylanase treatments can be implemented successfully with softwood, hardwood, and other lignocellulosic pulps. Reduced chemical loads are required for the bleaching sequence; if chlorine or chlorine dioxide is used, effluent properties, such as aromatic organic halides (AOX), chemical oxygen demand (COD), and color are reduced. Higher-brightness ceilings can be reached. Implementation of xylanase treatment into current industrial bleaching sequences can be done without extensive capital costs.

In general, the xylanase treatment is placed after the pulping and oxygen delignification steps and prior to chlorine, chlorine dioxide, and hydrogen peroxide steps; mills have implemented xylanase before or after ozone bleaching stages. In general, the higher the lignin content is prior to the xylanase application, the greater the reduction on subsequent chemical consumption or brightness gain. If hydrogen peroxide will follow, the xylanase treatment can be combined with chelation. Although the optimum reaction conditions vary with different xylanases, the pH generally lies between 4 and 9, with the temperature between 40 and 80°C. The xylanase is generally applied as a concentrated liquid at a rate near 100 ml per ton of pulp; too much can cause yield losses. Recent work has also found that mixtures of xylanases can have an improved effect. Most of the problems encountered with the xylanase treatment in mills have been due to poor mixing, reactor channeling, or poor pH and temperature control.

There are several proposals for the mechanism of xylanase efficacy. Xylanase may remove from the pulping process the reprecipitated xylans that have covered the lignin and limited access of subsequent bleaching chemicals. Or the removal of residual xylan in the cell walls may allow entrapped lignin to diffuse more easily out of the pulp fiber. Additionally, xylanases may play a role in altering lignin–carbohydrate bonding or in removing hexyneuronic acid groups.

Oxidative Enzyme Treatments

The extracellular ligninolytic enzymes of white-rot fungi have been the focus of significant development efforts over the past several years. These include lignin peroxidases (LiP), manganese peroxidases (MnP), and laccase, which can be used to replace chemical bleaching stages. While these enzymatic treatments do not usually brighten pulp (the pulp, in fact, often becomes darker after treatment) they do increase the effectiveness of subsequent brightening stages.

Manganese peroxidases are used in conjunction with hydrogen peroxide and manganese. Some pulps do not require additional manganese as they either already contain a sufficient amount of accessible manganese or chelators can be added to liberate sufficient amounts for full activity. Manganese and lignin peroxidases need a hydrogen peroxide source to be effective. Problematically, however, too high a level of hydrogen peroxide can inactivate these peroxidases, so glucose oxidase systems have been studied recently in order to generate low levels of hydrogen peroxide continuously. While these enzymes have become more available, an economical source for industrial application in pulp and paper has yet to be found.

Laccases work with oxygen and a mediator, a low-molecular-weight compound. These laccase-mediator systems (LMS) can achieve 40–60% delignification of kraft pulps. Researchers have commonly used 2,2′-azinobis-(3-ethylbenzothiazoline-6-sulfonate) (ABTS), 1-hydroxybenzotriazole (1-HBT), and violuric acid (VA) as mediators, but they are very expensive and may deactivate the laccase over time. Other mediators, such as extractives from wood and transition-metal complexes, are currently being studied. Furthermore, different laccases react differently with mediators and multistage laccase treatments, each with different mediators, will remove more lignin.

Laccases have also been used for reducing the energy of mechanical pulping. Peroxidases and laccases have also been used to polymerize and copolymerize materials with lignocellulosic fibers.

Mechanical Pulping

Mechanical pulping includes all processes that fiberize the wood chips with little or no application of chemicals. Not surprisingly, they require a considerable amount of energy, and they generally result in damage to the fibers. Thus two important goals are sought in advancing this technology. The first is to reduce the energy consumption in the mechanical refining. The second is to reduce the damage to the fibers. Recent developments have resulted in advances in both areas.

Biopulping

Biopulping is a process developed to improve the quality of mechanical pulps and significantly reduce the electrical energy required to pulp wood chips. High-yield mechanical pulps use wood resources efficiently, but consume considerable electrical energy during refining. The resulting pulp is considerably weaker than pulps produced by chemical pulping methods.

When wood chips are pretreated with an inoculum of fungi prior to refining, the wood chips become softened and more porous. Consequently, these treated chips are more easily broken apart when they are refined. The primary advantage of biopulping is the substantial savings in refining energy – as much as 30% depending on the wood species.

The biopulping procedure involves decontaminating wood chips with steam to eliminate competitive naturally occurring bacteria and fungi. Next they are sprayed with a dilute inoculum of a select fungus. Inoculated chips are incubated in an aerated chip pile for 2 weeks. Under warm, moist conditions the lignin-degrading fungi colonize chip surfaces and penetrate chip interiors with a network of hyphae. These treated chips are more readily broken apart during subsequent refining, saving as much as 30% of the electrical energy while producing more flexible, intact fibers compared to refining untreated chips. Various white-rot fungi have been used for biopulping; however, *Ceriporiopsis subvermispora* has proven to be very competitive both on softwoods and hardwoods and is one of the best energy conservers. Because this fungus consumes some of the pitch contained in the wood chips, both the toxicity and biological oxygen demand (BOD) content of mill process water are decreased and these pulps are more responsive to oxidative and reductive bleaching chemicals.

Because biopulping produces a superior mechanical pulp, it can be considered a viable alternative to chemical pulping and is a less costly alternative for constructing new mills because it requires simpler equipment and produces an effluent with reduced BOD. No additional equipment is required for biopulping in mechanical pulping mills. However, equipment for asepsis and inoculation, such as a conveyor system, steam, and inocula delivery, is needed.

Paper made from pretreated wood chips is stronger than paper made from conventional mechanical pulp and displays better optical properties, except brightness. Biopulping has been demonstrated successfully in mill trials in the USA and currently is being extensively trialed in a South American mill.

RTS

Thermal mechanical pulp (TMP) is the most common way to produce mechanical pulp. Wood chips are presteamed and passed through a pressurized refiner at high consistency. While this conventional process produces an acceptable mechanical pulp, considerable energy is required and pulp brightness is decreased. Recently a new refining process has been perfected. It has been termed RTS; it shortens the *r*etention time, lowers the *t*emperature of chip pretreatment, which is followed by rapid *s*peed refining through specially configured refiner plates. Use of this process significantly reduces the energy requirement and improves the brightness and quality of the resulting pulp. Savings are realized primarily from decreased energy consumption, but the decreased bleach requirement and higher-quality pulp also contribute to the desirability of this process.

Fiber Modification

In addition to the various innovations in fiberization of wood chips into pulps, a number of advances in the technology of fiber preparation have been reported. A few of these are included here. The first is related to enhancing the opacity of fibers through deposition of pigment particles within the papermaking fibers prior to formation on the paper machine. Two others are related to enhancing the recyclability of pulp fibers.

Fiber Loading

Fiber loading is a process for incorporating calcium carbonate made *in situ* and deposited within the lumen and cell walls of refined wood fibers during papermaking. This process requires two steps. First calcium hydroxide (hydrated lime) is mixed into moist pulp at high consistency. This alkaline mixture is then reacted with carbon dioxide within a pressurized refiner at ambient temperature. Calcium carbonate precipitates inside and on the surfaces of pulp fibers, where it is held tenaciously during subsequent papermaking.

Calcium carbonate is an important component of printing and writing papers. Papermaker's carbonate contributes opacity, smoothness, and brightness to high-quality paper; this filler also replaces some of the costly bleached kraft fiber.

Large paper mills often install a satellite plant on site to manufacture precipitated calcium carbonate (PCC) for their use. In conventional papermaking, a suspension of PCC is added to the pulp slurry prior to entering the headbox of the paper machine. Calcium carbonate added in this manner is located primarily between pulp fibers when made into paper. Fillers, such as PCC, interfere with fiber bonding essential to paper strength. Therefore, there is a limit to how much filler can be added without compromising the strength of paper.

In contrast, pulp fiber loaded with calcium carbonate has several distinct advantages over the conventional method of direct addition of PCC. Because a portion of the calcium carbonate formed during fiber loading is located within pulp fibers, more filler can be incorporated than by direct addition of PCC without losing paper strength. More filler incorporated within a paper furnish also reduces the amount of energy required to dry the paper.

Fiber loading has been demonstrated on mill scale. The only additional equipment required for manufacture is a pressurized chamber for introducing and reacting the carbon dioxide. Because the starting materials, hydrated lime and carbon dioxide, are inexpensive, this method of calcium carbonate production is cost-effective. Fiber loading can be used in small mills where a satellite PCC plant is not economically feasible.

All types of wood fibers can be fiber-loaded; this includes recycled fiber. Another benefit of paper made from fiber-loaded pulp is that the carbonate filler is better retained with the fiber during recycling than conventionally made paper. Disposal of sludge accumulated from paper fillers removed during recycling has become a major disadvantage of recycling mills. Fiber-loaded paper can minimize sludge production.

Enzymatic Deinking

Xerographic and laser-printed papers need to have the inks removed prior to recycling, but they are difficult to deink using conventional methods. This has resulted in a lower recycling rate for these types of papers at a time when they are being produced at growing rates. Cellulases have been shown to remove these toners and other contaminants from waste-paper pulps. In treatments, they are combined with nonionic surfactants, such as polyethylene oxide, and mechanical action. Cellulases likely improve deinking through several complementary mechanisms. They remove fibrils from the fiber surfaces and facilitate the removal of toner particles. Cellulases also separate fibrils from toner particles, which reduces toner particle size and makes them more hydrophobic for easier removal during the flotation and washing stages that follow. Researchers have recently improved cellulase action by linking surfactants directly on to the enzyme's amino acid groups.

Cellulases have also been shown to increase the freeness and flexibility and reduce the coarseness of dried fibers. They can also improve sheet density and smoothness. Cellulase treatments of recycled fibers may also reduce disintegration time and increase the bleachability of low-quality, recycled paper. However, excessive treatment can erode the fiber surface and ultimately reduce pulp strength.

Cellulase enzymes are commercially available and are used increasingly in the paper-recycling industry.

Pressure-Sensitive Adhesive Modification

The use of pressure sensitive adhesives (PSAs) has increased dramatically in the last decade. Prompted, in part, by consumer demand, adhesives were formulated to be more user-friendly – at least in their application. The problem caused by many of the PSAs did not surface until they entered the recycled-paper stream. Usually attached to envelopes in the form of self-sealing envelopes, postal stamps, and address labels, the PSAs became commingled with high-quality printing and writing papers. When subjected to high repulping temperature, alkaline pH, and vigorous agitation, many adhesives become plasticized, fragmented, or dispersed, enabling them to pass through pressure screens intended to retain and separate them and other macrocontaminants from recycling furnishes.

Because the US Postal Service (USPS) is a major user of PSAs in the form of stamps, labels, and postal stationery, it introduced and funded a research initiative to assure that the PSAs used in USPS products were recyclable. A consortium comprising adhesive manufacturers, printers, and recyclers was formed. A 5-year research program was undertaken to examine the recyclability of numerous PSA formulations. The essential characteristics of PSAs that made them removable under typical recycling conditions were identified. New guidelines for new PSA formulations were developed for adhesive manufacturers. Acceptable PSAs remain intact, thus were removed primarily by pressure screening, under typical warm, alkaline conditions used in recycling. Adhesives that were successfully removed during processing in pilot plant trials by pressure screening, cleaning, and flotation were subsequently confirmed in recycling mill trials. This research resulted in recyclable PSAs for the USPS products. The guidelines are likely to be adopted by other manufacturers of paper likely to be recycled.

See also: **Papermaking**: World Paper Industry Overview. **Pulping**: Bleaching of Pulp; Chemical Pulping; Environmental Control; Mechanical Pulping.

Further Reading

Akhtar M, Blanchette RA, Myers G, and Kirk TK (1998) An overview of biomechanical pulping research. In: Young and Akhtar MRA (eds) *Environmentally Friendly Technolgies for the Pulp and Paper Industry*. New York: John Wiley.

Dence CW and Reeve DW (eds) (1996) *Pulp Bleaching: Principles and Practice*. Atlanta, GA: TAPPI Press.

Gullichsen J and Fogelholm CJ (eds) (1999) *Chemical Pulping*. Helsinki, Finland: Fapet Oy.

Kenealy WR and Jefferies TJ (2003) Enzyme processes for pulp and paper: a review of recent developments. In: Goodwell N and Schultz (eds) *ACS Symposium Series 845. Wood Deterioration and Preservation: Advances in Our Changing World*.

Klugness JH, Stroika ML, Sykes MS, *et al.* (1999) *Engineering Analysis of Lightweight, High-Opacity Newsprint Production by Fiber Loading,* 1999 TAPPI Papermaking Conference, March 1–4, Atlanta, GA.

Weinstock IA, Barbuzzi EMG, Wemple MW, *et al.* (2001) Equilibrating metal-oxide cluster ensembles for oxidation reactions using oxygen in water. *Nature* 414(6860): 191–195.

Physical Properties

W E Scott, Miami University, Oxford, OH, USA

Structural Introduction

Paper has existed for over 2000 years and during that time it has found a myriad of uses, each of which requires its own unique set of paper properties. For example, high-quality printing papers need to be smooth, bright, opaque, dimensionally stable, and have good ink absorption characteristics. Paper towels, on the other hand, need to be soft, water-absorbent, and have a certain amount of strength when saturated with water. Neither of the two needs to have the strength characteristics required of packaging papers. In this article we will describe the most common paper properties referred to by papermakers and converters in their daily operations. For convenience, these properties will be grouped into the following four categories:

1. Structural properties.
2. Mechanical properties.
3. Appearance properties.
4. Barrier and resistance properties.

Lastly, we will consider the effects of atmospheric relative humidity on paper properties. Details about paper property testing will not be presented here unless they are necessary to define a specific property. You are referred to the Further Reading section for information about testing instruments and procedures.

The Structural Characteristics of Paper

Structural characteristics describe how the fibers are arranged in a sheet of paper. The topics of interest are listed in **Table 1**.

Basis Weight and Grammage

Papermakers keep track of their production in terms of tons produced and sell their products either on a weight basis or an area basis. This practice gives rise to the definition of the basis weight of paper as the weight, in pounds, of a predetermined number of sheets of a specified size. The number of sheets is known as the ream size. The size of the sheet is known as the basic size. The most common ream size is 500 sheets. There are a variety of basic sizes, several of which are listed in **Table 2**.

The system for specifying basis weight is very cumbersome. A simpler approach is taken in the SI system of units where the weight of paper is

Table 1 Structural properties of paper

Basis weight and grammage
Thickness
Formation
Directionality
Two-sidedness
Porosity
Smoothness or roughness

Table 2 Examples of basic sizes

Paper grade	*Dimensions (in.)*
Book, bible, offset, blotting	25 × 38
Bond, ledger, mimeo, writing	17 × 22
Glassine, news, tissues, wrapping	24 × 36
Postcard, wedding, Bristol	22.5 × 28.5
Cover stock	20 × 26

Table 3 Typical basis weights and grammages of various papers

Paper grade	*Basis weight (lb)*	*Grammage (g m^{-2})*
Grocery bag, sack	30–60	49–98
Bond	13, 16, 20, 24	48, 60, 75, 90
Folder stock	100–225	163–366
Corrugating medium	26	127
Kraft linerboard	16, 33, 38, 42, 47, 69	127, 161, 186, 205, 229, 337
Tissue and toweling	10–35	16–57
Newsprint	30	49

Reproduced, with permission, from Scott WE and Abbott JC (1995) *Properties of Paper: An Introduction*, 2nd edn. Atlanta, GA: TAPPI Press.

expressed in terms of grams per square meter, or grammage. **Table 3** gives some typical values for the basis weight and grammage of different kinds of paper.

Thickness (Caliper) of Paper

The thickness, or caliper, of paper is defined as the perpendicular distance between the two principal surfaces of paper and paperboard under specified conditions. The thickness of paper and paperboard ranges from 0.0003 in. for capacitor paper to 1 in. or greater for some construction boards.

Thickness is a very important property for the end-use and converting requirements of most grades of paper and paperboard. For example, the overall thickness of a book is directly related to the thickness of the paper used. The thickness of index cards and file folders determines how many can be filed in a given space. Thickness uniformity is also very important for most papers.

Formation, Directionality, Two-Sidedness

Paper is made from a mixture of heterogeneous particles having different shapes, densities, and chemical compositions. This mixture is subjected to a sheet-forming process where the flows are accelerated and drainage and filtration occur in one direction. The sheet is pulled in one direction during drying and substances are added to the outer surfaces of the formed sheet. In addition, the two-dimensional nature of a paper web imposes severe constraints on the different ways that sheet components can arrange themselves. The specific paper properties related to material distribution are called formation, directionality, and two-sidedness.

Formation The overall uniformity with which fibers and other solids particles are distributed in paper determines the formation of paper. Formation is an important property for printing papers—poor formation produces poor print quality. In the extreme, poor formation can also influence the strength of paper and its ability to absorb fluids uniformly.

Directionality Many paper properties are directional in nature. In other words, a given paper property might have one value when measured along one direction of the sheet and another value when measured at right angles to the first direction. The source of this behavior lies primarily in the relative alignment of fibers in the paper web. Few, if any, fibers have their axes aligned in directions other than parallel to the plane of the sheet. In addition, within the plane of the sheet, a majority of the fibers will often have their axes oriented toward the direction of forward movement on the paper machine. This preferential orientation arises as a result of accelerating forces exerted on the fibers in the headbox and on the forming section of the paper machine. Tension exerted on the sheet during drying also serves to enhance the effect. The terms 'machine direction' or 'grain direction' are assigned to the direction of paper parallel to the direction of paper machine travel, while the direction at right angles to the machine direction is called the cross-direction, cross-grain, or against-the-grain direction. The major influence of directionality lies in its effect on many mechanical properties of paper.

Folding, creasing, and scoring can be done more readily along the grain direction. The higher machine direction stiffness is taken advantage of in the design of file folders and some types of packages. Because the directionality of paper is so important in converting operations, the grain direction of sheets will always be indicated on the container of paper shipped from the mill to the converter. With roll stock, there is no ambiguity as to which direction is the machine direction.

Two-sidedness In addition to influencing the fiber orientation in paper, the manufacturing process can lead to nonuniform distribution of components through the thickness, or z-direction, of the sheet. Near the bottom side of the sheet, which is in contact with the fourdrinier wire during web formation and which is referred to as the wire side, there is a relatively low concentration of filler and fines. As you move through the sheet toward the top side, which is called the felt side, the filler and fines content increases. The outer surfaces represent the two extremes in component distributions and have very different characters.

The differences between the wire and felt sides of paper are significant due to their influence on other properties. As a rule, the gloss and smoothness of the two sides will be different. The two sides act differently in printing and it is important to identify them when setting up printing presses.

Porosity of Paper

Ordinary papers are about 50% air, by volume. Some of the air is present inside fibers, but most of it resides in pores within the sheet structure whose diameters are on the order of 1 μm (1×10^{-6} m). The ratio of pore volume to total volume is called the porosity of the sheet. This property, while being fundamentally very important, is rarely measured in papers except occasionally in laboratory studies. However, a related property, air permeability, is often determined. Air permeability is defined as the property of a paper that allows air to flow through it under a pressure difference across the sheet. It is a structure-related property depending on the number size, shape, and distribution of pores in the sheet. It should be emphasized that air permeability is not a measure of porosity and the two terms should not be used interchangeably.

Smoothness or Roughness of Paper

It is common to say that paper has a 'smooth' or 'rough' texture, meaning that the surface irregularities are small or large. A wide range of surface textures are available in papers today, ranging from very smooth, highly calendered papers to rough, uncoated grades of paper produced from coarse softwood fibers.

The quality of a paper surface is often referred to as its finish, which may be spoken of as high or low, good or poor, smooth or rough. Finish combines all those characteristics encompassed by the senses of sight and touch and, although a useful term, is an indefinite one from a technical standpoint. Appearance and mechanical qualities may also contribute to the perceived smoothness of paper.

Smoothness is a very important property in a wide variety of paper. Some papers are intentionally given very rough surfaces, while others must be very smooth, and still others must be carefully controlled somewhere in between. Smoothness is important in printing papers and in paper that serves as coating rawstock. It is possible for a paper to be too smooth and exhibit a tendency to slip in converting processes.

The Mechanical Properties of Paper

A sheet of paper, by virtue of its structure, exhibits the same general mechanical attributes as other structures encountered by the engineer in the field of construction materials. The term 'strength properties' is often used to refer to these characteristics of paper. They determine the durability and resistance to applied forces exhibited by paper during manufacturing operations, converting processes, and end-use performance.

While the fundamental mechanical properties of paper have been studied extensively, the more useful mechanical properties are applied in nature and are used for quality control during the manufacture and converting of paper and for specification of the specific qualities associated with each paper grade. **Table 4** lists the most common examples of such mechanical properties.

The mechanical properties commonly adopted by the paper industry are designed to yield values representing the resistance of a sheet of paper to stresses of various kinds at the point of paper rupture. The tests are arbitrary, as shown by the different specimen sizes, conditions, and instruments specified by the various test methods.

Tensile Properties

In a tensile strength measurement, a paper specimen of defined width and length is clamped between two jaws. The test instrument then causes the separation distance between the two jars to increase, which exerts a tensile stress (pulling stress) on the specimen. A mechanism is provided which indicates the tensile force when the specimen ruptures. This force is referred to as the tensile breaking strength (**Figure 1**). Most instruments can also indicate the stretch and tensile energy absorption of the specimen simultaneously with the tensile breaking strength.

Table 4 Common mechanical properties

Tensile properties
• Tensile breaking strength
• Stretch
• Tensile energy absorption
Bursting strength
Tearing resistance
Folding endurance
Bending stiffness

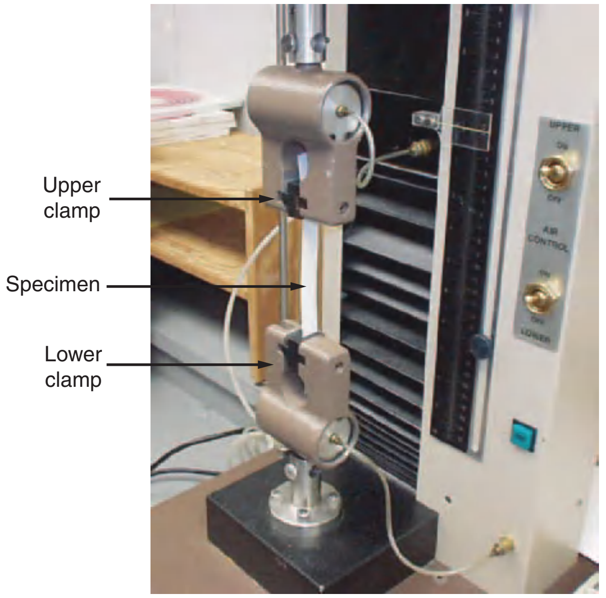


Figure 1 Illustration of a test specimen clamped in a tensile tester. During a test the specimen is stretched as the upper clamping jaw moves away from the fixed lower clamp. The tensile force being applied at the instant of rupture is called the tensile breaking strength. (TAPPI test method T 494 om-88.)

Tensile Breaking Strength

Tensile strength is a direct indication of the durability and potential end-use performance of a number of papers that receive direct tensile stresses in use, such as wrapping, bag, gummed tape, cable strapping, twisting papers, and printing papers. A certain minimum tensile strength is required of any paper that undergoes a web converting operation where it is subjected to tensile stresses while being pulled through the process. Printing papers are primary examples.

Stretch

The stretch of paper at rupture is usually expressed as a percentage of the original length of the test specimen. Stretch properties are important because they affect the way a paper withstands sudden impacts.

Tensile Energy Absorption

A tensile specimen absorbs energy during a tensile test. This phenomenon is known as tensile energy absorption (TEA) and it is directly related to a paper's ability to withstand sudden strains without breaking. TEA is strongly influenced by stretch and the most common way to increase the TEA in paper is to increase its stretch.

Tensile breaking strength, stretch, and TEA are known as directional tests because their values depend upon the direction (machine-direction versus cross-direction) in which a test specimen is cut.

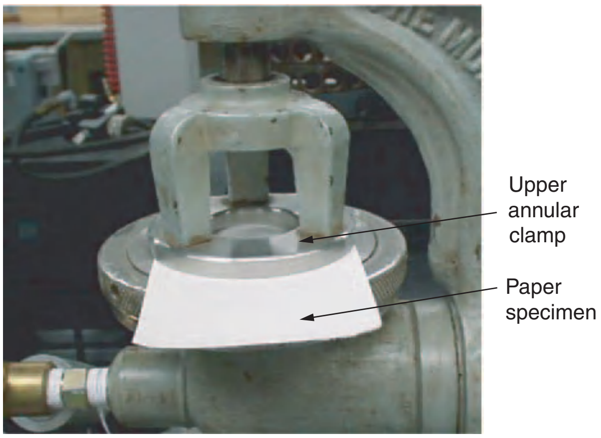


Figure 2 Bursting strength test. During the test a rubber diaphragm expands against the clamped test specimen causing the specimen to bulge into the annulus in the upper clamp. The test value is taken to be the pressure being exerted against the rubber diaphragm at the point of specimen rupture. (TAPPI test method T 403 om-91.)

Bursting Strength

Bursting strength is defined as the pressure required to rupture a paper specimen when it is held between annular clamps and subjected to pressure from one side. This causes the specimen to deform into an approximately hemispherical shape until failure occurs by rupture (**Figure 2**). The bursting strength test is one of the oldest tests used by the paper industry. The best use of the burst test is as a convenient, general indicator of strength or toughness of paper.

Tearing Resistance

The most common tearing resistance property used in the paper industry is called Elmendorf tearing resistance, after the specific instrument employed by the industry. The Elmendorf test measures the mechanical work required to continue a tear – which has already been started – through a fixed length of specimen using an Elmendorf tear tester. The mode of the tear is out-of-the-plane of the paper. **Figure 3** illustrates the tester.

The Elmendorf tear is particularly valued as a test for paper and paperboard, which will be subjected to tearing strains during converting or in end-use. Bags, wrapping papers, tissue papers, book, magazine and newsprint paper, and paperboard for bottle and can carriers are all papers or products where Elmendorf tear values are deemed important.

Elmendorf tearing resistance is affected by the direction in which the test is run, with the cross-direction tearing resistance being higher than the machine-direction tearing resistance in most instances.

Figure 3 Internal tearing resistance tester. A paper test specimen is clamped in a segmented clamp; the right side is fixed to the instrument base and the left side is attached to a segmented pendulum. The test specimen is slit along a line between the two clamp segments prior to the test. Thus, the test measures the force required to continue an internal tear within the paper specimen. During a test, the pendulum is released and swings upward (left to right in the figure), carrying the left clamp segment with it. This motion tears the paper specimen in a direction perpendicular to the plane of the paper in its original clamped configuration. The resistance exerted by the tearing specimen against the swinging pendulum is taken to be the internal tearing resistance. (TAPPI test method T 414 om-88.)

Folding Endurance

Many papers, such as currency and map papers, undergo repeated folding during end-use. The requirement here is one of durability or resistance to wear over a long period. In these instances, the folding endurance test is applicable.

As a rule, the machine-direction folding endurance is higher than the cross-direction folding endurance. Different papers exhibit a wide range of folding endurance values ranging from essentially zero double folds for very weak papers such as facial tissues to several thousand double folds for currency paper. **Figure 4** contains a picture of a paper specimen clamped in a folding endurance tester.

Bending Stiffness

Stiffness is defined as the resistance to a force causing a member to bend. Stiffness is very important to the end-use performance of many papers. For example, file folders and index cards must support themselves upright during use. Playing cards, posters, cups, and plates are also examples of paper that must have good stiffness in use. Stiffness is one of the most important mechanical properties of paperboard used in packaging. Packages must resist deformation, or bulging, when being filled and when the contents settle in a package while it is sitting on a shelf in the store. Folding cartons and corrugated shipping containers must also withstand bending stresses from loads imposed on them from containers stacked above.

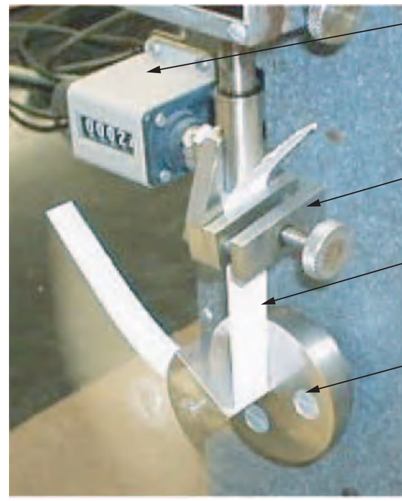


Figure 4 Folding endurance. In the folding endurance test the paper specimen is clamped between a rotating lower clamp and a stationary, spring-loaded upper clamp. The specimen is then subjected to a continuous folding motion of $\pm 135^\circ$ away from the unfolded configuration at the lower clamp while under tension from the upper clamp. The test value is taken to be the number of complete folds the specimen will undergo without rupture. (TAPPI test method T 511 om-96.)

Table 5 Factors affecting paper stiffness

Major	Thickness
	Young's modulus of pulp
	Restraint during drying
	Moisture content
	Surface treatments (wax, starch)
Minor	Fiber–fiber bonding
	Fiber orientation

A number of factors affect stiffness, several of which are listed in **Table 5**.

Stiffness can be thought of as a function of the product of Young's modulus and the thickness raised to the third power. Thus, thickness is a most important factor in controlling stiffness. As much as a threefold increase in machine direction stiffness can be achieved by increasing the tension on the sheet during drying. Cross-direction stiffness will be decreased by this action, however. Conversely, increasing the moisture content of paper will significantly decrease its stiffness. **Figure 5** illustrates a commonly employed stiffness-testing instrument.

Since stiffness is greatly affected by thickness, it is not surprising that paperboards exhibit by far the highest stiffness values, while tissue and toweling papers are the least stiff. In fact, a prerequisite for soft papers is that they have very low stiffness.

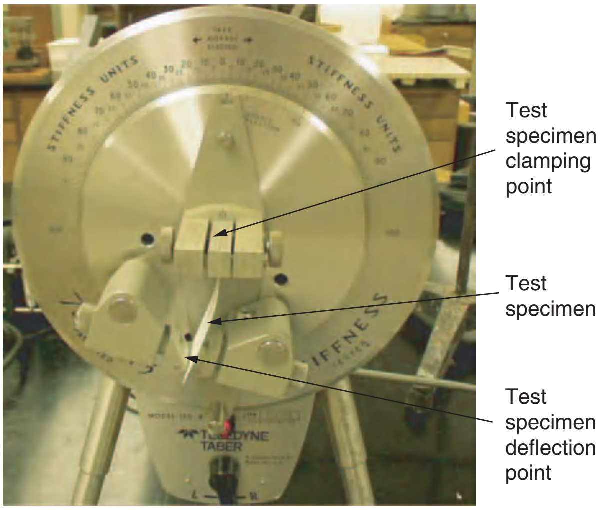


Figure 5 Taber stiffness test. The Taber stiffness test determines the bending moment necessary to deflect the free end of a vertically clamped specimen 15° from its center line when a load is applied 50 mm away from the clamp. This test is most commonly applied to paperboard. (TAPPI test method T489 om-92.)

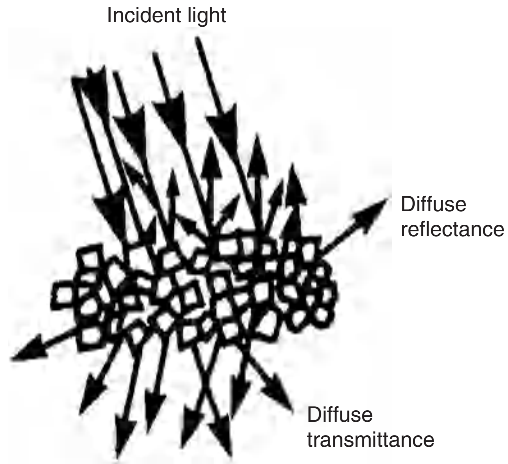


Figure 6 Schematic representation of diffuse reflectance and diffuse transmittance. Reproduced, with permission, from Scott WE and Abbott JC (1995) *Properties of Paper: An Introduction*, 2nd edn. Atlanta, GA: TAPPI Press.

The Appearance Properties of Paper

In this section, we will consider the appearance properties of paper, called transparency, opacity, brightness, color, and gloss.

A small piece of paper contains several million fibers and millions of small pieces of fibers that were torn away from the pulp fibers during the refining process. When illuminated with a beam of light, the fibers, fines, and filler particles in a sheet of paper cause some of the light rays to be reflected in all directions from the surface of the sheet. Since there are a great number of reflecting particles within the sheet, a great amount of light reflection occurs inside the sheet also. As a result of these multiple reflections, the transmitted light rays that emerge from the other side of the sheet and the reflected rays that emerge back out of the surface of the sheet are not parallel, but travel in all directions. This is indicated schematically in **Figure 6**.

The name given to this type of behavior is diffuse scattering. Hence, most of the light incident on white bond paper is either diffusely reflected or diffusely transmitted since the individual fibers and filler particles are essentially colorless. Materials that diffusely transmit light are said to be translucent. For white papers, the properties opacity, brightness, transparency, and gloss are all functions of the diffuse reflectance and diffuse transmittance of visible light. Colored papers involve light absorption, the topic to be discussed next.

The Color Properties of Paper

Color is used for identification, to attract attention, and to emphasize distinguishing characteristics in commodity papers and packaging. All white papers contain small amounts of dyes called 'tinting dyes.' These colorants produce a slight colored shade, or tinge, that is distinctive of a particular product.

The color of a sheet of paper is determined by the light absorption characteristics of its components. Dyes and colored pigments accomplish nearly all of the light absorption in colored papers. If you plot the diffuse reflectance from a thick pad of colored paper at different wavelengths across the visible spectrum, the resulting curve is called a spectral reflectance curve. Spectral reflectance curves for bleached, uncolored pulp, and the same pulp separately dyed with red, blue, and yellow dyes appear in **Figure 7**.

As is shown in the figure, the principal effect of the dyes is to cause the characteristic spectral reflectance curve of the white pulp to shift, and thus to cause its intrinsic color to change. By selecting industrial dyes having the desired light absorption characteristics, it is possible to create or match a full range of colors for any substrate within the physical limitations of the system involved.

Papermaker's Brightness

Another very important appearance property is called papermaker's brightness. True brightness refers to the lightness or overall spectral reflectance of paper, the energy distribution of the illuminant, viewing conditions and the characteristics of the viewer. Papermaker's brightness, on the other hand, is based on a measurement of the reflectance by white

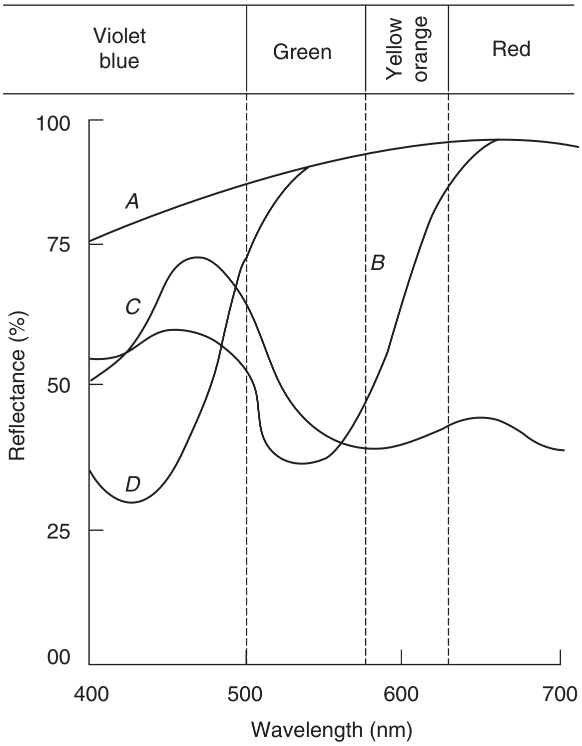


Figure 7 Typical spectral reflectance curves for dyes and undyed pulp. *A*, Bleached, uncolored pulp; *B*, *A* plus red dye; *C*, *A* plus blue dye; *D*, *A* plus yellow dye. Reproduced, with permission, from Scott WE and Abbott JC (1995) *Properties of Paper: An Introduction*, 2nd edn. Atlanta, GA: TAPPI Press.

or near-white papers at a single wavelength, 457 nm. Papermaker's brightness is primarily a measure of freedom from pulp yellowness associated with the presence of lignin and other impurities left by incomplete bleaching.

Unbleached kraft pulp will typically have a papermaker's brightness of 25–30%, while fully bleached kraft pulp will fall in the 80–90% range, depending upon its intended use. Newsprint papers have brightness typically in the 65–75% range.

Gloss

Gloss is the characteristic of a paper surface that causes it to reflect light at a given angle of reflection in excess of the diffuse reflection at that angle. Gloss is the degree to which the surface simulates a perfect mirror in its capacity to reflect incident light. In the case of a mirror, almost all of the light falling on the surface is reflected at an angle equal to the angle of incidence. This is known as specular reflection. Conversely, a completely matte surface will reflect the incident beam in all directions and the surface will appear the same from every angle.

Gloss measurements on paper have been made at many different angles of incidence, but most measurements on paper are made at an angle of 75° from the normal. Highly glossy papers, such as waxed papers, are measured at 20° from the normal. **Table 6** indicates the gloss values measured for a variety of papers.

Table 6 The gloss of different papers compared to polished black gloss as 100

Type of paper	*Gloss*
Lacquer-coated papers	96
Magazine cover	70
Machine-coated book	51
Supercalendered book	30
English finish book	12
Typewriter bond	6
Household waxed paper	57[a]
Bread wrapper	63[a]

[a] Measurements made at 20° from the normal. All the rest were made at 75° from the normal.

Reproduced, with permission, from Scott WE and Abbott JC (1995) *Properties of Paper: An Introduction*, 2nd edn. Atlanta, GA: TAPPI Press.

Opacity and Transparency

Transparency ratio is the preferred method of evaluating highly transparent materials, while opacity measurements are more suitable for relatively opaque papers.

Transparency

Transparency is important in tracing, reproduction, and packaging papers, to name a few. A completely transparent paper would be one that transmitted, without scattering, all of the light falling on it, and a clear view of an object would be had when the paper was placed between the object and a viewer, regardless of the distance between the paper and any object being viewed through it.

The transparency ratio of a paper, which is a true measure of transparency, is the ratio between the parallel transmittance of light and the total transmittance of light. Glassine, the most transparent paper, exhibits 10–40% parallel transmittance for a total transmittance of 60–85%. On a comparable basis, say 65% total reflectance, a tissue paper would have only 3% parallel transmittance.

Opacity

A perfectly opaque paper is one that is absolutely impervious to the passage of all visible light. The black paper used to wrap photographic films can properly be called 'opaque,' and most paperboards are opaque for all practical purposes. Many papers cannot be classified as opaque, yet opacity is a very important property for them. Printing, bond, and writing papers are good examples where this is true.

Opacity is determined by the amount of light transmitted by a paper. If all of the incident light is transmitted and none is reflected or absorbed, then the opacity will be zero. If no light is transmitted and all of it is reflected or absorbed, the opacity will be 100%. Most papers fall between these two extremes.

The Barrier and Resistance Properties of Paper

Introduction

Papers often come into contact with liquid water while being converted into final products or during their end-use. If it is desired that absolutely no water pass through the web, then the paper is said to exhibit barrier properties. Many packaging products must meet this requirement. Since paper webs are porous, some other material must be combined with it to produce the desired barrier characteristics. Plastic and wax coatings and metal foils are examples of materials that are employed for this purpose.

On the other hand, if it is necessary that a paper only retard or slow down the rate of penetration of liquid water in order to function properly, then the paper is said to exhibit resistance properties. Writing papers, offset printing papers, and coating base stock papers are examples of papers that must resist the penetration of liquid water in order to function effectively. However, if these papers come into contact with water over a long time period, then they will allow its penetration. Hence, they do not have barrier properties.

Another important group of papers must be able to absorb large amounts of water rapidly in use. These are called waterleaf papers. Examples are paper towels, facial tissues, filter paper, and blotting papers.

Table 7 lists the most important factors that affect water penetration rate in paper.

Paper webs are porous, having micron-size pore diameters. Those pores that connect the upper and lower sheet faces provide pathways for liquid penetration. The degree of wetting of fibers by liquids is expressed by the angle between the liquid and solid surface when the two come into contact. **Figure 8** illustrates this phenomenon.

A certain time is required for a liquid to wet paper. This time is called the wetting time. Wetting times ranging from 0.005 s to 0.3 s have been measured for different papers and liquid water.

Paper specimens increase in size (swell) when brought into contact with liquid water. The ratio of such swelling in the different sheet directions has been reported to be 1:2:50 for the machine-direction, cross-direction, and thickness-direction, respectably. This behavior will alter the internal pore structure of paper and affect the interactions that occur between the sheet and water.

It has been hypothesized that the diffusion and subsequent condensation of water molecules contained in the water vapor accompanying the advancing liquid water front aid in the penetration of liquid water through paper. It is expected that this will be a second-order effect that is only important in very dense papers.

Table 7 Factors that influence the rate of penetration of fluids into paper

Porous structure of the web
Degree of wetting of fibers by penetrating liquid
Wetting time
Fiber swelling
Diffusion

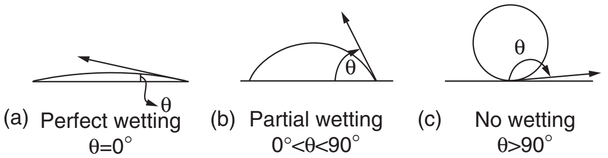


Figure 8 The different contact angles associated with perfect wetting, partial wetting, and no wetting. Reproduced, with permission, from Scott WE and Abbott JC (1995) *Properties of Paper: An Introduction*, 2nd edn. Atlanta, GA: TAPPI Press.

The Influence of Environmental Conditions on Paper Properties

Light, temperature, moisture vapor, and other atmospheric components can all affect paper properties. Of these factors, moisture vapor is by far the most important. Since moisture content can have a significant effect on paper properties, paper testing is usually done under well-defined atmospheric conditions – for example, 23°C and 50% relative humidity in the USA.

The effect of moisture content on mechanical properties is quite complex, as illustrated in **Figure 9**. The figure illustrates that nearly all possible behavior is observed. However, practically all mechanical properties will be adversely affected by relative humidities above 60%.

Changes in moisture content also affect the dimensional characteristics of paper. **Table 8** lists the major effects observed.

Paper expands in all directions when its moisture content increases, with the greatest expansion

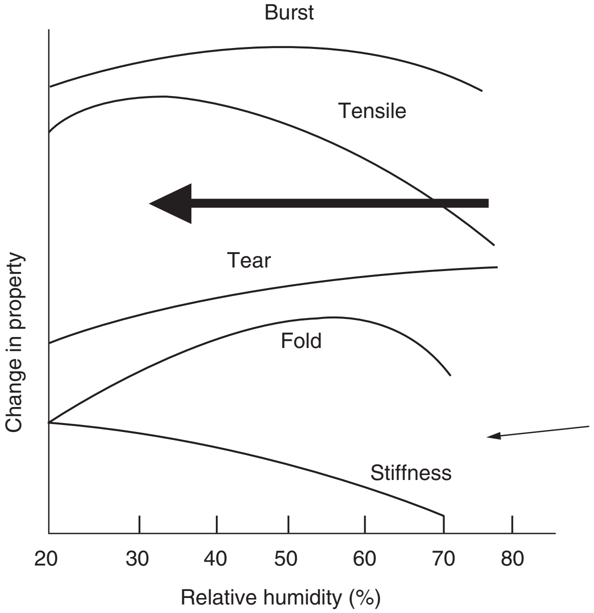


Figure 9 Effects of relative humidity on the mechanical properties of paper. Reproduced, with permission, from Scott WE and Abbott JC (1995) *Properties of Paper: An Introduction*, 2nd edn. Atlanta, GA: TAPPI Press.

Table 8 Influence of moisture content on the dimensional stability of paper

Expansion and contraction
Cockle
Curl
Wavy edges
Tight edges

occurring perpendicular to the plane of the sheet. Cockle refers to the 'puckering' that often accompanies an increase in moisture content. Curl refers to the tendency to 'roll up' into a tube exhibited by many papers as their moisture content increases. Wavy edges and tight edges are ramifications of curl that occur in stacks of paper where moisture content changes occur mostly at the exposed edges of sheets.

The dimensional changes listed in **Table 8** may be reversible or irreversible. In the latter case, they are almost always undesirable and it is necessary to guard against changes in sheet moisture content during conversion or end-use.

Conclusion

This concludes our overview of the most common paper properties important in the manufacture and use of paper. It was pointed out that paper has a highly complex structure and cannot be rigorously treated in fundamental terms. Consequently, papermakers and end-users rely on more empirical and arbitrary ways to characterize the common paper properties employed in manufacturing control and end-use performance. These properties can be grouped into the four categories of structural, mechanical, appearance, and resistance properties that provided a framework for this discussion. Many paper properties are also affected by atmospheric humidity and temperature conditions and the papermaker must take this into account when controlling the final moisture content of manufactured paper. End-users also often control the temperature and relative humidity of their operations because of this.

The intention of this discussion was to provide an introductory overview of the most common physical properties of paper. More detailed treatments can be found in the Further Reading section. In addition, there are other more specialized properties, such as electrical conductivity, that could not be discussed here. You are also referred to the Further Reading section for treatments of these subjects.

See also: **Packaging, Recycling and Printing**: Packaging Grades. **Papermaking**: Overview; Paper Grades; Paperboard Grades; Tissue Grades; World Paper Industry Overview.

Further Reading

Biermann CJ (1996) Paper and its properties. In: *Handbook of Pulping and Papermaking*, 2nd edn, pp. 158–189. London: Academic Press.

Conners TE and Banerjee S (eds) (1995) *Surface Analysis of Paper*, pp. 1–350. London: CRC Press.

Hahn LD (1992) *Testing Guidebook*, pp. 1–40. Atlanta, GA: TAPPI Press.

Kocurek M and Kouris M (eds) (1992) *Pulp and Paper Manufacture: Mill Control and Control Systems – Quality and Testing, Environmental, Corrosion, Electrical*, vol. 9, 3rd edn, pp. 1–233. Atlanta, GA: Joint Textbook Committee of the Paper Industry.

Levlin J-E and Soderhjelm L (eds) (1999) *Papermaking Science and Technology. Pulp and Paper Testing*, vol. 17, Helsinki, Finland: Fapet Oy.

Mark RE, Habeger CC, Borch J, and Lyne MB (eds) (2002) *Handbook of Physical Testing of Paper*, vols. 1 and 2. New York: Marcel Dekker.

Niskanen K (ed.) (1999) *Papermaking Science and Technology*, vol. 16, *Paper Physics*, pp. 1–324. Helsinki, Finland: Fapet Oy.

Scott WE and Abbott JC (1995) *Properties of Paper: An Introduction*, 2nd edn. Atlanta, GA: TAPPI Press.

Smook GA (1990) *Handbook of Pulp and Paper Terminology*, pp. 1–447. Vancouver, Canada: Angus Wilde.

Smook GA (2002) Properties and testing of pulp and paper. In: *Handbook for Pulp and Paper Technologists*, 3rd edn, pp. 332–344. Vancouver, Canada: Angus Wilde.

TAPPI Test Methods (2002–2003). Atlanta, GA: TAPPI Press.

Chemical Additives

M A Hubbe, North Carolina State University, Raleigh, NC, USA

Introduction

Chemical additives can be critical to the economic viability of paper machines. Relative to fibers (*see* **Pulping**: Fiber Resources), other materials are present in paper and paperboard at much lower levels. However, additives allow papermakers to differentiate their products to meet the differing needs of customers. They also use additives to make their operations more efficient. This article considers the most widely used papermaking additives, focusing on their composition, their modes of preparation and use, and their impacts on either product attributes or process efficiency. The fact that relatively small amounts of additives can make huge differences makes this a fascinating field of work and study.

Why use Additives During Paper Manufacture?

If you tour a typical papermaking operation you cannot help being struck by the capital-intensive nature of this business. To thrive in a capital-intensive industry it is essential to run the capital equipment as effectively as possible. In contrast, from the viewpoint of the papermaker, chemical additives represent an operating cost, not a capital cost. Those responsible for papermaking operations can decide on a month-to-month basis whether a given additive makes a big enough difference to justify its continued use.

There are two main classes of chemical additives applied in paper machine systems, and each of these involves different motivations concerning its use. The term 'functional additives' will be used here when referring to additives that change paper properties so that they better meet customer needs. A universal customer need is to cut costs; for this reason it makes sense to consider mineral fillers among the other functional additives to be described in this article. Other functional additives include materials to make paper stronger (dry-strength and wet-strength agents), materials to make paper resist water and other fluids (sizing agents), and materials to change the shade or brightness of paper (dyes, pigments, and fluorescent whiteners).

The term 'process additives' will be used here for materials that mainly affect the way the paper machine operates. Factors that determine the overall efficiency of papermaking operations include the speed of the paper machine. Papermaking involves rapid removal of huge amounts of water from fiber slurries (*see* **Papermaking**: Overview). Sometimes removal of water is the production-limiting step. So papermakers treat the furnish with drainage aids, an example of process additives, to allow water to be removed more easily. Another factor governing efficiency is the percentage of time during which the paper machine is successfully making product, i.e., up-time. A key enemy of up-time is the tendency of various materials to deposit on to papermaking equipment. Deposited material often becomes entrained again in the process, leading to spots or holes in the paper, web breaks, and costly downtime. Deposits in press felts, often called 'felt filling,' can cause moisture streaks or just make it necessary to slow down the machine. Chemicals used to fight deposits, as well as the related issues of slime and foam, are further examples of process additives.

Functional Additives for Papermaking

Mineral Fillers

Mineral fillers rank first among papermaking additives in terms of the amounts used. Many paper and paperboard grades contain little or no filler, while printing papers commonly contain up to 25% filler, by mass.

Though the word 'filler' would seem to suggest otherwise, there are numerous reasons to add mineral products to paper. These reasons include cost reduction, enhancement of opacity or brightness (*see* **Pulping**: Physical Properties), and enhanced smoothness of paper after calendering (*see* **Papermaking**: Overview). The minerals do not 'fill' all of the space between fibers in a sheet of paper. In fact, the use of fillers does not necessarily decrease the volumetric proportion of air space. Depending on their detailed locations, filler particles may act as spacers between fibers in the sheet, increasing its thickness or 'caliper' under given processing conditions or at a given target of paper smoothness.

The most widely used mineral products in paper manufacture, including those used in coating of paper (*see* **Papermaking**: Coating), are calcium carbonate, kaolin clay, titanium dioxide, and talc. The most common particle size range of fillers is between about 0.5 and 4.0 μm. An exception is titanium dioxide (TiO_2), the particles of which typically have diameters in the range 0.2–0.3 μm. Because TiO_2 is mainly used to improve paper's opacity, its size is dictated by the need to maximize the scattering of light.

Calcium carbonate Presently in the USA calcium carbonate ($CaCO_3$) is the major mineral additive for papermaking. The main varieties of $CaCO_3$ filler are as shown in **Table 1**.

The process for preparing precipitated $CaCO_3$ (PCC) can be represented by the following formulae:

$$CaCO_3(\text{crude}) + \text{heat} \rightarrow CaO + CO_2\uparrow \quad (\text{calcining}) \qquad (1)$$

$$CaO + H_2O \rightarrow Ca(OH)_2 \quad (\text{slaking}) \qquad (2)$$

$$Ca(OH)_2 + CO_2(\text{gas}) \rightarrow CaCO_3 + H_2O \quad (\text{carbonating}) \qquad (3)$$

Because the mass of CaO (lime) is only 56% of the mass of the corresponding $CaCO_3$, and in order to minimize transportation costs, it is common to carry out reaction (1) near to the mine, and to carry out reactions (2) and (3) adjacent to a paper mill. The precipitation process allows control of the particle sizes and shapes in ways that favor paper grades with differing requirements for brightness, opacity, smoothness, and strength.

The emergence of $CaCO_3$ as the major papermaking filler during the 1980s and 1990s profoundly affected operating conditions in paper mills, including the pH values and the kinds of sizing agents employed. The following reactions take place when $CaCO_3$ is placed in acidic solution, i.e., water with a pH lower than about 6:

$$CaCO_3 + 2H_3O^+ \rightarrow Ca^{2+} + H_2CO_3 + 2H_2O \quad (\text{dissolution}) \qquad (4)$$

$$H_2CO_3 \rightarrow CO_2\uparrow + H_2O \quad (\text{gas evolution}) \qquad (5)$$

Due to these reactions, the use of $CaCO_3$ typically implies neutral or weakly alkaline conditions during the manufacturing process, e.g., $6 < pH < 9$.

Kaolin clay Clay remains the most used mineral product for paper coatings (*see* **Papermaking**: Coating), but by the 1990s it was second to $CaCO_3$ with respect to use as a filler. Kaolinite is a hydrous aluminum silicate, $Al_4Si_4O_{14}(H_2O)_4$. Kaolin deposits in Georgia and South Carolina, having relatively narrow particle size distributions, were laid down by meltwaters from glaciers. The meltwaters slowed down when they entered the prehistoric ocean, allowing the particles to settle. After scooping the clay with a crane, it is commonly mixed with water under severe conditions of agitation in a process called 'blunging.' The clay particles in this initial mixture typically consist of 'bookettes' of clay platelets.

Two processes to modify clay for papermaking use are delamination and calcination. Delamination involves repeated overturning of a mixture of the clay bookettes and porcelain-grinding medium. The resulting shearing separates the clay into platelets. Papermakers favor delaminated clay when they want to decrease paper's air permeability, or when they want to improve brightness and opacity relative to conventional filler clay.

Calcined clay gets its name from the fact that the following reaction is carried out in the same kind of equipment that has been used to convert $CaCO_3$ to lime (see eqn [1]):

$$Al_4Si_4O_{14}(H_2O)_4 + \text{heat} \rightarrow Al_4Si_4O_{14} + 4H_2O\uparrow \qquad (6)$$

Calcination of clay fuses platelets together, and this has been found to be advantageous for bulking and optical properties of paper.

Titanium dioxide Papermakers use TiO_2 when high levels of opacity are needed, or when the market demands lighter-weight paper grades that match opacity levels of higher-weight samples. The major synthetic route for TiO_2 pigment is the so-called 'chloride' process, as follows:

$$2\ FeTiO_3(\text{ore}) + 3C + 7Cl_2 + \text{heat} \rightarrow 2TiCl_4 + 3CO_2 + 2\ FeCl_3 \qquad (7)$$

$$TiCl_4 + O_2 \rightarrow TiO_2 + 2Cl_2 \qquad (8)$$

A so-called 'sulfate' process is also used. By varying the manufacturing conditions it is possible to obtain TiO_2 in two crystal forms, rutile and anatase. Both mineral forms have high refractive indices, 2.7 and 2.5, respectively. By contrast, fibers, calcium carbonate, and kaolin all have refractive indices in the range of 1.5–1.6. The much higher refractive index of TiO_2 helps to explain its much greater ability to scatter light.

Table 1 Calcium carbonate filler types

	Crystal type	*Shape*
Precipitated calcium carbonate (PCC)		
Scalenohedral	Calcite	Rosette
Rhombohedral	Calcite	Blocky
Acicular	Aragonite	Needles
Ground limestone	Calcite	Irregular
Ground chalk	Calcite	Shell-like

Talc The most important characteristics of talc are its oil-loving surface, its platy shape, and its low hardness (1 on the Mohs scale). The low hardness makes it practical for filled paper with talc having large particles, e.g., in the range 3–10 μm. However, a more common application of talc is to control deposits of wood pitch in paper mills using mechanical pulp (*see* **Pulping**: Mechanical Pulping). Such applications require the use of finely divided talc, providing a high surface area of oil-loving material. The fine talc is also used to detackify sticky materials present in many recycled furnishes (*see* **Packaging, Recycling and Printing**: Paper Recycling Science and Technology).

Other fillers Aluminum trihydrate (ATH), having the composition $Al(OH)_3$, has high brightness, and it also acts as a flame-retardant when used at high levels. Gypsum, having a composition of calcium sulfate dihydrate, is also bright and inexpensive. Due to the high solubility of gypsum, some of it is dissolved in the process water during paper manufacture. Precipitated amorphous silicas, silica aluminates, and related products are used for specialty printing applications. These noncrystalline mineral products, having high specific surface areas, can help to hold fluid inks near to the surface of paper.

Dry-Strength Agents

Papermakers add water-loving polymers both at the wet end and at the size press to increase dry strength. Reasons for using a dry-strength additive usually go beyond just meeting specified strength requirements. For instance, a dry-strength agent can compensate for the tendency of fillers to interfere with interfiber bonding. A dry-strength additive can also compensate for low-quality fiber, including recycled kraft fibers that have lost some of their bonding ability. Though it is possible to increase strength by refining (*see* **Papermaking**: Overview), excessive refining hurts drainage of the paper web.

Starch products are by far the most important dry-strength agents presently used in the USA. At the wet end it is most common to use cationic derivatives of corn, waxy maize (a specialty corn variety), or potato starches. Wet-end starches are carefully handled to avoid lowering their molecular mass. The most popular cationic starches contain approximately 0.2–0.3% nitrogen, in the form of quaternary ammonium salt groups. One of the reactions used by suppliers of cationic starch products is shown in **Figure 1**.

Most wet-end starches require cooking (sometimes called 'pasting') at the mill site. In batch operations

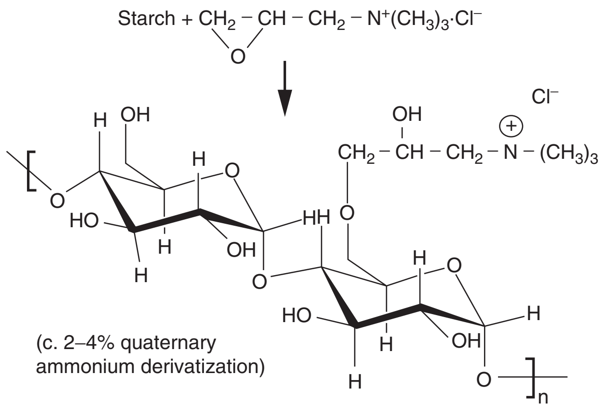


Figure 1 Synthesis of cationic starch.

the dispersed starch granules are heated at ambient pressure to just below the boiling point of water and agitated for about 20 min, at which time the granules have completed their swelling, rupture, and liberation of starch molecules. Starch can also be continuously 'jet-cooked' at higher temperature and elevated pressure. The combination of relatively high molecular mass and weak cationic charge makes it possible to adsorb at least 1% cationic starch, by mass, on to the fiber surfaces before formation of the sheet.

Other dry-strength additives include cationic guar gum, copolymers of acrylamide, and also various anionic polymer products such as carboxymethyl cellulose (CMC). Since fibers used for papermaking typically have a weak negative surface charge, anionic polymers added at the wet end are used in sequence with cationic additives.

Size-press addition of dry-strength agents offers the papermaker some freedom and also some more constraints. Freedom is provided by the fact that nearly 100% of material added to paper's surface becomes part of the product; this means that size press starches do not have to be cationic. But there is an added constraint relative to viscosity. Starch products to be used at the size press typically have to be reduced in molecular mass by treatment with a strong oxidizing agent or with an enzyme. Though the molecular mass reduction renders the starch less effective for strength, it is a necessary compromise to avoid nip rejection and other problems with size-press operations. It is common for the starch to be spread on to the surface of the paper or paperboard as a dilute solution of, say, 10% solids. Starch derivatives commonly used at the size press include unmodified starch, oxidized starch, hydroxyethylated starch, and cationic starch. In addition to starch, papermakers also use polyvinyl alcohol, carboxymethylcellulose (CMC), alginates, and copolymers such as styrenemaleic anhydride (SMA) to enhance the surface strength of paper.

Wet-Strength Agents

Polyamidoamine-epichlorohydrin (PAAE) copolymers are widely used in the USA to help maintain the strength of paper products even after they have become thoroughly wetted. Major applications include currency, paper bags, and paper towels.

Most materials that act as wet-strength agents are polymeric, and they contain some kind of reactive group capable of cross-linking the resin during drying of the paper. PAAE is basically formed as follows:

$$(COOH)(CH_2)_4(COOH) + NH_2(CH_2)_2NH(CH_2)_2NH_2 \rightarrow (COOH)(CH_2)_4(CO)NH(CH_2)_2NH(CH_2)_2NH(CO))(CH_2)_4COOH \quad [A] \qquad (9)$$

$$[A] + \text{epichlorohydrin},\ CH_2Cl(C_2H_3O) \rightarrow \text{PAAE resin} \qquad (10)$$

The PAAE resin has a positive charge in solution due to residual amine groups and cross-linkable azetidinium groups formed by the reaction with epichlorohydrin.

Other important wet-strength resins include gyloxylated polyacrylamide (GlyPAM) and traditional formaldehyde-based resins. GlyPAM is used in cases where a temporary wet-strength effect is desired, e.g., flushable products. Phenol formaldehyde (PF) and melamine formaldehyde (MF) resins offer many advantages, but their usage has decreased due to regulation of formaldehyde levels.

Internal Sizing Agents

The purpose of internal sizing agents, which are added at the wet end of a paper machine, is to inhibit wetting, spreading, or penetration of fluids on to and into the paper. The three major internal sizing agents are alkenylsuccinic anhydride (ASA), alkylketene dimer (AKD), and rosin products.

Alkenylsuccinic anhydride ASA is formed as follows, by the reaction between maleic acid and monounsaturated mineral oil from the distillation and cracking of petroleum:

$$RCH = CH - CH_2 - R' + \text{maleic anhydride},\ C_4H_2O_3 \rightarrow RCH(C_4H_3O_3)CH = CH - R' \qquad (11)$$

where $R = CH_3(CH_2)_n$, $R' = CH_3(CH_2)_m$, and $(n+m) = 13$, 15, 17, or 19. ASA oil needs to be emulsified before its addition at the wet end. Due to ASA's reactivity with water, the emulsification is carried out immediately before use, next to the paper machine. Cationic starch or a moderate-mass acrylamide copolymer can be used to stabilize the droplets of ASA that are formed by application of hydrodynamic shear. Sizing with ASA is generally understood to involve the formation of ester bonds as shown in **Figure 2** during the drying process.

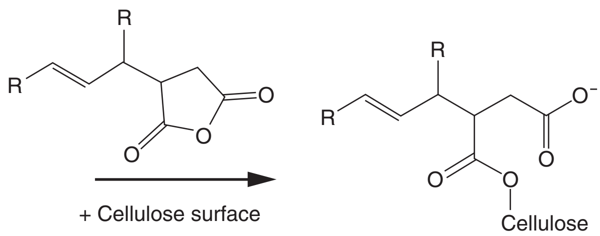


Figure 2 Reaction of alkenylsuccinic anhydride size with a fiber surface.

Alkylketene dimer AKD products are formed by reactions of fatty acids, as follows:

$$RCH_2COOH + SOCl_2 \rightarrow RCH_2COCl \quad \text{(acid chloride)} \qquad (12)$$

$$2RCH_2COCl - HCl \quad \text{(in triethylamine)} \rightarrow 2\ RCH = C = O \ \text{(ketene)} \qquad (13)$$

$$2RCH = C = O \rightarrow \text{alkylketene dimer(four-membered lactone ring)} \qquad (14)$$

where $R = CH_3(CH_2)_n$, and n is an even number between about 14 and 22.

Usually the AKD is emulsified by the chemical supplier and delivered to the papermaker as a ready-to-use dispersion. Stabilizers may include either cationic starch or various synthetic cationic polymers. Though the lower reactivity of AKD relative to ASA can make it easier to apply, it is more difficult to cure. For the curing of AKD it has been proposed by many authors that the ketene dimer's lactone ring opens to form a beta-keto ester with hydroxyl groups on the fiber surface. There has been continued discussion about whether esterification occurs extensively under typical drying conditions. Other factors that may contribute to sizing by AKD include the water-hating nature of the unreacted AKD itself, and its tendency to form insoluble condensation products on heating.

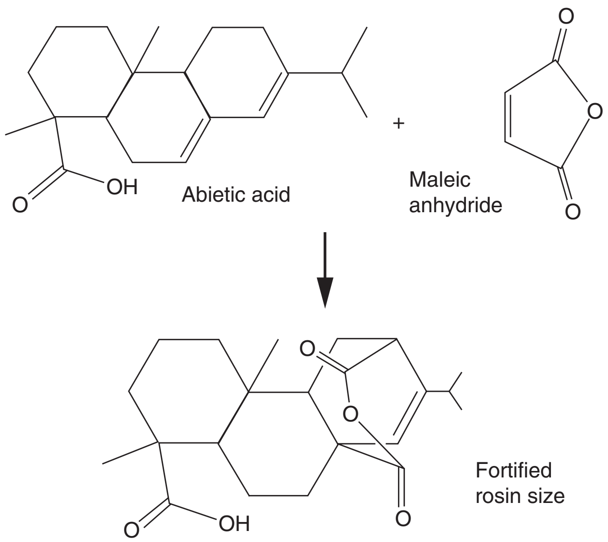


Figure 3 Fortification of rosin size molecule.

Rosin size products Crude rosin is most often obtained as a byproduct of kraft pulping (*see* **Pulping**: Chemical Pulping). The reaction shown in **Figure 3**, called 'fortification,' is carried out before the rosin is used for papermaking. Fortification tends to make rosin formulations easier to handle, less likely to crystallize during storage, and better able to react with aluminum compounds for retention and curing reactions.

Two main types of rosin size formulations are commonly used in the USA. The key difference involves the form of the carboxylic groups. In the case of emulsion-type rosin products, only enough base is added to convert a minor portion of the rosin to its salt form (saponification). The emulsion is stabilized by a cationic polymer or protein, much like the case of ASA, already described. Emulsion-type rosin products benefit from use of a retention aid to attach the particles to fiber surfaces in the wet end. During drying the rosin becomes distributed by vapor transport and a limited degree of spreading of rosin droplets on fiber surfaces. Aluminum byproducts at the paper surface can then bind the rosin. When using rosin emulsion products it is customary to use a reverse order of addition in which the aluminum compound, usually aluminum sulfate or alum, is added first, followed by the size.

Liquid rosin and traditional paste-type rosin soap products have high proportions of saponified, negatively charged carboxylate groups. This fact renders these products dispersible as micelles and monomeric ions in the water. The essential reaction for sizing takes place in the fiber slurry between rosin and a soluble aluminum or iron compound. Though papermakers often use the reverse order of addition when adding rosin soap products in the presence of hard water, the traditional approach is to 'set' the size by adding the alum after the size has been mixed with the furnish.

Colorants and Fluorescent Whitening Agents

With the exception of carbon black, which is polymeric, most colorants used for paper are monomeric organic chemicals. They derive their ability to adsorb light from multiple conjugation, i.e., extensive alternation of single and double covalent bonds.

The most widely used class of papermaking dye has the color index designation of 'direct.' Direct dye molecules contain negatively charged sulfonate groups. The molecules are relatively big and planar, attributes that help them to be retained on fiber surfaces even without the use of a fixative chemical. When papermakers want even higher retention of dye it is possible to use another class of dye, the cationic direct dyes. However, very high affinity is not always an advantage. To avoid an unintentional speckled appearance of the paper, cationic direct dyes need to be diluted and added at a point where there is good agitation. A class of dyes called basic dyes is widely used for yellow pages and other dyed products made from mechanical pulps. Pigment colorants, usually formed by precipitation or 'laking' of organic dye molecules, require the use of a retention aid, as in the case of the mineral fillers. Papermakers favor pigment colorants for products that have to resist fading on exposure to light.

Fluorescent whitening agents, often called 'optical brighteners,' are chemically very similar to certain direct dyes. However, they have the special ability to absorb light energy in the ultraviolet range and reemit some of that energy in the visible, blue part of the spectrum.

Process Additives for Papermaking

Retention and Drainage Additives

Papermaking involves separation between a solids-rich phase, the paper web, and a liquid-rich phase, the white water (*see* **Papermaking**: Overview). Chemicals that make this separation occur more completely or more quickly are called 'retention aids' and 'drainage aids.' There is so much overlap between the chemicals that perform these two functions that it makes sense to discuss them together. In colloidal chemical terms most of these additives can be grouped within the categories of coagulants, flocculants, and colloidal particles.

Coagulants

During papermaking one function of a chemical coagulant is to neutralize the surface charge of suspended materials and remove electrostatic barriers, preventing them from colliding with each other and sticking together. Because the fibers and many other materials used for papermaking typically have weak negative charges at their surfaces, coagulants usually consist of multivalent cationic materials, which can be either soluble inorganic products or organic polymers.

Among inorganic coagulants, the most widely used is aluminum sulfate, or 'papermakers' alum.' Alum derives its coagulating ability from the trivalent character of aluminum, plus a tendency to form oligomeric species. The system pH, contact times, and temperature profoundly affect alum's performance, with best results often obtained in the so-called 'acidic' range of papermaking, between pH values of 4 and 6. Polyaluminum chloride (PAC) and related products have extended the range of efficient coagulation to somewhat higher pH values.

The most important polymeric coagulants are the polyamines, including polydimethylamine-epichlorohydrin, as well as polyethylenimine (PEI) products and poly-diallyldimethylammonium chloride (DADMAC). The common feature of these polymeric coagulants is their high positive charge density, often with 100% of the monomeric groups bearing a charge. Molecular masses typically range from hundreds of thousands to about two million grams per mole.

Flocculants

The function of a flocculant is to cause suspended particles to stick together very strongly after coming into contact. The effect is achieved by use of very-high-mass polymers, which are capable of forming molecular bridges between the adjacent surfaces. When papermakers use the term 'retention aids,' they most often mean linear copolymers of acrylamide. Molecular masses of these retention aids range from about 4 million to upwards of 20 million $g\,mol^{-1}$. Retention aids with a wide range of charge density, either positive or negative, are widely used. Retention aids are most commonly delivered to the paper mill in the form of a water-in-oil emulsion, which needs to be inverted at high levels of dilution and agitation before it can be used. It is common to add a retention aid flocculant near the end of the wet-end process, after furnish has been conditioned by the addition of a lower-mass coagulant.

Colloidal Particulates

Since the 1980s there has been a trend toward the use of colloidal 'microparticles' or 'nanoparticles,' including colloidal silica and montmorillonite clay products. Under the right conditions, these have the ability to interact with the flocculants just discussed, producing a pronounced increase in drainage rates during paper formation.

Deposit Control

Papermaking operations are vulnerable to problems resulting from the deposition of tacky and pitch-like materials on to the equipment. In addition to talc, as already mentioned, deposit-control additives include organic detackifying agents, dispersing agents, and barrier chemicals. Effective use of a retention aid program, as just discussed, also helps to avoid deposition of fine materials on to chests, pipe walls, headbox surfaces, and in press felts and related equipment. Organic detackifiers include soluble polymers, such as polyvinyl alcohol products, designed to adsorb on to oil-loving surfaces and make them less tacky. Dispersing agents, including nonionic surfactants composed of short ethylene oxide chains attached to oil-loving groups, can be used to overcome deposition of tacky materials at specific locations in a papermaking process. The term 'barrier chemicals' describes materials sprayed directly on to the surface of a forming fabric or press felt to overcome deposit problems. Highly cationic polymers, i.e., organic coagulants, are used alone or in combination with surfactants to achieve this effect.

Biological Control

Papermaking systems, with their warm temperatures and content of starch and other biodegradable materials, can provide a wonderful medium for the growth of bacterial and fungal slime. Slime can become entrained and cause holes and breaks in the paper web, in addition to spots and bad smells. The two main categories of chemicals that papermakers use for slime control are oxidants and toxic organic chemicals. Chlorine dioxide has become a favored oxidant, especially for paper grades that use bleached kraft pulp. The selection of slimacides depends on factors such as temperature, the kind of slime in the system, and issues of effectiveness and biodegradability of the added material.

Foam Control

Due to the presence of air, water, high degrees of agitation, and various substances that can stabilize bubbles, there is the potential for severe foam problems during papermaking. Some of the problems can be minimized by avoiding overuse of surface-active materials and water-soluble polymers such as starches and wet-strength agents. Chemical defoamer formulations typically contain water-insoluble surfactants. They can also contain hydrophobic particles that help to rupture bubble surfaces when the surfactant molecules spread across those surfaces.

See also: **Packaging, Recycling and Printing**: Paper Recycling Science and Technology. **Papermaking**: Coating; Overview. **Pulping**: Chemical Pulping; Fiber Resources; Mechanical Pulping; Physical Properties.

Further Reading

Eklund D and Lindström T (1991) *Paper Chemistry: Introduction*. Grankulla, Finland: DT Paper Science.

Lindström T (1989) Some fundamental chemical aspects of paper forming. In: Baker CF and Punton VW (eds) *Fundamentals of Papermaking*, pp. 311–412. London: Mechanical Engineering Publishing.

Neimo L (1999) Papermaking Chemistry. *Papermaking Science and Technology*, vol. 4. Helsinki:/Fapet Oy, TAPPI Press.

Roberts JC (ed.) (1996) *Paper Chemistry*, 2nd edn. London: Blackie.

Scott WE (1996) *Principles of Wet End Chemistry*. Atlanta, GA: TAPPI Press.

Smook GA (1992) *Handbook for Pulp and Paper Technologists*, 2nd edn. Vancouver, Canada: Angus Wilde.

Environmental Control

D Peterson, Western Michigan University, Kalamazoo, MI, USA

Introduction

The basic operations of the paper industry involve the conversion of renewable resources using chemicals, energy, water, and human ingenuity to produce a universal consumer product. Wastewater, air emissions, and both dry and waterborne solids are generated during the process. Heat and noise also are generated and disbursed into the environment. The objectives of this article are to identify the sources of these emissions and the processes by which they can be managed.

An overview of the paper manufacturing process suggests that the sequence of events can be divided into distinct phases. The first phase involves the recovery of papermaking fiber from either wood or recycled fiber resources. The second phase involves the purification of the liberated fiber and preparation of that fiber for the papermaking process. The final phase includes formation of the paper mat and modification of its surface to meet specific moisture resistance, strength, and optical properties for designated paper or paperboard applications.

The pulping operation and papermaking operations often run at separate locations, while integrated operations combine both pulping and papermaking facilities at one manufacturing site. The pulping phase is accomplished using several different processes ranging from full chemical pulping to thermal and mechanical defibering with a large variety of sequential treatment combinations involving chemical, thermal and/or mechanical processes in between. The chemical pulping operations often are accompanied by a variety of complex chemical recovery processes depending on the chemicals involved.

The fiber purification processes involve both mechanical and chemical processes to remove unacceptable components and to brighten the fiber for specific applications.

The papermaking phase commonly involves the dispersion of the fiber in large quantities of water and other additives to modify optical, chemical, and physical properties. The thin slurry is distributed on a continuous moving forming fabric allowing the water to separate from the wet fiber mat. The wet mat is then pressed against an absorbent fabric to dewater the wet mat. The partially dewatered mat is dried by evaporating most of the remaining moisture to form a paper or paperboard sheet.

Depending on the use of the paper it may also have been surface treated with sizing to minimize moisture penetration and to prevent ink from feathering on a printed page or coated with additional material and/or treated mechanically to modify its surface and optical properties. Coating followed by calendaring are common treatments to obtain papers with excellent printing quality characteristics.

Before dealing with the treatment of some specific waste streams, it is important to recognize some of the waste streams that are characteristic of the production phases. Characterizing each of these by-product streams and assessing their reuse alternatives will enable the diversion of some of the waste streams to reuse elsewhere in the manufacturing sequence.

The following figures (**Figures 1** to **5**) depict several of the steps in the production of paper and identify some of the major emissions from the various stages. The process schemes describe the liberation of fiber from wood or the recovery of fiber from recycled paper sources (post consumer) through

	Process stage	By-products
	Roundwood	
Chip preparation	Wood handling	Dust, dirt, bark
	Debarking	Bark and shower water with wood extractives, suspended solids
	Chipping	Noise
	Chip screening	Undersize and oversize chip
	Wood chips	
Chemical pulping	Pre-steam	Vent volatile wood extractives
	Cook chips	Vent odorous digester gases
	Wash cooked chips	Discharge spent liquor (weak black liquor)
	Blow chips to blow tank	Vent odorous blow vent gases
	Brown stock washing	Vent washer hood gases
	Screen brown stock	Collect uncooked chips and knots
	Liberated chemical fiber	

Figure 1 Chemical pulping processes.

	Process stage	By-products
	Weak black liquor	
Recovery furnace operation	Evaporated	Foul condensate and vapor
	Reduced inorganics	Smelt and particulates
	Oxidize organics	SO_x, NO_x, CO_2, particulates$_x$
	Dissolve reduced chemicals	Odorous gases and insoluble dregs
	Green liquor	
Liquor production	Caustizing green liquor	Odorous gases and precipitate
	Clarify cooking liquor	Lime sludge
	Cooking liquor	
Lime kiln operation	Lime washing	
	Filtering	Weak cooking liquor
	Calcining	SO_x, NO_x, CO_2, particulates
	Slaking	Insoluble dregs
	Regenerated lime	

Figure 2 Chemical recovery processes associated with the Kraft process.

	Process stage	By-products
	Waste paper/paperboard	
Pulping of waste paper and board	Hydro-pulping	Hydropulper rejects
	Removal of heavies	Heavy rejects
	Removal of lightweight material	Light rejects
	Liberated secondary fiber	
Deinking	Washing or flotation	
	Deinking	Ink sludges
	Deinked fiber	

Figure 3 Recovery of post consumer fiber.

the purification stages and the production of paper or paperboard. The recovery of cooking chemicals from the major pulping process is included to emphasize the cyclic nature of the Kraft pulping process.

	Process stage	By-products
	Clean liberated fiber	
Bleaching	Multistage bleaching process	Soluble organics and inorganics
	Bleached fiber	

Figure 4 Chemical purification and paper making.

	Process stage	By-products
	Fiber stock	
Stock preparation	Refining	Soluble organics and fines
	Final cleaning and screening	Cleaner and screen rejects
	Prepared stock	
Sheet formation and dewatering	Diluted with white water	
	Distributed on paper machine	
	Water drained from slurry	Excess white water
	Water pressed from wet mat	Pressate wastewater
	Evaporate moisture in sheet	Humidity, heat, particulates
	Paper sheet	
Surface treatment	Apply surface size	Volatile organic compounds
	Evaporate moisture	Volatile organic compounds
	Apply coating surface treatment	Volatile organic compounds
	Coated paper sheet	

Figure 5 Stock preparation and papermaking.

Air Emissions and Control Processes

Sources

Air emissions from the manufacturing process include: dust from wood handling, chemical recovery operations, the recovery furnace and the calcining operation, and the drying processes associated with moisture removal from paper and applied coatings. Odorous gases are generated during the chemical pulping and chemical recovery operations. Odorous gases characteristic of the Kraft process include: sulfides (mercaptans) and total reducible sulfides (TRS) that are detectable in the 1–20 ppb concentration range. Small quantities of noxious gases are generated from the bleaching process that volatilize as fugitive emissions. Fugitive emissions including chlorinated organic compounds, such as chloroform, originate in small quantities from the chlorine bleaching process. In addition to the emissions from the manufacturing process the generation of power and steam needed to operate the manufacturing facility also generate air emissions. Energy generated from fossil fuels, biomass, and the incineration of wastes all involve the combustion of hydrocarbon material. The possible byproducts from the combustion include: CO_2, CO, H_2O, NO_x, SO_x, particulate matter, and waste energy (heat). The amount of each of these by-products depends on the fuel used in the process and the energy requirements of the facility.

Control

Particulates can be recovered by filtration (bag house operations), scrubbing (absorption), or settling induced by gravity or by electrostatic mechanisms. Gases are recovered either by collection in another media or by chemical conversion to a more benign compound. Media alternatives include the adsorption of the gases material on to a solid substrate or the absorption into a liquid media. The media selected may include chemicals that will ultimately react with the compounds sorbing the gaseous constituent.

Particulates

Treatments for particulates suspended in air are of three types: one is dependent on their density, the second is dependent on their physical size, and the third is dependent on generating a unique force that can be applied to the particle as it passes through a control device.

The density dependent control processes are based on the particle's inertia. Because of its inertia, the particle will tend to continue moving in a straight line as the carrier fluid (air) is forced to change direction. The resulting path of the particle is to impact (and be collected) on a collecting surface. The most common inertial control device, effective on relatively large particles (greater than 30 μm diameter), is a cyclone collector. Since the centrifugal force depends on the rate of directional change that takes place in the fluid stream, cyclones with small diameters are more effective but require larger pressure drops. A number of cyclones can be configured into a single body to save space. Scrubbers can be used to improve particle collection efficiency by first collecting the particles in a liquid droplet followed by the separation of the droplet from the gas stream. The liquid can be introduced in a number of ways including:

- a venturi device preceding the cyclone
- a liquid spray inside the cyclone
- directing the particle laden gas into a liquid before going into the cyclone.

The inertial phenomena also can be used effectively by impinging the gas flow through open structure forcing the gas to make many directional changes causing the particles to impact onto wetted surfaces within the erratic structure. One advantage with these control devices is that they can operate continuously. As the collected particles are continuously flushed from the collecting surfaces, the operation of the control device does not need to interrupt its operation to be cleaned.

The collection methods based on physical size are essentially screening processes. Particles that are larger than the openings in the filter media are trapped in the media, thus separating the particles from the fluid stream. Fabric filters are commonly configured with a number of cylindrical collection surfaces bunched in a common housing. The 'bag house' filter is limited to dry conditions and requires some interruption of the collection process to dislodge the collected material. The filter tends to plug as the surface becomes clogged with particulates and needs to be cleaned periodically. The cleaning cycle involves taking a portion of the filter off-line and cleaning it by back flushing with a burst of air or shaking it to dislodge the collected material. Collection efficiency and pressure drop depend on the size of the openings in the filter media.

The third type of collector functions by charging the particles electrically and exposing the charged particle to a surface with the opposite charge. The electrostatic forces cause the particle to migrate to the collecting plate where they accumulate. In this collection device the accumulated particulates are dislodged by shaking the plate, causing the accumulated layers of particles to slough off and fall to the bottom of the precipitator. Since the particles come off as a conglomerate, they are not re-entrained in the gas stream and thus are separated from the gas. This process is effective for very small particles but is limited by the dielectric property of the gas, which is heavily influenced by high temperature and the presence of moisture.

Gases

The controls for gases (sulfur oxides, sulfides, nitrogen oxides, volatile organics) might include or incorporate collection, destruction, or prevention. Collection can be accomplished by either absorption or adsorption while destruction can be accomplished by chemical reaction induced by either thermal destruction or imposed reactions. Prevention is the first choice where this alternative is feasible.

Absorption involves the transfer of the gas from the carrier gas to a liquid stream. The transfer is accomplished by contacting the carrier gas with an appropriate liquid in which the contaminant is soluble or with which it will react to form a soluble compound or precipitate.

Adsorption is used to transfer the contaminant to a surface. A highly porous surface is particularly effective. A good example is the use of activated carbon to adsorb volatile organic compounds.

Thermal processes utilize high temperature with or without a catalyst to convert the contaminant into benign compounds, or compounds that have less effect on the environment. Chemical reactions include specific reactions to convert contaminants into more agreeable compounds. Typical examples include oxidation of hydrocarbons to carbon dioxide and water or reactions that produce passive materials that do not have any impact on the environment.

One example of a prevention effort is the oxidation of odorous sulfides to sulfur oxides to reduce the foul odor associated with the spent cooking liquor generated in the Kraft pulping process.

Wastewater Emissions and Treatment Processes

Sources

Wastewater sources probably are the must numerous of all of the emissions sources from the paper manufacturing industry. Some mills use water to wash logs before treating the logs in a drum debarker, while others use high-pressure water to hydraulically debark the logs. In either case the wastewater generated contains both soluble and suspended solids.

The fiber liberation and purification processes also generate significant wastewater discharges. Except for accidental releases and leakage, all of the waterborne wastes from the chemical pulping process goes to chemical recovery. Chemical recovery releases foul condensate, and sludge from the slaking and smelting processes. Waterborne wastes from mechanical and thermal pulping processes, however, generate significant amounts of both dissolved and suspended solids.

Wastewater Treatment

To minimize maintenance concerns in the wastewater treatment train and to stabilize flow rates and loads many treatment systems include barrier screens and equalization basins. Barrier screens prevent oversize pieces of suspended solids from getting into the inlet flow stream that might interfere with the process equipment. Equalization basins serve to mix intermittent high concentration and large flows in a storage basin to provide a consistent feed rate to conventional primary and secondary treatment operations.

The primary clarifier is intended to remove the suspended solid portion of the wastewater. The primary treatment process is usually dependent on gravity settling to separate the suspended material from the liquid suspension. Because the settling rate is proportional to the square of the diameter of the particle, the raw wastewater is sometimes treated with coagulants that encourage individual particles to agglomerate forming large flocs. A typical primary clarifier is designed to handle between 500 and 1000 gpd/ft^2 of surface area removing 80–90% of the suspended material. Because some of the oxygen-demanding material is the suspended material itself or is attached to the suspended material, the removal of suspended material can also remove a significant fraction of the oxygen-demanding waste load. Another method of removing suspended material involves the use of a flotation clarifier. The flotation clarifier also used additives to agglomerate the suspended material with an air bubble, thus creating a particle that is less dense than the fluid causing the coagulated particle to float to the surface. The floating material can be skimmed from the surface and thus separated from the bulk of the liquid.

Biological treatment is intended to reduce the oxygen demanding components (biochemical oxygen demand, BOD) in the wastewater entering the secondary treatment system. The removal of the BOD components is accomplished by allowing bacteria to consume the BOD, usually in the presence of excess oxygen. The treatment occurs in aerated stabilization basins, activated sludge systems, large oxidation basins, or other biological contact processes. The key components in the process are aerobic bacteria, dissolved oxygen in water, and the oxygen-demanding material. The required residence time depends on the temperature, concentration of bacteria, concentration of oxygen, the BOD_5 load and nitrogen and phosphorus nutrients. The optimum temperature range is 20–30°C, the ideal BOD_5/N/P ratio is approximately 100/5/1, and the desired pH range is from 6.5 to 7.5, while residence times range from 3 h to more than 60 days. The residence times are 3–24 h for the activated sludge process, 5–10 days for the aerated basin process, and from 20 to 60 days for a storage aeration pond. The activated sludge process achieves BOD reductions in a short residence time by concentrating the bacteria in a highly oxygenated basin and recycling the bacteria by settling them in a clarifier and immediately returning them to the aeration chamber where they are combined with the flow of fresh wastewater. Another way to shorten the residence time is to inject oxygen-enriched air in the aeration chamber. The aerated stabilization basin process supplements the oxygen concentration by introducing oxygen by aerating the basin using surface mixers or subsurface aeration. The storage aeration process uses natural aeration of the basin's contents as the wind provides a natural wave action. The lower oxygen and bacteria concentrations require a longer retention time. This process generally follows one of the other aerobic processes. All of the above processes suspend the bacteria in the wastewater to accomplish the BOD reduction. The 'trickling filter' and 'rotating biological contactor' arrange to have the bacteria fixed on a structural media and provide for alternate contact between the bacteria and the BOD in the water and oxygen in air. The trickling filter requires a larger footprint than the activated sludge process but requires less energy to operate the system. These fixed media biological treatment processes are not widely used in the industry.

Another alternative for the treatment of mill wastewater is anaerobic treatment. As the name implies the process operates in the absence of oxygen. The carbon components are oxidized to CO_2 and reduced to CH_4. The methane gas is recoverable and can be used to provide heating to maintain reactor temperature or other combustion applications. The optimum temperature is approximately 35°C. One advantage of this process is that the amount of sludge produced per unit reduction of BOD is reduced to between 20% and 35% of that produced from the aerobic process. The anaerobic process is most effective for high BOD loads. This alternative is currently used at only a few pulp and paper installations and most of these are large covered-basin systems.

Effluent waters typically are treated by conventional means; primary treatment is followed by secondary treatment as needed. Mills in urban settings are likely to provide only primary treatment of their effluent before it goes to a municipal wastewater treatment facility. Mills in a more isolated setting would need to provide both primary and secondary treatment before discharge to a natural estuary or receiving water.

Solid Waste Sources and Management Alternatives

Sources

The solid waste components that accumulate around a manufacturing facility are the most diverse of all of the waste categories. Waste sources include: process wastes, raw material wastes, production wastes, spills, housekeeping, maintenance and remodeling wastes plus the residues that are generated by the treatment processes to manage air and water emissions. Solid wastes are generated from wood processing, chip preparation, pulping residuals, screening and cleaning rejects, and from nonpulpable components from secondary fiber sources. Sludges from wastewater treatment activities and recovered bottom ash and fly ash from power generation and incineration of other solids, fly ash from the recovery furnace, and fly ash from the calcining kiln are the result of environmental controls. Shipping containers, packaging materials, surplus and worn-out equipment, combined with numerous cleaning, housekeeping, maintenance and manufacturing remnants also contribute to the solid waste stream.

Wood pulping Process wastes generated by the industry are mostly derived from either organic sources (biomes or sludges containing biomes) or inorganic chemicals derived from inorganic minerals. Typically the largest source of organic waste comes from the log preparation, debarking, and chip screening operations. Some additional organic residual comes from the washing stages following the digester containing incompletely digested wood chives and knots. These mechanically separated materials can be dried and burned in the energy and power generation facilities associated with the mill. The resulting ash (both bottom ash and fly ash) plus the ash from the auxiliary fuel are additional waste components that need to be handled. Small quantities of solids are recovered from the purification and stock preparation processes that precedes the paper making operation.

Chemical recovery Chemical recovery operations generate a couple of inorganic wastes in the form of smelt dissolving dregs, green liquor clarifier and lime slaking dregs and fly ash from both the recovery furnace and the lime kiln. The fly ash components recovered from both of these sources are reintroduced back into the chemical recovery cycle.

Secondary fiber The recover of papermaking fiber from post consumer waste paper and paperboard generate a large variety of solid wastes. Nonpulpable material, dirt, sand and grit, staples, adhesives, sealing tape, labels, plastics, and packing materials are all separated from the reusable fiber. These materials each contribute to the wastes that are generated from the secondary pulping process. In the event that deinking and chemical purification of the secondary fiber is warranted, additional sludge containing ink, coating, and filler materials and soluble by-products are generated.

Treatment

Because of the diversity of materials that constitute the solid waste fraction, the treatment options are more diverse. Some of the materials are recyclable, some combustible, some can be land applied or composted while other fractions seem to have so little value that the most common option is to secure them in a well-designed landfill.

A major share of the solid waste stream is recovered because of its intrinsic value. Scrap metals, worn parts, and surplus equipment are notable examples. Components that are routinely replaced, shipping containers, and remodeling wastes are encouraged to be recycled by the supplier. Items of little intrinsic value generated by maintenance and housekeeping are commonly transferred to a waste disposal agent.

Organic wastes have a significant heating value; however, only those materials that can be effectively dewatered are viable candidates for energy recovery. Bark and wood wastes that are easier to dewater and dry are more likely to contribute to the energy needs of the mill. Most organic sludge materials are difficult to dewater though it is not unusual for these materials to be burned. Because of the moisture content of these wastes the remaining alternatives for treatment include biological treatment, land application/composting, or storage in a landfill.

Wastewater treatment sludges originate from either primary treatment or secondary (biological) treatment. Sludges from primary treatment will have either a high fiber content or a mix of fiber and filler material. Secondary treatment sludge is characterized as having a large amount of microbiological residue that is very effective at retaining moisture. The particular characteristics of each of these sludges prescribes how these sludges can be handled.

Secondary sludges have a large microbial cell content and are extremely difficult to dewater or stabilize. These sludges are difficult even to landfill because of their water content and unstable flow characteristics. One solution used often is to combine primary and secondary sludges to facilitate dewatering of the secondary portion. Alternatives for treatment include additional biological treatment, composting and anaerobic digestion. These additional processes reduce the quantity of the waste, which generally is easier to dispose.

Beneficial Use

Recycling is the most likely alternative for handling the largest share of solid wastes generated by a mill. Undersized and oversized chips are either burned for energy generation or the oversized are processed in a rechipping operation. Some operations focus on incompletely digested wood which can be treated in two different ways. One is to use the undigested wood as fuel and the second is to return it to the digester for another pass through the system.

Other beneficial uses for materials such as wastewater treatment solids include land application/composting, burning for energy, or use in by-products such as animal bedding, absorbent materials, concrete, fuel pellets, etc. Ash can also be used as a construction material or in by-products such as concrete.

Thermal Sources and Discharge

Thermal releases are associated with steam and power generation, pulping, chemical recovery, and drying process emissions. Manufacturing facilities recover and recycle as much of the thermal energy from these processes as practical. The lowest temperature energy residuals are discharged to the atmosphere as hot air or moisture generated by cooling tower operations or building vents. Some thermal energy is typically also released in wastewater discharges.

Noise Sources and Control

Noise is generated by the vibrations of rotation machinery and pumps, and by the flow of fluids through throttling valves. Treatment generally is accomplished by redesign and isolating rotating machines. Many pieces of equipment are mounted on vibration isolating pads and often are contained with noise insulated enclosures. Personal hearing protection is often used to protect personnel from the noise associated with some parts of the manufacturing process.

Summary

It is important to recognize that the various treatments of wastes (air, water, solids, heat, and noise) are often interdependent. The treatment of one type of waste can impact another type of waste. Management of any one of these environmental concerns can in turn affect other areas. Wastewater treatment commonly generates some sludge solids. Incineration of solids commonly generates some emissions to the air. Treatment of air pollutants generates either solid or liquid wastes. It is also important to recognize that most processes produce some by-products along with the desired product.

With these facts in mind, it makes sense to minimize the production of pollutants by modifying the manufacturing processes rather than treating pollutants after they are formed. The definitive solution to the environmental issues is to eliminate pollution sources where technically and economically feasible, minimize their production as much as practical, recycle by products as much as possible, and safely manage the remainder. The hope is that we can minimize waste streams and make them nontoxic and benign to our environment and us.

See also: **Packaging, Recycling and Printing**: Paper Recycling Science and Technology. **Papermaking**: Coating; Overview; Paper Raw Materials and Technology; World Paper Industry Overview. **Pulping**: Bleaching of Pulp; Chemical Pulping; Chip Preparation; Fiber Resources; Mechanical Pulping; New Technology in Pulping and Bleaching.

Further Reading

Springer AM (2000) *Industrial Environmental Control: Pulp and Paper Industry*, 3rd edn. Atlanta, GA: TAPPI Press.

Q

QUANTITATIVE GENETICS *see* GENETICS AND GENETIC RESOURCES: Quantitative Genetic Principles.

R

Reclamation *see* **Silviculture**: Bamboos and their Role in Ecosystem Rehabilitation; Forest Rehabilitation. **Site-Specific Silviculture**: Reclamation of Mining Lands; Silviculture in Polluted Areas. **Soil Development and Properties**: Soil Contamination and Amelioration; Waste Treatment and Recycling.

RECREATION

Contents

User Needs and Preferences

W E Hammitt, Clemson University, Clemson, SC, USA

Definitions

'Forest recreation' is defined as 'recreational activities and experiences conducted in forest and associated wildland environments that are dependent on the natural resources of these areas.' I include associated wildland environments along with forests in the definition, for forest recreation activities can occur above treeline at high attitudes and/or extreme latitudes, on streams and lakes in forested areas, and in old fields. The key point is that forest recreation is dependent upon the natural resources of the areas. Moreover, the resources and conditions of these forest/wildland settings are largely natural, and management strives to maintain a natural appearance.

'User needs' refer to physiological or psychological requirements for the well-being of an individual. Needs are the primary influences on an individual's behavior. When a particular need (physiological–emotional state) emerges in a recreationist, it determines the recreationist's behavior in terms of motivations, priorities, and actions taken. The unmet needs of recreationists are the basis for psychological and physiological forces, motives, and drives, which cause recreationists to pursue forest environments, recreational engagements, and desired recreational experiences. Driver and Tocher postulate that recreation is an experience that exists to the extent to which the needs or desires to recreate are gratified.

'Preferences' are related to needs gratification and refer to desired conditions and favored situations that recreationists expect will facilitate or satisfy their unmet needs during recreation engagements. Recreation managers need to know user preferences toward site facilities, services, programs, and management policies in order to design and manage conditions and situations to meet the recreation needs of users. They also must know users' psychological needs and preferences toward recreational experiences expected and desired, in order to provide opportunities for users to realize those needs and preferences.

User Need and Preference Relationships

User needs and preferences are essential components of forest recreation science and management, for the ultimate aim and product of forest recreation planning and management are quality recreation experiences. The relationships among user needs, preferences, quality experiences, and recreational benefits must be understood in the field of forest recreation (**Figures 1–3**).

Figure 1 A preferred campsite where the recreation user is offered the opportunity of naturalness and solitude in a nonimpacted site.

Figure 2 An unpreferred campsite where the natural conditions of the forest environment have been greatly impacted by heavy recreation use.

Figure 3 Nearness to water or in view of it is a major preference of forest recreation users. However, riparian sites can be sensitive to recreation use impacts.

Quality Experiences

Forest recreation, like any aspect of natural resource management, be it timber management, wildlife management, or water management, is ultimately concerned with enhancing the quality of the existing resource and the products and benefits derived from management. Long before professional forestry and forest sciences existed, forests were capable of producing timber, wildlife, water, and recreational benefits. However, because societal pressures and use of these resources can decrease the quality of products and benefits derived from them, professional management has aimed to maintain and enhance the quality of derived products and benefits, when possible. In the specific area of forest recreation, science and management have aimed to enhance the quality of resource conditions upon which various forest recreation engagements depend, the quality of visitor use of these dependent resources, and the interactions between the two. In order for forest recreation to enhance the quality of desired recreation resource conditions, and opportunities for quality recreation experiences, the recreational needs and preferences of users need to be identified. Once identified, managers can attempt to provide the resource and social conditions, and recreational opportunities, for users potentially to realize the quality experiences desired.

Diverse Opportunities

Many different types of users come to forest environments to engage in many diverse activities and resource settings, in order to realize quality and fulfilling recreation engagements. Associated with this diversity of user activities and resource settings is a diversity of user needs and preferences. In an attempt to meet these needs and preferences, scientists have researched the spectrum of needs and preferences, and management has developed recreation opportunity systems. Dr. Driver, long-time researcher at the University of Michigan and US Forest

Service, worked with colleagues to develop the recreation opportunity spectrum (ROS) as a system of diverse recreation opportunities to meet the many needs and preferences of forest recreationists in North America.

ROS has been formally adopted by the US Department of Agriculture Forest Service and the Department of Interior's Bureau of Land Management to manage forest recreation on their lands. The spectrum of recreation opportunities approach to forest recreation is based on understanding the recreation experience needs and preferences of users, and providing opportunities necessary to enhance the quality of recreation engagements, experiences, and outcome benefits.

Conceptual Models

Researchers have conceptualized the relationships among forest recreation, user needs, preferences, recreation opportunities, quality/experiences, satisfaction, and benefits (**Figure 4**). Driver *et al*. provide expanded discussions of the models and their theoretical/research foundations.

In **Figure 4**, it is proposed that unmet psychological and physiological needs result in internal drives and motivations to seek desired opportunities in order to fulfill need states and preferences, thus leading to satisfying experience outcomes and personal benefits. The model is based on Lawler's work with expectance theory. Lawler's approach is backed by the unmet-needs hypothesis of behavior, suggesting that the attractiveness of recreation experiences is determined by the extent to which it satisfies a human need. For example, the attractiveness to hike in a wilderness area is determined by the expectation that it will satisfy the human need for solitude and privacy in a natural outdoor setting. The focus of the Fishbein and Ajzen theory is upon salient beliefs regarding the outcomes of making a specific recreation choice.

In more practical terms of forest recreation science and management, the behavioral model of **Figure 4** can be restated to say that forest recreation users have needs, preferences, and expectations concerning resource settings, services, programs, and social setting use conditions. These user needs, preferences, and expectations toward recreation resource conditions and desired outcomes must be understood in order for managers to provide quality recreation opportunities and recreation experiences to gratify user needs and preferences and thus provide personal–social benefits. It must be realized that forest recreation cannot manage personal, psychological needs, preferences, and experiences; it can only attempt to understand user needs, preferences, and desired experiences so that diverse opportunities can be managed to meet the potential needs and preferences of users.

Figure 5 provides a more applied conceptual model of forest recreation-based needs-preference behavior. In the application, recreation visitors interact with forest environments because they have certain recreation needs. The needs are the determining factor behind their preferences and expectations concerning recreation opportunities and engagements. Management has the ability to enhance or diminish the quality (i.e., the plus and negative signs in the model) of recreation opportunities – experiences, and thus satisfaction – benefits of forest recreation to society.

User Need Determination

The determination of forest recreation needs has been influenced by Maslow's theory of hierarchy of needs. Maslow theorized that humans have five classes of needs and that various need states could be classified into these five categories in a hierarchical structure. The need hierarchy can be visualized as a climbing ladder where the individual must have

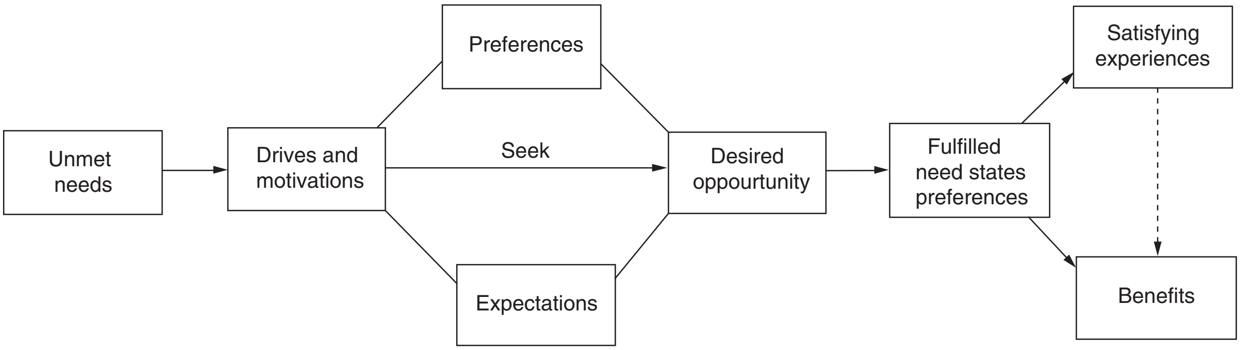


Figure 4 Conceptual model of relationships between user needs, preferences, desired opportunities, and satisfying recreational experiences.

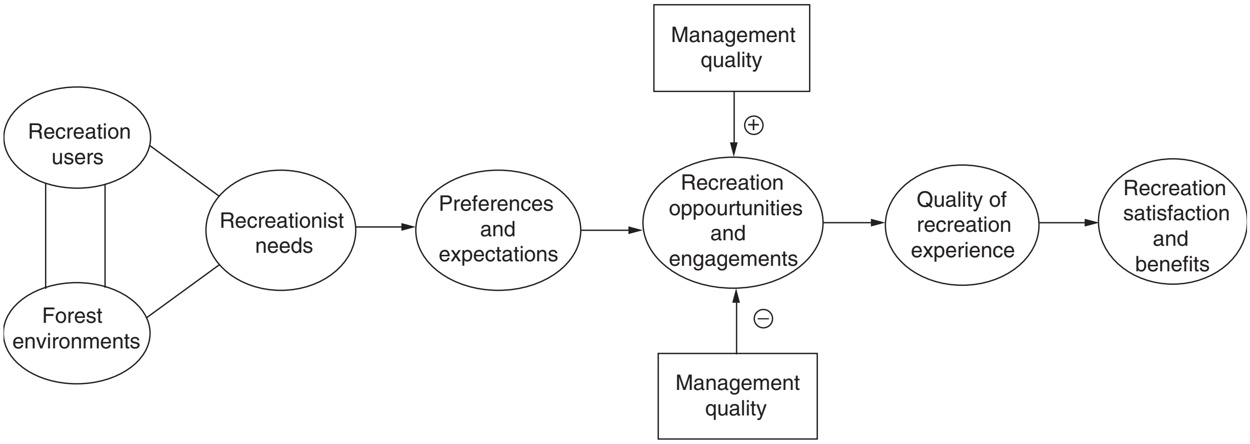


Figure 5 Conceptual model of forest recreation needs, preferences, and quality recreation opportunities – experiences.

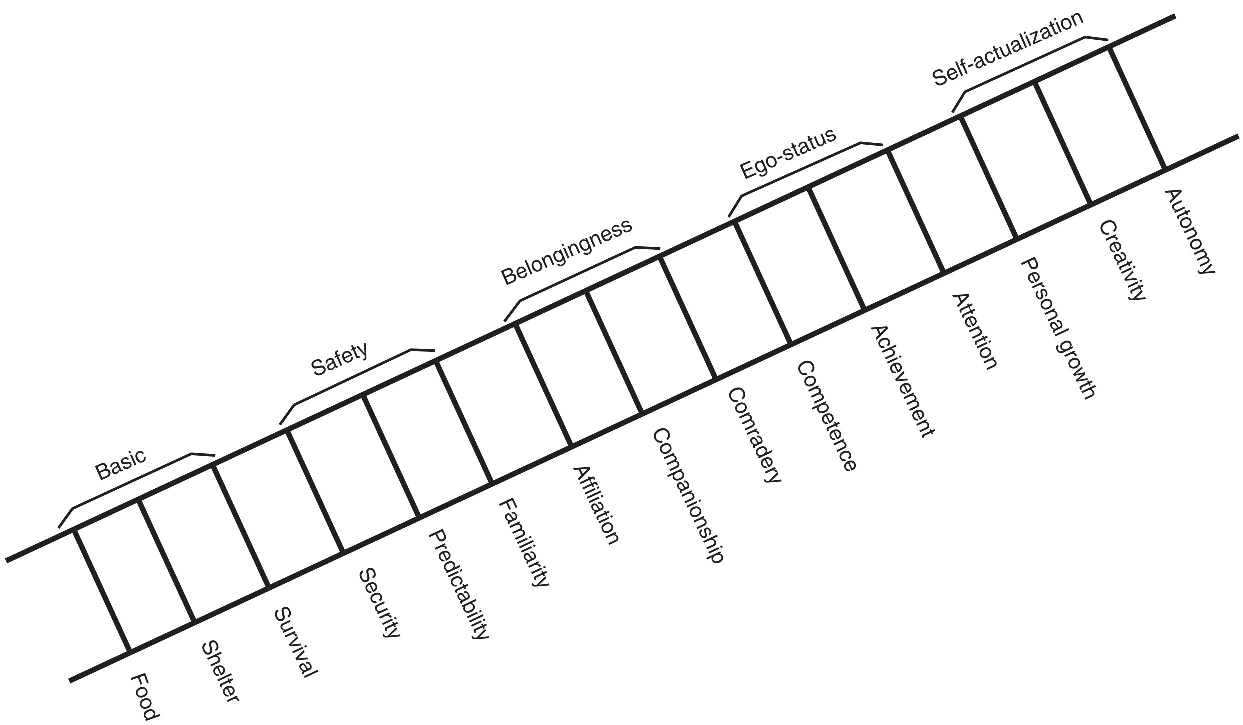


Figure 6 Maslow's ladder of human needs applied to forest recreation.

experienced a secure footing on the first rung in order to experience the need to step up to the next higher rung (**Figure 6**). He believed that there is a natural process whereby individuals fulfill needs in ascending order from the basic needs of food, shelter, survival, and other physiological needs, to the higher-order needs of self-actualization and personal creative growth.

Maslow's needs categories are related to needs-preference research in forest recreation. For example, survival skills and survival forms of wilderness recreation where self-reliance is necessary to participate successfully could be linked to basic-level needs. Safety and security needs are often at play when recreation planners, managers, and back country rangers design facilities, regulate visitor use, and rescue individuals from dangerous situations. The needs for affiliation, companionship, and comradery are commonly associated with many group activities and address the need level of belongingness. Ego-status is relevant to forest recreationists in terms of the need for competence and achievement that accompanies advanced skills necessary to participate in many risk-oriented and adventure activities. Self-actualization includes needs for personal growth, creativity, autonomy, and freedom to act, assets of many forms of remote-area recreation.

Tinsley and associates developed an inventory of psychological needs concerning leisure, using the paragraphs about leisure (PAL) inventory. The PAL inventory of recreation needs is based on the premise that leisure experiences result in the satisfaction of some of the psychological needs of recreation participants. The needs gratification helps to maintain and enhance the physical health, mental health, and life satisfaction of individuals which, in turn, stimulates personal psychological growth and increased self-actualization.

The PAL methodology consists of a series of single paragraphs which describe the gratification of a particular psychological need. Respondents are instructed to indicate the extent to which each paragraph is an accurate statement about the leisure activity being described. Ratings are done on a five-point rating scale with response alternatives ranging from 1 = not true to 5 = definitely true. This research resulted in the identification of 44 psychological needs that may be gratified by participation in leisure activities. Tinsley and associates also identified 27 of the 44 need-gratifying dimensions that varied the most across leisure activities. These two groups of leisure needs are shown in **Table 1**.

User Preference Determination

User needs are the psychophysiological antecedents that lead to the desired conditions and preferred situations (i.e preferences) that recreationists expect will facilitate and/or satisfy unmet needs. Driver's research, though similar in many respects to that of Tinsley's on leisure needs, concentrated on determining the recreation experience preferences (REP) of recreationists in natural environments. In particular, the research identified and assessed the relative importance of individual reasons or feelings of motivational implying reasons why recreationists selected certain activities and environments. A primary objective of this research was to enhance forest recreation managers' ability to specify management objectives and prescriptions that would provide quality recreation experience opportunities (i.e., the plus and minus aspects in **Figure 2**) identified by research on recreationists' motivations.

Like the PAL, the development of the REP scales was backed by the unmet-needs hypothesis that forest recreation was beneficial to helping people gratify needs not satisfied by their nonleisure behavior. Identification and evaluation of people's 'recreation experience preferences' was seen as a means to address the more difficult determination of human need states and as a managerial guide to provide the necessary recreational opportunities for quality recreation experiences. This research orientation later led to the practice of experience-based management of recreation settings, plus the development of the ROS.

The REP scales to measure recreationists' preferences were developed by means of survey questionnaires and interviews of individuals engaged in many activities in many environments. Each item in the REP inventory was assessed as to its 'importance' as

Table 1 Psychological needs of leisure

Leisure activity general: 17 needs which are satisfied to approximately the same degree by all leisure activities		
Abasement	Infavoidance	Relaxation
Autonomy	Justice	Self-control
Counteraction	Moral values	Succorance
Defendence	Order	Task generalization
Deference	Recognition	Tolerance
Harm-avoidance	Rejection	
Leisure activity specific: 27 needs which can be satisfied to a significantly greater degree through participation in some leisure activities than by participation in other leisure activities		
Ability utilization	Creativity	Security
Achievement	Dominance	Self-esteem
Activity	Exhibition	Sentience
Advancement	Getting along with others	Sex
Affiliation	Independence	Social service
Aggression	Nurturance	Social status
Authority	Play	Supervision
Catharsis	Responsibility	Understanding
Compensation	Reward	Variety

Reproduced, with permission, from Tinsley HEA, Barrett TC, and Kass RA (1977) Leisure activities and need satisfaction. *Journal of Leisure Research* 9: 110–120.

a reason for deciding to recreate in a particular activity at a certain place. Recreationists rated the reasons on a five-point importance basis, ranging from not at all important to extremely important. Years of research by Driver and colleagues resulted in 43 reliable and valid REP scales to measure the extent to which specific experiences are preferred and expected from recreational activities. **Table 2** demonstrates 19 general recreation experience preference domains into which the 43 REP scales are grouped empirically (i.e., factor analysis). Note the degree of similarity and difference between the human needs of Maslow, the leisure needs of Tinsley, and the REP of Driver.

The REP scales have dominated the determination of user needs and preferences in forest/wildland recreation, involving over 30 years of research by many different scientists. This research has yielded REP profiles for many recreational activities in an array of natural environments. **Table 3** summarizes the overall mean scores and rank order of 16 REP domains (i.e., groups of REP scales) of users of 15 different areas ranging from low-use designated wilderness to highly used outdoor areas. Note the patterns of commonality across areas in those REPs ranked the highest (i.e., enjoy nature, reduce tensions in wilderness). In areas offering a more diverse array of undeveloped and developed facilities and activities than wilderness, more variation in preference profiles, specific to activity and place, have been produced.

Site Needs and Preferences Application

While recreation scientists, planners, and managers have been interested in the physiological–psychological needs and preferences underlying why people recreate and the experiences preferred, they have also been interested in user needs and preference about on-site facilities, services, and other amenities desired. The behavioral needs and preferences of users are directly, and indirectly, related to the amenity needs and preferences of forest recreationists, for the amenity-site facilities and services can influence the type of experience derived by users. For example, the many amenities of a developed campground can provide for the needs of affiliation and family cohesion while an undeveloped wilderness area is better suited for solitude and self-reliance.

There have been many management-oriented studies on the site needs and preferences of users in many activities in many environments. Manning provides a major review and synthesis of this research, which will be summarized here.

Table 2 Recreation experience preference (REP) scales making up the recreation experience preference domains[a]

1. Enjoy nature
   A Scenery
   B General nature experience
2. Physical fitness
3. Reduce tension
   A Tension release
   B Slow down mentally
   C Escape role overloads
   D Escape daily routines
4. Escape physical stressors
   A Tranquility/solitude
   B Privacy
   C Escape crowds
   D Escape noise
5. Outdoor learning
   A General learning
   B Exploration
   C Learn geography of area
   D Learn about nature
6. Share similar values
   A Be with friends
   B Be with people having similar values
7. Independence
   A Independence
   B Autonomy
   C Being in control
8. Family relations
   A Family kinship
   B Escape family
9. Introspection
   A Spiritual
   B Personal values
10. Be with considerate people (social security)
11. Achievement/stimulation
   A Reinforcing self-confidence
   B Social recognition
   C Skill development
   D Competence testing
   E Seeking excitement
   F Endurance
   G Telling others
12. Physical rest
13. Teach/lead others
   A Teaching/sharing skills
   B Leading others
14. Risk-taking
15. Risk reduction
   A Risk moderation
   B Risk prevention
16. Meet new people
   A Meet new people
   B Observe other people
17. Creativity
18. Nostalgia
19. Agreeable temperatures

[a] Individual REP scales are designated by the capital letters if there is more than one scale per domain and by the name given the domain when there is only one scale per domain.

Reproduced, with permission, from Driver BL, Tinsley HEA, and Manfredo MJ (1991) The paragraph about leisure and recreation experience preference scales: results from the two inventories designed to assess the breadth of the perceived psychological benefits of leisure. In: Driver BL, Brown PJ, and Peterson GL (eds) *Benefits of Leisure*, pp. 263–286. Pennsylvania: Venture Publishing.

Table 3 Mean scores and ranks (in parentheses) of 16 recreation experience preference domain by users of 15 recreation areas[a]

	Experience preference domains	Designated wilderness							
		Weminuche (CO) (n = 313)	Maroon Bells (CO) (n = 268)	Flattops (CO) (n = 135)	Eagles Nest (CO) (n = 271)	Rawah (CO) (n = 212)	Linville Gorge (NC) (n = 249)	Shining Rock (NC) (n = 297)	Joyce Kilmer (NC) (n = 80)
1.	Enjoy nature	1.5 (1)	1.5 (1)	1.5 (1)	1.5 (1)	1.7 (1)	1.5 (1)	1.6 (1)	1.4 (1)
2.	Physical fitness	2.4 (4)	2.0 (2)	2.5 (5)	2.3 (2)	2.3 (3)	2.1 (2)	2.2 (2)	1.8 (2)
3.	Reduce tensions	2.1 (2)	2.3 (4)	2.1 (2)	2.4 (3)	2.2 (2)	2.3 (3)	2.3 (3)	2.1 (3)
4.	Escape noise/crowds	2.2 (3)	2.2 (3)	2.2 (3)	2.4 (3)	2.2 (2)	2.3 (3)	2.3 (3)	2.2 (4)
5.	Outdoor learning	2.1 (2)	2.4 (5)	2.4 (4)	2.5 (4)	2.2 (2)	2.3 (3)	2.4 (4)	2.2 (4)
6.	Sharing similar values	2.8 (5)	2.9 (6)	3.2 (8)	2.8 (4)	2.8 (4)	2.7 (4)	2.9 (5)	2.7 (6)
7.	Independence	3.1 (7)	2.9 (6)	2.8 (7)	3.3 (7)	3.0 (6)	3.0 (7)	3.0 (6)	3.0 (8)
8.	Family kinship	3.0 (6)	3.0 (7)	2.6 (6)	3.2 (6)	2.9 (5)	3.4 (9)	3.1 (7)	3.0 (8)
9.	Introspection/spiritual	3.5 (8)	3.1 (8)	3.3 (9)	3.7 (8)	3.5 (7)	2.8 (5)	2.9 (5)	2.6 (5)
10.	Considerate people	3.6 (9)	3.4 (9)	3.2 (8)	3.8 (9)	3.7 (8)	3.0 (7)	3.3 (8)	2.8 (7)
11.	Achievement/ stimulation	3.9 (11)	3.1 (8)	3.4 (10)	4.0 (11)	3.9 (10)	2.9 (6)	3.1 (7)	3.0 (8)
12.	Physical rest	3.8 (10)	4.3 (10)	2.5 (5)	3.9 (10)	3.9 (10)	3.2 (8)	3.3 (8)	3.4 (9)
13.	Teach/lead others	3.7 (10)	4.3 (10)	3.5 (11)	3.9 (10)	3.8 (9)	3.6 (10)	3.7 (9)	3.9 (10)
14.	Risk-taking	4.7 (12)	4.8 (12)	4.8 (13)	4.6 (12)	4.8 (10)	4.1 (11)	4.5 (10)	4.6 (12)
15.	Risk reduction	4.8 (13)	4.7 (11)	4.7 (12)	4.7 (13)	4.8 (11)	4.7 (13)	4.7 (11)	4.7 (13)
16.	Meet new people	5.6 (14)	5.3 (13)	5.5 (14)	5.5 (14)	5.8 (12)	4.6 (12)	4.5 (10)	4.5 (11)

	Experience preference domains	Undesignated wilderness				Nonwilderness areas		
		Indian Peaks (CO) (n = 101)	Vermont (VT) (n = 415)	Commanche (CO) (n = 424)	Shoshone (WY) (n = 165)	Little Sahara (UT) (n = 421)	Arkansas River (CO) (n = 442)	Lake Shelbyville (IL) (n = 1567)
1.	Enjoy nature	1.8 (1)	2.5 (2)	1.7 (1)	1.9 (1)	2.4 (4)	1.7 (1)	3.1 (2)
2.	Physical fitness	2.8 (4)	2.7 (4)	2.4 (2)	2.2 (3)	2.2 (3)	2.3 (4)	3.1 (2)
3.	Reduce tensions	1.9 (2)	1.9 (1)	2.4 (2)	2.0 (2)	2.7 (5)	2.2 (3)	3.3 (4)
4.	Escape noise/crowds	2.8 (4)	2.8 (5)	2.5 (3)	2.0 (2)	3.1 (9)	2.1 (2)	3.3 (4)
5.	Outdoor learning	2.4 (3)	2.5 (3)	2.5 (3)	2.2 (3)	2.9 (8)	2.3 (4)	3.8 (6)
6.	Sharing similar values	3.3 (6)	3.0 (7)	3.5 (7)	3.1 (7)	1.2 (1)	2.3 (4)	3.1 (2)
7.	Independence	3.2 (5)	2.9 (5)	3.2 (4)	3.1 (7)	2.7 (6)	2.7 (5)	3.7 (5)
8.	Family kinship	3.4 (7)	3.6 (9)	3.6 (8)	2.5 (4)	2.1 (2)	2.1 (2)	3.2 (3)
9.	Introspection/spiritual	3.3 (6)	3.2 (8)	3.4 (6)	2.6 (5)	3.5 (12)	3.5 (8)	4.1 (8)
10.	Considerate people	3.1 (4)	—	3.3 (5)	3.0 (6)	—	—	4.8 (10)
11.	Achievement/ stimulation	3.6 (8)	3.3 (9)	3.8 (9)	3.1 (8)	2.8 (7)	3.1 (6)	4.2 (9)
12.	Physical rest	3.1 (4)	5.0 (11)	3.4 (6)	3.3 (9)	3.2 (10)	3.1 (2)	3.0 (1)
13.	Teach/lead others	4.2 (9)	—	4.1 (10)	3.9 (10)	3.6 (13)	3.1 (6)	5.2 (11)
14.	Risk-taking	4.6 (10)	3.2 (8)	5.1 (13)	2.2 (3)	2.2 (3)	2.2 (3)	5.3 (12)
15.	Risk reduction	4.7 (11)	—	4.5 (11)	4.9 (11)	3.3 (11)	3.4 (7)	—
16.	Meet new people	5.1 (12)	4.5 (10)	4.9 (12)	4.9 (11)	3.5 (12)	4.0 (9)	4.0 (7)

[a] Ratings were made on the following nine-point response format (with numerical codes used to compute means); adds (to satisfaction): most strongly (1), strongly (2), moderately (3), a little (4), neither adds nor detracts (5), detracts: a little (6), moderately (7), strongly (8), most strongly (9).

Reproduced, from Driver BL, Nash R, and Haas GE (1987) Wilderness benefits: a state-of-knowledge review: In: Lucas RC (Comp.) *Proceedings, National Wilderness Research Conference: Issues, State of Knowledge, Future Directions.* General technical report INT-220, pp. 294–319. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station.

Environmental Preferences

Recreation experiences are seldom derived from a single on-site recreation activity (i.e., camping), but rather, result from a package of amenity-related events. For example, trail hiking and/or driving to sightsee the surrounding forest environs are popular and rewarding outdoor recreation activities while camping. Trail preferences among North American forest recreation users indicate they prefer trails of less than 10% slope, that have many bends to create an element of mystery in terms of what lies around the corner, a natural but somewhat open understory so they can see into the forest, views of large and otherwise unique features, including wildlife, and the most important preference, nearness to water.

Sightseeing involves larger-scale environmental forest preferences. Sightseers in North America prefer vistas and corridors that offer views into the forest, large trees and mature forests that have open, park-like understories that offer visual penetration into the forest, viewsheds that include water (i.e., rivers, lakes, falls), mountains offering multiridge and valley views, and unique features and landmarks. These sightseeing needs and preferences of forest recreationists are essential to understand and manage, for driving-for-pleasure remains one of the most popular forest recreation activities. Scenic byway, parkways, and natural-roaded areas are the preference of 'windshield visitors' to forested areas.

Developed Recreation Areas

Campsites and campgrounds have been researched the most and offer insight as to what campers prefer, and what planners need to consider when designing camping-related recreation opportunities.

Most campers find partial-to-full shade desirable, strongly prefer vegetative screening between adjacent campsites, and prefer spacing between campsites in the 50–100 ft (15–30 m) range, to be located between 100 and 200 ft (30 and 60 m) from both comfort station and drinking water, strongly prefer flush toilets, and favor fireplaces constructed of metal. Nearness to lakes, rivers, and other water, as well as major tourist attractions, are universally desired amenities of developed camping. However, it should be noted that there are several types of developed campgrounds and a diversity of camper preferences, meaning that management for the average preferences of the average camper may not meet the diverse preferences of many campers.

Undeveloped Recreation Areas

Several studies have researched the preferences of backcountry and wilderness users toward management policies, and facilities and services. Preferences toward management policies suggest that:

1. Most users prefer restrictions on the number of users in crowded areas.
2. There is no consensus on the preferred method of use rationing, although queuing seems most favored and lottery the least favored procedures.
3. Opinions are mixed on the desirability of fixed-travel routes or itineraries (via, permits).
4. A majority of users support self-registration permits.
5. Degree of preference is mixed on spatial zoning by method of travel (i.e., horse versus hiking), lowering trail standards, and restricting or downgrading access routes.
6. Most users prefer limits on group size.
7. Most users do not favor prohibition of campfires, although this may change as more areas restrict campfire use.
8. Most wilderness users do not prefer policies requiring use of designated campsites.

Studies of backcountry–wilderness user preferences for facilities and services (**Table 4**) suggest:

1. Relatively low-standard trails are preferred to high-standard trails.
2. Most users prefer bridges at large streams difficult or dangerous to ford.
3. Information signs along trails (i.e., trail names, directions, and distances) are preferred, while campsite and interpretive signs are less favored.
4. Fireplaces and picnic tables are not preferred at campsites, while fire rings are.
5. Degree of preference is mixed on pit toilets and other types of sanitary facilities at campsites.
6. Degree of preference is mixed on trail shelters.
7. Special equestrian facilities (i.e., corrals and hitching racks) are generally not preferred.
8. Emergency telephones are generally not favored, although cell phones are more commonly being carried into wilderness areas.
9. Maps and informational pamphlets about areas are preferred by the majority of areas.
10. The majority of users favor the presence of wilderness rangers.

In both developed and undeveloped areas, there is considerable evidence that users tend to prefer or respond favorably to the facilities and services they find on-site when recreating; in other words, site supply determines preference demand. Manning suggests this finding might be explained by the fact that visitors may sort themselves, or self-select,

Table 4 Percentage of users preferring selected backcountry facilities and services

Location	*Facility*	*%*
Mt. Marcy, NY	Pit toilets, sanitary facilities	70
	Emergency telephones	50
Boundary Waters Canoe Area, MN	Pit toilets, sanitary facilities	50
	Emergency telephones	26
High Sierras, CA	Pit toilets, sanitary facilities	36
	Emergency telephones	45
Three wilderness areas	High-standard trails	m
	Information signs	M
	Interpretive signs	m
	Fireplaces	25
	Picnic tables	40
	Trail shelters	60
	Corrals	20
	Maps/pamphlets	M
Bob Marshall Wilderness, MT	High-standard trails	25
	Information signs	90
	Fireplaces	34
	Picnic tables	34
	Trail shelters	15
	Emergency telephones	62
Mission Mountains Primitive Area, MT	High-standard trails	32
	Information signs	62
	Fireplaces	24
	Picnic tables	24
	Trail shelters	34
	Emergency telephones	32
Glacier National Park, MT	High-standard trails	10
	Information signs	67
	Fireplaces	52
	Picnic tables	52
	Trail shelters	76
	Emergency telephones	12
Boundary Waters Canoe Area, MN	High-standard trails	37
	Pit toilets, sanitary facilities	63
	Maps/pamphlets	60
	Wilderness rangers	70
Bob Marshall Wilderness, MT	High-standard trails	35
	Bridges across large rivers	67
	Campsite signs	52
	Pit toilets, sanitary facilities	43
	Corrals	25
	Hitching racks	26
	Maps/pamphlets	52
	Wilderness rangers	58
Bridge Wilderness, WY	High-standard trails	31
	Bridges across large rivers	65
	Campsite signs	30
	Pit toilets, sanitary facilities	22
	Corrals	4
	Hitching racks	4
	Maps/pamphlets	60
	Wilderness rangers	68
High Uintas Primitive Area, UT	High-standard trails	335
	Bridges across large rivers	62
	Campsite signs	26
	Pit toilets, sanitary facilities	25
	Corrals	11
	Hitching racks	16
	Maps/pamphlets	55
	Wilderness rangers	67
Appalachian Trail	Low-standard trails	M
	Interpretive signs	50
Cranberry Backcountry, WV	Trail shelters	35
	Wilderness rangers	63
Appalachian Trail	Trail shelters	49
Nine wilderness areas	High-standard trails	m
	Low-standard trails	M
	Bridges across large rivers	M
	Information signs	M
	Fireplaces	mx
	Fire rings	M
	Picnic tables	m
	Pit toilets, sanitary facilities	m
	Corrals	mx
	Maps/pamphlets	M
	Wilderness rangers	M
Three wilderness areas	Information signs	68
	Picnic tables	41
	Maps/pamphlets	74/90
	Wilderness rangers	62
Three rivers	Wilderness rangers	16
Desolation Wilderness, CA	Low-standard trails	M
	Bridge across large rivers	M
	Interpretive signs	M
	Fireplaces	mx
	Fire rings	M
	Pit toilets, sanitary facilities	mx

M, majority; m, minority; mx, mixed.
Reproduced, with permission, from Manning RE (1999) *Studies in Outdoor Recreation*. Corvallis, OR: Oregon State University Press.

among areas and facilities according to their preferences. Preferences may also be based on the types of areas and facilities previously encountered, and familiarity. For example, field observation research shows that users tend to camp at previously used and familiar sites rather than seek out and establish new sites.

Use Impact Preference

User perceptions and preferences regarding various types and levels of recreation-caused impacts to environmental and experiential conditions are of interest to recreation researchers and managers, for impacts can degrade the quality of recreation places and experiences. However, forest recreationists seem to have few reactions to impacted site conditions, and are often not perceptive of existing impacts. Some exceptions are severe disturbances to site conditions (i.e., deep trail erosion) and experience conditions (i.e., crowded users); both examples of impacts that can be managed to improve the quality of forest recreation. In addition, forest recreationists are very sensitive about litter in natural areas. Litter is not only a site impact; it is also an experience impact. Litter decreases the naturalness of a site, can indicate that an area is overused and/or misused, and detracts from the preferred conditions and, thus, quality of recreation experience received by users.

While forest recreation users exhibit preferences against some major impacts as listed above, they are not perceptive of and/or demonstrate preferences toward the majority of recreation resource impacts. For example, worn-out campsites and trails, as well as water pollution and wildlife disturbance, are not perceived by the majority of users as impacts or unpreferred conditions. A study of camper perceptions of site impacts at three Indiana state park campgrounds indicated that the majority of campers rated ground cover conditions as satisfactory to excellent, even in areas where over 75% of the campsites were 100% bare-ground and severely compacted. Two-thirds of the campers did not notice damage to trees or shrubs, despite the fact that damage was extensive in several areas. In addition, even the minority of users who rated the campsite conditions as poor reported that these conditions did not detract from their enjoyment of the area.

The lack of perception and reaction of recreationists toward recreation resource impacts has been troublesome to recreation resource managers, whose responsibilities include maintaining and enhancing the quality of the recreation resource. It seems the perceptions and preferences of users do not always match those of recreation scientists and managers. Managers tend to be more perceptive of site and experience conditions, and prefer higher standards of conditions than the majority of users. This is true for developed campgrounds, backcountry campsites, wilderness areas, roaded forest lands, and state parks. Impacts and problems studied in these areas have included litter, vandalism, theft, human waste, environmental impacts at campsites and along trails, water pollution, wildlife disturbance, excessive noise, rule violations, and conflicts among recreationists. Managers also tend to rate such issues as greater problems than do site users. Similar differences between managers and users have been found to occur concerning motivations and reasons for area and activity participations, and preferences/attitudes toward recreation management policies and practices. Thus, forest recreation scientists and managers not only need to understand the needs and preferences of recreation users, they must also understand the differences that exist between scientists, managers, and users of resources.

See also: **Landscape and Planning**: Forest Amenity Planning Approaches; Perceptions of Forest Landscapes; The Role of Visualization in Forest Planning. **Recreation**: Inventory, Monitoring and Management.

Further Reading

Driver BL and Tocher SR (1970) Toward a behavioral interpretation of recreational engagements, with implications for planning. In: Driver BL (ed.) *Elements of Outdoor Recreation Planning*, pp. 9–31. Ann Arbor, MI: University Microfilms.

Driver BL, Nash R, and Haas GE (1987) Wilderness benefits: a state-of-knowledge review. In: Lucas RC (comp.) *Proceedings, National Wilderness Research Conference: Issues, State of Knowledge, Future Directions*. General technical report INT-220, pp. 294–319. Ogden, UT: US Department of Agriculture Forest Service, Intermountain Forest and Range Experiment Station.

Driver BL, Tinsley HEA, and Manfredo MJ (1991) The paragraph about leisure and recreation experience preference scales: results from the two inventories designed to assess the breadth of the perceived psychological benefits of leisure. In: Driver BL, Brown PJ, and Peterson GL (eds) *Benefits of Leisure*, pp. 263–286. Pennsylvania: Venture Publishing.

Hammitt WE and Cole DN (1998) *Wildland Recreation: Ecology and Management*. New York: John Wiley.

Jubenville A (1976) *Concepts in Recreation Planning. Outdoor Recreation Planning*. Philadelphia, PA: W.B. Saunders.

Knopf R (1983) Recreational needs and behavior in natural settings. In: Altman I and Wohwill J (eds) *Behavior and the Natural Environment*, pp. 205–240. New York: Plenum Press.

Manfredo M (1984) Comparability of onsite and offsite measures of recreation needs. *Journal of Leisure Research* 16: 245–249.

Manning RE (1999) *Studies in Outdoor Recreation*. Corvallis, OR: Oregon State University Press.

Schreyer R and Beaulieu J (1986) Attribute preferences for wildland recreation settings. *Journal of Leisure Research* 18: 231–247.

Tinsley HEA, Barrett TC, and Kass RA (1977) Leisure activities and need satisfaction. *Journal of Leisure Research* 9: 110–120.

Inventory, Monitoring and Management

T Sievänen, Finnish Forest Research Institute, Helsinki, Finland

Introduction

Outdoor recreation in forested settings is a use of forest resources which has become more and more important for urbanized societies. It plays a prominent role in people's leisure time. Forests together with other natural areas offer an environment where people can participate in many kinds of recreation activities, and where they can feel close to nature and natural resources. This article offers an overview of the key issues and research regarding the evaluation and management of forest recreation.

This article includes a brief history of recreation research, a description of methods and types of data gathered for recreation information concerning both demand of recreation and supply of recreation resources, and an overview of management methods of recreation resources and visitors.

History of Recreation Research

Research on forest recreation started to develop in the USA and European countries such as Germany in the late 1950s and 1960s. One of the first authors to discuss the information needs and provide a theoretical basis for producing information on outdoor recreation was Dr. Marion Clawson. The Outdoor Recreation Review Commission (ORRRC) was established in 1958 in the USA, and that started the process of producing regular nationwide recreation participation surveys. The ORRRC report was first published in 1962, with recreation participation surveys taking place at 5–12-year intervals up to that of 2000, led by Dr. H. Ken Cordell. Canada also has a long tradition of recreation participation surveys since the early 1980s. In Europe, some countries have done long-term monitoring for decades. Sweden was one of the first to produce outdoor recreation information on a population basis in 1964 and 1974, and repeated a population study in the 1990s. In Denmark, the first nationwide recreation participation survey was done in 1976–1977 by Niels Elers Koch, and repeated in 1993–1994. The Netherlands has also monitored outdoor recreation since the 1970s. In countries such as Finland and Italy, the first nationwide recreation participation surveys were done in the 1990s and early 2000.

In addition to nationwide surveys, development work for producing visitor information on recreation areas was needed. Visitor surveys and visitor-counting methods have been studied since the 1960s. Dr. George A. James in the USA and Dr. Lars Kardell in Sweden were the most prominent pioneers of this work. In the 1990s, a number of handbooks were produced to help park personnel to monitor visitation.

Science-based visitor management in recreation areas, national parks, and wilderness areas has demanded growing attention. Research related to concepts of ecological and social carrying capacity and conflict management, done by Dr. David Lime and others, have been important in improving management methods in the 1970s–1980s. That line of research was adopted into a planning system or framework, e.g., limits of acceptable change (LAC) in the 1980s, developed by Dr. George Stankey and others. The LAC approach has been adopted in many countries as a tool for planning the sustainable recreational use of natural resources. Studies on recreation experiences and benefits gained from recreation have produced systematic development frameworks for visitor management, i.e., benefit-based management or outcomes approach to leisure, developed by Dr. Bev Driver and his colleagues in the 1980s and 1990s.

Beside the recreation participation surveys, research on recreation resource inventories has developed over the years. In the USA, the ORRRC report included a recreation resource classification. Next, the theoretical framework for classifying recreation environment, i.e., recreation opportunity spectrum (ROS), was developed by Dr. Bev Driver and Dr. Perry Brown and their colleagues in the late 1970s. The nationwide application of broad-scale resource inventories in the USA was led by that country's Forest Service in the late 1970s and 1980s. Methods to implement these scientific-based approaches into resources management were also developed, such as the early visual management system developed in the 1970s by the US Forest Service (*see* **Landscape and Planning:** Visual Resource Management Approaches). Recently, geographic information system (GIS)-based planning methods and participatory planning processes have advanced recreation planning and management in many countries.

Methods and Data for Recreation Information Gathering

Studies on recreation inventory and monitoring fall into two basic types – studies of user needs and activities (demand), and studies of the recreation facilities and land-based resources (supply).

Recreation Demand Surveys

Nationwide population surveys Recreation demand refers here to the actual or potential participation in recreation activities. There is a need to know how many people, and how many times, or how many days per year they walk for pleasure, hike, ride a bicycle, and do other recration activities. The need for nationwide information on recreation demand was recognized 40 years ago, when the first National Recreation Survey (NRS) was conducted in 1960 in the USA. Monitoring of recreation demand will help forest managers in allocation and planning of the use of forest resources in the future. The continuity of a core set of participation and demographic questions has ensured that trend construction and comparisons of recreation have been possible at the national level over the years. Similar efforts have been made in other countries like Canada, Denmark, and Sweden but the contents and extent of the nationwide recreation surveys vary considerably.

The latest National Survey of Recreation and Environment 2000 (NSRE) includes several themes of recreation research. In particular, information concerning recreation participation and recreation trips serves to monitor recreation demand. The survey covers 50 different outdoor activities. The survey had about 75 000 responses.

Denmark has conducted a series of recreation surveys, which offer the possibility of comparing forest recreation participation over time: Danish surveys covered overall visitation into the forestland, and included a remarkable set of data on forest and landscape preferences. The survey in 1993–1994 as well as the 1993–1994 survey reached a response rate of over 80%, from samples of almost 3000 persons. In Finland, only one nationwide recreation survey has been conducted but the study is planned to be repeated in 2008–2010. The Finnish survey data included about 10 000 respondents. The main issues measured were participation in outdoor activities, recreation trips close to home, and nature trips including an overnight stay. In southern Europe, Italy has conducted its first nationwide recreation survey. Even though there are still many discrepancies in use of concepts, terms, and units of measurement, some international comparisons can be made. **Table 1** shows participation rates of some of the most typical recreation activities in six countries, expressing the diversity, similarity, and differences in recreation behavior among different nations. The issue of harmonizing policy and procedures for recreation information monitoring internationally has been discussed in the research community and may provide more comparable data in the future.

On-site user inventories: monitoring visitor flows and gathering visitor information On-site recreation inventories, i.e., visitation monitoring systems, are an important part of the management policy of recreational and protected areas in many countries.

Table 1 Participation rates in some recreation activities in six countries in the 1990s. Participation rate means the portion of population which recreate doing the activity at least one time during one year

Recreation activity	*Participation rate (%)*					
	Canada[a]	*Denmark*[b]	*Finland*[c]	*Holland*[d]	*Italy*[e]	*USA*[f]
Walking		63	68	74	40	67
Hiking			19		38	24
Bicycling			55	68	6	29
Jogging, running		14	16	16	4	26
Camping	19		18		2	14
Picnicking	26	10	28		45	49
Hunting	5	1	8		4	7
Picking berries or other forest fruits	11	2	57			
Picking wild mushrooms		3	41		21	
Cross-country horseback riding	2	1	2	6	3	5
Studying and enjoying nature	31	56	51		21	
Cross-country skiing	4		40		2	3

Empty spaces infer that a comparable figure was not available.
[a] The Nature Survey; sample of 86 951 Canadians by Statistics Canada in 1997. DuWors E, Villeneuve M, Filion FL, *et al.* (1999) *The Importance of Nature to Canadians: Survey Highlights*. Ottawa, Canada: Environment Canada.
[b] A mail questionnaire regarding forest recreation on a sample of 2826 of the Danish adult population in 1993–1994, conducted by the Danish Forest and Landscape Research Institute. Jensen FA and Koch NE (1997) *Frilutsliv i Skovene 1976/77–1993/94. [Forest Recreation 1976/77–1993/94.]* Forskningserien nr. 20. Copenhagen, Denmark: Forskiningscentret for Skov & Landskap, 215 s., ill.
[c] A telephone survey, sample of 12 709 among the whole population conducted by Statistics Finland and Finnish Forest Research Institute in 1998–2000. Sievänen T (2001) Luonnon virkistyskäyttö 2000. [Outdoor recreation 2000.] *Metsäntutkimuslaitoksen Tiedonantoja 802*.
[d] A diary survey by Statistics Netherlands (CBS) in 1995–1996. Statistics Netherlands (CBS) (1997) *Dagrecreatie1995/'96. [Daytrips 1995/'96.]* Voorburg/Heerlen, The Netherlands: Statistics Netherlands.
[e] A mail questionnaire on a sample of 3000 of the whole Italian population in 1995; recreation activities in forest. Scrintzi G, Tosi V, Agatea P, and Flamminj T (1995) Gli Italiani e il bosco. Coordinate quali-quantitaitve dell'utenza turistica in Italia. [Italians and the wood. The forest recreation demand in Italy.] *Communicazioni di Ricerca ISAFA 95/1*, Trento.
[f] NRSE telephone survey of sample of 12 000 people in 1994–1995. Cordell KH (principal investigator) (1999) *Outdoor Recreation in American Life: A National Assessment of Demand and Supply Trends*. Sagamore.

Recreation monitoring as applied is most often a science-based system for data collection, data management and reporting, which supplies managers with baseline, updated visitor information on a continuous basis. Monitoring systems differ between countries, but often standardization of methods and harmonization of information content have taken place within one country or at least within one public land agency.

The most common visitation information measured includes number of visits, duration of visit, and distribution in the area. Information gathered from visitors often consists of socioeconomic factors such as sex, age, income, and municipality/region/country of residence, length and means of travel, and money used. Visitor behavior pattern describes recreation activities participated in, length of stay in the area, and company of visit. Visitor satisfaction, motives, and expectations of visit and experiences are also studied in most cases.

In the USA, the National Park Service implements a mail-back customer satisfaction card (referred to as the visitor survey card or VSC), which is similar to surveys used by other agencies. All National Park Service units systematically measure and report annually on visitor satisfaction. The customer satisfaction card enables parks, clusters, regions, and national program offices to measure their progress toward meeting annual and long-term goals of park management. The US Forest Service has implemented a sophisticated on-site visitor monitoring system called the National Visitor Use Monitoring (NVUM) system. With this system, one-fourth of the 160 national forests in the country are sampled each year through a system of site-day sampling. Activities, duration of visit, satisfaction, trip spending profiles, and sites visited are collected and geographic information systems (GIS) referenced to provide location-specific, regional, and national estimates to guide policy, management, maintenance, budgeting, and customer responsiveness.

In Denmark, automatic monitoring of the car-based forest visitation at four selected forest areas was established in the mid-1970s and has been going on since that. In addition, on-site inventories have been carried out in more than 300 forest areas in 1976–1977 and again in 1996–1997 in more than 500 Danish forest and nature areas. In the UK, visitor counting and surveys are also applied widely and used in planning and management processes. Finland has standardized visitor study procedures in order to get comparable visitor information from all state-owned recreation and protected areas. The national recreation management policy directs the conduct of visitor countings and visitor surveys in order to develop customer-driven management in recreation areas. In many other European countries, visitor information collection systems are still in a developmental stage.

In New Zealand, the Visitor Asset Management System (VAMS) was created to provide a basis for an integrated visitor counting and reporting system. The VAMS is an interactive database on key management information about the 4000 designated visitor sites throughout New Zealand.

Inventories of Recreation Resources

Geographical information system GIS-based methods have become important for collecting information on recreation resources. GIS-based recreation resource inventories are useful for GIS-based management systems. Countries using GIS-based recreation supply databanks are, for example, Denmark, Finland, the Netherlands, and the USA. GIS offers several benefits of analyzing recreation resources. The most important aspect is that it is possible to gather inventory information on natural resources such as forest types, water bodies, and topography from other GIS data sources, which decreases the costs of data collection. Also, the same information is easily used on a local, regional, and national level.

The most essential components of recreation supply are the number and land area of recreational areas, trails or trail networks, and the array of facilities and services supporting recreation participation. The quality aspects of natural resources are important in terms of scenery, topography, water elements, nature values, accessibility, and safety. The factors and indicators measured must be valid in order to support the ecologically and socially sustainable recreational management of natural resources. The recreation specific criteria and indicators of ecologically and socially sustainable use vary among different countries and between the types of recreational area according to ROS classification. Landscape preference studies have produced a strong information basis to assess the landscape quality in many countries e.g., BC (Canada) tourism capability and recreation features/activity mapping (*see* **Landscape and Planning**: Visual Analysis of Forest Landscapes). In general, people appreciate forested landscape with a variety of different types of forest: old growth, a mix of broad-leaved, and conifer stands with some open views are appreciated in many countries. Water elements – ponds, rivers, streams, lakes, and sea – are appealing landscape elements. Accessibility means first, distance and need of transportation, and second, safety and tranquillity of route to recreation site. The importance of distance and other factors of accessibility depends on the type of recreation areas and recreation activity. Close-to-home recreation areas, which allow daily visits, stress the safety and close distance, preferably a walking possibility. Areas used during a weekend or annual vacation may be located at longer distances, but then the demand for other qualities is of much higher importance (*see* **Recreation**: User Needs and Preferences). Recreation opportunities (i.e., resources provided for people's use) needed depend on both the time and money budget of the population. The mobility of the population is a detrimental factor to determine the recreation behavior patterns and thus the demand of different types of recreation areas and other recreation resources.

Management of Recreation and Nature-Based Tourism in Forests

Approaches and Concepts Related to Managing Recreation Resources and Visitors

The carrying capacity concept describes a sustainable level of recreational use. The ecological carrying capacity is defined as the number of visitors or visits an area can sustain without degrading natural resources. The social carrying capacity refers to level of recreational use where the fulfillment expectations of visitor experiences are not threatened because of crowding or misbehavior of other visitors. Most professionals agree that both ecological and social carrying capacity factors must be considered for effective area planning and management. For managerial applications, it is essential to learn about the user attitudes, user preferences, and site use impacts relating to management objectives.

The ROS is a management framework designed to respond to the diversity of experiences desired by recreationists and is used by many recreation resource management agencies all over the world. The original ROS framework describes six levels of recreation opportunities as a spectrum of natural to more developed categories – primitive, semiprimitive, nonmotor, semiprimitive motor, roaded natural, rural, and urban. Recreation opportunities comprise of activity, setting, and recreation experience.

The term limits of acceptable change (LAC) is the management process developed for recreation and wilderness planning and management. The focus is to determine the degree of change caused by recreationists which is acceptable in a specific area. The LAC principles include ecological, economic, and social dimensions of recreation and nature-based tourism. The LAC concept is based on nine steps, where different parameters, such as vegetation and littering, and their indicators (e.g., presence of seedlings and litter) are monitored to detect when the limits are reached. In the LAC process, the general principles of recreation and nature tourism management are divided into more detailed aims and indicators. Furthermore, the management actions will be defined beforehand if the LAC of a certain indicator is being approached or reached. The LAC process can also be applied as a tool for assessing the impacts of recreation and nature tourism on natural areas as well as managing visitor conflicts and other visitor-related problems.

Applying theoretical approaches of carrying capacity and limits of acceptable change into planning and management processes sets a demand of monitoring both of recreational use and its impacts on natural resources. A contemporary framework for managing carrying capacity in the US national parks is visitor experience and resource protection (VERP), which focuses on formulating indicators and standard of quality for desired future conditions of park resources and visitor experiences.

A broad management framework was developed in order to combine both resource and visitor management, paying more attention to the final desired outcomes of resource use. The benefit-based management (BBM) approach focus on optimizing net benefits of use for recreation resources. The BBM requires benefits-oriented management prescriptions, guidelines, and standards to assure provision of optimal recreation opportunities to citizens.

The most advanced visitor management approach is the outcomes approach to leisure (OAL). It focuses on both ecologically and culturally sustainable use of natural resources and the realization of satisfying recreation experiences of recreationists. It stresses applying science-based knowledge in planning and management systems. It also includes the notion of creating and maintaining collaborative partnerships with affected stakeholders. OAL covers all aspects of recreation production, both input and output elements, facilitating outputs as well as final outcomes, i.e., benefits gained on an individual and societal level. Inputs refer to the agency efforts such as time, knowledge, and capital investments used for the production of recreation opportunities as a whole. Facilitating outputs are the results of provider actions, i.e., recreation services such as trails and information. Outcomes can be beneficial or unwanted consequences resulting from the management and use of recreation resources.

Related concepts and frameworks on visitor resources are discussed in the article on VRM (*see* **Landscape and Planning**: Visual Resource Management Approaches).

Implementation: Development Programs and Planning Systems

Forest recreation is nowadays an essential component when planning the use of forest resources. There are many ways to integrate different components of forest uses into the planning system. One goal of integrated, multiobjective forest planning is improving the quality of forest planning by utilizing advanced decision-support tools. Decision makers' values, including recreation-related values, which can be either in conflict or compatibility with other values, could be added into the planning process in a systematic way by using recreation criteria and indicators.

The planning processes are to a great extent developed into a direction where public involvement plays an essential role (*see* **Social and Collaborative Forestry**: Public Participation in Forest Decision Making). The participatory planning principle is used widely in many countries. Visitor studies, public meetings, and recreation user group participation are the most typical ways to get public input into the agency-driven planning and management system for recreation resources.

There are two important research fields, which offer valuable additional information into the planning process for recreation. The first is economic valuation, which includes the methods of travel cost modeling and contingent valuation. The contingent valuation method measures with the help of survey techniques people's personal valuation of unpriced recreation opportunities by using contingent markets. For example, people are asked how valuable in monetary terms for them is the possibility to use the neighborhood park. Values related to the recreational use of forests can be compared to other forest values. The economic valuation procedures also provide forecasting models, revenue potentials, and equity analysis components. The second is economic impact assessment, which produces income, employment, local tax generation, and other macroeconomic statistics for recreation scenarios. These tools, integrated with participation surveys, resource inventories, ROS, LAC, and other approaches to planning, provide a broad overview and a more complete picture for more effective recreation planning management.

Planning of forest recreation in designated recreation areas has many styles and scales in different countries. In some countries, there are rather standardized styles, applied by forest and park services and other state land agencies, to produce management plans, which cover both the management of resources and visitors. The management plan of a recreation area, for example, includes the strategic and tactical policies and decisions of how much use is appropriate, what kind of activities are acceptable, and how visitor use is to be managed. An important part of the plan is to define the management tools for implementation, such as how to limit access or what regulations are needed to limit length of stay or group size.

In the USA, broad-scale studies of the demand and supply of outdoor recreation and wilderness, for the first time, paid attention to social change and its consequences to recreation, and have reported long-term outdoor recreation trends. The research indicates rapid and continuing growth in recreation demand in the USA. The same trend applies to many other countries with urbanized societies. Responding to the growing demand for outdoor recreation, large national programs and plans for development of recreation and nature-based tourism are conducted to enhance welfare and positive economic impacts of forest recreation. The development actions are directed to improve recreation resources supply, to rationalize recreation resource management and administration, and to increase research and education.

See also: **Landscape and Planning**: Visual Analysis of Forest Landscapes; Visual Resource Management Approaches. **Social and Collaborative Forestry**: Public Participation in Forest Decision Making. **Recreation**: User Needs and Preferences.

Further Reading

Anderson DH, Lime DW, and Wang TL (1998) *Maintaining the Quality of Park Resources and Visitor Experiences: A Handbook for Managers*. St Paul, MN: Cooperative Park Studies Unit, Department of Forest Resources, University of Minnesota.

Arneberger A, Brandenburg C, and Muhar A (eds) (2001) *Monitoring and Management of Visitor Flows in Recreational and Protected Areas*. Conference proceedings. Vienna, Austria: Institute for Landscape Architecture and Landscape Management, Boden kultur University of Vienna.

Clawson M and Knetch JL (1966) *Economics of Outdoor Recreation. Resources for the Future, Inc*. Baltimore, MD: Johns Hopkins University Press.

Cordell HK (1999) *Outdoor Recreation in American Life: a national assessment of demand and supply trends*. Washington, DC: Sagamore.

Cordell HK, Green GT, and Carter JB (2003) *Outdoor Recreation for 21st Century America*. State College, PA: Venture.

Dale M, Foley M, and Macgregor C (1993) *Visitor Monitoring Training Manual*. Edinburgh, UK: Scottish Natural Heritage.

Driver BL, Brown PJ, and Peterson GL (1991) *Benefits of Leisure*. State College, PA: Venture.

Driver BL, Brown PJ, and Stankey GH (1987) The ROS planning system: Evolution, basic concepts, and research needed. *Leisure Sciences* 9: 201–212.

Gartner WG and Lime DW (eds) (2000) *Trends in Outdoor Recreation, Leisure and Tourism*. Wallinford, UK: CAB International.

Manning RE (1999) *Studies in Outdoor Recreation: Search and Research for Satisfaction*, 2nd edn. Corvallis, OR: Oregon State University Press.

McCool SF and Cole DN (1997) *Proceedings – Limits of Acceptable Change and Related Planning Processes: Progress and Future Directions*, May 20–22 1977, University of Montana, Ogden, UT.

Shelby B and Heberlein TA (1986) *Carrying Capacity in Recreation Setting*. Corvallis, OR: Oregon State University Press.

Stankey GH, Cole DN, Lucas RC, Petersen ME, and Frissel SS (1985) *The Limits of Acceptable Change (LAC) System for Wilderness Planning*. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station.

US Department of Agriculture, Forest Service (1995) *Landscape Aesthetics, A Handbook for Scenery Management*. US Agricultural Handbook no. 701. Washington, DC: Government Printing Office.

US Department of the Interior, National Park Service (1997) *VERP, The Visitor Experience and Resource Protection (VERP) Framework. A Handbook for Planners and Managers*. Denver, CO: US Department of Interior, National Park Service, Denver Service Center.

Watson AE, Cole DN, Turner DL, and Reynolds PS (2000) *Wilderness Recreation Use Estimation: A Handbook of Methods and Systems*. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-56. Ogden, UT.

Yuan S, Maiorano B, Yuan M, Kocis SM, and Hoshide GT (1995) *Techniques and Equipment for Gathering Visitor Data on Recreation Sites*. Washington, DC: US Department of Agriculture Forest Service, Technology and Development Program.

Reduced Impact Logging *see* **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Forest Operations under Mountainous Conditions; Harvesting of Thinnings; Roading and Transport Operations; Wood Delivery.

Regeneration *see* **Ecology**: Reproductive Ecology of Forest Trees. **Plantation Silviculture**: Forest Plantations. **Silviculture**: Natural Regeneration of Tropical Rain Forests; Natural Stand Regeneration; Silvicultural Systems; Unevenaged Silviculture. **Site-Specific Silviculture**: Ecology and Silviculture of Tropical Wetland Forests.

Rehabilitation *see* **Silviculture**: Bamboos and their Role in Ecosystem Rehabilitation; Forest Rehabilitation. **Site-Specific Silviculture**: Reclamation of Mining Lands; Silviculture in Polluted Areas.

Remote Sensing *see* **Resource Assessment**: Forest Change; Forest Resources; GIS and Remote Sensing; Regional and Global Forest Resource Assessments.

Reproduction *see* **Ecology**: Reproductive Ecology of Forest Trees. **Genetics and Genetic Resources**: Genetic Systems of Forest Trees; Propagation Technology for Forest Trees. **Silviculture**: Natural Stand Regeneration. **Tree Breeding, Principles**: Conifer Breeding Principles and Processes. **Tree Physiology**: Physiology of Sexual Reproduction in Trees; Physiology of Vegetative Reproduction.

RESOURCE ASSESSMENT

Contents

Forest Resources

E Tomppo, Finnish Forest Research Institute, Helsinki, Finland

Introduction

The term 'inventory' means the preparation of a detailed list of articles according to their properties. Similarly, forest inventory means tabulated, reliable, and satisfactory tree information related to the required area unit. An essential feature is the assessment of the area and quality of each unit. The principal purpose of forest inventories has been to provide accurate information for sound planning and management of resources and for the planning of forest industry investments and nature conservation. Accordingly, optional cutting possibilities with future forest development scenarios have been computed on the basis of inventory results. These scenarios have formed the basis for forest policy and forest utilization.

The needs for information in forestry have increased during the last decades because of the awareness of forest health status, particularly since the beginning of the 1980s, and the status of biological diversity, as well as the recognition of the role of forests in reducing the effects of global warming. At the same time, the pressure to increase timber consumption is increasing in some regions of the world. Therefore, reliable forest information is important to plan the sustainable use of forests.

The Food and Agricultural Organization of the United Nations (FAO) and International Union of Forest Research Organizations (IUFRO) collect and agree globally accepted concepts and definitions used in forest inventories.

FAO has also collected global-level forest resource information since 1947. Since the beginning of the 1950s, various regional and global surveys have been conducted every 5–10 years. As knowledge on the forest resources has improved at national levels and as technology has advanced, the Global Forest Resources Assessments have increased in breadth and quality. Forest Resource Assessment 2000 (FRA 2000) is so far the most comprehensive in terms of the number of references used and information analyzed on forest cover, forest state, forest services, and nonwood forest products (NWFP). FRA 2000 applies for the first time a single technical definition of forest at the global level, based on 10% crown cover.

There are also several types of forest inventories, such as operational, management, and national forest inventory. The information from operational and management inventories is used to make short- and long-term plans for the management of specific forest ownership while national forest inventories are used as the information basis for national forestry policy, forestry programs, and strategic planning of forestry and forest industry. Forest inventory is considered here from the point of view of national forest inventory. There are several definitions for the term 'forest inventory' in the forest inventory literature. A modern national forest inventory could be defined as follows:

> *Forest inventory is a procedure involving planning of inventory design, data collection, data analysis and reporting about forest resources of a large forested area or entire country. It is designed to insure continuous flow of information about the current status and rate of changes over time about forest resources and the characteristics of the land area on which trees are growing.*

Forest inventory information is related to administrative or other area units and presented in the form of tables and forest maps together with reliability assessments. Basic information is timber quantity and quality by tree species and by tree size as well as tree growth, mortality, and removal by harvest. Inventories have also provided information about land use, site quality, vegetation cover, description of topography, ownership and protection patters, accessibility, transportation facilities, accomplished and needed silvicultural and cutting regimes, and forest damage. When needed, additional information may be collected on recreational resources, wildlife resources, and so forth. Further examples of more recent other elements are information related to biodiversity, either its indicators or surrogates, like quantity and quality of decaying wood, or direct components, like abundance and distribution (diversity) of vegetation species, as well as carbon pools in soil, trees, and coarse woody debris, together with carbon sinks and sources. The need for diverse information has stimulated the development of integrated or multiresource inventories. The forest inventory information is collected in the field and through remote sensing.

The number of variables measured in the field in the current inventories is usually high, typically varying from 100 to up to 400. The great challenge is to develop inventory methods which respond to diverse information needs and still are simpler, cheaper, and yet more accurate in taking measurements and deriving population estimates than the old ones.

The planning of sampling design data collection and statistical inference is a highly statistical problem whose solution needs advanced knowledge in statistical sampling design, current forest inventory systems, forest mensuration, remote sensing, and computer science as related to forest inventory.

This article discusses basic principles and concepts in forest inventory, sampling methods, and statistical inference, including field measurement-based inventory and multisource inventory.

Statistically Designed Forest Inventories

The history of statistically designed forest inventories dates back to the end of the nineteenth century and the beginning of the twentieth century, when county-level and municipality-level forest resource inventories were carried out in Norway, Sweden, Finland, and the UK. The early Nordic forest inventories inspired some of the pioneering work on the statistical accuracy assessment in the context of systematic sampling, particularly error estimation of linewise survey sampling. Statistical knowledge has thus been utilized and also promoted in Nordic forestry literature between 1900 and 1930. This knowledge became common in other parts of the world between 1930 and 1950.

Statistical Problems in Forest Inventory

The total counting of quantities of forests is not possible due to large areas and large numbers of trees (often tens or hundreds of billions within one country). Therefore, either rapid visual assessment by units, e.g., by forest stands, must be applied, or total counting in small subareas. Visual assessment is often the method in operative and management inventories. Estimates may be biased and statistical analysis of reliability is difficult. National and regional inventories are based on sampling with accurate measurements, and error components are known or estimated, in which case statistical error estimation is possible.

Forest inventory is a good and far from trivial application for statistical sampling methods. Difficulties arise from the large number of parameters to be estimated and the dependencies between different variables, even in different scales. Nearby trees are more similar than those farther apart from each other. Large-scale trends like changes in forest parameters are common. Some of the classical statistical questions are:

- What kind of sampling design is ‘optimal’? Simple-minded optimization approaches are not possible in forest inventories, because different variables have different covariance structures and presume different sampling designs. A compromise must often be searched for.
- What type of estimators should be used?
- How does one avoid bias?
- How does one assess the reliability of the estimates?

In present inventories, the field measurements are sometimes combined with satellite images and other georeferenced data into a multisource inventory. It produces both statistics and digital thematic maps for computation units and enables accurate small area estimation and wall-to-wall mapping.

Planning of Sampling Design

The inventory design usually involves designing the layout of the field sample plots, choice and decisions concerning the proportion of temporary and permanent field plots, statistical inference method, as well as the possible role of remote sensing material and technique. The principles and factors affecting field sampling design are discussed in this article.

Examples of the factors affecting sampling design are the purpose of the inventory: which parameters are of interest, the accuracy requirement for different parameter estimates, topographic, economic and transportations conditions, and the spatial correlation of the variables of interest. The design-planning procedure is also affected by existing information on the forest area.

Examples of possible field sampling designs are: (1) simple random sampling; (2) systematic sampling;

(3) stratified random and systematic sampling; (4) multistage sampling; and (5) multiphase sampling. It can be shown that systematic sampling is always more efficient than random sampling if the variables of interest are positively spatially correlated.

Stratification is usually an efficient tool in sample surveys to reduce the variances of the estimates and to increase the efficiency of the survey. In forest inventories, stratification can be done on the basis of aerial photographs, satellite images, or on earlier information. In multiresource inventories, it is a problem to find a stratification which is efficient for most of the variables. Another problem is that the boundaries of strata may change over time. Poststratification is an estimation procedure which avoids the problems related to prestratification. Sample units are drawn independently of the stratification system, stratification is done after selecting the sample, and stratified sampling formulae are applied to the unstratified sample.

A further problem related to prestratification, particularly earlier when photointerpretation was used, was that it could be expensive to do for a large area. Digital analysis of satellite images currently reduces this problem. The advantages of stratification can be preserved but the costs of stratification were decreased using a double sampling for stratification design. The first phase is usually a high number of plots with low intensity of measurements and the second phase is a low number of plots with a high intensity of accurate measurements.

Stratified Random and Stratified Systematic Sample

In stratified systematic sampling, a population of N units is divided into subpopulations of known size, $N_1, N_2 \cdots N_H$ units, respectively, and the sample is selected in each population. These populations are not overlapping, and together comprise the whole population, so that:

$$N_1 + N_2+, \ldots, +N_H = N$$

If sample units are allocated wisely among the strata, the estimates of the population are more precise than those with the same size of sample and without stratification. The following advantages for stratified sampling in forest inventories can be achieved:

1. Separate estimates of the means and variances can be made for each forest subdivision.
2. Sampling problems may differ markedly in different parts of the population.
3. Administrative convenience may dictate the use of stratification.
4. For a given sampling intensity, stratification often yields more precise estimates of the forest parameters than does a simple random sample of the same size. This will be achieved if the established strata result in a greater homogeneity of sampling units within a stratum than for the population as a whole.

The disadvantages are that the size of each stratum must be known or at least a reasonable estimate must be available, and sampling units must be taken in each stratum if an estimate for that stratum is needed. In forest inventories, stratification is often based on the percentage of forest area, mean volume, topographical features, or site classes. Theoretically, the stratification should be based on the values of the variables of interest. However, there are numerous variables in a normal forest inventory. In practical inventories, aerial photographs and/or satellite images are employed for stratification.

The disadvantage that the sizes must be known can be overcome by means of poststratification, i.e., stratification after selecting the sample. This procedure also has the advantage that the stratification can be done separately for different variables.

Methods to allocate units to strata are found in the sampling literature. The sample sizes can be proportional to population sizes, e.g., forest areas, or they can be optimized taking into account within-strata variances and sampling costs.

Multistage sampling is a design where the ultimate sampling units are selected in stages and samples at each stage are taken from the clusters of sampling units of the previous stage. The principal advantage is to concentrate measurement work close to the locations of the chosen primary sampling units rather than spreading it over the entire forest area.

Many sampling techniques require or gain from advance covariate information either in the design phase (stratification, PPS (probability proportional to size) sampling) or in the estimation phase (regression, ratio estimation). If this information is not available, it can be collected with first-phase sample collecting data on a covariate which is easier and cheaper to measure than the variable of interest itself. Multiphase sampling is primarily used to reduce sampling by collecting a relatively large amount of data of covariates that are easier and cheaper to measure than the variable of interest. Special cases are two-phase sampling or double sampling and double sampling for stratification, if the first-phase sample is used to estimate the sizes of the strata.

For practical reasons, e.g., for reducing the moving time of field crews, and also for increasing cost-efficiency, the sampling units are organized to clusters or line strips. However, line strips are usually less efficient than clusters of plots due to spatial correlation. In practice, there are two different alternatives: systematic clusterwise sampling and stratified systematic clusterwise sampling. In the systematic clusterwise sampling, the clusters are spaced at uniform intervals throughout the population. Rectangular spacing or square grids are often applied in practical inventories.

The relevant questions in planning are: (1) what are the spacing of the clusters? (2) what is the shape of the cluster? (3) what is the number of plots per cluster? (4) what is the ratio of remeasured (permanent) plots and only once-measured (temporary) plots? and (5) what is the size and shape of the field plot? To answer these questions, preliminary information about the spatial distribution of the variables of interest is needed. Correlation as a function of distance between field plots and semivariograms can be used to compare the efficiencies of optional sampling designs. An effective way to compare sampling designs is sampling simulation if a model of forest area is available. This can be obtained from a previous inventory or from satellite image-based estimation of variables of interest. An example of the standard errors of optional sampling designs for mean volume of growing stock is shown in **Figure 1**. The land area is 6.47 million hectares, forest land area 4.19 million hectares, and mean volume on forest land 52.7 $m^3 ha^{-1}$. The test site is in North Finland.

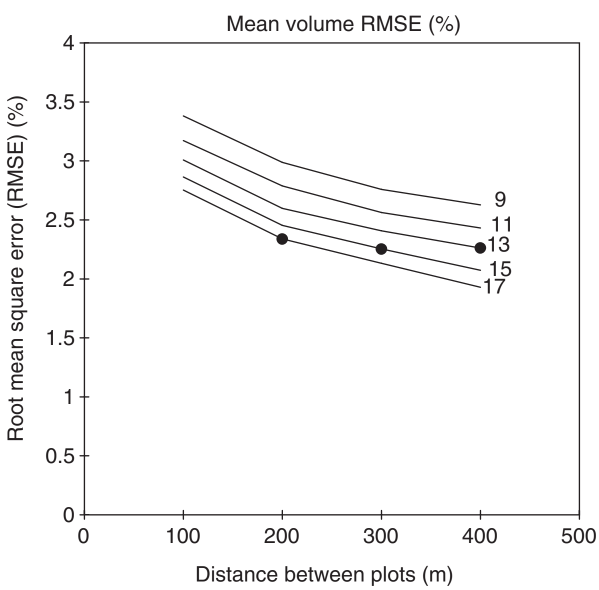


Figure 1 Standard errors based on sampling simulations with different distances between field plots and with number of plots per clusters between 9 and 17. The distance between clusters is 10 km.

One selection concerning the size and the shape of field plot is between a fixed-area sample plot and a sample plot with a varying size for different size of trees. Circular plots are often used in forest inventories. The shape and size problem can be solved using sampling simulation and possible earlier information of the forest area. An example of field sampling design with sample plots is shown in **Figure 2**.

Measurements

The estimates of interest in forest inventories can be grouped into area, volume, and increment estimates. Today, variables describing diversity of ground vegetation as well as carbon pools, sources, and sinks are measured. The measured field plots are usually small for assessing the values of area-based variables, e.g., mean age of trees, or needed silvicultural regimes, so these variables are assessed from a homogeneous forest area intersecting the field plot. This homogeneous forest area is called stand and the variables are stand variables. Examples of stand characteristics are land use, site quality and fertility, and mean characteristics of the growing stock, like tree species composition, number of stems, mean diameter, mean height and mean age of trees, basal area of trees, as well as accomplished and proposed silvicultural, cutting, and drainage measures.

Tree stem volumes and increments by tree species are typical examples of variables whose estimates are based on measurements on field sample plots. Direct measurement of these quantities is, however, not possible. Relationships between direct measurable variables (tree diameter, height) and desired variables (volumes) have to be derived. Measurements are usually done at different intensity levels. Few variables are measured from trees called tally trees, and more variables are taken from a subsample of tally trees, called sample trees. Sampling ratio and variables are selected in such a way that the inventory is as efficient as possible. Tree species and diameter are examples of tally tree variables while height and height increment and diameter increment are examples of sample tree variables.

Tree Level Volume and Increment Estimation

Tree stem volume is still one of the key variables in forest inventories. It is usually measured over bark and is defined as above-stump volume and can be expressed as an integral $v = \int_a^b A(X)\mathrm{d}X$ where *A(X)* is a cross-sectional area of the stem at height *X*. The cross-section is usually assumed to be a circle when *A(X)* can expressed as a function of

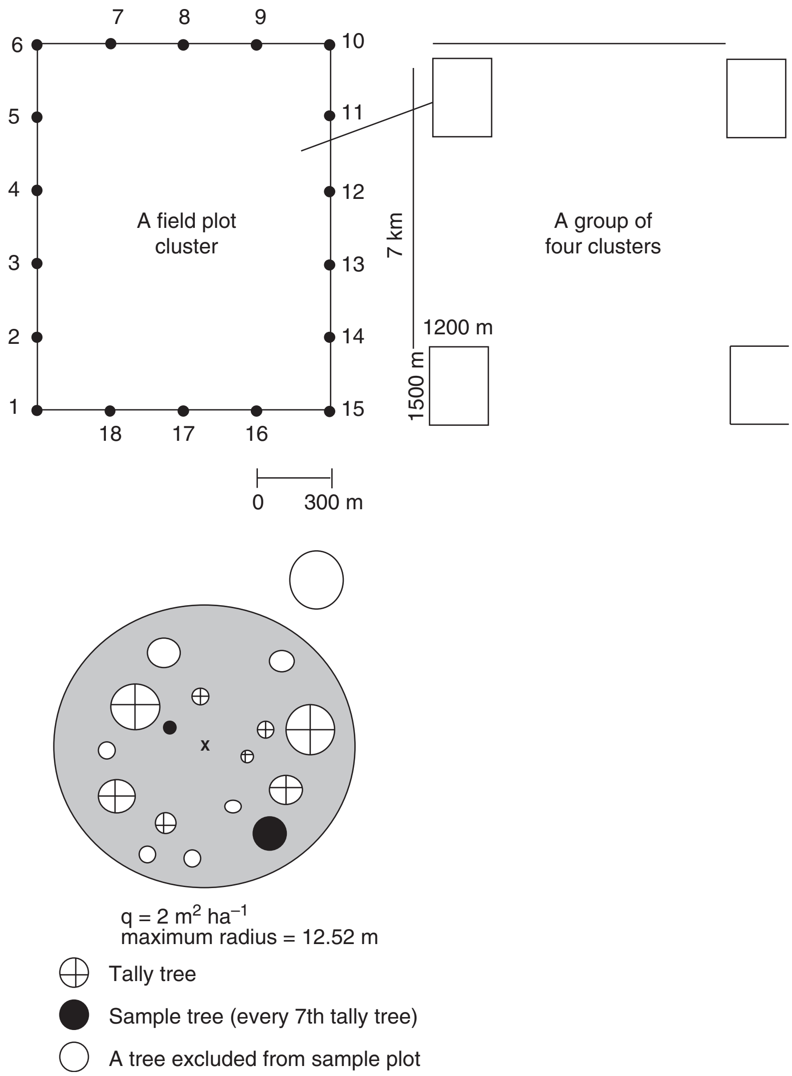


Figure 2 Sample plot and sampling design of the ninth National Forest Inventory (NFI9) in Central Finland. Three of four clusters consist of temporary plots (18 plots) and one is established permanently (14 plots; the plots 11–14 are not measured).

tree diameter at height X. This function is often called taper curve. Sample tree volumes are often predicted as a function of variables which can be measured in the field, e.g., current volume over bark $v_{ob,0} = f$ (tree species, d_{h_1}, d_{h_2}, h) where d_{h_i} is the diameter of the stem at the height of h_i and h is the height of the tree. Taper curve models can be used to predict the volumes of logs. The volumes for tally trees are estimated by strata using the volumes of sample trees, measured tally tree variables, and either parametric or nonparametric regression analysis.

Tree Growth

Tree growth consists of elongation and thickening of roots, stem, and branches and causes changes in tree stem form and dimensions. Tree stem volume increment can be predicted as a function of measurements, e.g., as a function of height increment and diameter increment at certain heights. The increase in a tree dimension is qualified by the period of time during which the increment has occurred. Current annual increment is the difference between dimensions at the beginning and end of the current year. Periodic annual increment is the average increment for a periodic of years. Increment can be predicted directly from the measurements or indirectly as a difference of the current volume and the volume at the beginning of the growth period, e.g., as a function $v_{ob,-5} = g$ (tree sp, $v_{ob,0}, g_{ub,0}, g_{ub,-5}, h$) where $g_{ub,t} =$ basal area under bark at time point t. The annual increment for sample trees is $i_v = (v_{ob,0} - v_{ob,-5})/5$ if the period is 5 years.

Estimation and Error Estimation from Field Data

The estimates in forest inventory can be divided into area and volume estimates as well as mean values and totals, for example, area of forest of a certain age class and mean volume of a pine-dominated forest. Both the sampling design and the parameter estimation can be done in different ways. One basic division is into design-based inference and model-based inference. Stratification can be done by the design and by a model. As noted earlier, stratification can be done either before or after sampling. The interesting parameters in forest inventory are often of the form:

$$M = \frac{Y}{X} \tag{1}$$

where Y and X are expectations of two random variables x and y, e.g., y is an indicator of land class or the volume of a tree species and x is the indicator of a stratum of interest, e.g., forestry land. Let $x_{id'}$ and y_{id} be their observed values on sample plot i in the domains of interests d' and d. The ratio estimator of M is

$$\hat{m} = \frac{\sum_{i=1}^{n} y_{id}}{\sum_{i=1}^{n} x_{id'}} = \frac{\overline{y_d}}{\bar{x}_{d'}} \tag{2}$$

where n is the number of sample plots in the inventory area.

When stratification is applied, the ratio estimator is:

$$\hat{m}_{st} = \frac{\hat{Y}_d}{\hat{X}_{d'}} = \frac{\sum_h^H W_h \overline{y}_{hd}}{\sum_h^H W_h \overline{x}_{hd'}} \tag{3}$$

where W_h are the stratum weights, $\overline{y}_{hd}$ and $\overline{x}_{hd'}$ stratum sample means in the stratum h and domains d and d'.

When double sampling for stratification is applied, i.e., stratum weights are not known, the estimator is of the form:

$$\hat{m}_{st} = \frac{\hat{Y}_d}{\hat{X}_{d'}} = \frac{\sum_h^H \frac{n'_h}{n'} \overline{y}_{hd}}{\sum_h^H \frac{n'_h}{n'} \overline{x}_{hd'}} \tag{4}$$

where n' and n'_h are the sample size and sample size in the stratum h in domain d'. The variance estimator of equation (4) is:

$$v(\hat{m}_{st'}) = \frac{1}{\hat{X}_{d'}^2} [v(\hat{Y}_d) + \hat{R}^2 v(\hat{X}_{d'}) - 2\hat{R}\,\mathrm{cov}(\hat{Y}_d, \hat{X}_{d'})] \tag{5}$$

where $v(\hat{Y}_d)$ and $v(\hat{X}_d)$ are the variance estimators for (double) sampling for stratification.

The normal variance estimator is not necessarily a good measure for the reliability of estimates in forestry applications due to the spatial autocorrelation and possible trend-like changes of the target variables. Matérn suggested the quantity $E(m - M)^2$, the error variance, as a measure of reliability of the estimator and also proposed an estimator for the error variance. He considered the groups of field plot clusters within possible strata and deviances of the cluster means from the stratum mean. The quadratic forms of the deviances, computed from groups of clusters, often from groups of four clusters, can be used as terms of the error variance estimator. The method can be applied to stratified sampling as well. The standard error estimators for the whole area of interest can be obtained by combining the stratum-specific estimators with the usual formula for stratified sampling.

Multisource Estimation

Aerial Photographs

Aerial photographs have been used in large-area forest inventories since the late 1920s in Canada, the 1930s in the USA, and the 1940s in Europe, the tropics, and Russia. Mapping, land cover classification and measurements, e.g., tree dimensions, are typical applications. In large-area inventories, a natural statistical framework for the use of the images is double sampling for stratification. Photo interpretation or estimation represents phase 1 and field inventory phase 2. Areas of strata are estimated using aerial photographs. A kind of application of double sampling is also the grouping method applied in the Finnish national forest inventory (NFI) in North Finland. A great benefit of the procedure is that each photo plot receives a formally complete data vector. Large-scale (aerial photographs) (1:5000 to 1:10 000) can be used to measure tree dimensions, such as height of trees and canopy dimensions.

Digital analysis of aerial photographs is still problematic due to varying illumination conditions and viewing angle of targets within one image. The trend in both stratification and estimation is today towards the use of digital satellite images and digital analysis.

Satellite Images

It was long considered that the resolution of natural resource satellites like Landsat TM, or ETM+, Spot XS, is not high enough for forest inventory purposes. The often-applied classification approach was not sufficient for forest inventory purposes, except for stratification. Standard errors at picture element (pixel) level are still high with all methods and for most forest variables. However, the developments during the last 10–15 years have shown that satellite images have a role in forest inventories, in spite of their limitations. The new very high resolution image may in future have a similar role as high-altitude aerial photographs.

There are already operational and some semi-operational applications based on co-use of field measurements and satellite images, sometimes supplemented by digital maps or land cover data.

The goal of using satellite images in national forest inventories may either be to compute estimates for smaller areas than is possible using field measurements only, e.g., for areas typically of a size of some 10 000 ha (the Finnish NFI) or to decrease the standard errors at medium-level areas, e.g., some 1–2 million hectares (the USA NFI). These goals and methods are not independent. However, the previous one is closer to synthetic small-area estimation while the latter one involves poststratification, or double sampling for stratification. The possibility of producing wall-to-wall digital forest maps in both systems is an extra benefit of the use of satellite images (**Figure 3**). The estimation method in both applications is what is called k-nearest neighbor (k-NN) estimation. The basic idea is as follows.

The procedure utilizes a distance metric, $d_{pi,p}$, which is computed in the feature space from pixel p to each pixel p_i, whose ground truth is known (to pixel with sample plot i). Data from the k plots, $i_1(p)\ldots i_k(p)$ with the shortest distances are employed

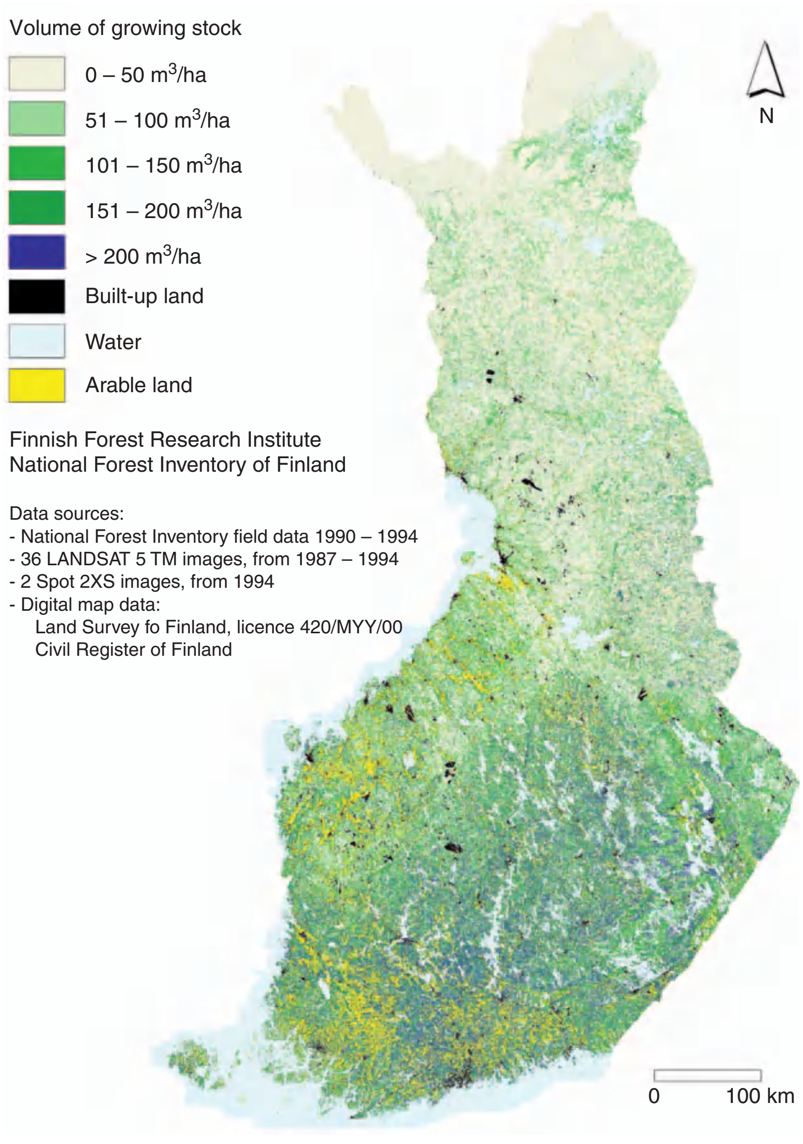


Figure 3 Mean volume of growing stock ($m^3 ha^{-1}$) based on multisource national forest inventory. Pixel size is 25×25 m and volumes are given with a resolution of $1\ m^3 ha^{-1}$.

in the analysis of pixel p. A maximum distance in the geographical space (usually 50–100 km in the horizontal direction and some hundreds of meters in the vertical direction) is set from the pixel p to the sample plots in order to avoid utilizing sample plots from very different vegetation zones.

The weight of the ground data vector of plot i to pixel p is then defined by:

$$w_{i,p} = \frac{1}{d^2_{p_i,p}} \Big/ \sum_{j \in \{i_1(p),\ldots,i_k(p)\}} \frac{1}{d^2_{p_j,p}} \quad \text{if } i \in \{i_1(p),\ldots,i_k(p)\}$$
$$= 0, \quad \text{otherwise.} \qquad (6)$$

Sums of weights $w_{i,p}$ are calculated by computation units (for example, by forest counties) in the image analysis process. The weight of plot i to computation unit u is then:

$$c_{i,u} = \sum_{p \in u} w_{i,p}. \qquad (7)$$

This quantity can be interpreted as the area represented by plot i in unit u, or stratum weights when each stratum consists of one plot only. The estimation returns to the estimation using field data only.

The accuracy of the estimates can be improved if land use or land cover classes can be distinguished by means of digital maps, as in the Finnish NFI.

Information from field plots and maps can be employed to remove the effect of map errors from the estimates.

Error Assessment in Multisource Inventory

Estimation of sampling error in forest inventory presents some difficulties, even if only field sample plots are applied. The reasons are systematic sampling, spatial correlation, and trend-like changes in the target variables. The assessment of reliability of the estimates is even more difficult when a multisource technique is applied.

If the k-NN method is used for stratification, variances of stratified sampling can be used as error estimates. In the case of synthetic estimation, the analytic error estimation is yet to be found.

For the k-NN method, the RMSE of the pixel level estimates can be statistically assessed by cross-validation. However, the error in the estimate of a forest parameter in one pixel is highly dependent on the true value there, and thereby the errors are spatially correlated. The error structure is made even more complex by the spatial dependencies in the image itself. The inevitable inaccuracies in locating the field plots on the image must clearly have a stronger effect on the pixel level estimates than those for larger areas. Developing an operationally usable statistical error assessment technique is a highly challenging task, and a fully satisfactory solution is yet to be found.

Future Directions

Both increasing timber production demands and ecological and environmental needs for forest information necessitate the further development of the inventory methods. To achieve these requirements, it is necessary to have up-to-date georeferenced forestry data systems with precise knowledge about log specifications and the status of the forest ecosystem.

Technical progress in satellite and airborne imaging will bring radiometrically and spatially improved sensors and imaging systems. Examples are very-high-resolution optical area images (Ikonos, QuickBird), imaging spectrometers and laser instruments and active microwave instruments. Microwaves penetrate through clouds without changing and imaging is, in principle, possible under any condition. Research has shown, however, that the backscattering depends very much on the canopy and soil moisture conditions, so interferometry and multitemporal images are needed.

Forest inventories have traditionally produced information about forest biodiversity. The extent and quality of habitats which maintain valuable flora and fauna, and volume and quality of dead decaying wood are examples of new characteristics describing forest biodiversity. The output wall-to-wall maps of multisource inventories can be employed to assess the landscape level biodiversity and the effect of the structure of the growing stock on the abundance of species.

The measurement technique is developing as well. Digital instruments are already employed in many large-area inventories. Digital imaging of tree stems and canopies provides new methods to estimate the volumes of stem parts and biomass of trees.

The future global forest inventories may be based on the co-use of digital field measurements, airborne instruments, such as imaging spectrometers, laser instruments, and scatterometers as well as satellite images of optical and microwave area. Old inventory data, together with mathematical forest development models and new data sets, will be applied in the estimation. The roles of different input information sources vary depending on the application and information needs. Sampling at different resolutions will be applied. Results will consist of estimates of parameters with reliability assessments and digital maps describing forest resources and the forest ecosystems.

See also: **Inventory**: Modeling. **Mensuration**: Forest Measurements; Timber and Tree Measurements; Yield Tables, Forecasting, Modeling and Simulation. **Resource Assessment**: Regional and Global Forest Resource Assessments.

Further Reading

Avery TE and Burkhart HE (1983) *Forest Measurements*. New York: McGraw-Hill.
Cochran WG (1977) *Sampling Techinques*, 3rd edn. New York: Wiley.
Cunia T (1978) On the objectives and methodology of national forest inventories. In: *Forest Resource Inventory*, pp. xi–xxxi. Joint Meeting of IUFRO Groups S4.02 and S4.04. 18–26 June 1978. Bucharest: Institutul de Cerctari si Amenageri Silvice.
FAO (2001) *Global Forest Resources Assessment 2000. Main Report*. FAO forestry paper 140. Rome: FAO.
Husch B, Miller CI, and Beers TW (1982) *Forest Mensuration*. New York: John Wiley.
Ilvessalo Y (1927) The forests of Suomi Finland. Results of the general survey of the forests of the country carried out during the years 1921–1924. [In Finnish with English summary.]. *Communicationes ex Instituto Quaestionum Forestalium Finlandie* 11: 321–395.
Loetsch F and Haller KE (1973) *Forest Inventory*, vol. I. Munich: BLV Verlagsgesellschaft.
Loetsch F, Zöhrer F, and Haller KE (1973) *Forest Inventory*, vol. II. Munich: BLV Verlagsgesellschaft.
Matérn B (1960) Spatial variation. Meddelanden från statens skogsforskningsinstitut. 49(5). Stockholm, Sweden. Also appeared as Lecture Notes in Statistics 36 (1986). New York: Springer-Verlag.
McRoberts RE, Nelson MD, and Wendt DG (2002) Stratified estimation of forest area using satellite imagery, inventory data, and the k-nearest neighbors technique. *Remote Sensing of Environment* 82: 457–468.
Poso S (1972) A method of combining photo and field samples in forest inventory. *Communicationes Instituti Forestalis Fenniae* 76(1): 1–133.
Ranneby B, Cruse Th, Hägglund B, Jonasson H, and Swärd J (1987) Designing a new national forest survey for Sweden. *Studia Forestalia Suecica* 177: 29.
Särndal CE, Swenson B, and Wreteman J (1992) *Model Assisted Survey Sampling*. New York: Springer-Verlag.
Schreuder HT, Gregoire TG, and Wood GB (1993) *Sampling Methods for Multiresource Forest Inventory*. New York: John Wiley.
Study on European Forestry Information and Communication Systems (1997) *Reports on Forestry Inventory and Survey Systems*, vols 1–2. Brussels, Belgium: European Commission.
Tomppo E (1996) *Multi-source National Forest Inventory of Finland. New Thrusts in Forest Inventory*. Proceedings of the Subject Group S4.02-00 'Forest Resource Inventory and Monitoring' and Subject Group S4.12-00 'Remote Sensing Technology,' vol. 1. IUFRO XX World Congress 6–12 August 1995, Tampere, Finland. EFI Proceedings no. 7. Tampere, Finland: European Forest Institute.

Regional and Global Forest Resource Assessments

A V Korotkov, UN Economic Commission for Europe Timber Section, Geneva, Switzerland
T Peck, European Forest Institute, Vaud, Switzerland
M Köhl, Dresden University of Technology, Dresden, Germany

Introduction

Forests and other wooded lands have been recognized and highly valued as important natural resource for centuries. The list of benefits that people gain from forests is very impressive. Forest resources play a vital role not only for the economic, social, and cultural well-being of local and regional communities, but also for the maintenance of life on earth as a whole. The majority of forest functions, both wood and non-wood goods and services, are well known. For some forest functions and services, their features and potential still need additional research, but all forest resources need a comprehensive and reliable assessment, as a basis for their proper utilization and management in an efficient and sustainable manner.

The Food and Agriculture Organization of the United Nations (FAO) and UN Economic Commission for Europe (UNECE) have implemented assessments of forest resources at the regional and global levels for more than half a century. The assessments are carried out in collaboration with countries and partner organizations. The UNECE, one of the five UN regional commissions, contributes to the forest resources assessments from the regional perspective. Other partners, notably the United Nations Environment Programme (UNEP), carry out multicountry surveys reflecting the global or regional situation regarding different aspects of forest resources.

The periodic international Forest Resources Assessments at the regional, subregional, and global levels are an important source of knowledge about forests and other wooded lands. Traditionally, the Forest Resources Assessments focus on a number of key parameters/variables (areas, growing stock, increment, species composition, ownership categories), their status and changes over time. The list of parameters to measure is evolving from assessment to assessment under the pressure of demands for new and more detailed and accurate information. The FAO and UNECE/FAO Forest Resources Assessments have been carried out at 5–10-year intervals and provided a unique source of data for many forest- and forestry-related activities, including the ongoing top-level international forest policy dialogue.

International Forest Resources Assessment: What It Is and Whom It Serves

The information compiled, analyzed and disseminated by FAO (Rome) and UNECE/FAO (Geneva) in the framework of international forest resources assessments gives a comprehensive picture of the main features and values of forests, their status, health, and condition. This defines the role of Forest Resources Assessments as an important instrument for many users. Reliable, consistent, and accurate information on the status and trends of forest resources facilitates the development of national and international forest policies.

The list of users of Forest Resources Assessments is long: governments and other decision makers, nongovernmental organizations, researchers and scientists, forest inventory and monitoring specialists, current and potential donors, international aid agencies, the private sector and industries, the general public, and many others needing reliable information on forest resources. Accurate, validated, and harmonized forest resources data are required for monitoring and assessment of the sustainability of forest management by international processes. The Forest Resources Assessment information is also helpful for addressing impending risks of possible misuse or undesirable changes in forest condition.

The United Nations strongly supports the international efforts aimed at promoting sustainable management and development of forests and other wooded land. These efforts have become the subject of many political processes at different global and regional levels. The UN Forum on Forests, the UN Convention on Biological Diversity, the UN Framework Convention on Climate Change, the Kyoto process, and other global and regional processes and initiatives represent the examples of top-level work in this area. The Ministerial Conference on the Protection of Forests in Europe and the Montreal process are examples of regional processes, where countries and their governments have made policy commitments to achieve sustainable management of forests. All these processes require monitoring, assessment, and reporting on state and changes in forest resources.

FAO and UNECE/FAO Forest Resources Assessments constantly make efforts to harmonize and streamline reporting, notably by improving assessment concepts and methods, and harmonizing forest-related terms and definitions. The Forest Resources Assessment databases serve as the major components of the long-term efforts for establishing a worldwide forest resources information system.

Governance of Global and Regional Forest Resources Assessments

The work of Forest Resources Assessments received a strong impetus from the UNCED Rio Conference (1992). Agenda 21 'The Non-Legally Binding Authoritative Statement on Principles on the Management, Conservation and Sustainable Development of All Types of Forests' and the UN Conventions on Biodiversity, Desertification and Climate Change have made an important impact on Forest Resources Assessments work. One of the program areas of Agenda 21 set up the objective:

> to strengthen or establish systems for the assessment and systematic observation of forests and forest lands with a view to assessing the impact of programs, projects and activities on the quality and extent of forest resources…

The World Summit on Sustainable Development (WSSD) held in Johannesburg in September 2002 re-enforced the regional aspects of this work.

The guidance provided by the UN Commission on Sustainable Development (CSD), the UN Forum on Forests (UNFF), and the Collaborative Partnership for Forests (CPF), as well as activities within a number of regional initiatives, have had a direct influence on the scope, coverage, and methodology of Forest Resources Assessments. The links between the Forest Resources Assessment work and criteria and indicators for sustainability of forest management processes have become closer at the regional and global levels.

The FAO Committee on Forestry (COFO), the most important FAO forestry statutory body, provides overall political guidance and gives directions for the global Forest Resources Assessments work. The UNECE Timber Committee and FAO European Forestry Commission have been leading the regional work on forest resources assessment. Periodic global Forest Resources Assessments expert consultations provide technical guidance for the forthcoming rounds of the assessment. The global Forest Resources Assessments advisory group and the regional UNECE/FAO team of specialists also provide advice and detailed specifications, at the global and regional levels respectively.

Historical Overview of Forest Resources Assessments

Periodicity, Scope/Contents, Coverage, Evolution

When reviewing the historical development and evolution of the international forest resources assessments during the last five decades, one should keep in mind the changes that the world has undergone during this period. The scope of changes, not only those on the geographic or political map of the globe, but also economic, social, and ecological has been very impressive. The needs of countries and society for goods and services provided by forests have been constantly evolving, with corresponding shifts in the objectives, scope and coverage of forest resources assessments. FAO and UNECE have provided the required information, independent analysis, and policy forum for the sector as whole, adapting their activities to the evolving needs.

These needs have ranged from statistics on wood/timber resources available for roundwood production, sawn timber or wood-based panels to much more sophisticated information relating to biological diversity or carbon sequestration. Of course, all these far-reaching global and regional changes, and consequently evolving demands for the knowledge about forest resources from the simple data on the potential of forests to supply wood to the market, to profound scientifically based analysis, have had a continuous impact on the contents and methods of Forest Resources Assessments.

Initially, the assessments were focusing on the collection of data revealing the existing potential of forests to supply timber. This was motivated by the need for timber and wood products for the reconstruction of Europe after World War II, and the need for defining national forest policies. The quality, comprehensiveness, and comparability of the earlier forest resources data, which were collected from countries with weak (or destroyed in the war) forest inventory systems, varied significantly from country to country. This created a challenge to come up with regional or global totals that would allow reliable analysis and conclusions.

The *World Forest Inventory 1958* stated that the formulation of a sound national forest policy required a precise knowledge of wood (forest) resources. The *World Forest Inventory 1963* already assessed a number of important parameters: forest area (productive and protective), ownership and management status, species composition (softwoods and hardwoods), growing stock and removals. The increasing importance of forests as a source for the environmental and other non-wood goods and services was stated in the forest resources assessments of the 1980s and 1990s. Wood production meanwhile had remained so far the most important function of the forest, especially for the industrialized countries. The public attitudes towards the forest and forestry has continued to change over the past two to three decades, with increasing concern being expressed in many countries for the protection of the environment, conservation of forests, biodiversity and fuller development of the socioeconomic functions of forests.

The multiple uses of forests, forest protection, water regulation and quality, nature conservation received increasing emphasis in national forest policy and planning. The Global Forest Resources Assessment nowadays aims to report not only on the status, but also on trends of forest resources, their management and uses. Under pressure of demand from the wide range of users, the latest regional Forest Resources Assessment 2000 addressed about 700 parameters ranging from the traditional forest inventory data to very sophisticated information relating to biodiversity, forest conditions, protective functions and carbon sequestration capacities, and potential of forests and other wooded land.

The Information Needs of the Forest Resources Assessments

The scope and coverage of each Forest Resources Assessments round is based on the estimate of information needs. The information needs have traditionally been defined in advance of launching the new assessment round on the basis of consultation with major stakeholders and interested parties, also by means of specifically elaborated questionnaires. The most recently identified information needs have been the criteria and indicators for sustainable forest management adopted by different regional and global processes.

The list of reporting themes/components, parameters/variables, and data items that are chosen on the basis of the information needs analysis determines the scope of the statistical summary tables, geographical information, graphical and descriptive information, special studies, and other elements, which constitute final outcome of the assessment. The information about forest resources required by policy makers, forest managers, researchers, and many others has become increasingly complex and diverse. Their needs have to be constantly reassessed and classified at the local, national, regional and global levels, and the scope and coverage of the Forest Resources Assessment have to be defined and adopted correspondingly.

The management of knowledge on forest resources and other forest-related information, especially in the light of regional and global processes on criteria and indicators for sustainable forest management, is of paramount importance. Analysis of the policy implications, and responses of governments and other stakeholders to the assessments' findings have always been an important element of the Forest Resources Assessments' work.

Role of the Global Expert Consultations in Forest Resources Assessments

The international Forest Resources Assessments are traditionally based on the technical guidance and the common platform (framework) elaborated in the process of the global Forest Resources Assessments expert consultations. The necessity to agree on the strategy for the next round of Forest Resources Assessments, to assess the current and future information needs, to elaborate a global platform for the assessments, including the guidelines and definitions to be applied, to set up modalities of implementation, and a number of practical guiding aspects have materialized through the expert consultations. The last four global expert consultations were organized in the Finnish town of Kotka and came to be widely known as the Kotka meetings.

Methodological Approaches in the Forest Resources Assessment

The methodological approaches in the Forest Resources Assessment are defined by a number of factors. Among them are: data sources and analysis, reliability of data, comparability between countries and continuity in Forest Resources Assessment concepts (in order to assess trends over time), adjustment procedures, links to other processes (criteria and indicators for sustainable forest management), clear understanding of results by a wide range of users, responsiveness to new demands for information from different processes and a wider audience, and aspects of the governance of Forest Resource Assessments at the regional and global levels.

The information published before the 1980s was mainly collected by means of questionnaires sent to countries, but in the latest Global Forest Resources Assessment methodology such elements as remote sensing, analysis of country information sources by experts, and statistical modeling prevail. The main instrument for the regional data collection traditionally was an enquiry (questionnaire) based on a proposed global platform. The elaboration of internationally agreed terms and definitions, which are indispensable for guiding the collection, analysis, and dissemination of information, is an important element and a difficult task in the process of Forest Resources Assessment.

The *Global Forest Resources Assessment 2000* was based on validated country information, mainly from national forest inventories, and consisted of a number of activities, including a remote sensing survey of forest cover change at the pan-tropical level, mapping of global forest cover and ecological zones, and the establishment of a forestry information system. The main results include analytical components relating to the stocking of forests, wood production, and non-wood goods and services. All the Forest Resources Assessment 2000 information including the main report, global forest map, country profiles and working papers is posted on the Internet.

The UNECE as the major FAO partner in this area contributed to the *Global Forest Resources Assessment 2000* by the publication of *Forest Resources of Europe, CIS, North America, Australia, Japan and New Zealand* (**Figure 1**). This is the latest in the series of surveys of temperate and boreal forests carried out at the regional level, and feedback received from many users and major clients has shown that it was a successful study. Many experts consider it to be the most comprehensive international assessment ever made of the temperate and boreal forests resources of industrialized countries.

Careful data checking and validation are important methodological stages of the Forest Resources Assessment process. The UNECE/FAO secretariat in cooperation with the national correspondents has managed to settle a number of difficult issues and points in the country data sets, that concerned the completeness of the replies from some countries and their consistency, and the comparability of the supplied data.

Driving Forces and Partnerships

Each round of Forest Resource Assessments raises high expectations, and it would not be possible to respond to those expectations satisfactorily without extensive support from countries in providing expertise and funding, and without building the close cooperation and partnership with many stakeholders. For example, the implementation of such a challenging project as the regional Forest Resources Assessment 2000 would not be possible with the limited manpower and financial resources that were available to the UNECE/FAO secretariat. The role and input from national correspondents and the team of specialists were decisive, and the countries' support was invaluable.

The Forest Resource Assessments process has revealed that there are still major information gaps at the national level, especially in the developing and some central and eastern European countries. First of all, this concerns nontraditional parameters, such as biomass, biodiversity, and non-wood goods and services. These countries need support and capacity building in forest inventory and assessment, including methodology development.

(a) (b)

Figure 1 (a) *Global Forest Resources Assessment 2000*, Food and Agricultural Organization of the United Nations (reproduced with permission), (b) a *Regional Forest Resources Assessment 2000* report (reproduced with permission).

FAO and UNECE should continue working with countries and the donor community to revive and/or maintain the interest in committing resources to national forest assessments, as being an important part of national policy development. The capacity building and capacity maintenance should constitute an important component of this work. The coordination of efforts in the field of forest resources assessments is especially needed given the limited resources available.

UNECE and FAO cooperation in this area is the most important feature of the process. The advantages of running the regional forest resources assessments by intergovernmental bodies like FAO European Forestry Commission and UNECE Timber Committee is obvious. Their status allows the collection of official national data, and these two bodies complement each other in a number of aspects. In particular, not all countries of the UNECE region are the members of FAO, so the cooperation of the two bodies in Forest Resource Assessment work allows a comprehensive coverage of the region.

National Forest Inventories (Accounts, Assessments) as the Main Source for Forest Resource Assessments

The main value of Forest Resource Assessment information is in its original nature. Much of the information called for in the enquiries and provided by countries was derived from data collected in the national forest inventories. The information comes from original sources, where it is obtained by direct measurement. The main sources of the information in the Forest Resource Assessments is national forest inventories, periodic observations of different variables and their changes by countries and institutions, also on permanent plots, as well as remote sensing techniques. The success of the forest resource assessment depends, to a great extent, on the level of the national forest inventory systems, and the ability of national correspondents to provide comprehensive, consistent and reliable replies to the questionnaires.

National forest inventories and data collection at the country level are being carried out for a variety of purposes. The main national forest inventories and assessment objective is to serve national information needs, to provide aggregated information for the entire nation and subregions within the nation, and to provide basic information for the development of national forest policies and decision making processes.

The ability of national forest inventories and assessments to contribute to the international Forest Resources Assessment is more responsive and efficient if the demand for information originates from national forest policy processes. The Forest Resources Assessment process helps countries to evaluate their forestry sectors within the regional and global context. The great incentive and motivation for countries to provide data for the regional and global assessments is the opportunity to estimate their own levels of knowledge about forests and to make efforts to improve the situation when necessary.

The network of country correspondents, whose knowledge is based, along with the traditional forest inventory methods, on aerial photos, satellite images and geographical information systems (GIS), and supported by high-level experts' judgment, remains one of the main driving forces of the assessment and sources of information. The importance of national data for the international Forest Resources Assessment will definitely be maintained in the future.

The Forest Resources Assessment 2000 confirmed that not only developing tropical countries but also a number of central and eastern European countries need financial support for national forest inventory and national forest assessment work. This issue is linked to the question of cost of the assessment work, which should be taken into account when planning future Forest Resources Assessment rounds. Countries should themselves assess whether they need external assistance to implement national forest assessments and consider seeking such help, for example through the National Forest Programme Facility implemented by FAO, which has a mandate to offer support.

Terms and Definitions and Issues of Harmonization

From the first Forest Resources Assessment publications to the latest regional *Temperate and Boreal Forest Resources Assessment 2000* and *Global Forest Resources Assessment 2000*, the international assessments (although regular and systematic) unfortunately do not provide a series of data comparable over time. This is mainly due to differences in terms and their definitions, which had been changing from one Forest Resources Assessment survey to another. Just to note that the common definition of 'forest' based on 10% crown cover (or equivalent level of stocking) was applied globally for the first time in Forest Resources Assessment 2000.

The following terms (and their dates) related to a major component of forest area and used in different Forest Resource Assessments illustrate the situation:

- accessible productive forest (1947)
- forest in use (1953, 1958)
- forest in use (for industrial or commercial purposes) (1963)
- operable closed forest (1970)
- exploitable (operable) closed forest (1980)
- exploitable forest (1990)
- forest available for wood supply (2000).

It is obvious that the definitions of these variables are not comparable, although some harmonization of the data would still be possible. Moreover, some variables (e.g., growing stock or increment) that were linked to 'forest area' were also not directly comparable over time (e.g., 'growing stock on forest' or 'growing stock on forest in use').

Bearing in mind the wide range of parameters and indicators to be covered by the assessment, the role of 'well-informed' and 'qualified' estimates in closing the information gaps in the Forest Resources Assessment databases is important. For every key parameter for which data are missing, whether the country is small or large, no regional or global totals can be prepared. Such a situation would significantly reduce the usefulness of the Forest Resources Assessment data sets. It should also be noted that the national inventories in individual countries, to which the given data referred in all the Forest Resources Assessments, took place in different periods.

Despite the intensive efforts to harmonize forest-related definitions, which are being applied in different international initiatives and processes, major challenges still remain. Definitions are not comparable within the range of Forest Resources Assessment datasets and between different processes. It is already expected that although no major revision of definitions is foreseen in the next rounds, Forest Resources Assessment 2000 terms and definitions may be amended, in order to build synergies and be more consistent with other international processes, in particular the UN Framework Convention on Climate Change and the UN Convention on Biological Diversity.

To maintain a sense of ownership and continuity of the global (regional) forest resources databases there is an urgent need to stop changing terms and definitions in each following round of Forest Resources Assessments. For that it is necessary to reach agreement on definitions of the main parameters/variables among the main stakeholders. This is by no means an easy task, as was proved by the intensive FAO-led discussion on 'Harmonizing forest-related definitions for use by various stakeholders.' This forum showed that each process has its own agenda, but still there are some common denominations.

Data Availability and Accuracy

The FAO collects, analyses, interprets, and disseminates forest resources information. Quite often large forest areas are lacking in information, and the level of existing national forest inventories does not allow assessing some more sophisticated variables, mainly relating to environmental functions of the forest.

Research is needed for some parameters/variables so that they can be assessed at the country level, and brought to a common platform at the international level for comparison, or for monitoring changes over time. The generally quite satisfactory state of Forest Resources Assessment data does not mean that all data are perfect for every country, but that the general quality (scope and comparability) is good enough to give a realistic picture of the situation with regard to the parameter under consideration.

One major objective of international Forest Resources Assessment data sets, including those from the regional Forest Resources Assessments, is to make it possible to carry out analysis of the situation at the regional or global level. To do this, it is absolutely necessary to have regional and global totals that are complete and comparable between themselves and with other parameters, e.g., land area or population. A total for Europe with one or two countries missing is almost useless, especially if the 'European total' in other tables is missing for some other countries. For this reason, it is of the highest importance that, for the most vital parameters, data or at least informed estimates are presented for every participating country, without exception.

The references to sources of data, e.g., sample plots (field measurements), remote sensing, maps, aerial photography, as well as reference years (dates) of observations are important for evaluating the collected information, and for future Forest Resources Assessment data analysis. The statements on accuracy and data quality control are a relatively new feature of the regional and global Forest Resources Assessment.

Forest Resources Assessment and Criteria and Indicators for Sustainability of Forest Management

The wide range of indicators for sustainable forest management from different regional and global processes constitutes the core information that is needed at the local, national, regional, and global levels to ensure the monitoring and promotion of sustainable forest management. Of course, some of the indicators are highly important for individual countries and regions, others are less important, but all of them have proved to be necessary for overall monitoring and estimation of levels of sustainability of utilization of forest resources. The existing lists of criteria and indicators for sustainable forest management could be considered as forest policy instruments for monitoring, evaluating, and reporting on progress towards sustainable forest management.

The cooperation of the Forest Resources Assessment process with regional sustainable forest management processes and initiatives appears to be not only fruitful, but also mutually beneficial. This cooperation helps to avoid countries having to reply to multiple enquires and to make the best use of the competitive advantage of the cooperating organizations. The *Global Forest Resources Assessment 2000* platform was designed keeping in mind the criteria and indicators, and the regional Forest Resources Assessment enquiry incorporated an important part (as many as possible) of pan-European indicators for sustainable forest management. The data collection with regard to most of indicators should be combined also in the future with the broader, more detailed and comprehensive data collection exercise like the Forest Resources Assessment.

Continuous work is needed to improve the methodology and implementation of international Forest Resources Assessments with regard to sustainable forest management needs. In practical terms, it is necessary to examine systematically to what extent the data collected through the Forest Resources Assessment process have satisfied the criteria and indicators processes' needs, notably with regard to the quantitative indicators for sustainable forest management.

There is still a long way to go to achieve a system of collecting fully reliable, comprehensive and comparable information which would respond to the requirements of criteria and indicators on all functions of forests, especially those relating to environmental and social aspects.

Outlook for Future Regional and Global Forest Resources Assessment Work

The Forest Resources Assessment variables relating to wood and non-wood goods and services, and functions of forests and other wooded land which provide commercial and noncommercial benefits to society, have been constantly extended during recent years. A broader and more holistic assessment of forest resources will be the main challenge of future assessments. The global Forest Resources Assessment will be more focused in the future on protective functions of the forests and other wooded land, biological diversity, forest health, climate change and carbon-related parameters, and variables relating to hydrology and water cycles.

The meeting of the UNECE/FAO team of specialists on the forest resources assessment, held in Krakow (Poland) in May 2002 noted that future global and regional Forest Resources Assessments should aim (to the extent possible) at evaluating all benefits from forests. The team stressed that the Forest Resources Assessment work should be integrated with international processes on criteria and indicators for sustainable forest management.

The next global Forest Resources Assessment will be based mainly on national reporting and supported by independent surveys. Intensive communication with countries and partner organizations should be the key element of the assessment. The process of incorporating national data into the international Forest Resources Assessment database should be open/transparent and well documented. The country forestry profiles should continue to be an important supplementary element of the assessment work. The international Forest Resources Assessment process will maintain in the foreseeable future its main objective: to collect, analyse, and disseminate information on forest resources at the global and regional levels.

The future global Forest Resources Assessment, and *Forest Resources Assessment 2005* in particular, should be structured along the following lines of the commonly agreed thematic areas of sustainable forest management:

1. Extent of forest resources.
2. Biological diversity.
3. Forest health and vitality.
4. Productive functions of forest resources.
5. Protective functions of forest resources.
6. Socioeconomic functions.
7. Legal, policy, and institutional frameworks.

These global thematic areas correlate closely with the pan-European and other processes criteria and indicators for sustainable forest management, and this global Forest Resources Assessment approach might facilitate the sharing of forestry information all over the world in a unified way.

Prerequisites for Successful Implementation of Forest Resources Assessments

Experience with the previous rounds shows that the success of the FAO and UNECE work on Forest Resources Assessment was determined by the following factors:

- The process should be initiated and supported by participating countries, and its general scope and coverage should be defined from the very beginning with countries' involvement and support.
- The process should be transparent for all stakeholders, and these should be involved in the process during its different stages, so as to ensure credibility and consistency of the process.
- A network of national correspondents should be established/re-established on an official, ministerial (or governmental) basis, and in a good time before the initiation of the project.
- A good level of cooperation with national correspondents is vital; it enables sufficient response to be obtained from countries to demanding and challenging enquiries.
- The participating countries, through their national correspondents, have to demonstrate their goodwill, and provide the necessary support at each and every stage of the project implementation.
- The network of national correspondents (focal points) has to be kept operational from the very beginning of the process through different information needs enquiries, discussion of data adjustment issues, data checking and updating figures for interim relevant publication, other queries relating to the process, and briefing ('training') meetings.
- Cooperation between the regional and global sustainable forest management processes and initiatives is an important and stimulating factor for developing and accelerating the whole Forest Resources Assessment process.
- The regional Forest Resources Assessment work should constitute a part of the global process, and it needs to receive the necessary support and partnership from FAO and other international organizations.
- The contribution of the UNECE/FAO team of specialists and the FAO global advisory group on Forest Resources Assessments is significant as a factor in the successful development of the project.
- International organizations involved in the collection and dissemination of information on sustainable forest management should continue to cooperate and harmonize their activities, sharing information collection and dissemination activities as appropriate.
- Internet links between the national and international Forest Resources Assessment databases would be a step towards the continuous assessment of forest resources in the future (European Forestry Information and Communication System (EFICS), European Forestry Information System (EFIS)).
- The main Forest Resources Assessment publications should be accompanied by supplementary studies and papers, which would help to analyze specifically the situation on sustainable forest management in individual countries and in the region as a whole. All modern means (Internet, CD-ROM, etc) should be used for the publication and dissemination of the information.

Planning the Forest Resources Assessment 2005 Round

The work on improving the quality, relevance, and credibility of forest resources information continues to be the focus of FAO, UNECE and their partners. Close cooperation between the major stakeholders is indispensable for successfully achieving this goal, already in the next round of the Assessment (*Global Forest Resources Assessment 2005*).

The UN Forum on Forests conference to be held in 2005 has to consider the situation and developments in the international forest policy dialogue, and it is supposed to decide on further possible arrangements to promote sustainable forest management. The *Global Forest Resources Assessment 2005* update is expected to be an important contribution to this top-level international forum.

Concluding Remarks

The three pillars of sustainable development (economic, social, and environmental) constitute the core of sustainable forest management. Sustainable forest management may only be achieved if it is based on comprehensive and reliable information on forest resources, i.e., if forest policy makers, managers, and practitioners are well informed. Reliable national forest inventory and assessment systems are vital for sustainable forest management and monitoring. The ultimate objective of the Forest Resources Assessment program is to provide a comprehensive picture of the status, developments, and trends of the world's forest resources, so that users may make conclusions and take measures aimed at sustainable forest management in different countries and regions.

The information on forest resources should adequately respond to demands and needs of in-depth forest policy dialogues, which involve all major stakeholders, cover major concepts, strategies and monitoring of sustainable forest management. The global Forest Resources Assessment actively moves in this direction. The regional dimension of the international forest policy dialogue has received during the last decade increasing attention.

The international Forest Resources Assessment work provides important guidance for countries; it serves as a 'standard' for forest inventory, assessment, and accounting at the national level. The national realities concerning the forest inventory and assessment at the country level, especially for a number of developing countries and some central and eastern European countries, should be taken into full consideration.

Outside financial, material, and methodological support from donor countries and organizations is needed for the setting up, reinforcement or further development of national forest inventory and assessment systems in many developing and central and eastern European countries. The lack of forest resources information at national level undermines the process of the development of effective national forest policies. Support for national forest assessments and building the national forest inventory capacities should be an important part of the global Forest Resources Assessment program.

It is extremely important for Forest Resources Assessment that the profile and importance of forestry at the country level should be maintained at a sufficient level. The close links of developing and central and eastern European countries in transition to market economies with the international forest community is an important prerequisite for establishing comprehensive and reliable data sets, and ultimately for sustainable forest management in these regions.

See also: **Inventory**: Large-scale Forest Inventory and Scenario Modeling; Multipurpose Resource Inventories. **Mensuration**: Forest Measurements. **Resource Assessment**: Forest Resources. **Sustainable Forest Management**: Certification; Overview.

Further Reading

FAO (2001) *Global Forest Resources Assessment 2000 (FRA 2000): Main Report*, FAO Forestry Paper no. 140. Rome: Food and Agriculture Organization of the United Nations.

FAO (2003a) *State of the World's Forests 2003*. Rome: Food and Agriculture Organization of the United Nations.

FAO (2003b) *Harmonizing Forest-Related Definitions for Use by Various Stakeholders*, Proceedings of the 2nd expert meeting, 11–13 September 2002, Rome. Rome: Food and Agriculture Organization of the United Nations.

FAO/UNECE/UNEP (2002) *Kotka-IV: Expert Consultation on Global Forest Resources Assessment*, 1–5 July 2002, Kotka, Finland. Rome: Food and Agriculture Organization of the United Nations.

FAO/ECE Joint Working Party on Forest Economics and Statistics (2003) *Twenty-Fifth Session*: Document TIM/EFC/WP.2/2003/4, 24–26 February 2003, Geneva, Switzerland. Rome: Food and Agriculture Organization of the United Nations. http://www.fao.org/forestry/fo/fra/index.jsp, http://www.cfm2003.org/en/index.php

Korotkov AV (2003) UNECE/FAO Forest Resources Assessment: an efficient tool for monitoring sustainable forest management in Europe. International Conference of UNECE/FAO, May–June 2003, Geneva, Ohrid (Macedonia), Freiburg (Germany).

Ministerial Conference on the Protection of Forests in Europe (1993) Documents, 1st Conference of MCPFE, 16–17 June 1993, Helsinki. http://www.mcpfe.org
Ministerial Conference on the Protection of Forests in Europe (1998) Follow-up Reports on the 3rd Ministerial Conference on the Protection of Forests in Europe, vol. 2. Lisbon, Liaison Unit: http://www.mcpfe.org
Ministerial Conference on the Protection of Forests in Europe (2001) Background Documents on the Evaluation of Pan-European Indicators, 1st Workshop on the Improvement of pan-European Indicators for Sustainable Forest Management, 26–27 March 2001, Triesenberg/Liechtenstein. http://www.mcpfe.org
Ministerial Conference on the Protection of Forests in Europe (2003) Documents, 4th Conference of MCPFE, 28–30 April 2003, Vienna. http://www.mcpfe.org
UNECE (2001) *Structural, Compositional and Functional Aspects of Forest Biodiversity in Europe*. Geneva Timber and Forest Discussion Papers no. 22. New York: United Nations.
UNECE/FAO (2000) *Forest Resources of Europe, CIS, North America, Australia, Japan and New Zealand*, UNECE/FAO Contribution to the *Global Forest Resources Assessment 2000: Main Report*, Geneva Timber and Forest Study Papers no. 17. New York: United Nations.
UNECE/FAO (2002) *Report of the Meeting of the UNECE/FAO Team of Specialists on the Forest Resources Assessment*, May 2002, Krakow (Poland) and Geneva. Geneva: United Nations.
UNECE/FAO (2003) *Analysis of the Development of European Forest Resources (1950–2000)*, Geneva Timber and Forest Discussion Papers no. 32. Geneva, Switzerland: United Nations.
UNECE/FAO/MCPFE (2003) *State of Europe's Forests 2003*, the MCPFE Report on Sustainable Forest Management in Europe, Jointly prepared by UNECE/FAO and the MCPFE Liaison Unit Vienna for the 4th Ministerial Conference on the Protection of Forests in Europe. Vienna, Austria: United Nations.

Non-timber Forest Resources and Products

J L Chamberlain, US Department of Agriculture Forest Service, Blacksburg, VA, USA
M Predny, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

Introduction

Forests provide resources that are gathered from the canopy, the understory, the forest floor, and below ground level. The diversity of flora within these strata ensures forest health and productivity. Although many of the products fashioned from these resources are important for household subsistence, as well as for generating income, their ecological and economic value has not been fully appreciated nor integrated into forest management. Without management, many of these resources may be lost, reducing forest ecosystem diversity, sustainability, and greatly affecting peoples' livelihoods. To ensure that the collection is sustainable, forest management practices need to include assessments of growth, yield, and productivity, as well as inventories of the resource from which the products originate. A small body of knowledge exists that addresses resource and product inventory and assessments. In a few countries, this knowledge is being used to incorporate more prominent non-timber products into forest inventories, and these may be useful models for other less advanced countries.

Although a great deal of effort has been given to assessments of market and economic development opportunities for non-timber forest products, the primary focus of this article is biological, ethnobotanical, and social resources. Wong and others summarized much of the body of knowledge concerning inventory and resource assessments of non-timber forest resources and associated products in a seminal document published by the UN Food and Agriculture Organization. While some discussions of non-timber forest products may include wildlife and other fauna, the generally accepted definition excludes animals, and therefore they are not included in this article.

Non-Timber Forest Resources and Products

A variety of terms have been used to describe the flora collected from forests for products that are not timber based. The Food and Agriculture Organization of the United Nations describes them as 'nonwood forest products,' a term that includes food and game, fibers, resins, gums, and plant and animal products used for medicinal, cosmetic, or cultural purposes. The US Department of Agriculture Forest Service, in a recently released national strategy, uses the term 'special forest products,' which excludes sawtimber, pulpwood, cull logs, small roundwood, house logs, utility poles, minerals, animal parts, rocks, water, and soil. Recently, the US Congress, in legislation that supports improved management for these products, introduced the term 'forest botanicals' and defined them as naturally occurring mushrooms, fungi, flowers, seeds, roots, barks, leaves, and other vegetation (or portions thereof) that grow on National Forest System lands.

A more common term, non-timber forest products (NTFPs), relates to plants, parts of plants, fungi, and other flora that are collected or cultivated from within and on the edges of natural, manipulated or disturbed forests. This definition excludes animals, but embraces all flora and botanical resources. Non-timber forest resources (NTFRs) include fungi, moss, lichen, herbs, vines, shrubs, or trees. Many parts are harvested, including the roots, tubers, leaves, bark, twigs, and branches, the fruit, sap, and resin, as well as the wood. NTFPs may be marketed with little processing, such as dried roots and herbs, graded and bundled leaves and twigs, or live plants. Some are processed into finished products, such as carvings, walking sticks, jams, jellies, tinctures, or teas. The following product categories are recognized in this article: building materials, crafts, decoratives, edibles, and medicinals.

Whatever term is used to describe these products, the fact is that very little effort has been made to manage these forest resources for their sustainable production. NTFPs seldom appear as a major objective in forest management. For many of the plants, little is known about their population biology or the impact that harvesting has on population dynamics, especially on associated species. In general, silvicultural treatments that include non-timber products are lacking because insufficient information is available to address these resources adequately. Inventory and monitoring protocols for some products have been examined, but they are not fully integrated into forest management.

Inventory Methods for NTFPs

In general, inventory methods for most natural resources are well developed and utilized in the formulation of management strategies. Inventory protocols for commonly harvested timber and wildlife species are fully integrated into forest management. Vegetation inventories are now used for biodiversity conservation. Market and economic inventories have been widely used to assess current and potential contributions to community development. Much of what is known concerning these subjects is organized and consolidated into standard approaches, which are accessible to forest managers. The body of knowledge concerning inventory of non-timber forest resources does not reflect such development, but it is developing rapidly, and many of the approaches are being generated from developing countries.

Quantitative inventory methods for NTFRs and NTFPs must deal with enumerating the number and spatial distribution of plant populations. These inventories may describe the number of individuals of a particular species, measure various characteristics of the species of interest, and/or examine relationships between individuals and biological or ecological functions. The overall methods, including sampling designs and plot configurations, are dependent on scale of analysis, product life-form, and plant part harvested.

The sampling designs used in NTFP inventory studies vary extensively. Aerial surveys of large forest tracts have been used to measure occurrence of a single large species, such as trees or bamboo. A census, where 100% of all useful plants are measured, provides information that can be used for stock surveys to describe the abundance of species. Regularly laid out, systematic plots have been used in the Pacific Northwest of the United States and Finland to measure annual mushroom production. In India, large tracts of bamboo are stratified into smaller zones in which sampling is undertaken independently to estimate volume. Multistaged sampling techniques used for rattan entail establishing test plots within small blocks, which are nested within larger plots within a contiguous survey area.

Basic plot configurations include measured plots with fixed dimensions, plotless sampling, cluster sampling, and transect intercepts. Square, rectangular, and circular plots have been used to enumerate rattan, perennial herbs, and lianas. Plotless sampling, such as the point-centered quarter method, or 'random forest walks,' has been used to inventory particular species of trees, palms, and shrubs. A systematic group of subplots in a fixed pattern commonly referred to as cluster sampling has been used to inventory rattan. Line-plot transects of varying widths have been used to count the number of plants and percent cover for fiber and tubers. More research and development may be necessary to determine optimal and efficient designs and configurations.

Estimating Growth, Yield and Productivity

Management decisions based on information that lacks evidence of growth and regeneration rates could have serious ramifications on plant populations. To achieve sustainable management of NTFPs, data are needed on population dynamics as well as regeneration and productivity. In general, NTFP inventories require measuring certain aspects for an individual and then aggregating that to the population. Estimates of total yields can be made by sampling individuals and then using predictive models to extrapolate to the population. Estimating growth, yield and productivity are important outcomes of NTFP inventories; yet undertaking the inventory may be problematic due to the nature of the product being harvested.

Permanent sample plots, which have been used extensively to estimate growth and yield of timber, are needed for NTFPs. Some work has been done to establish permanent plots for fruit production in tropical forests and more recently for mushrooms in the Pacific Northwest and medicinal plants in the southern Appalachian Mountains. Protocols for permanent plots of fruit tree yields include single, subjectively located plots configured in 1-ha squares which are subdivided into contiguous subplots. They call for measuring specific attributes that relate to production of fruit bearing trees and potential productivity of saplings. Configurations that include contiguous plots make statistical analysis difficult, as the plots may not be independent.

Growth and yield assessments are often undertaken using paired sites, which allow for comparisons of management approaches. One site is designated as an unharvested control, while the other is subjected to different degrees of harvesting. To achieve best results, local harvesters are used to gather the product. Alternatively, researchers simulate harvest methods based on experience. The main advantage of paired sites is that they allow for statistical testing. For better results and credibility, multiple replications and successive observations over several years are needed.

Development of methods to quantify product yields is lagging, and methods that have been developed have limitations. For example, methods for calculating yield of fruit trees may misrepresent actual yield because some fruit is inaccessible, other fruit may rot on the plant, and in general not all fruit is needed to meet market demand. Various techniques used to estimate fruit yields, such as ground level traps, repeat counting of fruit on trees, and random sampling of fruit on branches, each have their limitations. Repeat counting is good for fruit that do not fall when ripe, but requires marking fruit that have been counted. Branch counts are useful only for branches that are accessible. Litter traps only catch fruit that have dropped, which may not represent total yield for the tree.

For NTFPs where the desired products are below ground, such as tubers and roots, inventories are especially problematic as there is little or no way to correlate aboveground biomass to belowground yield. Attempts have been made to relate leaf width to bulb size, but further research is needed to find more reliable inventory methods. Understanding these limitations allow for development of improved protocols.

Methods for Product Categories

One of the confounding issues that affect NTFP inventory and monitoring is the tremendous diversity of products. Many different parts of the plants are harvested to produce many different products. Vines and other climbing plants are harvested for building materials and furniture. Saps and resins extracted from palms and trees are used for medicinal and culinary products. All plant parts are harvested for medicinal uses. Edible forest products may grow above or below the ground. Parts harvested for decorative and craft products include flowers, moss, twigs, branches, and cones. Building materials, such as bamboo, rattan, poles, and thatch, require different inventory approaches. Specific inventory methods may be required for each product or plant part. With so many different products, developing and implementing standardized inventory protocols is challenging. However, commonalities exist between inventory methods that create potential for the transfer and sharing of techniques.

Building Materials

Several NTFPs, especially bamboo, rattan and palms, are useful for building materials in tropical climates. A great deal of work has been done on various aspects of bamboo, particularly in India and other South Asian countries. As bamboo is a nationalized product in India, keeping track of supply and demand is legislated. It is included in national timber surveys, and volume tables have been developed to allow for accurate estimates of density per hectare. Large-scale aerial photographs and satellite imagery have been tested as a means to inventory bamboo at the District level in India. In Central and South America, demographic studies examining population dynamics of palm species used for building materials have been undertaken in forest reserves. Studies of this nature allow for estimating potential sustainable harvest levels.

Vines collected from forest lands are used as building materials, in furniture production, and in fashioning crafts. In Southeast Asia, where rattan is a major commodity, a great deal of work has been undertaken to develop inventory protocols. Efforts in this region have determined efficient and optimal sampling techniques as well as established permanent sample plots to monitor long-term impact. Results from inventory studies concerning rattan and other vines are providing valuable information that will help management. Optimal and alternative harvest methods and sustainable yields have been developed based on statistical analysis and efficient plot layout. Methods and subsequent results for rattan could have implications for management of other vines, such as grape (*Vitis* spp.), smoke (*Aristolochia macrophylla*), and smilax (*Smilax* spp.).

Crafts

NTFPs are used in the production of crafts for personal benefits and to augment household economies. Products such as statues, baskets, hats, and weavings are commonly fashioned from materials collected from forests. Perhaps the best-known example of an NTFP being fashioned into a craft is the tauga (*Phytelephas* spp.) nut from Ecuador that is used to produce buttons and carvings. This NTFP was one of the earliest examples of market development for conservation of a non-timber forest resource. Growth models established for the tauga nut help understand the impact of harvesting. Much of the work on craft materials has focused on harvest methods and levels. Findings from these studies provide insight into total production and optimal harvesting patterns that can aid in evaluating management alternatives. Inventory and assessments of craft materials is an area where more research is needed to address the multitude of products used to fashion these products.

Decoratives

A great many NTFPs are used to produce decorative products that provide aesthetic and spiritual benefits to people in their homes and workplaces. These products are used in churches and other places of worship to decorate altars as well as coffins and wedding tables. They decorate hotel lobbies and entranceways in offices and other buildings. Products made from gathered or cultivated forest plants decorate many different venues.

The international floral industry is full of products collected from or cultivated within forests. Moss, harvested from the Appalachian forests of the USA, is shipped throughout the world and finally consumed through retail and wholesale craft stores. Wreaths made from vines from China are available in craft markets in eastern United States. Lycopodium (*Lycopodium* spp.) pulled from the forests of northern Michigan is cleaned, dyed and turned into wreaths that grace the mantels of consumers in Germany and other European countries.

Many decorative NTFPs originate from diverse natural forests where they are gathered by hand or with simple equipment. Inventorying the resources for these products is extremely challenging due to the vast number and diversity of products and life-forms. Although work may be under way to develop inventory and monitoring protocols for many of the more common products (e.g., leaves, moss, twigs, cones) there are few fully developed approaches integrated into forest management. The inventory of twigs and branches produced through an agroforestry scheme could be readily developed and implemented.

In the USA, work is under way to develop protocols to inventory and monitor galax (*Galax urceolata*) and salal (*Gaultheria shallon*), two prominent species in the floral industy. For galax, permanent sample plots using a point-intercept approach have been established along the Blue Ridge Parkway in North Carolina to monitor harvesting impact. Within each plot, leaves that intercept the transect lines are recorded and measured for diameter.

Harvesting and exploitation inventories for decorative NTFPs provide information that may be useful in determining optimal management practices. Parallel transects, with attached circular and square plots of varying size and grid shapes, provide data that are analyzed using simple spreadsheets and more complicated statistical methods such as linear regression. These types of studies (**Figure 1**) allow for tracking changes in population densities, and provide information on long-term impact of harvests.

Edibles

A great deal of inventory and assessment work has examined NTFPs harvested for foods and other culinary products, particularly berries, mushrooms, and sap. Much of this work is based in Europe where mushrooms and berry-producing shrubs have been included in forest management inventories for several decades. At the same time, some of the early work on developing inventory methods for resins and saps has occurred in Southeast Asia.

National legislation in many European countries, including the Czech Republic, Estonia, Finland, Lithuania, Russia, Sweden, and Poland, mandates the inventory of these products. Although most of the available literature concerning inventory assessments in Europe comes from Finland, results are available from these other countries and could serve as models for other areas. The greatest impediment to this information getting wider distribution is the lack of translation services; the literature is mostly only available in the language of its country of origin.

In general, the main objective of berry and mushroom inventories in Europe has been to produce national-level production statistics. In the Czech Republic, household surveys are used to demonstrate the national importance of these edible forest products. Work in Estonia is helping to improve

Figure 1 Monitoring log-moss harvests and determining sustainable yields of this important non-timber forest product is essential to finding ways to manage for this product. Courtesy of Gary Kauffman, USDA Forest Service.

the understanding of production levels under various conditions. The mapping of berry and mushroom populations in Lithuania is mandated by law and provides the basis for sustainable management planning. In Poland, where edible forest products have been included in national inventories since the 1960s, valuable information is provided to analyze spatial distribution and to aid in development of yield tables.

A great deal can be learned from the berry and mushroom inventory assessments in Finland. Thousands of permanent sample plots have been established throughout the country. Volunteers are mobilized to enumerate berry production. Measurements are taken throughout the season to provide information on the progression of fruit production. Systems are in place that provide for regular national- and local-level yield forecasts. Product information is sent electronically to a central database for distribution through various media (e.g., newsprint, internet, radio) to aid pickers in their quest to collect berries.

Inventory efforts for forest foods in other regions are far less advanced. In Central and South America, demographic and yield studies have looked at various fruit-producing trees. This work is providing information on potential harvesting scenarios, changes in population dynamics, and the feasibility of commercial harvesting. While some studies have used small plots of less than 1 ha, others have taken a wider scope with more than 25 ha in a single plot. Lessons can be learned from these differences that may lead to improved protocols. For example, large plots may be necessary when the distribution of plant species is so thin that gatherers are forced to search greater distances. In areas where species density is quite low, large plots may better reflect local harvesting practices. In several studies throughout this region, plots were located with the aid of local inhabitants. Certainly using local inhabitants to locate plots will better reflect what local people want the researcher to experience.

Resins and saps are used for culinary, medicinal, and lubricating purposes. In the late 1960s, an aerial survey in Papua New Guinea was used to estimate the standing volume for production of copal (*Agathis labillardieri*) gum. Protocols developed with basket makers in rural villages in Zimbabwe allowed for the inventory and monitoring of dye production from the palm *Berchemia discolor*. Multipurpose resource inventories in Sudan have been used to estimate the potential for producing gum arabic (*Acacia senegal*), fuelwood, and building materials. In South Africa, measuring the amount of sap that is collected from the palm *Hyphaene coriacea* by local tappers allowed for assessing the potential production of wine. In North America, inventory protocols for maple syrup from *Acer saccharum* will improve forest management for that delicacy.

A variety of methods, scales, and complexities have been used in resin studies. Aerial surveys and special computer software allow for tracking large distribution of species that are tapped for resin. Regional, District and plot level analysis of resin-producing species provide information to improve management at different geopolitical levels. Grid patterns for laying out plots and condition scoring of trees impacted by harvesting provide details that will aid in replicating studies and assessing impact at a tree or stand level.

Medicinals

Inventory studies on medicinal forest products span the globe. In Cameroon, average bark production for individual trees of *Prunus africana* has been determined using systematic and subjective plot layout. In South and Southeast Asia, ethnobotanical inventories have generated lists of useful medicinal plants. In Nepal, studies have developed protocols that would integrate medicinal plants into national forest inventories. Through an assessment of medicinal plants in Sri Lanka, researchers have assessed management options for commonly collected species. Other inventory studies in the region are providing insight into the responses of plant populations to other forest activities, particularly logging. Alternative inventory approaches, modified for various plant distributions, is a critical need to improve protocols.

In Central and South America, inventory studies have strived to quantify the value of managing forests for medicinal NTFPs. Studies in this region have included economic valuation inventories as well as ethnobotanical and biodiversity inventories. They have varied in scale from 10-ha forest reserves to small research plots in local forests. Transects with random plots have been used to inventory medicinal plants in the forests of Nicaragua. Interviewing local people to identify sites and species names has been integral to some studies. Data collected include a count of all plants and collection of voucher specimens, as well as volume of green and dried product prepared for sale.

The results of studies from Central and South America provide useful information for management. The value of medicinal plants to local communities can be estimated and provides for calculating the present value of sustainable harvest levels. Knowledge gained also provides insight into the impact of management practices, particularly logging, on medicinal plant populations. Methods developed in this region may be useful in other areas where medicinal plant collection is a concern.

In North America, efforts to develop inventory and monitoring protocols primarily focus on American ginseng (*Panax quinquefolius*), goldenseal (*Hydrastis canadensis*) and Pacific yew (*Taxus brevifolia*). Recent initiatives to develop inventory protocols for black cohosh (*Actaea racemosa*) and bloodroot (*Sanguinaria canadensis*) are too new to provide substantive recommendations (**Figure 2**). An inventory assessment in British Columbia, which was based on previous research by the US Department of Agriculture Forest Service to inventory Pacific yew bark, examined two alternative approaches to inventory bark production. Bark volume was estimated using linear regression, with bark thickness against tree diameter and bark shape. Protocols recommended from studies in North America are directed at ecoregional and provincial scales, and provide information to estimate minimum viable populations and growth rates. Information generated from ginseng and goldenseal protocols allow for modeling harvest at various critical life stages and aid in projecting productivity levels. All of these studies provide approaches that may be applicable to other bark and root products.

Summary

Timber is not the only flora-based product that is harvested from the forests. Many other plants and fungi are collected, and when these are included in forest management the diversity of biological material increases tremendously. In fact, more different plant parts are used to make non-timber forest products than are used to make timber products. The

Figure 2 US Department of Agriculture Forest Service field technicians install permanent plots to inventory medicinal plant populations. Volunteers also help monitor medicinal plant populations on Forest Service lands. Courtesy of Gary Kauffman, USDA Forest Service.

magnitude of this increases significantly when one considers the number of life-forms that are gathered for subsistence, spiritual, aesthetic, and economic reasons. Although it may be impossible to determine the aggregate social value of these products, the global economic benefits from NTFPs may exceed timber.

The complexity of forest management increases when NTFRs are considered. Inventory and assessment of these resources, which is essential for sustainable forest management, is not sufficiently institutionalized. Some countries, particularly in Europe and South Asia, have incorporated a few NTFPs into multipurpose resource inventories. These countries have recognized the social and economic benefits of berries, mushrooms, and bamboo, and have taken action to manage their forests for these products. Greater efforts and investments are needed to integrate fully the inventory and assessment of NTFPs into forest management.

The greatest body of knowledge concerning NTFP inventories is based on experiences in developing countries. The proportion of literature from Europe is about half that which has been generated from developing countries, but almost twice that from North America. The rest of the world is far more advanced than North America in developing NTFP inventory protocols. Certainly, there are lessons to be learned from efforts in developing countries that could help to advance efforts in more developed nations.

To ensure the sustainable management of forest for NTFRs, inventories need to be multidisciplinary, embracing social, ecological, and economic scientific methods. Local gatherers have tremendous anecdotal knowledge and need to be included in NTFR inventories. When forest management decisions might impact the lives of local inhabitants, the local people should be involved in determining resource and harvest levels. Their involvement in ecological assays and impact assessments could help to assuage the cost issues of undertaking NTFP inventories. Methods designed to inventory and assess economic and market opportunities may be more advanced, but need to be better organized and accessible to forest managers.

The choice of inventory methods depends on the purpose of the inventory, as well as the products, plant part, and life-form. Single resource inventories are less complex and require different approaches than multipurpose resource inventories. Although there are no standard methods for bark, sap, fruit, or any of the other many products, there is a solid body of knowledge from which to formalize more rigorous protocols. The many life-forms (e.g., trees, shrubs, palms, vines, grasses, and herbs) increase the challenges of developing standard methods. Inventories of NTFPs in natural forest settings are more complex than inventories set in agroforests or other planted arrangements. Optimal and efficient methods will be based on combinations of methods from these areas.

Fundamentally, there is a strong and growing body of knowledge on which to build an inventory program for non-timber forest resources and products.

But there are currently insufficient data and a lack of common reporting methods in many countries to fully integrate NTFP inventories into forest management. Efforts are further constrained by a lack of field skills, time, personnel, and fiscal resources. Until these issues are addressed, the inventory and assessment of NTFRs will remain underutilized in forest management.

See also: **Biodiversity**: Biodiversity in Forests; Plant Diversity in Forests. **Genetics and Genetic Resources**: Forest Management for Conservation. **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Inventory**: Multipurpose Resource Inventories. **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest; Forest Biodiversity Prospecting; Medicinal and Aromatic Plants: Ethnobotany and Conservation Status; Tribal Medicine and Medicinal Plants. **Mensuration**: Forest Measurements. **Non-wood Products**: Resins, Latex and Palm Oil; Rubber Trees; Seasonal Greenery. Bamboos and their Role in Ecosystem Rehabilitation; Managing for Tropical Non-timber Forest Products. **Sustainable Forest Management**: Definitions, Good Practices and Certification.

Further Reading

Alexiades MN (1996) *Selected Guidelines for Ethnobotanical Research: A Field Manual*. New York: Botanical Garden.

Burkhart HE and Gregoire TG (1994) Forest biometrics. In: Patil GP and Rao CR (eds) *Handbook of Statistics, vol. 12, Environmental Statistics*, pp. 377–407. New York: Botanical Garden.

Cunningham AB (1987) Commercial craftwork: balancing out human needs and resources. *South African Journal of Botany* 53(4): 259–266.

Falconer J (1992) *Non-Timber Forest Products in Southern Ghana: Main Report*. Chatham, UK: Natural Resource Institute.

Jong RJ and Bonnor GM (1995) *Pilot Inventory for Pacific Yew*, Forest Resource Development Agreement Report no. 231. Victoria, BC: Canadian Forest Service and British Columbia Ministry of Forests.

Lund HG (1998) *IUFRO Guidelines for Designing Multipurpose Resource Inventories*, IUFRO World Series vol. 8. Vienna, Austria: International Union of Forest Research Organizations.

Lund HG, Pajari B, and Korhonen M (eds) (1998) *Sustainable development of non-wood goods and benefits from boreal and cold temperate forests*, EFI Proceedings no. 23. Joensuu, Finland: European Forest Institute.

Peters CM (1994) *Sustainable Harvest of Non-Timber Plant Resources in Tropical Moist Forest: An Ecological Primer*. Washington, DC: World Wildlife Fund.

Peters CM (1996) *The Ecology and Management of Non-Timber Forest Resources*, World Bank Technical Paper no. 322. Washington, DC: World Bank.

Pilz D, Fischer C, Molina R, Amaranthus M, and Luoma D (1996) Study 10: Matsutake productivity and ecology plots in Southern Oregon. In: Pilz D and Molina R (eds) *Managing Forest Ecosystems to Conserve Fungus Diversity and Sustain Wild Mushroom Harvests*, General Technical Report no. PNW-GTR-371, pp. 75–77. Portland, OR: US Department of Agriculture Forest Service, Pacific Northwest Research Station.

Salo K (1993) Yields of commercial edible mushrooms in mineral forest soils in forests in Finland, 1985–1986. *Aquilo Ser. Botanica* 31: 115–121.

Wong JLG, Thornber K, and Baker N (2001) *Resource Assessment of Non-Wood Forest Products: Experience and Biometric Principles*. FAO Non-Wood Forest Products Series no. 13. Rome: Food and Agriculture Organization of the United Nations.

Wong JLG (2000) *The Biometrics of Non-Timber Forest Product Resource Assessment: A Review of Current Methodology*. London: UK Department of International Development.

Forest Change

T Krug and J R dos Santos, National Institute for Space Research, São José dos Campos, Brazil

Introduction

Forest inventories constitute the basic documentation containing data (tables, maps) and information relevant to the planning and management of forest practices. Depending on the purpose of the forest inventory, a multitude of different data and information is collected, including, for example, measurements of some tree biophysical characteristics, production assessment, the industrial and economic value of the forest, all of which may be relevant to the efficient use of the forest resources. Different types of inventories, from reconnaissance inventories (a preliminary survey of low intensity that guides the more intensive inventory) to a large area inventories exist. The identification of the areas covered by forests constitutes the first step to initiate the forest inventory.

In order to identify the areas covered by forests, the 'own' definition (see below) of forest (which is necessarily linked to other forest-related definitions, such as deforestation, afforestation, reforestation, forest degradation) needs to be agreed. Unfortunately, there is no universal definition that is used worldwide and for all purposes. An exhaustive compilation of forest definitions has been prepared and includes more than 650 different definitions.

Similar work was carried out for other forest-related terms, such as deforestation, afforestation, and reforestation. An attempt to harmonize the different forest-related definitions to facilitate the country's reporting under different international conventions and processes (such as the United Nations Convention on Biological Diversity, the United Nations Framework Convention on Climate Change, the Forest Resources Assessments, for instance) has been carried out by the Food and Agriculture Organization of the United Nations (FAO). Complications arise in using a country's data in global forest assessments, since each country usually develops and applies its own definition of forest, based on the particular characteristics of its vegetation cover and the application to be given to the data and to the information collected. By 'own' definition it is meant the country's choice of the biophysical parameters of the vegetation cover (minimum height, minimum area cover, crown cover density) or minimum corresponding carbon stock that will be associated with a forest typology.

Most forest definitions include some threshold parameters (usually presented as ranges) associated with biophysical characteristics of the forests (such as minimum height, minimum crown cover) and/or relate to the land use status of the land. Land use refers to the way the land is being used or the intents of use (it is, in general, a political/management decision). Since deforestation, afforestation, and reforestation activities are associated with changes in forest (in particular, changes in forest area), and considering that most of these terms are defined as conversions from one state to another (either forest to nonforest, or vice versa), the implications of the forest definition are multifold.

Part of the definition of forest provided by FAO (and in the Kyoto Protocol to the United Nations Framework Convention on Climate Change) indicates that areas that are normally part of the forest area but which are temporarily unstocked (due to human intervention or natural causes) and which are expected to revert back to forest, are included under forest. The temporarily unstocked condition, if not associated with a land use change but only due to a temporary land cover change, does not characterize a convertion from a forest state into a nonforest state, and hence, deforestation. The status of the land is maintained as forest.

Forest Inventories

Forest inventories may be carried out at country, regional, or global level. The methodologies used to develop the inventories vary widely. Even at the country level, a full coverage of all the forest area is seldom carried out. Some parameters to be estimated entail destructive sampling to generate mean values that are used as representative values for certain forest components. In general, two approaches are used (either jointly or separately) in forest inventories: (1) remotely sensed data (aerial photographs, satellite imagery), and (2) statistical sampling techniques. Although some information can be provided via remote sensing, the main share of data is usually obtained through field measurements, hence the need to rely on sampling techniques.

Aerial photographs and satellite imagery may be useful to stratify the forest area into vegetation types, or even tree species, depending on the scale of the aerial photographs or the spatial resolution of the sensor on board the satellite. Through stratification, a number of strata containing relatively homogenous elements is defined. Then sampling can be applied in each stratum, ensuring that all the classes of interest (vegetation types or tree species, for instance) are included. Multistage stratification can also be applied. First, the broad classes of forest types are stratified, and then each stratum is further stratified according to tree species, height, age, wood volume, or productivity, for instance.

One common practice for stratifying the forest area according to different forest types (broad categories) is to integrate fine spatial resolution satellite data (around 30 meters) with available national vegetation maps in a geographical information system (GIS). Satellite data can be used to update the vegetation maps and, on the other hand, the existing vegetation maps may be useful in providing the spectral characteristics of broad vegetation types, improving the thematic classification (digital or based on visual analysis).

Despite the relevance of remotely sensed data to the forest inventory process, they are not adequate to provide data or information on the full range of forest parameters that may be included in a comprehensive inventory. Even very high resolution satellite data, such as the 1-m spatial resolution data from Ikonos or Quick Bird are not suitable for providing accurate data on the diameter (or the circumference at breast height) of trees which is used in several allometric equations to estimate forest biomass.

Forest Change

Changes in forest are normally associated with the variations in the biophysical characteristics of the trees (due to natural growth or decay) and/or to total or partial structural changes due to natural causes (such as pest attack, wildfires) or anthropogenic activities (such as selective logging, pruning). In general, these changes are not related to changes in the forest area, depending on the definition of forest used. Structural changes due to wildfires, for instance, may cause part or all of the forest area to be temporarily unstocked, but if land use does not change, the unstocked area is still regarded as forest, according to the FAO definition of forest. For several purposes, the estimation of the change in forest area is critical. These changes can be either positive (through reforestation, afforestation, or natural expansion) or negative (through deforestation). All these changes (biophysical, structural, and area change) are directly connected to other forest-related changes, such as change in biomass and in carbon stocks. Changes in the soil carbon may also result from the conversion of forest into pasture or agriculture. Changes in forest may also be associated with changes in the products and services (social and economic, aesthetic, cultural, or historical values) provided by the forests.

Some forests can also undergo periodic changes that are not directly human-induced, but result from a natural phenomena related to the climate region where the forest is located. This is the case of the so-called deciduous or semideciduous tropical (or subtropical) forests, where 20–50% of the tree species composition is characterized by a complete or partial loss of foliage. This loss occurs during the biological driest period, and does not promote a structural change in the forest. The ecological concept related to this type of vegetation involves two climatic aspects: (1) tropical, characterized by high levels of pluviometry in the summer, followed by a persistent drought period (4–6 months); and (2) subtropical, which does not have a dry period, but goes through a physiological drought resulting from an intense cold (mean temperature of 15°C for 3 months) during the winter.

Many efforts exist to identify the determinants of forest change, which are fundamental for the development of models to predict the rate and trend of change. However, the ability of these models to reliably predict the new fronts of deforestation and the rates of change is most commonly not very good. The traditional determinants are usually related to demographic factors (such as density, population movement), economic factors, governmental incentives, agriculture expansion, agrarian reform, infrastructure (road building), and technology (improved seeds). However, they seem insufficient to provide good predictions of where and how the changes in forest will occur (see **Figure 1**). The definition of deforestation adopted to generate the rates in **Figure 1** refers to the conversion of areas of primary forest physiognomy by anthropogenic activities, for the development of agriculture and cattle raising, detected from orbital platforms. Gross deforestation indicates that the areas in process of secondary

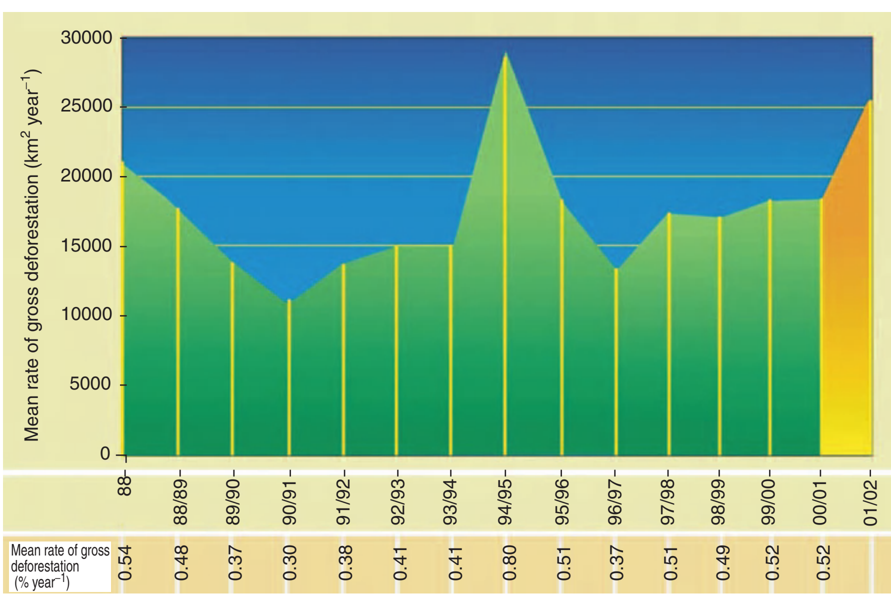


Figure 1 Evolution of the mean rate of gross deforestation in Brazilian Amazonia (km^2 year^{-1}). This illustrates the variation in the annual rate of gross deforestation from the period 1988–2001, and provides an estimate, based on a sample of 50 images, of the rate of gross deforestation from 2001 to 2002. Mean rate of gross forestation (percent per year) is given relative to the area of remaining forest. Data from 1993 and 1994 refer to an estimate of the mean rate of gross deforestation for the period 1992–1994. The mean rate gross deforestation for 2002 was based on the analysis of 50 TM Landsat images from that year.

succession or forest recovery are not subtracted in the calculation of the extent and the rate.

Forest changes can be estimated at various levels (global, regional, country, tree stand). In general, global estimates of change are provided for forest cover, forest volume, and biomass, using a range of methods from information provided by each individual country, through their national forest inventories (usually carried out at every 10 years) and/or the use of remote sensing. The advent of satellite imagery in the mid-1970s motivated the use of data from sensors on board earth observation and meteorological satellites for global assessments purposes. From the practical point of view, data from coarse spatial resolution satellite systems, such as those from the 1.1-km spatial resolution Advanced Very High Resolution Radiometer (AVHRR) sensor on board the National Oceanic and Atmospheric Administration (NOAA) series of satellites (1.1-km spatial resolution) seemed appropriate to map the extensive areas and to detect changes in forest cover. However, with this coarse spatial resolution, it was only expected that major changes in the vegetation cover would be detected. The advantage of the NOAA satellites, however, relates to their daily coverage of large areas at very low acquisition and processing costs.

At the country level (or smaller administrative units), forest assessments or estimates of forest change are usually developed from field observations, existing surveys and maps, in addition to high spatial resolution satellite data (around 30 m). This spatial resolution has demonstrated to be very appropriate for mapping land cover and to detect land-cover or land-use changes. However, the temporal resolution of these orbital systems (Landsat, SPOT, CBERS) ranges at present from 16 to 28 days, and most are based on optical sensors, which present mapping limitations over cloud-covered areas. For regional assessments, an intermediary spatial resolution of approximately 250 m is normally adequate. One difficulty associated with estimating forest cover or forest cover changes relates to the accuracy of the estimates. Field data collection and classification of remotely sensed data (digital or by visual analysis) are subject to errors of different nature. The accuracy of the satellite-derived forest estimates depends on the spatial resolution of the system and the classification process. The accuracy can be estimated from existing or sampled ground data, aerial photographs, and/or data from very high resolution satellite systems.

Forest-related estimates can also be developed from data collected in a sample selected according to a specific sampling design, the most common one being the stratified sampling design. The stratified sampling design aims at subdividing the population into a number of strata so that the variance within each one of them is smaller than the overall variance of the population. If ancillary data are available to support the stratification of the population, then it is expected that stratified sampling will increase the sampling efficiency. However, regardless of the method used, there are uncertainties associated with the estimates. How close is an estimate based on sampling from the true population parameter being estimated? This uncertainty is usually expressed by coupling the point estimate with the maximum error of the estimative, to a given probability. The question then becomes: what is the probability that the sample estimate deviates from the true value by a given amount? Ideally, this amount would be small. However, it is closely linked to the number of samples to be observed which, in turn, is a function of the variance of the population or area unit to be sampled.

In addition to identifying the occurrence of changes in the forests, whenever there is land use change, it may be important also to identify the new land associated to the previously forest area (e.g., annual and perennial agriculture, pasture, settlements). The most common approach is to make use of transition matrices, which indicate, for a sequence of time periods, through sampling or complete analysis of fine spatial resolution satellite data, how much of the original forest was converted to other land uses, and vice versa. Markov chain models may also be used to provide the likelihood of transition from one land cover or land use to another. Transition sequences can be obtained from the observation of fine spatial resolution satellite imagery at different points in time. The use of coarse spatial resolution data is only justified if only the transitions between very broad classes are of interest.

Global Forest Area and Area Change Estimates

The best-known effort to inventory the state of the forests around the world and their change (including area and stock) is carried out by the FAO through its Forest Resources Assessments (the latest one being Forest Resources Assessment 2000) (*see* **Resource Assessment**: Regional and Global Forest Resource Assessments). In addition to estimating the area and stock of the world forests, estimates of the rate of change, what triggers the changes, and what are their economic, environmental, and social impacts are also addressed.

Data on forest area and forest area change are provided by FAO by country, and at regional and global levels. This task is carried out using, wherever available, data provided by the countries (in general surveys of national forest inventories and mapping reports) and remotely sensed data. Since many countries lack data on forest area and/or a consistent time series to allow forest change to be estimated, it is important to evaluate the uncertainties associated with any global mapping or estimates. This, in general, is not an easy task, particularly when different methods are used to generate the maps or the estimates.

The estimates provided in the FRA Forest Resources Assessment 2000 report for the area covered by forests in the world was around 3.9 billion ha, which corresponds to approximately 30% of the world's land area. About 95% of the forest cover was in natural forest and 5% in forest plantations. Natural forests, in this context, refers to forest stands predominantly composed of self-sown native trees (trees which have germinated and grown from spontaneous seedfall, either wholly naturally or influenced by various silvicultural activities).

The net change of the forest area (the difference between the area deforested and the expansion of natural forest and forest plantation) was approximately 9.4 million ha year^{-1}, from 1990 to 2000. Presently, the largest changes in forest area occur in the tropics and are mostly due to deforestation activities (approximately 14.2 million ha year^{-1} in the period 1990–2000, against 0.4 million ha outside the tropics). Increases in forest area are estimated to be on the order of 3.3 million ha in the nontropics and 1.9 million ha in the tropics, totaling an annual increase of 5.2 million ha (1.6 million ha from afforestation and 3.6 million ha from natural expansion of forests (natural succession on to previously nonforested lands). All these figures represent annual estimates for the period 1990–2000. The remote sensing survey in Forest Resources Assessment 2000 revealed that the deforestation process in the tropics is dominated by direct conversion of forests to agriculture.

Of the total forest area, 47% is concentrated in the tropics, 33% in the boreal zone, 11% in the temperate areas, and 9% in the subtropics. The distribution of the forest area by region is presented in **Table 1**.

Another initiative at global level, focusing on the tropical forests of the world, was carried out by the Joint Research Centre and was known as the TREES (Tropical Ecosystem Environment Observations by Satellites) project. As the name indicates, the main sources of relevant data to detect changes in forest cover were fine or coarse spatial resolution satellite data. Methods such as image differencing, spectral bands ratios, and regression models are normally used to detect changes from images collected at two different points in time. If images acquired at several different time periods are available, it is possible to identify deforestation 'hot spots' areas which, with the help of local forest experts to adjust for possible inconsistencies, can be of significant value. The TREES project provided maps of 'hot spot' areas for southeast Asia, west and central Africa, and south and central America. 'Hot spot' areas, in the context of the TREES project, was defined as 'an area where major changes of the forest cover are going on at present (past 5 years) or are expected to take place in the near future (next 5 years).'

The knowledge of the deforestation 'hot spot' areas guides the selection of statistical samples to estimate the annual rate of deforestation, for instance. In the Brazilian Amazonia basin, this annual rate is estimated through the analysis of data from approximately 50 TM Landsat images selected in the so-called 'arc of deforestation' (**Figure 2a**) which accounts for nearly 75% of the total rate of gross deforestation in the region (covered by 229 TM Landsat images). The difference between the estimated and observed (analysis of all the images) rates has demonstrated that the estimates were off by at most 5%.

Table 1 Forest area by region (FAO Global Forest Resource Assessment, 2000)

Region	*Land area (ha × 10⁶)*	*Total forest (natural forests and forest plantations)*				*Natural forests (ha × 10⁶)*	*Forest plantations (ha × 10⁶)*
		Area (ha × 10⁶)	*% of land area*	*% of all forests*	*Net change*		
Africa	2978	650	22	17	−5.3	642	8
Asia	3085	548	18	14	−0.4	432	116
Europe	2260	1039	46	27	0.9	1007	32
North and Central America	2137	549	26	14	−0.6	532	18
Oceania	849	198	23	5	−0.4	194	3
South America	1755	886	51	23	−3.7	875	10
World total	13064	3869	30	100	−9.4	3682	187

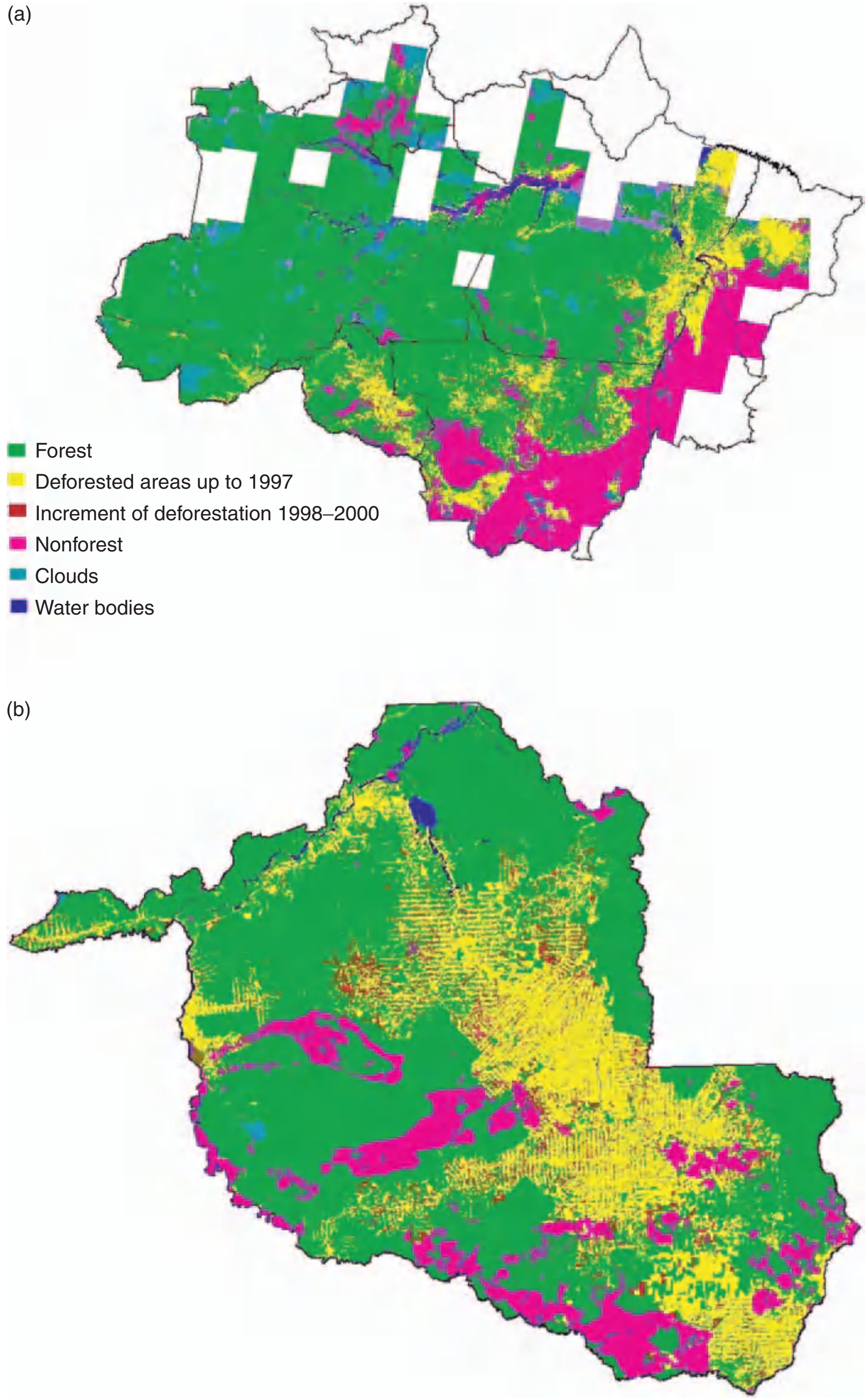


Figure 2 Mosaic derived from digital classification of TM Landsat imagery containing the deforested areas up to year 1997 and increments of deforestation from 1998 to 2000, (a) in the Brazilian Amazonia; (b) Zoom in Rondonia State.

Estimating the Rate of Deforestation

One key issue in the forestry sector concerns the estimation of rates of change. In particular, the rate of deforestation is of special interest, for many reasons. The contribution of land use, land-use change, and the forestry sector to climate change (through the increase of the concentration of some greenhouse gases in the atmosphere) is of particular interest, since the largest contribution from the nonindustrialized countries is associated with deforestation activities.

Reliable estimates of the rate of deforestation in the tropics can be generated from the analysis of high spatial resolution satellite data (approximately 30 m), which provide spatially explicit observations of changes in the forest cover. The Brazilian Ministry of Science and Technology, through its National Institute for Space Research (INPE) conducts annual estimates of the gross deforestation rates of Brazilian Amazonia, whose original forest cover was 4 million km^2 (400 million ha), corresponding to approximately 60% of the tropical rainforest in South America (cerrado vegetation not included). The estimates are based on the visual analysis of all 229 TM Landsat imagery (30 m spatial resolution) that cover the region (the so-called 'wall-to-wall' coverage).

Since the estimates are generated on an annual basis and is based on the visual interpretation of satellite imagery, the spatial distribution of the gross deforestation can be displayed and, through use of GIS, integrated with other database such as vegetation maps. This particular integration allows the identification of the forest types affected by deforestation activities. This information is relevant in estimating the carbon stock change associated to the deforestation activity. The visualization of the annual spatial distribution of deforestation helps to identify the deforestation 'hot spot' areas. In the case of the Brazilian Amazonia, approximately 75% of the annual gross deforestation concentrates on 50 out of the 229 images that cover the region. Estimates of the rate of deforestation can be made from the analysis of these 50 images, since the deforestation activities do not shift significantly from one place to another each year. Thus, changes in forest area can be estimated with 'reasonable' accuracy from a sample of images selected from the set of images that concentrate the images covering 'hot spot' areas.

Figure 2 presents the spatial distribution of the deforestation detected up to 1997 in the Brazilian Amazonia, the aggregated deforestation from the period 1997–2000, and the increments of deforestation 2000–2001. The use of GIS to integrate georeferenced databases allows the identification of the vegetation physiognomies affected by the deforestation activities each year. **Figure 3** presents the distribution of the main vegetation types in

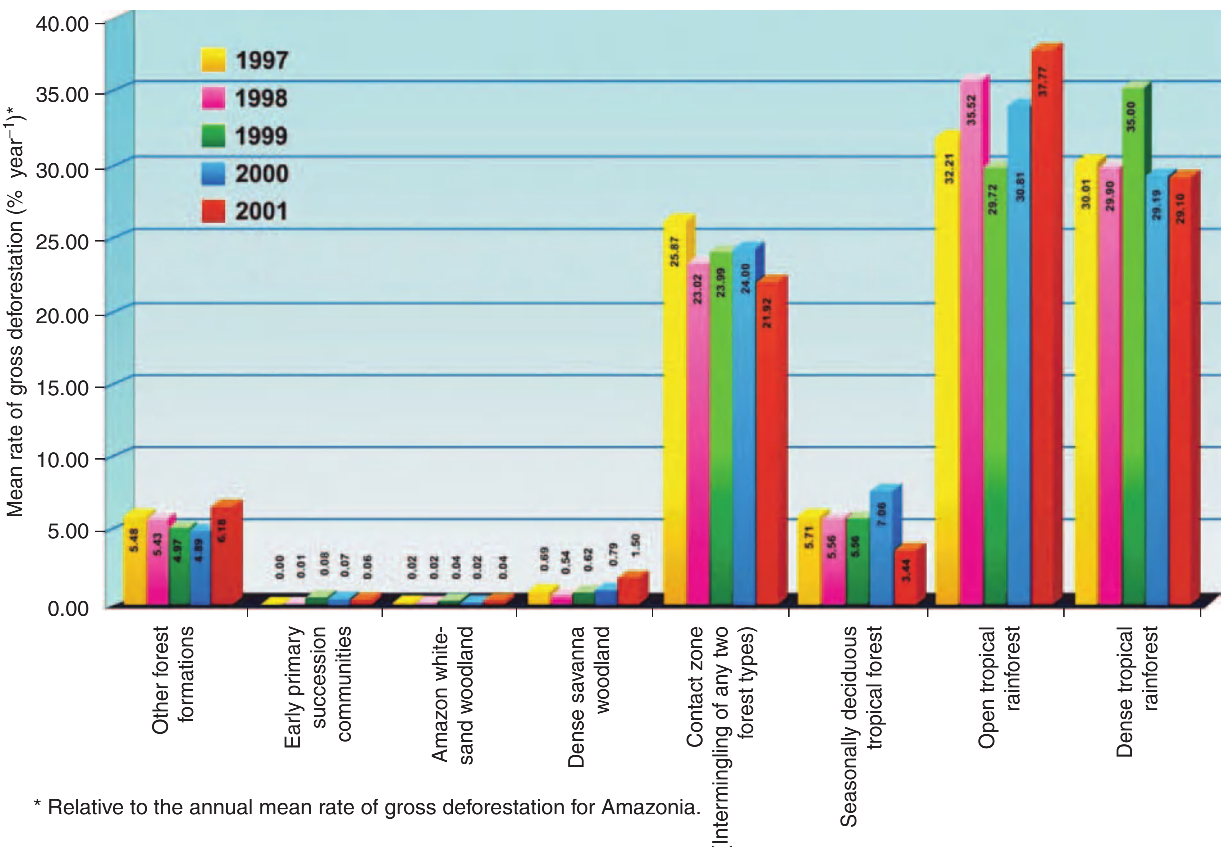


Figure 3 Distribution of the mean rate of gross deforestation (percent per year) (relative to the annual mean rate of gross deforestation for Amazonia) by forest physiognomy from 1997 until 2001.

Amazonia and the percent amount of deforestation affecting each of the vegetation physiognomies.

Biomass and Related Changes

Biomass, from the forest point of view, is defined as the total amount of aboveground living organic matter in trees expressed as oven-dry tonnes per unit area (tree, hectare, region, or country). The term biomass density is used when the biomass is presented as mass per unit area. The product between the estimated forest biomass density and the corresponding forest area gives the total biomass. The total biomass for a country or region, when different forest types exist, is estimated from the sum of the individual total biomass for each type.

Many methods exist to estimate biomass density, and these can be found in the related literature. These methods are provided for individual trees, plantations, and forest stands. The already existing data (from national forest inventories, for instance) may prove to be not always useful, since they may have been developed for other purposes and may lack the necessary information to generate reliable estimates. The estimates of the changes in the forest area, if provided by broad vegetation types, can be coupled with estimates of biomass density of these types to generate estimates of the changes in the total biomass. This approach may be satisfactory for generating changes in total biomass at regional or global levels. However, the statistical reliability of the estimates, at country level, is in general low.

The use of radar remotely sensed data to estimate biomass and to detect changes in aboveground stocks is an ongoing line of research. The main problem with the existing radar systems (the Canadian RADARSAT or the European Union ERS-2, for example) is that their signal saturates at low biomass levels. Hence, above this saturation level, the differences in biomass are no longer captured. There are many orbital radar systems available, but none has yet succeeded in providing reliable estimates of biomass, unless for low biomass content forests (regrowing forest areas, for example). Simulated P-band SAR (synthetic aperture radar) data from aircraft-based radar sensors indicated the potential use of these data to detect biomass in forests up to 200 tonnes ha^{-1} (dry aboveground biomass), which represent substantial improvements when compared to the available C or L band radar systems. However, there are no space-borne systems presently operating in this frequency. P-band sensors operate in the range 30–100 cm of the electromagnetic spectrum, whereas C and L bands operate in the ranges of 3.75–7.5 cm and 15–30 cm, respectively.

The contribution of the different components of the biomass (stem, branches, leaves, understory vegetation) to the total biomass depends on the type of the forest (natural or planted, closed or open). Studies in the Brazilian Amazonia indicate that approximately 65% of the total aboveground live biomass corresponds to trunks, and 35% to the canopy, where leaves account for approximately 12%.

The average annual change in biomass stocks for a given forest type can be estimated from the ratio between the difference of total biomass estimated at two different points in time (t_1 and t_2) and the number of years that separate the estimates ($t_2 - t_1$). Another method is based on the annual growth rate of the forest, the annual change of forest area, and the annual loss of biomass (due to commercial harvest, natural mortality, pruning, pest attack, etc. For the estimation of the annual growth rate, which is defined as the annual increase on aboveground and belowground living biomass, equations are available and usually rely on the use of biomass expansion factors. The annual total biomass loss is in general computed as the sum of biomass losses due to harvesting, fuelwood gathering, and natural or anthropogenic disturbances.

Another approach to estimate biomass change is based on field observations: permanent sample plots are established in areas representative of the vegetation types of interest, and are monitored. In this respect, high resolution satellite imagery can be useful. Measurements collected on at least two points in time are necessary to estimate change. From the biomass changes observed in the permanent sample plots for each vegetation type and the changes in their corresponding area, and estimate of the total biomass change can be derived. Since the variance of the biomass change in the permanent plots, as well as the variance in area change, the uncertainty related to the change in total biomass can be provided (area change and biomass change can be considered independent variables; in this case, the variance of the total biomass change is simply the sum of the two variances).

Modeling is another approach that can be used to estimate total biomass change. However, these models rely on the understanding of the relationship between biomass density and factors that influence its change, in particular those associated directly or indirectly with humans, such as population density and movement, socioeconomic aspects, forest fragmentation, establishment of infrastructure such as roads and railways, etc. This approach, at present, is still in its early stages. The potential use of these models will depend on the ability to understand better how humans intervene in the process and how to account for these interventions.

Changes in Forest Carbon Stocks

Trees are composed of carbon that results from the photosynthesis process. Their growth results from the removal of carbon dioxide from the atmosphere (through respiration), justifying the label of forests as carbon sinks. Carbon from trees can also be emitted to the atmosphere through, for instance, the decomposition of wood, stumps, and leaves from deforestation. In this case, the trees are referred to as carbon sources. Trees stock carbon not only above ground (stem, branches, foliage, and understory vegetation) but also below ground (all living biomass of live roots). Carbon pools also include dead organic wood (nonliving woody biomass), litter, and soil organic matter (including organic carbon in mineral and organic soils). Anthropogenic changes in carbon stock normally result from changes in land use, such as conversion of natural ecosystems (such as forests) to cropland, grazing land, or pasture or abandonment of croplands; and activities such as harvesting of timber and establishment of tree plantations. Estimating forest carbon stocks and their changes is not a trivial task and the associated uncertainties are very high. Some changes cannot be reliably estimated in small intervals of time, as is the case with soil carbon. The estimation of carbon stock changes from the land use, land use change, and forestry sector is one of the components in the national greenhouse gas inventory that countries have to calculate annually. A very comprehensive report on methodologies for estimating changes in carbon stocks in all these pools has recently been published by the Institute for Global Environmental Strategies (IGES) for the Intergovernmental Panel on Climate Change (IPCC) and should be available in 2004.

See also: **Inventory**: Large-scale Forest Inventory and Scenario Modeling. **Resource Assessment**: Forest Resources; GIS and Remote Sensing; Regional and Global Forest Resource Assessments.

Further Reading

Brown S (1997) *Estimating Biomass and Biomass Change of Tropical Forests: A Primer*. FAO Forestry Paper no. 134. Rome: Food and Agriculture Organization.

FAO (2002) *Proceedings of the Second Expert Meeting on Harmonizing Forest-Related Definitions for Use by Various Stakeholders*. Rome: Food and Agriculture Organization.

Fearnside PM (1997) Wood density for estimating forest biomass in Brazilian Amazonia. *Forest Ecology and Management* 90: 59–87.

INPE (National Institute for Space Research) (2003) Monitoring of the Brazilian Amazonian Forest by Satellite: 2001–2002. Available online at www.grid.inpe.br

IPCC (Intergovernmental Panel on Climate Change) (2004) *Good Practice Guidance for Land Use, Land-Use Change and Forestry*. New York: Cambridge University Press.

Joint Research Centre (JRC) of the European Commission (2003) *Land Use Change Monitoring in the Framework of the UNFCCC and its Kyoto Protocol: Report on Current Capabilities of Satellite Remote Sensing Technology*. Ispra, Italy: JRC EU.

Kleinn C (2002) New technologies and methodologies for national forest inventories. *Unasylva 210* 53: 10–15.

Lund HG (coord.) (2003) *Definitions of Forest, Deforestation, Afforestation, and Reforestation*. Available online at http://home.att.net/~gklund/DEFpaper.htm.

Schoene D (2002) Assessing and reporting forest carbon stock changes: a concerted effort? *Unasylva 210* 53: 76–81.

TREES (Tropical Ecosystem Environment Observations by Satellite) (1998) *Identification of Deforestation Hot Spot Areas in the Humid Tropics*. TREES publication series B, Research Report no. 4, 104 pp. Global Vegetation Monitoring Unit, Ispra, Italy: Space Applications Institute.

GIS and Remote Sensing

M A Wulder, Canadian Forest Service, Victoria, BC, Canada

Introduction

Forest inventory data are the primary information source for forest management. Forest inventories are undertaken to provide a survey of the location, composition, and distribution of the forest resource and their relative amounts over a given area. Forest inventories are required to derive the information for resource evaluation enabling management decisions at a variety of levels, such as harvest plans through to the development of provincial or state level strategies. The production of a forest inventory data set follows a series of stages, the ultimate being the development of a digital spatial database. Forest inventory, stored and manipulated in a geographic information system (GIS), is a key information source for operational-level planning and strategic-level planning and management. Operational-level forest inventories are often calibrated with field-sampled measurements and are used to develop location-specific information required for harvest planning, road layout, and silvicultural activities. At the strategic level, forest inventories provide data for longer-term forest management, analysis, and decision-making. The general approaches to the development of information for operational- and management-level inventories are similar.

Remotely sensed data, excluding aerial photography, provide opportunities to update forest inventories, estimate inventory attributes, capture forest disturbances, and to estimate nontraditional forest characteristics such as habitat and biodiversity. Remotely sensed data are georeferenced and are therefore easily integrated with GIS databases. For example, forest disturbances related to insect damage or fire, that are captured in remotely sensed data, can be incorporated as unique attributes for individual polygons in an existing forest inventory database. These inputs aid in maintaining the currency of the forest inventory database, and, as a result, contribute to the informed management of remaining forest resources.

Forest Inventory GIS

A GIS has the capability to capture, store, integrate, analyze, and display spatially referenced data. In the case of forest inventory, a GIS facilitates initial database development through data capture; storage; integration of forest inventory information with other spatial data sets; analysis and modeling of the forest inventory attributes (spatially and aspatially); and graphical display of the spatial layers on screen or as hardcopy plots. The cartographic capabilities of a GIS provide the user with a wide range of options for portraying data and producing powerful thematic outputs.

The creation of a forest inventory facilitates the generalization of complex forest resources into meaningful units. The units created are useful for forest management, as the attributes attached to a particular management unit, or polygon, were developed for this purpose. Recent developments in forest management have resulted in an expansion of the range of attributes attached to each polygon. Historically forest management inventories have focused on capturing information necessary to support harvesting and silviculture activities. These volume-based resource inventories have given way to vegetation resource inventories (VRI). A VRI captures a more diverse range of information required to support an increasingly broad range of management activities such as biodiversity conservation and habitat retention. Forest inventories are commonly the only data set capturing the forest structural characteristics over large areas. Information regarding forest structure is of interest to a large audience of practitioners engaged in every facet of natural resource management.

Traditionally forest inventory production was an analog process that culminated in the drafting of a paper map. The pervasiveness of GIS today has broadened the utility and importance of forest inventory data beyond the realm of its traditional users. Current forest management is based upon forest inventory databases which are both digital and spatially explicit. The general procedure for the map production component in the development of forest inventory databases is as follows:

1. Planning (e.g., sample design, creation of a data model, identification of attributes required).
2. Photo acquisition.
3. Photointerpretation (analog or digital-assisted).
    - Field reconnaissance
    - Calibration
    - Quality control
4. Digitization.
    - Capture of photo-interpreted polygons (including forest stand, lake, and swamp boundaries)
    - Attribute entry
    - Linkage of spatial and attribute data
    - Input of base map features (such as roads, rivers, utilities)
    - Inclusion of administrative boundaries
    - Edge matching at map boundaries of map sheets
    - Label placement
    - Quality control
    - Creation of final data set
    - Generation of outputs (hard-copy maps, reports).

The photo scale selected influences the information content, and subsequent detail of attributes that may be mapped. Typically, for forest inventory purposes, a photo scale in the range of 1 : 10 000 to 1 : 20 000 is used. Photointerpretation is the most important element of the inventory process, as the quality of the inventory is dependent on the quality of the photo interpretation. The use of experienced photo-interpreters is important. Quality control and interpreter calibration, with field data, are important elements of the photointerpretation process. The entire production cycle, from planning to generating final outputs, can take several years. Forest inventory production cycles may be shortened by using a process where the photointerpretation is done direct to digital (e.g., softcopy photogrammetry). Forest inventory databases can suffer from issues related to the length of time required to complete the inventory cycle. Forest disturbances, such as those due to fire and insects, may go undetected and not be captured in forest inventory databases. The inventory process may also be inconsistent over large areas due to operational constraints or issues of land tenure. As a result, inventory data for adjacent mapsheets may be collected at significantly different points in time. Remote sensing facilitates the continuous collection and updating of forest disturbances within the forest inventory cycle.

Remote Sensing

Air photos and digital images record energy properties at a point in time for a portion of the earth's surface. Using different combinations of film sensitivity and filters, air photos can selectively record certain wavelength ranges of the electromagnetic spectrum. Digital sensors can also be considered to use filters, but rather than using halide crystals in a film emulsion to record the image, energy detectors are used. Photographic film is generally limited in sensitivity to a narrow range of the electromagnetic spectrum (400–900 nm), while digital optical sensors can operate in a wider range of the electromagnetic spectrum (400–14 000 nm). Energy incident upon a detector, representing a wavelength range of electromagnetic energy, is typically converted to a digital number. The pattern of these digital numbers forms an image. Digital images can be considered a function of spectral, spatial, temporal, and radiometric resolution characteristics. Spectral resolution indicates range of wavelengths captured in the imagery. Spatial resolution is the pixel size or unit of area on the ground. Small pixels less than 1 m^2 in size, commonly referred to as high-spatial-resolution data, provide detailed images, conferring tree-level information. Larger pixels, such as those captured by Landsat sensors (30×30 m) capture stand or landscape-level characteristics. As a result, the types of attributes that can be estimated are closely linked to image spatial resolution. Temporal resolution indicates the frequency that a particular type of imagery is collected. A high temporal resolution (frequent acquisition) allows for capturing time-specific forest characteristics, and also allows for overcoming the presence of clouds. Radiometric resolution is generally interpreted as the number of intensity or quantization levels that a sensor can use to record a given signal. For example, 8-bits is a common quantization level, enabling a digital number range from 0 to 255. The radiometric resolution influences the precision with which attributes may be estimated and the categorical detail present. Greater radiometric resolution increases the level of attribute or categorical detail that may be attempted to be extracted from the imagery. These four image resolution characteristics (spatial, spectral, temporal, and radiometric) also combine to result in specific image characteristics. For instance, high spatial resolution imagery generally has a small spatial extent (i.e., covers a small area on the ground), is generally costly and collected infrequently, whereas lower spatial resolution data have a larger spatial extent and is collected frequently, often with data available at a lower cost.

Despite the potential and demonstrated abilities of remotely sensed data, the practical use by forest managers has been limited to date. Key to increasing the use of remote sensing in forestry are its integration with GIS technology and databases, as well as an understanding of the information need relative to the capabilities of the technology. In the following sections we present successful and nascent application areas where the integration of remotely sensed and GIS data enables the generation of unique data for forest characterization.

Forest Inventory Information from Remotely Sensed Data

The demands for current inventory information at increasingly finer levels of detail are resulting in opportunities to incorporate inventory derivatives from remotely sensed data in at least two ways: polygon decomposition and individual tree crown recognition. Polygon decomposition is a process whereby attributes generated from remotely sensed data may be integrated with existing forest inventory databases. When the spatial resolution of a given remotely sensed data source is finer than the inventory polygon size, multiple pixels may be generalized and a new forest inventory attribute developed. Even at a Landsat Thematic Mapper satellite resolution of 30 m, there are over 20 pixels within a minimum mapped forest stand polygon size of 2 ha. For instance, new forest inventory attributes indicative of forest change may be developed following a polygon decomposition approach. To achieve this result, a change detection procedure can be applied to multiple dates of satellite imagery to create a pixel-based change map. The pixel-based change may then be generalized to create new forest inventory attributes for each polygon, such as area and proportion changed. These new attributes may in turn be analyzed in conjunction with existing forest inventory attributes or viewed alone to provide for a landscape-level representation of forest disturbances. Given that the development of forest inventory databases is primarily from the manual interpretation of aerial photographs, remotely sensed data can be used to update the inventory database with harvest information for quality control and audit purposes. Biases in forest inventory databases (due to vintage, map sheet boundaries, or interpreter preferences) may also be detected using landscape-level remotely sensed land cover information.

Individual tree crown recognition is based on high spatial resolution images from which individual tree characteristics such as crown area, stand density, and volume may be derived and integrated with the forest inventory database. There are growing demands for these tree and stand attributes to be collected at increasingly finer levels of detail, and to collect others such as gap size and distribution to ensure forests are being managed sustainably for a multitude of timber and nontimber values. Information needs such as these can only be provided through the seamless integration of remote sensing and GIS technologies.

Fire, insects, and disease are among the major natural disturbances that alter our forested landscapes and their impacts need to be determined on a timely basis to ensure inventory databases are continuously maintained and updated in support of forest management planning and monitoring of sustainability. Remote sensing and its integration with GIS are technological tools that provide the capability to monitor the health of our forests. The roles that integrated remote sensing and GIS systems may serve when addressing forest pests, including:

1. Mapping and detecting insect outbreak areas.
2. Characterizing patterns of disturbance (by determining spatial relationships to mapped stand attributes).
3. Modeling and predicting outbreak patterns (such as through hazard rating).
4. Provision of data to GIS-based pest management decision support systems.

These roles result in information products that are intended for management planning, supporting impact studies, and contributing to regional or national reporting on the status of forests.

Fire is an ecological process that governs the composition, distribution, and successional dynamics of vegetation on the landscape. As a result, knowledge of fire disturbance is useful in:

1. Understanding fire impacts on timber and nontimber values.
2. Definition of salvage logging opportunities.
3. Understanding climate change effects on forest fire occurrence.
4. Quantification of the influence of fire on regional, national, and global carbon budgets.

To address this range of issues, current methods employ a range of data sources, including field observation and measurement, global positioning system (GPS) occurrence locations, forest inventory, and from remote sensing (including airborne and satellite). A similarly wide range of methods is applied to address unique forest conditions, characteristics, and fire information needs. Applications have been developed to capture a unique temporal domain to address differing management needs. Airborne infrared and thermal remote sensing systems enable real-time applications, where active fires and fire hot spots are detected. Data telemetry systems will transmit observations about fire location and size from the aircraft to field-based systems from which precise directions can be given to water-bombers and fire-fighting crews. Near real-time remote sensing GIS systems have also been developed to identify where fire activity is occurring over large areas and to aid in targeting locations for collecting finer precision information. Near real-time systems are generally based on daily satellite observations from the coarse-resolution (1 km pixel size) National Oceanic and Atmospheric Administration (NOAA) Advanced High Resolution Radiometer (AVHRR) data. Postfire applications are undertaken to map burned areas, from aerial photographs or satellite imagery, to aid in assessing fire damage.

Future Directions

High spatial resolution remotely sensed data are available from a wide range of sensor/platform configurations, including aerial photography, digital aerial photographs, video and digital cameras, and multispectral airborne and space-borne sensor systems. The multitude of possible high spatial resolution image data sources are increasing the possibilities to extract detailed information about forest structure, function, and ecosystem processes. The extraction of forest structure and biophysical information from high spatial detail imagery requires nontraditional digital analysis approaches and, often, the careful use of complementary data. Lidar is an example of a complementary data source for combination with high spatial resolution optical data. Lidar provides unprecedented accuracy in estimates of forest biomass, height, and the vertical distribution of forest structure. Samples of high spatial resolution remotely sensed data may be combined with more spatially extensive, yet less detailed information sources such as Landsat or existing GIS inventory database, to provide for landscape-level characterizations. Hyperspectral sensors collect data over many narrow spectral bands, rather than the few broad bands represented by most optical sensors. The ability to purposely select specific bandwidths of spectral information is intended to allow for improved discrimination of cover and physiological attributes. Additional research is ongoing to determine the utility of hyperspectral data in a forest management context. High spatial resolution, lidar, and hyperspectral data are examples of information sources poised to impact forest management operations. As the availability of these alternate data sources improves, as their associated costs decline, and as optimal methods to extract information from these data become better understood, data integration opportunities, and subsequent management options, are expected to increase. Landsat, and Landsat-type, sensors are also envisioned to play a continuing role in map update, broad area characterization, and change detection applications.

Conclusions

Remote sensing and GIS are complementary technologies that combine to enable improved mapping, monitoring, analysis, modeling, and management of forest resources. Forest inventory, as a cornerstone of forest management activity, has benefited from developments in GIS and may be further improved through the judicious integration of remotely sensed data. Additional information on forest inventory attributes, insect and fire damage, habitat, and biodiversity can be developed through the integration of remotely sensed and GIS data. As the availability of multiresolution, multisource data increases, so should the capability to generate timely and accurate maps of forest composition and structure. In turn, the future should see operational capabilities improved for routine mapping of a range of attributes as well as improvements in the extraction of characteristics at a precision commensurate with strategic-level forest management scales, which will contribute to efforts aimed at assessing the sustainability of our forests. The combination of remotely sensed attribute estimates with the analytical utility of geographic information systems and advanced forest process models is a powerful means to generate information that describe forests and contributes to a better understanding of the influence of disturbances, management practices, and a changing climate on the sustainability of forest ecosystems.

See also: **Ecology**: Natural Disturbance in Forest Environments. **Inventory**: Forest Inventory and Monitoring. **Landscape and Planning**: Spatial Information. **Resource Assessment**: Forest Change.

Further Reading

Aldrich RE (1979) Remote sensing of Wildland Resources: A State-of-the-Art Review. General technical report RM-71. Rocky Mountain Forest and Range Experiment Station, Forest Service, US Department of Agriculture. Available online at: http://www.fs.fed.us/rm/ftcol/publications/outofprint/remotesensing.htm.

Avery T and Berlin E (1992) *Fundamentals of Remote Sensing and Airphoto Interpretation*, 5th edn. Toronto, Canada: Maxwell Macmillan.

Avery T and Burhart H (2002) *Forest Measurements*, 5th edn. New York: McGraw-Hill Higher Education.

Fotheringham S and Rogerson P (1994) *Spatial Analysis and GIS*. London: Taylor & Francis.

Franklin SE (2001) *Remote Sensing for Sustainable Forest Management*. Boca Raton, FL: CRC Press.

Glackin D and Peltzer G (1999) *Civil, Commercial, and International Remote Sensing Systems and Geoprocessing*. El Segundo, CA: Aerospace Press.

Jensen J (1996) *Introductory Digital Image Processing: A Remote Sensing Perspective*, 2nd edn. Englewood Cliffs, NJ: Prentice Hall.

Lillesand T and Kiefer R (1999) *Remote Sensing and Image Interpretation*, 4th edn. New York: John Wiley.

Longley P, Goodchild M, and Maguire D (1999) *Geographical Information Systems: Principles, Techniques, Applications and Management*, 2nd edn. New York: John Wiley.

Longley P, Goodchild M, Maguire D, and Rhind D (2001) *Geographic Information Systems and Science*. New York: John Wiley.

Schowengerdt R (1997) *Remote Sensing, Models, and Methods for Image Processing*. San Diego, CA: Academic Press.

Wolf P and DeWitt B (2000) *Elements of Photogrammetry (with Applications in GIS)*, 3rd edn. New York: McGraw-Hill Higher Education.

Wulder M and Franklin SE (2001) Polygon decomposition with remotely sensed data: rationale, methods, and applications. *Geomatica* 55(1): 11–21.

Wulder M and Franklin S (2003) *Remote Sensing of Forest Environments: Concepts and Case Studies*. Dordrecht, The Netherlands: Kluwer Academic.

S

Sawn Timber *see* **Solid Wood Products**: Glued Structural Members; Lumber Production, Properties and Uses; Structural Use of Wood.

SILVICULTURE

Contents

Silvicultural Systems

P Savill, Oxford Forestry Institute, Oxford, UK

Introduction

A silvicultural system is a planned series of treatments for tending, harvesting, and reestablishing a stand. The main systems, their variations, and applications are described in this article. There is no fundamental difference between the systems practiced in tropical and temperate parts of the world. Variations often have to be introduced in both, for example in the wet tropics to accommodate the species-rich nature of the forests, and the relatively small number of species with timber that is commercial by current standards.

Classification of Systems

The classification of silvicultural systems, which are by their nature often flexible and imprecisely defined, is not easy. They differ, and can therefore be classified in three major ways. First, the method of regeneration used can be from coppice or root suckers, or by planting, direct seeding, or natural regeneration. Although coppice systems are clearly distinguished, most others can use any of the other three techniques. Secondly, the even-agedness of a stand puts selection systems at one extreme, and clear-cutting and coppice systems at the other. Other systems have two or more age classes for at least part of the rotation. Finally, systems can also differ in the size of the silvicultural unit. This ranges from the compartment in shelterwood and clear-cutting systems to progressively smaller areas in strip and group systems. The place of the selection system in this hierarchy is debatable, depending on whether one considers that each felling is applied to the stand as a whole, or whether each tree is treated individually.

A consideration of these three axes of variation suggests the following classification:

1. (a) Stands originating from stool shoots or suckers of vegetative origin: coppice systems.
   (b) Stands predominantly of seedling origin: high forest systems—**2**.

2. (a) Felling and regeneration are distributed continuously over the whole area, giving rise to an uneven-aged (irregular) stand: selection or polycyclic systems.
   (b) Felling and regeneration are concentrated on one part of the forest area only at any one time—**3**.
3. (a) Systems of successive regeneration fellings such that the old stand is removed by several fellings over a period of years. This gives rise to an approximately two-aged stand for a period in the regeneration cycle: shelterwood systems.
   (b) Old stand is cleared by a single felling, giving rise to an even-aged stand: clear-cutting (or clear-felling) system.

There are also various group, strip, wedge, and edge systems that are considered here (but not by all authors) as variants of the three basic high forest systems, as determined by the age structure within each. These are discussed later.

Coppice System

Coppice shoots arise primarily from concealed dormant buds that grow from the stump of a tree following cutting (**Figure 1**). They can also develop from buds on roots in some species, to give rise to root suckers, and a few reproduce by both methods.

The coppice system relies upon these methods of vegetative production after each stand of trees has been felled to provide the next generation. Coppice regeneration has an advantage over seedlings in that ample supplies of carbohydrates are available from the parent stool and its root system, so new shoots grow very vigorously from the start. However, coppice shoots of most species seldom grow to the dimensions of trees grown from seed, so the system is used to produce small-sized material. The ability to coppice is far more common in broad-leaved trees than in conifers. Species also vary greatly in their vigor of coppicing: poplars, willows, and eucalypts are generally very good. The longevity of a stool varies with its health, species, and site. Some are relatively short-lived, lasting only two or three rotations, while others, such as *Tilia cordata*, are almost indestructible. Among suitable species, no method of regeneration has a greater certainty of such rapid and complete success, and in the rather rare circumstances today where coppicing is profitable, no other method of regeneration is cheaper. The system can be attractive financially because coppice rotations are much shorter than those in high forest where trees are grown from seed.

Variants of coppicing include coppice-with-standards, pollarding, and shredding, the latter two being mostly associated with wood pasture and isolated trees rather than woodland.

- Woodlands managed as coppice-with-standards usually consist of simple even-aged coppice as the underwood, and an overwood of standards which are normally trees of seedling rather than coppice origin (**Figure 2**). The latter are uneven-aged and the two components have quite different rotation lengths. The system provides both large and small stems from the same piece of land, and is the oldest of all deliberately adopted systems of forest treatment. Cuttings are made in both the overwood and underwood at the same time. When the coppice underwood has reached the end of its rotation and is cleared, standards which have reached the end of theirs are also removed and new ones introduced.

Figure 1 Coppice shoots growing from a sweet chestnut (*Castanea sativa*) stump in Sussex, UK.

Figure 2 Oak coppice with standards in Germany. In this picture, the coppice has recently been cut for fuel wood, after growing for about 25 years, and has been stacked ready for removal. Most of the standards, which are trees of seedling origin, are left and a good indication of the range of ages (sizes) can be obtained.

Figure 3 *Eucalyptus globulus* grown on a 7–10-year coppice cycle for paper pulp production in Portugal.

- In pollarding the trees are cut 1.5–3.5 m above the ground, rather than at ground level, and allowed to grow again. This puts the regrowth out of reach of cattle and other browsing animals. Any tree that can be coppiced will respond to pollarding, except those where suckers are depended upon. Today, pollarding is mostly done for ornament.
- Shredding involves the repeated removal of side branches on a short cycle, leaving just a tuft at the top of the tree. It was practiced in Europe to feed cattle on the leafy shoots removed from trees, especially elm on land where there was little grass. Today it is sometimes carried out in countries with Mediterranean or monsoon climates, such as parts of Nepal, where there is a long, dry, grassless season, while deeper-rooting trees can provide ample fodder from their leaves.

Coppicing is one of the oldest forms of forest management, but it has been in decline in many temperate regions since at least the mid-1800s as a result of industrialization. Plastic, metal, and other alternatives are now available to replace the many objects and implements formerly made of wood of small dimensions. Improvements in infrastructure for distributing gas, electricity, and coal also means that wood is seldom required as a fuel outside the tropics.

In its modern form, coppice is extensively used for the production of pulpwood (e.g., from *Eucalyptus*; **Figure 3**), and for short-rotation energy crops (from

Salix and *Populus*), as well as for fuelwood, mostly in the tropics (e.g., *Leucaena leucocephala*). It is normally worked on a clear cutting system.

High Forest Systems

Selection System

Selection systems involve the manipulation of a forest to maintain a continuous cover, to provide for the regeneration of the desired species and controlled growth and development of trees through a range of diameter classes which are mixed singly (in single-tree selection systems) or in groups (group selection systems). Successful management can be very complex. It depends on a sound ecological knowledge, experience, in which considerable intuition may be involved, and silvicultural judgment. It aims for the maintenance of a stable and relatively unchanging forest environment.

Stands managed on a selection system are, at all times, an intimate mixture of trees of all age classes (**Figure 4**). There is no concept of a rotation length, or of a regeneration period, as both harvesting and reestablishment take place regularly and simultaneously throughout the stand. The only silvicultural interventions are selection fellings, which are typically carried out every 5–10 years throughout the stand. These fellings are a combination of regeneration tending, cleaning, thinning, final felling, and regeneration felling. This can be difficult as the needs of each of the age classes must be taken into account and trees of all sizes are removed. An important feature of selection felling is that it concentrates on improving the quality of the stand rather than felling to remove the largest and best stems, which may result in impoverishment.

Without careful intervention there is usually a tendency for a more even-aged structure to evolve, and also for the different age classes to become spatially separated, so that a group structure develops. In an extreme case, this would result in even-aged, single-storied groups. This occurs with light-demanding species, and such a group selection system is the only form of the selection system which is appropriate to them.

The length of the period between successive selection fellings varies. Short periods (less than 5 years) allow better stand management, particularly of young trees. Long periods result in larger volumes of timber being removed at each visit, making them more economical. They also improve the success of regeneration of light-demanders because the canopy is opened up more.

Selection or polycyclic systems are appropriate for the management of tropical high forests in, for example, West Africa. The best European examples are in the silver fir (with beech and Norway spruce) forests of central Europe. In temperate regions, selection systems are largely confined to mountainous areas where a continuous protection of the soil against erosion and often against avalanches is of great importance. They also protect the soil against leaching and are suitable for regeneration of frost-sensitive species. Selection forests are probably the ideal for conserving landscapes, and appropriate for forests around towns where an apparently unchanging view is important, but contrary to popular belief they do not necessarily even approximate to natural forests in many places where they are applied.

The term ‘group selection’ is widely used and loosely applied to any irregular or group system. It should strictly refer only to systems in which a stand

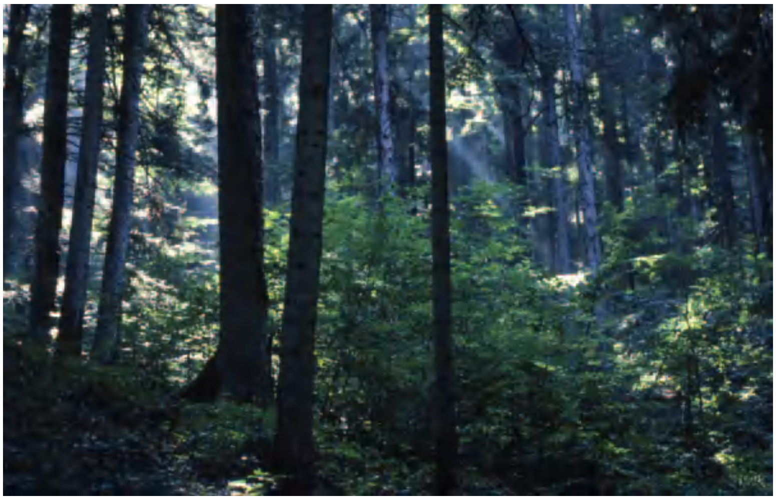


Figure 4 A selection forest of predominantly Norway spruce (*Picea abies*) and European silver fir (*Abies alba*), with some beech (*Fagus sylvatica* L.) in the Jura mountains, France.

is subdivided into groups, each of which is, for a large part of its life, uneven-aged, and has more than one storey. They are also referred as 'irregular shelterwood' systems. In practice, group selection closely resembles the selection system, as there is usually no fixed rotation length or regeneration period. It differs in that a time eventually comes when all remaining old trees must be removed, whereas in true selection working no such time ever arrives. There is, therefore, a shelterwood notion: an older stand providing protection for a younger one which is replacing it, but the period of shelter is often over 50 years. It also differs from a selection system in that more emphasis is placed on obtaining and developing regeneration in groups rather than uniformly through the stand.

Shelterwood System

The essential feature of the system is that even-aged stands are established, normally by natural regeneration, under a thinned overstory that produces sufficient shade and a moderated environment for young trees to establish. It is removed as soon as establishment is complete. Treatments usually include the following (**Figure 5**):

1. Preparatory felling: essentially a late thinning to encourage the development of the crowns of future seed bearers.
2. Seeding felling: once it is clear that there is going to be a good seed crop, a third to a half of the stems are removed. The understory and any regeneration already present are also removed. Cultivation may be carried out to assist seedling establishment (**Figure 6**).
3. Secondary fellings: usually two to four fellings, at 3–5-year intervals, with timing and intensity carefully regulated to allow seedlings to grow, but also to prevent rank weed growth (**Figure 7**).
4. Final felling: the last secondary felling in which the remaining overstory is removed. The damage done to regeneration in later fellings is not usually serious, especially if the regeneration is young and supple, dense and even-aged.

The whole series of operations normally takes 5–20 years. Infrequent mast years and frost-sensitive seedlings both necessitate long regeneration periods. The secondary fellings for a light-demanding species must be few and rapid and the whole process may be completed in 5 years.

If seed production is infrequent, then it may take 20 years to obtain adequate regeneration. The stand will then be somewhat uneven-aged and patchily distributed, in which case the system grades into the group shelterwood. Some authors state that one of the main advantages of this system is its simplicity, but in areas where mast years are infrequent,

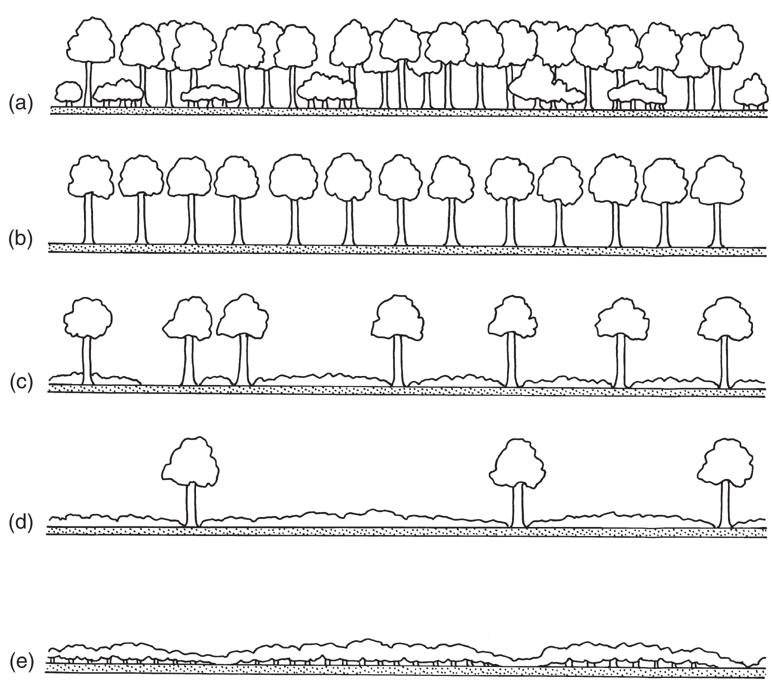


Figure 5 Uniform shelterwood system, showing successive stages of regeneration in oak forest. It typically takes 5–8 years from a successful seed fall to removing the last of the adult trees. (a) The forest before regeneration begins, with understory trees and shrubs; (b) after the seeding felling; (c) a secondary stage where adult trees have been removed around successfully established regeneration; (d) a late secondary stage where very few adult trees remain; (e) the young regenerated stand with all the previous generation of trees removed.

Figure 6 Shelterwood system with oak (*Quercus petraea*). A seeding felling has just been carried out, removing a third to a half of the trees. The understory and any regeneration already present have also been removed and the ground has been cultivated to assist seedling establishment. Bellême forest, Normandy, France.

Figure 7 Shelterwood system with oak (*Quercus petraea*). A late secondary felling, at an intensity and time to allow the prolifically produced seedlings to grow, but also to prevent excessive weed growth. Bellême forest, Normandy, France.

obtaining a fully stocked, even-aged regeneration is a major managerial problem. The shelterwood system can also be used with planted stock where natural seeding is insufficient or irregular, where a change of species is required, and where seed-bearers are insufficient in number or quality.

Variants to the system include both group and strip systems that consist of shelterwood regeneration fellings carried out in a strip ahead of the advancing edge of the final felling. They are sometimes considered more suitable than the shelterwood systems for light-demanding species.

Group shelterwood systems involve retaining an overstory for a short period to provide shelter for the new stand, which is approximately even-aged. The main difference from the shelterwood system, apart from the small size of the areas worked, is the fact that if advance or existing regeneration is present, it is used as the focus of a regeneration felling. (In a strict shelterwood system, existing regeneration would be removed with the understory.) Groups are gradually enlarged by carrying out regeneration fellings (seeding, secondary, and final fellings successively) around the edges until eventually they meet and merge. The regeneration period is generally longer (15–40 years) than with the shelterwood system, and the resulting stand is therefore somewhat more uneven-aged.

Stands managed under a shelterwood system have many features in common with those established by planting under a clear-cutting system. They can be pure, even-aged, and uniform in structure and density over large areas.

Clear-cutting System

This system is universally applied and is likely to remain the predominant silvicultural system in forests managed primarily for profitable wood production. Its main advantages include simplicity, uniformity, and, in particular, the ease of felling and extraction. The use of clear-cutting does not necessarily preclude the use of natural regeneration (as is done in a variant, the ‘seed tree’ system, where a small number of widely spaced adult trees are retained for seed production), but the system almost always operates with establishment by planting (**Figure 8**). The main advantages of planting arise from its artificiality and minimum reliance on unpredictable natural events. Enough plants can be ordered for the desired year and can then be evenly distributed across the whole area, in rows, to facilitate subsequent tending. This makes reliance on natural regeneration seem like a technique inherited from a primitive ‘hunter–gatherer’ technology, whereby the time of arrival and dissemination of seed, the genetic quality, and even the species of the regeneration are largely outside the control of the manager.

However, planting is expensive, losses may be high, especially through drought, and since stocking is usually orders of magnitude lower than with good natural regeneration, the resulting stand may be of lower quality. Disadvantages of clear-cutting, rather than of planting, largely arise from the lack of protection, leading to a rise in the water table, extremes of temperature including frost, leaching and soil acidification, and rank weed growth. Clear-cutting is widely regarded as the least desirable system for both landscape and conservation but these disadvantages can be reduced by the use of small coupe-fellings (0.2–2 ha).

Clear-cutting is based strongly upon principles of economics and finance. It provides good opportunities for using labor-saving equipment and machinery efficiently; management is simple and work can be carried out with little skilled supervision. Management can, in fact, be intensive, and hence cost-effective. For production systems where profit is a major motive, clear-cutting is invariably the choice, unless some biological or environmental factor of the locality rules it out.

Group clear-cutting involves felling all the trees in a group prior to restocking. The stand within each group will always be even-aged, but the stand as a whole will contain groups of a wide range of ages, and possibly of all ages. The individual groups may be pure or mixed in species composition, and may be established by natural regeneration, or planting, or a combination. Group clear-cutting is particularly appropriate to strong light-demanders as the only protection given to the young trees is from side shelter. Group sizes commonly range from coupes of about 50 m in diameter (0.2 ha) to areas of a hectare in extent.

Group, Strip, Wedge, and Edge Systems

The various group systems are considered here to be variants of the three main high forest systems, giving group clear-cutting, group shelterwood, and group selection systems. A whole compartment of a group clear-cutting system may therefore be uneven-aged, but each individual group will be even-aged and managed on a clear-cutting system. Similarly, strip,

Figure 8 Extensive even-aged plantations of Sitka spruce (*Picea sitchensis*) in Scotland.

wedge, and edge systems can be considered as variants of each of the three basic high forest systems, depending on the type of stand treatment that is carried out ahead of the advancing felling edge. This gives strip-felling, and strip-shelterwood systems, and also strip variants of the group systems, such as strip-group shelterwood.

In all group systems, the size of the group is a critical characteristic. Large groups are easier to manage, and are essential for light-demanders. The most useful range is probably 0.1–0.5 ha; larger groups are needed in taller and more uneven-aged stands. The shape and orientation of the groups can have a major influence on the variation of microclimate within them, and considerable emphasis is laid on this in central Europe. General observations are that a north–south orientation of an elliptical or rectangular group provides a good compromise between wind and sun, and that light-demanders should be near the north edge, and frost-tender species near the south.

The layout of groups is vital in facilitating management of the stands. Wherever possible, the first groups to be regenerated are those located furthest from the road, thereby minimizing the amount of timber that has to be extracted through a young stand. Fencing costs for small groups are inordinately high and this has always been considered a major disadvantage of any group system.

Group systems come closest to imitating the structure of a natural stand, at least in many temperate regions, and are therefore increasingly recommended for use.

Choice of Silvicultural System

Foresters continually have to choose between different silvicultural and management systems to achieve different mixes of products and benefits from specific forest areas. No single system is ideal for all situations. The choice is most often between even-aged monocultures that are usually, but not always, based on planting and clear-cutting and various uneven-aged systems based on natural regeneration.

The factors that govern the choice of a silvicultural system are silvicultural, economic, and socioeconomic, and include:

- the reproductive requirements and habits of the desired tree species
- the site itself may indicate, or at least rule out certain systems. Where conditions are particularly suitable for seeding and germination, systems for regenerating large coupes can be used, but where they are less certain, much smaller coupes are preferable
- constraints and requirements imposed by wildlife
- likelihood of problems arising from insect pests, fungal diseases, fire or climatic hazards, such as frequent high winds. The latter usually necessitate use of the clear-cutting system, and put the shelterwood system at extreme risk
- the size, age, and vigour of the existing trees may dictate the system
- the introduction of a new species to a site, or genetically improved strains, usually requires planting and even-aged systems
- the nature of the topography and soil may dictate the system
- constraints on manpower, money, equipment, and markets all have considerable influence on the choice of system.

Woodland management can be thought of as grading from intensive through to extensive. The former implies careful and expensive tending to produce valuable high-quality timber and the latter a lower-input approach, accepting mixed and uneven-aged stands, and producing, cheaply, rather lower-quality timber. Intensive management is normally associated with clear-cutting and shelterwood systems. The less intensive approach is more appropriate to selection and group systems, which need careful, but not capital-intensive, management to run well.

The same distinctions apply to the strategy adopted for obtaining and using natural regeneration: one could either invest time and money in trying to get a full stocking from any one seed year (i.e., a shelterwood system with careful preparatory thinnings, cultivation, and weed control) or one could operate a group, or selection, system with minimum preparation for seed, but accepting and using the steady trickle that establishes itself, largely unaided. Both approaches have their merits and the high-input one is not always the most profitable. The low-input approach is particularly appropriate to owners of small woodlands who do not have large sums to invest or where the forest is composed of many species, few of which are merchantable, as in many tropical forests.

Stands of irregular structure and tolerant (shade-bearing) species are best suited to uneven-aged silviculture, and it is also best practiced on fragile sites, steep slopes, sites with high water tables, and very dry sites that would be adversely affected by complete removal of the forest cover, even for short periods. Even-aged systems are most appropriate in stands of intolerant (light-demanding) species and should be used to return over mature, decadent, diseased, or insect-infested stands to productivity.

See also: **Afforestation**: Species Choice. **Plantation Silviculture**: Multiple-use Silviculture in Temperate Plantation Forestry; Rotations; Sustainability of Forest Plantations. **Silviculture**: Coppice Silviculture Practiced in Temperate Regions; Natural Stand Regeneration; Unevenaged Silviculture. **Windbreaks and Shelterbelts**.

Further Reading

Burns RM (1983) *Silviculture Systems for the Major Forest Types of the United States. Agriculture Handbook No. 445*. Washington, DC: US Department of Agriculture.

Dawkins HC and Philip MS (1998) *Tropical Moist Forest Silviculture and Management*. Wallingford, UK: CAB International.

Lamprecht H (1986) *Waldbau in den Tropen (Silviculture in the Tropics)*. Hamburg, Germany: Verlag Paul Parey.

Matthews JD (1989) *Silvicultural Systems*. Oxford: Clarendon Press.

Palmer J and Synnott TJ (1992) The management of natural forests. In: Sharma NP (ed.) *Managing the World's Forests: Looking for a Balance Between Conservation and Development*, pp. 337–373. Iowa, USA: Kendall/Hunt.

Parren MPE (1991) *Silviculture with Natural Regeneration: A Comparison Between Ghana, Cote d'Ivoire and Liberia*. AV. no. 90/50. Wageningen Agricultural University, The Netherlands: Department of Forestry.

Poore D (ed.) (1989) *No Timber Without Trees – Sustainability in the Tropical Forest*. London: Earthscan Publications.

Smith DM (1986) *The Practice of Silviculture*, 8th edn. New York: John Wiley.

Troup RS (1955) *Silvicultural Systems*. Oxford: Clarendon Press.

Whitmore TC (1990) *An Introduction to Tropical Rainforest*. Oxford: Clarendon Press.

Bamboos and their Role in Ecosystem Rehabilitation

I V Ramanuja Rao, International Network for Bamboo and Rattan (INBAR), Beijing, China

Introduction

Bamboos are a treelike, 'woody' plant of the grass family and botanically, one of the closest relatives to rice. It thus combines the best of both worlds – it grows speedily like a grass and in much the same way, while at the same time, it produces a considerable amount of high-strength and easily processed woody material with similar properties. It can grow in very poor soils, but also responds admirably to fertilization and irrigation, much like the modern rices, resulting in a doubling or more of size and annual biomass production.

Within the area of their natural distribution, bamboos are the plant equivalent of the domesticated animal like the cow, sheep, and goat. The high strength-to-weight ratio of the poles, and the absence of cross-fibers that lends bamboo to easy linear splitting, are characteristics that have made rural communities choose bamboo over other trees when it comes to structural as well as diverse subsistence uses. Over 1 billion people on earth live in houses that are reinforced with bamboo, even where wood is available nearby.

There are hundreds of traditional uses of bamboo, from food, construction material, housing, and bridges to household articles, and use in agriculture, fisheries, transportation, and in village industry. Bamboo also finds use today as a structural material, as a wood substitute, food, fuel, and a filtration medium.

Diversity

Bamboos are the most diverse group in the grass family, and the most primitive subfamily. The taxonomy of bamboos remains poorly understood, though the general consensus seems to be that the subfamily Bambusoideae has between 60 and 90 genera with 1100 to 1500 species, with the vast majority being tropical. The main reason for this large variation in diversity estimates is that flowering bamboos are few and far between. Most bamboos flower once in several years (and die thereafter), with the vegetative period extending up to several decades, but commonly 30–60 years for the more useful species. Hence taxonomists have to contend with having to do species determination mainly on the basis of vegetative material, which results in open-ended results that need a flowering specimen for confirmation.

Propagation

Bamboos are commonly propagated using vegetative (clonal) means and, when available, by seeds. The latter method is more common in tropical areas where the bamboos flower and set seed more frequently. Most bamboos produce copious quantities of seed (botanically termed caryopses that are technically fruits); these are called 'bamboo rice' and are even used as such. The rare exceptions are species such as *Melocanna baccifera* that produce large fruits, often the size of small mangoes. In some bamboos, infertility is rampant, with few viable seeds being produced.

More commonly, vegetative propagation methods are used. The methods primarily use (1) rhizome cuttings (or with attached culms (stems)), (2) culm (main stem) cuttings, and (3) branch cuttings. It is observed that the success rate commonly considerably decreases from rhizome cuttings to branch cuttings, but this needs to be considered against the larger number of cuttings available from branches as against the few rhizome cuttings (often one to two from a plant), and the damage the parent plant suffers on removal of material for propagation, which is significantly greater with rhizome removal.

Tissue culture has also been used to propagate bamboos, and has been widely employed where facilities, and availability of seeds that easier starting materials for culture, are available. Fewer bamboos have been mass-propagated by tissue culture from mature adult plants.

Production and Characteristics

The annual incremental biomass production on air-dry basis for a bamboo plantation can range from 10 to 40 tonnes ha^{-1} depending on the species, planting density, soil, and climate, including slope and aspect of a hill. An increase in strength is reported to occur until about 3–4 years and thereafter it decreases. Therefore the maturity period of bamboo is commonly considered 3–4 years with respect to density and strength, although for other applications, younger bamboos from ages 1–2 are used.

The mechanical properties of bamboo differ with species, age, climatic factors, moisture content, and different heights of the culm. Because of its hollowness, the effectiveness of bamboo as a beam is 2.9 times better than a wood beam. Bamboo possesses excellent strength properties especially tensile strength. It is as strong as wood and some species even exceed the strength of timbers such as *Shorea robusta* and *Tectona grandis*.

The density of bamboo varies from 500 to 800 $kg\,m^{-3}$. The general mechanical properties of bamboo are:

- tensile strength = 1000–4000 $kg\,cm^{-2}$
- compression strength = 250–1000 $kg\,cm^{-2}$
- bending strength = 700–3000 $kg\,cm^{-2}$
- modulus of elasticity = 100 000–300 000 $kg\,cm^{-2}$.

Ecological Requirements and Distribution

Bamboos are important ecologically because of the vast area over which they are distributed, the total quantum of the resource, and the diversity of species and the ecological habitats they occupy. According to an estimate, bamboo accounts for one-quarter of the biomass in tropical regions and one-fifth in subtropical regions. Bamboos occur in latitudes as far north as 46° N and as far south as 47° S, and at elevations from sea level to as high as 4000 m in the Himalayas. Most bamboo is found in the area between the Tropic of Cancer and the Tropic of Capricorn, and its principal distribution completely girdles the world like a belt around the equatorial region, with extensions both to the north and the south into the subtemperate areas.

Bamboos thrive in a semi-evergreen and moist deciduous forest, with the wet evergreen and dry deciduous types as its two extreme limits. The controlling factors for its abundance, distribution of species, growth, and development within these typical limits are mainly annual precipitation, relative humidity, and the nature of the soil. Bamboos can grow as an understory in almost all the forests excepting mangrove vegetation and form a rich belt of vegetation in well-drained parts of tropical and subtropical habitats.

Most clump-forming (or pachymorph) bamboos grow at temperatures ranging from 7°C (sometimes 2–3°C) to 40°C and can tolerate higher temperatures for short periods. Altitude affects the distribution of bamboo even in the tropical region. The clump-forming type is observed to predominate in low and medium altitudes, while the nonclump-forming running (or leptomorph) type occurs more abundantly at high elevations. Altitude and temperature are closely related and it is difficult to separate one from the other, for example, some species of *Phyllostachys* are cultivated at high elevations in India and Nepal but also occur at low elevations in countries of the temperate zone.

Bamboo commonly grows well in areas with an annual rainfall of 1000–6000 mm, but is also found in areas with lower (800 mm) and higher annual rainfall levels.

Role in Ecosystems

Bamboos grow in a vast diversity of ecosystems, both natural and human-made. In general, bamboos are one of the first members to colonize a new site in a seed year and perhaps the last to leave it. Once established on a site, it is relatively difficult to eradicate, with the rhizomes being found throughout the forest area. Even if the bamboos are felled with the trees, the underground rhizomes remain alive and give out new shoots in the following growing season. In the absence of tree regeneration the site would become a pure bamboo forest; with tree regeneration the bamboo comes up as undergrowth.

Generally, one bamboo species will grow in a pure condition. It is rare to encounter a mixture of two or more species.

Their unique biological properties have enabled the bamboos to adapt to diverse situations. Their role in ecosystem rehabilitation is best understood in terms of (1) their role in various natural and human-made ecosystems, and (2) the unique combination of characteristics and properties of this plant that increase the comparative advantage of the plant, and have enabled it to survive and spread around the globe. Principal amongst these are its treelike stature, the aggressive spreading underground rhizome, the strong adventitious root system, the rapid shooting of the pointed and leafless new culms, the production of leaves and branches from the tip downwards, the considerable tensile strength of the culms, the often several decades-long lifespan, and the gregarious flowering of bamboo, all of which together enable the remarkable adaptability of bamboo to diverse ecological conditions.

Treelike Stature and Dense Canopy

Bamboos commonly grow to 15 m; some species are diminutive, some are climbers, while others reach a height of up to 40 m. Bamboos have a dense canopy. A bamboo produces considerable biomass, and a significant part of this is in the form of foliage. For example, in *Gigantochloa scortechnii*, the amount of biomass is 50–100 tonnes ha^{-1}, divided into 60–70% for culms, 10–15% for branches, and 15–20% for the leaves.

Bamboos are not purely evergreen plants. Most of the clump-forming types in the tropical regions shed their leaves in winter when it is dry and renew the leaves simultaneously in a short time. The amount of leaf fall from *Melocanna baccifera*, *Oxytenanthera nigrociliata*, *Bambusa tulda*, and *Dendrocalamus giganteus* is 6.0, 5.6, 5.8, and 7.0 tonnes ha^{-1}, respectively. Bamboos contribute approximately 20 kg $tonne^{-1}$ of organic matter to the soil, which is largely similar to that of other broadleaved species. The abundant leaf fall and rhizome growth in the topsoil layer serves to ameliorate soils.

The spreading foliage takes the impact of the fierce tropical rains and softens their impact on the ground. Leaves that fall up to 10 cm thickness per year also help absorb the impact of rain. A project in China conclusively proved that the canopy and leaf litter of temperate bamboo stands can intercept rainfalls much higher than those for conifers and pines.

Strong Adventitious Root System

The strong and solid underground rhizome of bamboos produce copious roots. Eighty-three percent of the roots of a well-grown clump of *Bambusa tulda* were reported to be present in the upper 33 cm of the soil; 12% between 33 and 66 cm, 4% between 66 and 100 cm, and only 1% between 100 and 135 cm below the surface. Bamboos are thus a superficial grower and feeder, and this characteristic gives them the ability to bind soils and prevent erosion. A study estimated that a single bamboo plant could bind up to 6 m^3 of soil. The weight of the soil bound is considerably more than the weight of the over-ground light tubular, cross-reinforced plant – the considerable dead-weight prevents it from being easily uprooted.

Underground Rhizome

The complex branched and robust underground rhizome system and infrequent flowering also distinguish the bamboo from common trees. The rhizome system spreads horizontally and produces culms from new rhizome growth. Even if a bamboo species is 30 m or more in height, the rhizome seldom grows more than 75 cm deep within the soil, mostly occurring within the top 20–50 cm.

There are two principal categories of bamboos – the clumping type (pachymorph bamboos) and the running type (leptomorph bamboos). The extent of spread of the former is dependent on the length of the rhizome neck, while in the latter, the running rhizome produces buds that grow up into culms. Bamboos can well be called the ‘walking tree.’ A bamboo can thus quickly expand and consolidate its ‘territory’ compared to most trees. In more dense wet tropical forests, climbing bamboos are not uncommon.

The underground rhizome network is a function of the type of bamboo. Clumping or pachymorph bamboos would have a clustered set of rhizomes under the clumps with limited spread outwards. Pachymorph bamboos like *Melocanna baccifera* but having an open and diffuse type of rhizome system with long rhizome necks of 1–2 m, form a complete underground network over the entire area that gridlocks the soil and do not give way even under considerable pressure from liquefied soils under strong monsoonal rains. Running or leptomorph bamboos have rhizomes that criss-cross the ground. This kind of rhizome system is stronger than the clumping bamboos but not as strong as that of the diffuse pachymorph type.

Importantly, the underground rhizomes enable bamboo to survive forest fires, including fires set for clearing land for slash-and-burn agriculture. Thus they are fairly tenacious, and difficult to kill or eradicate. In burnt lands that previously had growth of bamboo, it is often the first plant to regenerate.

Once established, the early formation of rhizome protects seedlings from grazing. Even if the tops get eaten, new shoots are produced from the rhizome.

Rapid Shooting of New Culms

The new shoots grow to full height within 2–4 months which is the total time taken from when the newly forming bamboo culm (pole) starts to break ground as a new bamboo shoot to the attaining of full height. This period is the same for a short-stature bamboo and one whose culms reach up to 40 m with a diameter of up to 30 cm. During this period the bamboo shoots can grow 1.2 m in 24 h. The pointed, leafless culms reach full height before branches and leaves are produced on the naked culm from the apex downward. The culms can therefore fully occupy even small open spaces in the forest before spreading their branches.

Annual Production of Culms

Bamboo produces several new full length culms each year. Thus a clump ordinarily produces several kilometers of culms during its lifetime. Since culms are produced each year, annual harvests are possible and recommended. Bamboo therefore combines characteristics of an annual and a perennial, and hence can span agriculture and forestry. Given that there is no secondary growth in bamboo (it being a grass), but that several tonnes of new woody biomass are produced *de novo* each year as new culms, bamboo offers the opportunity to sequester considerable carbon throughout its lifetime. *Guadua* in Costa Rica has been calculated to sequester 17 tonnes ha^{-1} of carbon each year throughout its lifetime.

Considerable Tensile Strength of the Culms

Bamboos poles have a remarkably high tensile strength – weight for weight, this is greater than that of steel. It therefore can withstand very high winds and typhoons.

Bamboo poles mostly attain full strength by the third year, while trees take a considerably longer time to mature. Yet another very important characteristic is that the total quantum of bamboo wood is produced in the very first year of growth, although its composition undergoes a change from year to year.

Gregarious Flowering of Bamboo

Depending on the periodicity of flowering, bamboos fall into three groups: (1) annual flowering (or nearly so), (2) irregular flowering, and (3) gregarious and periodical flowering. Many species that flower gregariously also flower sporadically. Gregariously flowering clumping species generally have vegetative periods of around 25–35 years within a larger range of 15–60 years, while many running bamboos flower after 60–120 years. There are also bamboos such as *Bambusa vulgaris* that have not been known to flower, or do so rarely without seed set and concomitant death, but never gregariously. Gregariously flowering species from the same cohort will flower at the same time even if separated geographically across the globe.

More recently, bamboo hybridization has become possible through an ingenious nutrition control means that seeks to physically bring together naturally flowering bamboos and maintain them in a flowering state. Interspecific and intergeneric hybrids have been produced. The flowering of bamboos *in vitro* has also been demonstrated. Once *in vitro* flowering is established, the bamboo can be alternated between the flowering and vegetative states.

Most species of bamboo die after gregarious flowering at the end of a long vegetative period of growth, often three decades and more, depending on the species. This event with catastrophic economic and social effects (because of the suddenness and scale) has a major impact on the local ecosystem, and affects the vegetation with which it is associated. There is also the possibility of increased soil erosion, effects on wildlife, and also significant social and food security effects. The latter is mostly due to its nutritious seeds and fruits that form food for field rats (commonly called bamboo rats) which increases the number of litters and the live pups per litter. When the bamboo seeds/fruits are exhausted, the ferocious rats turn to household grain stocks. In Mizoram, which is a state in the northeastern part of India, a revolution was spawned as a result. In Thailand, the flowering of *Dendrocalamus asper* brought a flourishing edible shoots export industry to its knees. In Zambia, whole communities were uprooted when the bamboo that was the mainstay of their life and livelihood flowered and died.

The natural regeneration of bamboos occurs profusely after each gregarious flowering. Masses of seedlings form and there is intense competition with consequent natural thinning. By around 6 years, the area again has fairly uniformly spaced clumps, unless there is human intervention, intense grazing or fire. The first year or two are critical since there is little protection, except for refuges in the dead clumps.

Much learning is rapidly taking place in this area, with the result that where prior data of flowering is known, advance steps can be taken to reduce its impact. Mapping of flowered areas on to the geographical information system (GIS) with dates and species/cohorts have started in some areas.

Preventing Soil Erosion in Uplands and Lowlands

The extensive underground root-and-rhizome system makes bamboo a good instrument for arresting the ravages of water erosion in areas prone to it (such as slopes and lowlands). Researchers in Puerto Rico, who experimented with several plant species, found bamboo to be one of the most effective in controlling landslides. It is reported that the *Guadua* bamboo in Colombia has effectively prevented millions of tonnes of mountain soil from being washed down into the ocean. In China it has been observed that the mixed bamboo stands that adorn the southwest mountainous area are instrumental in ensuring that the quantity of soil that reaches Yangtze River through sheet erosion is just half that of the quantity washed out into the Huang River (Yellow River). The plant is so effective in binding soil on steep slopes that Malaysia has planted bamboos on hillsides to block mud and stones sliding on to roads.

Watersheds

Bamboo is commonly used in watersheds for increasing rain interception, reducing impact on the ground of heavy rain, reducing soil erosion, increasing water recharge, and for increasing postmonsoonal flow. In Ecuador, it is common for farmers to plant *Guadua* on the slope above farms since it increases water availability.

Riverbanks, Dam Sites, Lakes, and Ponds

As a plant that, unlike trees, spreads horizontally because of its rapidly growing rhizome and its pronounced ability to bind soil, bamboo is excellent for protecting riverbanks, dam sites, lakes, and ponds. It is also able to tolerate intermittent flooding which helps in this function. For this reason, bamboo cultivation in Japan has been recommended since the sixteenth century.

Bamboo's efficacy as a soil binder has been successfully used in Puerto Rico, Costa Rica, Nepal, the Philippines, and China. Bamboo planted at certain strategic points along the course of a river, especially at points where the river curves, have solved the problem of damage to the riverbank and also flooding. Not only is this due to the soil-binding capacity, but also the clumping bamboos often tend to 'mound,' leading to an increase in the height of banks as well. In Dayingjiang River in Yunnan Province and Jiulongjang River in Fujian Province in China, bamboo succeeded in protecting riverbanks after soil-rock engineering efforts and the planting of other trees had failed to yield results. It was shown that each clump can protect up to $12\,m^3$ of river embankment.

Windbreaks

Bamboos, particularly the clumping type, are an effective shield against the onslaught of wind. The flexibility of the culms (for green culms the modulus of elasticity is about $9000–10\,000\,N\,mm^{-2}$ and the modulus of rupture $84–120\,N\,mm^2$) helps them to bend but not break even in relatively strong winds. Bamboo can bend even until it touches the ground in very strong winds, cyclones, and typhoons without getting uprooted like trees. Because of this bamboo is commonly used as a wind barrier along boundaries of farms, and to protect agricultural land from wind erosion during fallow periods.

Bamboo is also now being planted as an inner line plantation behind coastal mangrove and casuarinas to shield the interior from the effects of strong winds and cyclones.

Inundated Areas and Saline Environments

Bamboo does not grow naturally under saline coastal inundation. However, in Bangladesh, it is common practice for people in coastal areas to cultivate bamboo in homesteads and farmlands. The most successful species is *Bambusa vulgaris*. Another such bamboo is *B. atra* (*B. lineata*) which is found in the tidal swamp forest of the Andaman Islands (India).

Species such as *Ochlandra scriptoria*, *O. stridula*, and *O. travancorica* that are indigenous to the states of Kerala and Tamilnadu in India are mostly found in marshy areas and riverbanks that get flooded in the monsoons. *Phyllostachys purpurata* (*P. heteroclada*) and *P. atrovaginata* are monopodial species that can grow in wet soils and waterlogged areas. Interestingly, the rhizomes of these monopodial species have air canals.

Most bamboos can tolerate a period of inundation. With longer periods of inundation there is death of a considerable number of culms, especially if this occurs during the growing season (up to 60% death of new culms), but the plant usually recovers in the subsequent growing season.

Fish and Shrimp Farming in Water Bodies

Bamboos growing on the banks of water bodies contribute to an increase in aquatic life, including algae, fish, and shrimps. In Puerto Rico, despite the fact that bamboo litter is different from riparian inputs of the indigenous forest species bamboo displaces, the leaves decompose at similarly fast rates. There is also significant increases of filter-feeders (*Atya* spp.) and predators (*Macrobrachium* spp.) in bamboo pools. Data from experiments suggest a structural consideration in shrimp preference for bamboo substrata, in addition to the relative qualities of the leaves as food.

In India, villagers increasingly plant bamboo on water body margins. Even in new ponds established in degraded agricultural land from which the topsoil has been dug out for brickmaking, bamboo planted on the pond banks results in an increase in the fish population because of the leaf fall into the pond (which also reduces the amount of additional feed required). In Bangladesh, bottom mud from the ponds is dug out and used as a fertilizer for the bamboo clumps.

Wastelands

Bamboo is especially useful in converting wastelands, previously used only for grazing based on natural grass growth, to productive agriculture. Such lands after planting with bamboo have been successfully intercropped with soybean, groundnut, and maize, and the results have prompted several farmers to adopt this approach.

Because of the ability of bamboo to grow in poor soils, it has been used in dense plantations at close intervals to build up considerable woody and leafy biomass over ground, considerable leaf litter, and an extensive rhizome system. Together these contribute to a substantial build-up of organic carbon in the soil, an increase in soil microflora, increase in water holding capacity, and amelioration of soil pH from acidic towards neutrality. Bamboo soil is a commodity in some countries because of its fertility.

Agroforestry Systems

A variety of agroforestry systems exists for bamboo. It is common to see bamboo interplanted in fruit orchards in Thailand, and in tea estates in Bangladesh. Agricultural crops are mostly interplanted in the first 4 years of establishment of a bamboo plantation before canopy closure takes place. A diversity of crops are grown depending on the local agroclimatic condition, such as watermelon, soybean, sweet potato, sugar cane, and vegetables in the initial years. Within adult bamboo stands, the raising of pineapple, ginger, turmeric, and shade-tolerant varieties of sweet potato, etc. is undertaken in places where land is scarce. Continued agriculture is possible in situations where bamboo is the interplant.

A large number of mushrooms are also raised in China in bamboo stands which satisfy the fungi's need for humidity, shade, and a fertile bed. Key amongst these are *Dictyophonra tomentose*, *Plenrotus ostreatus*, and *Auricularia auricular-judoe*.

Medicinal plants are also interplanted with bamboo.

Interplanting with Trees

Bamboo is interplanted with conifers and broadleaf timber trees; in the latter case this is especially successful with trees with deciduous light crowns rather than heavy canopies. Interplanting of bamboo plantations and even dense bamboo plantations with casuarinas (and with eucalyptus) has been done successfully over the past two decades in western India.

Degraded Lands

Bamboo has proved to be ideal for making productive land degraded by removal of the clayey topsoil down to 3 m for producing bricks, down to the sandy layer. The bamboo that is grown interspersed and also on boundaries of farms acts as a shelterbelt. It prevents further soil erosion due to wind action, improves the microclimate at the crop level, improves moisture retention, and contributes to soil rebuilding by increasing organic carbon content from leaf fall, including an increase in water holding capacity. Increases in groundwater levels have been recorded using this method.

The method is increasingly being used following the initial successes, and has significant implications for the over 3 million ha of land that are degraded in India, and similar lands elsewhere.

Ecological Role of Bamboos in Forests

Bamboos grow naturally as a component of forests, often as the understory. Their role in deciduous forests in areas with a pronounced dry season appears to be more significant in that the understory bamboo results in a reduction in soil erosion. The association of teak with bamboo is a common one, with significant benefits in controlling soil erosion.

The gregarious flowering of bamboo has been said to be the reason for development of bamboo brakes and pure bamboo stands; it probably occurs when there is complete death of all tree saplings growing in the understory of the closed bamboo canopy.

Bamboo also appears to play a role in the protection and regeneration of forests. Detailed studies in Asiatic old-growth forests with a bamboo understory have also noted the influence of the life cycle of the bamboos on the age structure of tree populations, and the tendency of synchronization of tree regeneration following bamboo dieback following flowering.

In Costa Rica, oak (*Quercus*) forest regeneration is pulsed as a consequence of the synchronous life cycle of the *Chusquea* bamboos due to gregarious flowering. The *Chusquea* bamboo normally grows as the understory in the oak forests. In the steady state, the understory *Chusquea* clumps are small because of limited light conditions. If there are fires or gap creation through tree fall, the *Chusquea* rapidly responds to the increased availability of light, and grows up to become the local dominant species with a closed canopy under which saplings of trees now grow in a suppressed state because of the low light conditions under the bamboo canopy. When the *Chusquea* flowers gregariously and dies, the forest floor is more illuminated, and the already established suppressed saplings shoot up. The new generation of bamboo then grows under the newly formed tree canopy.

Bamboos in Fire-Disturbed Lands

Bamboos are one community that colonizes disturbed lands in the tropics especially after fire, because of its well-developed underground rhizome system. The widespread distribution of *Melocanna baccifera* throughout eastern India, Bangladesh, northern Myanmar, and Thailand and of species of *Thyrsostachys* in Thailand and *Schizostachyum* in Vietnam mainly occurs as secondary vegetation due to the destruction of tropical rainforest by fire, shifting cultivation, and logging.

As a result of shifting agriculture, huge expanses of bamboo forests have been established in Asia. In northeast India, bamboos constitute the major vegetation after slash-and-burn agriculture, and due to their adaptability and nutrient conservational role, they play a special role in succession. Shortening of the cycle when the bamboos are still the dominant species largely results in the reduction and often elimination of tree species, such that the fire-tolerant bamboos that survive through the underground rhizomes become the permanent dominant species. Repeated firing over short cycles results in almost pure stands of bamboo over vast areas in the hills. While shrubs and trees tend to grow more slowly, the competitive bamboos have rapid rates of dry matter production, continuous stem extension and leaf production during the growing period, and rapid phenotypic adjustments in leaf area and shoot morphology in response to shade. The competitive bamboos also store more nitrogen, phosphorus, and potassium than stress-tolerant shrubs and trees while the reverse is true for calcium and magnesium. Overall it is seen that bamboos follow a strategy of faster uptake and storage of essential elements and a quicker turnover to supplement the soil fluxes, thus efficiently dominating the stress-tolerant shrubs and tree species for a long duration. Overall, bamboos promote stability in the ecosystem through regulation of its functions like other competitive early successional species.

See also: **Tropical Ecosystems**: Bamboos, Palms and Rattans. **Tropical Forests**: Tropical Dry Forests; Tropical Moist Forests; Tropical Montane Forests.

Further Reading

Banik RL (2000) *Silviculture and Field Guide to Priority Bamboos of Bangladesh and South Asia*. Chittagong, Bangladesh: Bangladesh Forest Research Institute.

Farelly D (2003) *The Book of Bamboo: A Comprehensive Guide to this Remarkable Plant, its Uses and its History.* San Francisco, CA: Sierra Club Books.

Kumar A, Rao Ramanuja IV, and Sastry CB (eds) (2002) *Bamboo for Sustainable Development*, Proceedings of the 5th International Bamboo Congress and the 6th International Bamboo Workshop, Bali, Indonesia. Utrecht, The Netherlands: VSP.

Rao Ramanuja IV, Gnanaharan R, and Sastry CB (eds) (1990) *Bamboos*: *Current Research*, Proceedings of the International Bamboo Workshop, Cochin, India. Peechi, India: Kerala Forest Research Institute.

Rao Ramanuja IV, Rao IU, and Roohi FN (1992) Bamboo propagation through conventional and *in vitro* technologies. In: Baker FWG (ed.) *Rapid Propagation of Fast-Growing Woody Species*, pp. 41–56. Wallingford, UK: CAB International.

Rao Ramanuja IV and Sastry CB (eds) (1996) *Bamboo, People and Environment*, Proceedings of the 5th International Bamboo Workshop and the 4th International Bamboo Congress, Bali, Indonesia. New Delhi, India: International Network for Bamboo and Rattan.

Natural Stand Regeneration

J Huss, University of Freiburg, Freiburg, Germany

Introduction

There are two possible methods of forest stand establishment, namely natural and artificial regeneration. The process of natural regeneration involves the renewal of forests by means of self-sown seeds, root suckers, or coppicing. In natural forests, conifers rely almost entirely on regeneration through seed. Most of the broadleaves, however, are able to regenerate by means of the emergence of shoots from stumps (coppice) and broken stems. This type of forest reestablishment has obviously been important in temperate natural forests, as well as in tropical forests. A few broadleaves, such as aspen (*Populus tremula)*, Oriental plane (*Platanus orientalis*), and Oriental beech (*Fagus orientalis)*, can regenerate from root suckers, if their roots have been injured. Vegetative reproduction by means of sprouts and suckers merely renews the aboveground parts of plants and the old roots remain. Strictly speaking only sexual reproduction from seeds that results in a total natural renewal of the stand can be defined as regeneration.

In Europe regeneration by natural distribution of seeds was the standard means of forest renewal for thousands of years until overexploitation, in combination with intensive grazing, which has taken place since the late Middle Ages, led to a gradual depletion of the forests and severely inhibited regrowth. At the beginning of the nineteenth century, extensive afforestation took place in Central Europe by means of sowing and planting, predominantly with conifers. Since then, natural regeneration has been limited to the renewal of beech (*Fagus sylvatica*) and its main associates, such as ash *(Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*), and wild cherry (*Prunus avium*).

At the end of the nineteenth century, however, an early back-to-nature movement brought about an increasing interest in the natural regeneration of managed forests, and the creation of a variety of silvicultural systems such as shelterwood strip, strip and group, and wedge system. Most of these systems were geared towards the creation of favorable ecological conditions for the production and germination of seeds, as well as adequate growing conditions for seedlings and saplings. The new ecological movement towards nature-orientated, nature-based, or seminatural silviculture and forestry, which began in the 1980s, has once again revived an interest in natural regeneration.

Planting nevertheless will remain the dominant regeneration method for various reasons, such as the conversion of species, the need for suitable provenances and ease of operation.

Nature-orientated forestry is based on the adaptation of natural dynamics as much as possible, and mimics natural regeneration processes in particular.

Therefore, it is necessary to highlight some of the ecological factors essential to the regeneration process in natural forests, before natural regeneration in naturally managed forests can be discussed.

Natural Regeneration in Natural Forests

Regeneration in natural forests is very much influenced by abiotic stress conditions, such as drought, or catastrophic events like fires, storms, snow, and ice (**Figures 1** and **2**).

On sites with medium to good nutrient and water supplies, the following situations are possible:

- Landslides, fires, and floods create large bare areas, which are colonized by the seeds of pioneer species distributed by the wind, including poplars, willows, and birches. According to succession models, this initial forest cover acts as a nurse crop, improving soil and ecological conditions, paving the way for intermediate successional stage species such as Norway spruce (*Picea abies*) and sycamore (**Figures 3** and **4**). These intermediate species will in turn gradually be replaced by shade tolerant species such as hornbeam (*Carpinus betulus*), beech, and silver fir (*Abies alba*).
- On storm-felled stands, a mixture of pioneer and late successional species may develop together, if advance regeneration already exists beneath the original stand, which is usually the case.

Figure 1 Small-scale storm damage from 1999 in the natural beech dominated forest Suserup, Denmark, which has not been managed since about 1850.

Figure 2 Large-scale storm damage from 1990 in beech/Norway spruce stands (Sobernheim, Germany).

Figure 4 Birch acting as a nurse crop for Norway spruce (South Sweden).

Figure 3 Natural regeneration of birch, Scots pine and a few oaks in a 1985 storm-damaged area which does not need much enrichment (Hesse, Germany).

- In the absence of the above situations, smaller gaps are created by individual old trees gradually dying. These smaller gaps provide conditions under which shade-tolerant species, such as beech, silver fir (*Abies alba*), and yew (*Taxus baccata*) can develop, rising up through the canopy and eventually filling the gaps.

On extreme sites (very dry, wet, or cold), however, these general successional trends do not reach any definitive climax stage, as only stress tolerant species are able to grow on them.

Tree species employ different strategies in order to colonize ground effectively. Some of the more important characteristics of a number of selected species are illustrated in **Table 1**.

Flowering

Flowering begins early in the very light demanding pioneers and decades later for most of the shade-tolerant species. Not all species, however, follow this strategy, e.g., hornbeam flowers relatively early. Pioneers usually flower on an almost annual basis. In the case of intermediate and late successional species in particular, flowering is induced by the weather conditions of the preceding summer, and possibly even two growing seasons earlier. This has only recently been discovered for beech. Dominant individuals with large crowns begin flowering earlier and flower more abundantly.

Seed Production

Seed production requires favorable weather conditions during flowering and the development of seeds, as well as the absence of damaging insects. Pioneers, in general, produce more and lighter seeds. Only the oaks (*Quercus* spp.) do not follow this rule. Storage conditions become important immediately after ripening of the seeds. These are usually released from the tree, distributed by wind or animals and deposited on the ground, where they can germinate. Once on the ground, seeds are subject to predation by mammals, birds and insects, as well as fungal attack. Seed survival rates are higher on mineral soils after uprooting of trees by storm. Survival rates are even higher when seeds are buried in the soil, for example by wild boars (*Sus scofra*), 'sown' by jays (*Garrulus glandarius*) or stored in the soil by mice. Therefore, storage conditions are important in determining the proportion of seeds that eventually germinate.

Germination

Germination of the seeds of pioneer species begins immediately upon deposition on the ground. Pioneer seeds have no nutrient reserves and require subsoil conditions that permit easy penetration and access to water, such as mineral soils. The seeds of most other species have a chilling requirement and only germinate after winter has ended and the conditions are again suitable for seedlings to grow. Such seeds exhibit a period of dormancy, which is broken by a change of temperature. Oak again is an exception. Provided that temperatures are adequate in late autumn, the acorns generally develop a radicle, in order to secure a supply of water.

Germination is induced by an adequate temperature and humidity. In contrast to some species in the tropics light is not necessary for the first phases of germination of the species in the temperate zones. Direct light becomes essential once the cotyledons have spread and photosynthesis starts.

Following germination, the further development of the seedlings is very much dependant on the following ecological conditions:

- The water supply becomes a vital factor shortly after germination. Seeds that have germinated in

Table 1 Seed production strategies of some representative tree species

Species	*Light requirement*	*Succession type*	*Beginning of seed production (age in years)*	*Weight of seeds (mg)*	*Agent of seed dispersal*
Populus tremula		Pioneer	10–15	<0.2	Wind
Betula pendula	Very light demanding		10–15	0.2	
Pinus sylvestris			15–20	6	
Fraxinus excelsior			20–30	56	
Quercus petraea		Long-lived pioneer	40–50	3030	Birds, rodents
Acer pseudoplatanus	Light demanding		15–25	125	Wind
Picea abies	Intermediate		30–40	8	
Carpinus betulus	Shade-tolerant	Late successional species	15–20	33	
Fagus sylvatica	Very shade tolerant		40–50	192	Birds, rodents
Abies alba			40–60	44	Wind

leaf litter or needles regularly die during dry periods, which are particularly frequent in European regions with a continentally influenced climate. In mountainous areas, a maritime climate usually prevails and regeneration tends to be more successful. Seedlings on mineral soils tend to suffer fewer losses, as their roots can extend into the lower soil horizons and the water supply. Decayed coarse woody debris acts as a sponge, making it a perfect substrate for seedlings to grow on and is of great relevance in natural forests. Norway spruce, in particular, profits from the presence of dead wood (**Figure 5**).
- The further development of the young trees is subject to the light conditions. In open areas, light-demanding pioneers are highly competitive in the early decades because of their fast growth and will dominate the stands at the establishment stage. Under the shelter of old trees, however, the shade tolerance of the seedlings will determine their ability to survive. Even young shade-tolerant plants die if the canopy remains closed, however. The greater the nutrient reserves stored in the seed, the longer a seedling will be able to endure in a waiting position.
- Various biotic stress factors may decimate the seedlings from the moment of germination. They can become infected by fungi. Mice, birds, and snails often reduce the numbers sharply (**Figure 6**). Saplings are very susceptible to browsing and bark peeling by larger mammals, such as roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) (**Figures 7** and **8**). Under the natural conditions prevalent in times past, the density of these animals was probably not very high and browsing pressure not too severe. There is, however, intense debate over the ecological impact of megaherbivores on the forest cover prior to large-scale interference by humans.

Figure 5 Regeneration of Norway spruce seedlings on coarse woody debris (North Sweden).

As a general conclusion the natural regeneration of natural forests is steered by a great variety of abiotic and biotic factors, and their interactions. Undoubtedly, natural forests exhibit a high degree of site adaptation. The characteristics of a forest type will mirror the prevailing site factors, such as climate and soils. Additionally, the soil mosaic often leads to a further differentiation of the tree species distribution. The aforementioned 'catastrophes' may pave the way for the early stages of pioneer forests, which will evolve towards later successional stages over the course of centuries. In many cases, a form of climax forest may never be achieved, as the process is set back by further catastrophes. Even in the climax phases the species composition may vary purely as a result of chance, depending on, for example, which species produces seed in a given year and develops on a certain spot in the forest, whereas in another year a different species may have regenerated and conquered the available space.

Figure 6 Bark peeling by voles destroying beech seedlings and saplings (Zwiefalten, Southwest Germany).

Figure 7 Browsing by red deer heavily affecting the growth of young beech (Kempfeld, Germany).

All successional models, therefore, only show a general direction leading to later stages of development.

Natural Regeneration in Managed Forests

The management of forests generally aims towards production and/or service goals. This is never the case for purely natural forests, however. Nature-based silviculture seeks to make use of natural forest dynamics to as great a degree as possible, to meet both ecological and economic targets, yet aims to avoid or minimize the disadvantages.

There are several reasons both for and against the practical application of natural regeneration as a means of stand establishment (**Table 2**).

Although some of the advantages of natural regeneration are very appealing, many of the disadvantages provide serious practical obstacles to large-scale natural regeneration (**Figure 9**). Included in the disadvantages are a lack of experience, shortage of qualified and motivated personnel and, of course, impatience – the greatest problem in forestry.

Preconditions

Apart from the sociological and organizational constraints mentioned above, some preconditions must also be met in order to make use of natural regeneration processes.

During the afforestation period of the last two centuries in Europe, which continues to this day,

Figure 8 Browsing of Norway spruce by roe deer. The saplings start to grow normally as soon as they exceed the browsing height (Grafing, Germany).

Table 2 Arguments for and against using natural regeneration in practice

	Comments
Arguments for	
Preservation of site-adapted autochthonous populations	Reduced risk of receiving the wrong provenances from private nurseries.
High degree of adaptation of young plants to the site mosaic	Effective use of microsite differences by the species in mixed stands.
Undisturbed growth of young plants	Development of a regular root system; no deformations following planting, a particular problem on heavy soils.
Saving on high investment costs of plant material and planting procedures	Remarkable savings can be made in the establishment phase. Natural regeneration may require spending on site preparation and fencing, however.
Possible production of wildlings	Uses of site adapted wildlings for: • filling in incomplete young stands • transfer of plants to other regeneration areas • production of transplants in the nursery.
Increased number of potential crop trees for selection at later tending phases	Good sapling quality due to the high density of individuals and the intensive natural differentiation in the young stands; often results in savings on tending costs.
Arguments against	
Dependence on seed production and volume of seeds produced	Requires economic flexibility on the part of forest enterprises because of the irregularity of mast years
Irregular densities of natural regrowth and additional costs of filling in	Risk of reduced sapling quality, especially bordering on gaps. Necessity of filling in gaps in certain areas and of lowering the densities at other places. Difficulties of surveying naturally regenerated young stands, resulting in improper tending measures.
Greater risk to seedlings and saplings	Extended period of exposure to fungi, insects, birds, rodents, and game, especially in the seedling phase, not to mention increased competition with ground vegetation.
Technical problems involved in felling old trees over regrowth	Natural regeneration mainly takes place under the shelter of old trees. The several cuttings necessary to remove the old trees result in damage during harvesting and extraction procedures. Removal of damaged individuals is necessary.
Extended tending efforts/expenditure in the thicket/pole stage	The following measures, not required in the case of plantations, are necessary for the: • reduction of high plant densities • correction of stocking irregularities • elimination of excessively vigorous and coarse trees (wolves) • elimination of unwanted mixture trees.
Extended duration of the regeneration period	The length of time between seed production and the end of the tending process is normally much longer than in plantations. This presents problems of continuity for forest enterprises.

Figure 9 Natural regeneration of different species often early needs tending procedures.

conifers, in particular, have often been planted on the wrong sites. Unfortunately, some of them now regenerate freely and have to be removed at great expense. One of the most important examples of this is the natural regeneration of Norway spruce on compacted soils, with anaerobic subsoil conditions, for example, pseudogleys. Such stands are often prone to storm damage (**Figures 10** and **11**). To avoid further species selection mistakes, a site classification survey would prove to be an invaluable source of basic information.

The use of unsuitable provenances in years gone by, due to a lack of knowledge of the importance of genetically adapted plant material, with respect to abiotic and biotic site factors, would appear to be just as serious a problem. Conifer provenances such as Norway spruce from the lowlands have been planted at high elevations, where they are susceptible to ice and snow break (**Figure 12**), and Scots pine (*Pinus sylvestris)* and European larch (*Larix decidua*) transferred from continentally influenced regions into maritime areas suffer from fungal attacks.

Significantly fewer mistakes have been made with broadleaves because of their lower economic value.

Figure 10 Norway spruce with a flat root system on a shallow pseudogley soil after having been uprooted by a storm (Schaidt, Germany).

Figure 12 Norway spruce from the lowlands suffering from storm, ice, and snow at high elevations (Freiburg, Germany).

Figure 11 Beech, also with a flat root system, uprooted by storm on a pseudogley (Schaidt, Germany).

In order to be successful, it is important, therefore, that there is an adequate distribution of site-adapted tree species in the forest stand to be regenerated, or in its vicinity.

Active Promotion of Natural Processes

In order to minimize the disadvantages and the problems associated with natural regeneration, the following procedures may be helpful and are used in practice.

Promoting seed production As has already been mentioned, some pioneer species flower annually. Most other trees, however, flower irregularly. Their seed production is highly dependent on the prevailing climatic conditions, as well as conditions in the preceding years, and cannot, therefore, be influenced by the forester. However, vigorous dominant trees with large crowns and sufficient growing space begin to flower earlier, and they do so more frequently and more intensively. Early and continued crown thinning will improve seed production effectively and sustainably, but requires continuity and a great deal of staying-power. Often thinnings are neglected, especially in the case of most broadleaves (**Figure 13**).

It has been shown, however, that dominant individuals of certain species, including beech and oak, increase seed production when their crowns receive more light. This is true even after very late crown thinning. The process of natural regeneration, therefore, normally begins a few years in advance of seed production, with an intensive crown thinning of the dominant individuals in the stand.

Influencing tree species proportion Tree species distribution and proportion can be influenced using the following procedures.

Choice of an appropriate silvicultural system Silvicultural systems are geared towards creating favorable ecological conditions for particular species, depending on its demands (**Figures 14–16**). Ensuring protection against the main wind direction, as well as providing an infrastructure for felling and extraction, with an adequate road and timber extraction line system, are further components.

Some silvicultural systems are listed in **Table 3**, according to the ecological needs of the respective tree species.

Generally, natural regeneration of intermediate and late successional species is more important in Central Europe. Therefore, stronger emphasis is laid on these systems compared with regeneration of light demanding species on bare land.

Choice of mast year Flowering and fruit development can be observed and inventoried during the growing season. In a mast year, natural regeneration is usually initiated by opening the canopy slightly and, if necessary, preparing the soil. If the sheltering stands, or those nearby, contain the desired species, the initial procedures can begin once the trees start to produce seed.

Regulating the light regime In the event of two or more tree species germinating, with each likely to establish themselves, it is possible to manipulate their proportions by regulating the light regime within the

Figure 13 Poorly thinned beech with very small crowns will not be able to produce seeds later on (Tuttlingen, Germany).

Figure 14 A relatively open uniform shelterwood stand enables young Scots pine to grow in the initial years but has to be removed fairly early to allow sufficient light to reach the young growth (North Sweden).

Figure 15 Beech being regenerated in the group shelter system, protected for many years against late frost and drought (Kelheim, Germany).

forest stand. This is done by varying the intensity of cuttings. Under the canopy of old trees the suppression of young growth of light-demanding species is possible. The seedlings may even disappear because of a lack of light. On bare ground or in larger gaps this problem will not arise, however. The mixed montane forests common in Central Europe provide a good example of the way of regulating the light conditions according to the needs of the species. These forests consist mainly of three species: silver fir, beech, and Norway spruce. Very gradual, light shelterwood cuttings will maintain relatively dark conditions within the stand, which results in the dominance of the very shade-tolerant silver fir. Larger openings favor beech. More dramatic openings in the canopy are required in order to promote Norway spruce (**Table 4**). To increase the proportion of sycamore, a further component of these mixed montane forests, gaps must be made and enlarged further after a few years.

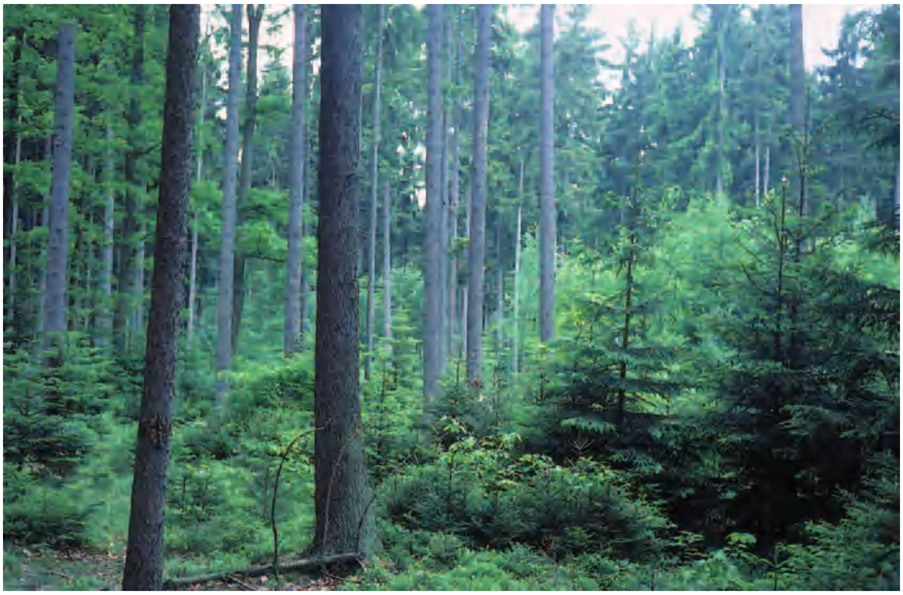


Figure 16 Silver fir and Norway spruce saplings naturally regenerated in a group shelterwood stand (Kelheim, Germany).

Table 3 Main silvicultural systems with regard to the ecological requirements of forest tree species

Silvicultural system	*Size of opening*		*Ecological type*	*Tree species*[a] *(examples)*	*Comments*
Clear-cut	Large	>5 ha	Pioneer	*Betula* spp., *Populus* spp., *Alnus* spp., *Salix* spp.	No practical importance in Central Europe
	Small–medium	0.5 – 5 ha		*Pinus sylvestris*, *Larix decidua*	Common traditionally
Gap/strip felling	Small	0.05–0.5 ha <100 m wide	Intermediate	*Picea abies*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *A. platanoides*, *A. campestre*, *Quercus petraea*, *Q. robur*, *Prunus avium* (*Pinus sylvestris*)	Shelterwood system important traditionally. Transition to small-scale free mixture of the three adjacent systems becoming increasingly important.
Uniform shelterwood		Regular crown openings in large stands	Intermediate/ late successional	*Fagus sylvatica*, (*Quercus petraea*), *Tilia* spp., *Carpinus betulus*	The speed with which the crown cover is opened can be adapted to suit the demands of the species.
Group shelterwood; combination of shelter and strips		Groups of >30 m in diameter	Late successional	*Abies alba*, *Fagus sylvatica*, *Picea abies*	Beech should be kept under shelter for 15–20 years, oak for only 5 years.
Selection		Single tree removal		*Abies alba* (*Fagus sylvatica*)	Special site conditions necessary, therefore restricted to specific areas.

[a]Tree names in brackets indicate species of minor importance within the system mentioned.

Another important example is beech, with its many potential admixed tree species. Beech will outcompete almost every other species, including oak (*Quercus petraea* and *Q. robur*), ash, and sycamore, if the canopy is not opened following the initial stand establishment phases. The only exceptions are even more shade-tolerant species, such as yew and silver fir. This has proven to be a very common problem.

Of course, it is important to bear in mind that, flexibility with regard to varying the tree species

Table 4 Effect of the rate of opening of canopy on the species distribution of the regrowth. The regeneration period begins when the initial openings of the canopy are made in order to encourage the development of seedlings and ends when the last tree is removed

Rate of progression of shelterwood treatments		*Dominance of species*	
Very slow	>50 years	Silver fir	*Abies alba*
Slow	~25 years	Beech	*Fagus silvatica*
Frequent and gentle	~15 years	Norway spruce	*Picea abies*
Cutting gaps and enlargement	~5 years	Sycamore	*Acer pseudoplatanus*

Table 5 Silvicultural means of improving conditions for the storage of seeds in the forest floor, for germination, and for the first phases of establishment

Procedure	*Specification*	*Description of procedure*	*Comments*
Conversion of surface layers not conducive to natural regeneration	Opening of the canopy in order to stimulate soil activity by improving the temperature and water supply	Removal of all individuals that create heavy shade and intercept precipitation, i.e., dominant trees with large crowns, as well as intermediate and suppressed trees	Common starting procedure of many silvicultural systems. Slow, long-term response. Possible development of competing ground vegetation if employed too rigidly.
	Soil preparation to promote soil activity	Breaking up the uppermost organic soil layers and mixing with mineral soil	Necessary in areas with thick raw humus layers or inhibited mineralization.
	Mineral fertilization to promote soil activity	Distribution of limestone dust or compound fertilizer across the whole area; occasionally combined with opening of the canopy and soil preparation	On poor or acid soils, this is only to be recommended if carried out several years in advance of the start of regeneration. Promotes the development of nutrient demanding species, as well as increment growth of the old trees.
Removal of surface layers not conducive to natural regeneration	Exposing mineral soil by removing surface layers in strips or patches (Figs 18 + 19)	Use of small tractors with soil preparation fittings	Important means of improving the germination rate, especially of beech and Scots pine. Growing concerns over soil compaction as a result of driving in the stands. Increasing importance as a measure for mitigating soil acidification.
	Burning of surface layers	Mainly the result of accidental forest fires; controlled burning also possible	Improves establishment conditions, especially for pioneers. Mostly in dry areas, with increasing importance worldwide.
Removal of competing ground vegetation	Removal of ground vegetation in strips or patches prior to germination	Use of small tractors with fitted weeding equipment	Gaining importance with increasing problems with the development of grass cover.
		Herbicides	More and more herbicides have been banned as a result of environmental/ecological concerns.

composition is only possible if the desired species have regenerated naturally.

Improving the seed storage, germination and early development conditions of the young plants In managed forests, the soil surface often fails to provide favorable conditions for storage, germination, and plant establishment. This is true of 'normal' conditions, as well as special climatic situations, which arise only periodically. There are frequently neither sufficient volumes of coarse woody debris nor large enough areas of mineral soil to support the regeneration process. It may, therefore, be necessary to promote it by employing one or a combination of the procedures mentioned in **Table 5**. These measures are very much specific to each site, however (**Figures 17–19**).

The following developments have taken place in Central Europe in the last two to three decades, with regard to the procedures mentioned in **Table 5**:

- The intensification of thinnings has led to better crown development in the stands of a number of forest enterprises. Preparatory fellings have tended to become less important in certain areas.

- During the last two decades, an increase in seed production has been very obvious for most tree species. Therefore, foresters no longer rely on isolated mast years, as in the past.
- Soils have recovered remarkably from centuries of overuse in the production of timber and firewood, as well as litter extraction. Raw humus layers have become rare. To date, nitrogen inputs from pollution (NH_4 from agriculture and NO_X mainly from traffic) have had an advantageous effect, in spite of increasing acidification. The necessity of soil preparation has, therefore, decreased in some areas.
- Compensatory fertilizing has been used widely as a means of combating acidification. A side effect of this is that, more demanding species are favored in the regeneration process.

Figure 17 Scarification of the soil to improve soil activity and promote natural regeneration (Fuhrberg, Germany).

Figure 19 Mineral soil allows for improved germination of Scots pine (North Sweden).

Figure 18 Line plowing to promote Scots pine regeneration (Sellhorn, Germany).

- Ground vegetation has evidently profited greatly from the rehabilitation of soils and nitrogen inputs, seriously impeding natural regeneration in many places. The problematic species include grasses, such as *Calamagrostis epigejos* and *C. villosa*, *Avellana flexuosa*, *Carex brizoides*, as well as climbers and shrubs including *Rubus fruticosus*, *R. idaeus*, *Clematis vitalba* and *Prunus serotina*. This tendency appears set to continue (**Figures 20** and **21**).

Minimizing biotic damage Seeds, seedlings, and young plants are very prone to damage caused by snails, rodents and game. Snails feed on seedlings shortly after germination, but will not harm them after the woody tissue has formed. Snails profit from the humid conditions under the shelter of the canopy.

Mice (Microtinae) live in grass cover and prefer warm open areas. They feed on the bark of hardwood saplings and are able to destroy whole groups of them up to the thicket stage. Regeneration under

Figure 20 Grasses (in this case *Calamagrostis epigeios)* increasingly cover large areas and are a serious obstacle to natural regeneration (Berlin, Germany).

Figure 21 Bramble (*Rubus fruticosus)* profits from nitrogen input as well as the recovery of soils, and increasingly competes with young forest plants (Saxony, Germany).

the canopy normally brings about a decline in the ground vegetation, resulting in the loss of their habitat. Unfortunately, keeping the canopy closed for a longer period of time is not possible in many stands. This also requires long-term planning and will favor shade-tolerant species, such as beech.

Game, the omnipresent roe deer, in particular, but also red deer, fallow deer (*Cervus dama*), and some other locally distributed species, such as mouflon (*Ovis ammon musimon*) and chamois (*Rupicapra rupicapra*), are the greatest hazard to young plants. Broadleaves are especially susceptible. Roe deer, for example, prefers rare species such as occasional hardwoods in conifers as well as specific hardwoods like ash and sycamore in beech. Some of these trees have become almost extinct in certain areas because of the high browsing and debarking pressure, and damage caused by fraying. In general, there has been a widespread decline in the species mix and a tendency towards conifer monocultures. As the hunting lobby in almost all countries of the temperate zones has succeeded in resisting a

Figure 22 Fencing in order to promote growth, especially of endangered broadleaves, is often inevitable – and very expensive.

Figure 23 Individual tree protection as a possible method for the promotion of a small number of endangered plants.

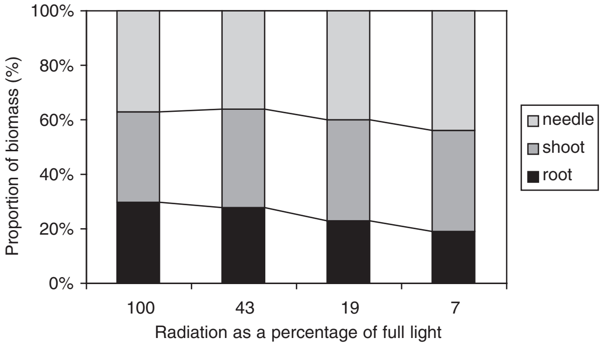


Figure 24 The change in biomass proportion (%) of needles, shoots, and roots of 4-year-old Norway spruce (*Picea abies*), after growing three years in a shading experiment. Apart from the general reduction of biomass, the additional reduction of the root biomass was disproportionately great. Young plants may, therefore, be greatly endangered in the event of water stress and often die in dry periods. (From Huss J 1971 *Untersuchungen über die Wirkung von Beschattung und Düngung auf das Wachstum junger Fichten*. Habilitation thesis, University of Göttingen, Germany.)

reasonable reduction of the high game stocks, fencing or single tree protection is the likely means of protection in many cases (**Figures 22** and **23**).

Securing a species mixture The canopy of an old stand provides shelter against late and early frosts, high temperatures, and desiccation. The regeneration of shade-tolerant tree species susceptible to these climatic stresses therefore normally takes place under the shelter of the old trees. The longer the regrowth is kept under shelter, however, the greater the likelihood of not only the light-demanding components of the mixture of trees dying or being overgrown, but also the risk of the shade-tolerant species suffering as a result of the low irradiation. Unlike in the tropics, all tree species found in Europe exhibit the greatest biomass production under full light. Under a closed canopy, biomass production and growth in diameter and height are reduced. For instance the biomass production of young Norway spruce was reduced to less than 10% when the global radiation was only 7%. Moreover biomass allocation (**Figure 24**), as well as stem and crown form, may also be affected **Figure 25**. The degree of canopy closure is regulated according to the development phase of the young plants (**Figure 26**).

Combining and optimizing all the different possible effects and goals of management, such as excluding ecological stress conditions on the one hand, and regulating growth and the species mix on the other, is a great challenge for the forester.

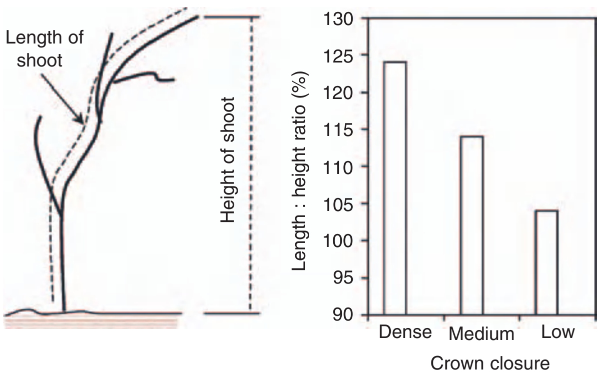


Figure 25 Changes to the stem form of beech wildings (*Fagus sylvatica*) after 9 years growing under the shelter of differentially thinned 55-year-old Norway spruce (*Pinus abies*). The 1–3-m high beech saplings show significant differences in the degree of bending, depending on the density of the canopy, as influenced by the thinning variation. Saplings in deep shade are bent to a much greater extent, and are less stable because their slim stems are more susceptible to snow damage, or even heavy rain.

The Future Role of Natural Regeneration in Forest Practice

It has been shown that the rehabilitation of the soil, as well as increased seed production rates, have improved the potential for natural regeneration over recent decades. The main obstacle to an increase in the use of natural regeneration, however, remains high game densities. There are some examples in Germany where the deer population has been successfully reduced, resulting in an overwhelming

Figure 26 Seedlings and saplings (here Norway spruce) show uneven growth according to varying light conditions in unevenly opened canopy (Gaildorf, Germany).

Figure 27 Rowan and other rare species return when protected by fences or where the deer numbers have been reduced (Hinterzarten, south-west Germany).

recovery of the forest by means of natural regeneration, including species very sensitive to browsing and, consequently, quite rare. Rowan (*Sorbus aucuparia*) is an illustrative example in this regard (**Figure 27**).

Ecological and silvicultural problems aside, sociological and economic factors have, in a way, contributed to the increased acceptance of natural regeneration and its practical application. Three such factors are:

1. The 'green' movement amongst the public, which favors all procedures promoting natural forms of management.
2. Forestry in Central Europe has reached a phase in its development where there is a trend away from afforestation, towards nature-based forestry. Most forests are being reconstructed, and provide the opportunity for more demanding species to regenerate under the shelter of existing stands.
3. Forestry is suffering from the same problems as all other industries within the primary sector: falling revenues from the production of raw materials and a steady increase in the costs. All forest enterprises have, therefore, been forced to reduce their costs. Natural regeneration is one possible way of achieving this.

See also: **Afforestation**: Stand Establishment, Treatment and Promotion - European Experience. **Ecology**: Natural Disturbance in Forest Environments. **Genetics and Genetic Resources**: Forest Management for Conservation. **Silviculture**: Coppice Silviculture Practiced in Temperate Regions; Natural Regeneration of Tropical Rain Forests. **Sustainable Forest Management**: Overview. **Tree Physiology**: Physiology of Sexual Reproduction in Trees; Physiology of Vegetative Reproduction.

Further Reading

Burschel P and Huss J (1997) *Grundriß des Waldbaus*, 2nd edn. Berlin: Parey Buchverlag.

Huss J 1971 *Untersuchungen über die Wirkung von Beschattung und Düngung auf das Wachstum junger Fichten*. Habilitation thesis, University of Göttingen, Germany.

Matthews JD (1989) *Silvicultural Systems*. Oxford, UK: Clarendon Press.

Smith DM (1986) *The Practice of Silviculture*, 8th edn. New York: John Wiley.

Forest Rehabilitation

D Lamb, University of Queensland, Brisbane, Australia

Introduction

Rehabilitation is a form of reforestation that differs from more traditional approaches because it seeks to achieve outcomes other than just timber production. As well as creating a supply of goods such as timber, many rehabilitation projects aim to achieve functional changes and re-establish the ecological processes that once supported the original forest ecosystems. These changes then increase the supply of ecological services from a forest such as increased topsoil organic matter and fertility, enhanced hillslope stability, or improvements in watershed protection. Most rehabilitation projects try to do this by restoring some, though not necessarily all, of the original biodiversity (unlike ecological restoration which seeks to restore all of the plant and animal communities that were once present in the original forest).

One of the potential advantages of rehabilitation is that it can provide greater benefits for humans living in and around the new forest than most of the more traditional forms of reforestation. This may be through the socioeconomic benefits the forests provide from new goods such as timber, fruit, nuts, or medicinal plants leading to improvements in human livelihoods. Alternatively, it may come from the environmental and cultural benefits generated (**Table 1**). Finding the right balance between improving human well-being and improving the ecological integrity is difficult. This is because there may be more than one stakeholder involved at a particular site and each may have different priorities. Rehabilitation therefore represents a particularly difficult form of silviculture.

Some say it is too difficult – we should simply separate these different objectives and do each on different parts of the landscape. That is, we should continue to carry out intensive commercial production on those parts of a landscape that are suitable and protect or restore biodiversity in other, residual areas less suited for production. This view ignores the fact that the world's landscapes are being simplified and homogenized as agricultural areas have spread and natural forests are lost. Many now question the sustainability of these agricultural landscapes. Indeed, the provision of ecological services from new forests to ensure the sustainability of some agricultural landscapes may be a far more valuable outcome than any goods these forests may supply.

What is needed, therefore, is a more sophisticated array of silvicultural options to match the range of socioeconomic and ecological dilemmas that land managers are facing. This does not mean that traditional forms of reforestation are superseded. Indeed, in many situations they may continue to be the predominant method by which cleared land is reforested. What it does mean, however, is that they should not be seen as the only way in which reforestation is undertaken.

This article reviews some of approaches that have been developed to achieve these purposes. It also considers the problems limiting the application of these and some of the issues involving scaling up from these site level interventions to reforesting at a landscape scale.

Table 1 Goods and services provided by forest rehabilitation

Goods	*Ecological services for*	
	Individual landowner	*Community*
Industrial timbers	Hillslope stabilization	Biodiversity
Firewood	Improved soil fertility	Watershed protection
Fruits	Windbreaks and shelter	Hillslope stabilization
Gums and resins	Aesthetic benefits	Clean water
Animal protein	Cultural benefits	Carbon sequestration
Medicinal plants	Recreational benefits	Aesthetic benefits
Other food crops		Cultural benefits
		Recreational benefits

A Typology of Rehabilitation

Rehabilitation may take place under two circumstances. One is where deforestation is not complete and where logging or agricultural clearing has left some residual forest. This residual forest may consist entirely of remnants of the original forest or it may also include regrowth that has developed since the disturbing event occurred. The other circumstance is where deforestation has been complete and only grassland or shrublands persists. In either situation the prevailing conditions may prevent natural recovery occurring as quickly as is needed meaning that some form of silvicultural intervention is needed. These two conditions generate alternative silvicultural options. These options are summarized by the typology in **Table 2**. Typologies such as this necessarily disguise the fact that, in practice, these alternatives sometimes merge or overlap.

Some Residual Natural Forest Still Present at Site

Protect residual forest If a significant stocking of trees remains at the site the most obvious silvicultural

Table 2 A typology of forest rehabilitation approaches

1. Some residual forest still present

- Protect forest and allow natural recovery
- Protect and manage forest to encourage favored species
- Protect forest and enrich with commercially desired species (e.g., timber trees, fruit trees, etc.)

2. No existing forest remains: canopy trees must be replanted

2.1 New plantations with a more or less constant canopy tree composition

- Monoculture of tree species with preference given to native species
- Mosaic of tree monocultures across the landscape using mostly native species
- Tree monoculture with underplantings or inter-row plantings of economically or socially useful agricultural crop plants
- Multispecies tree plantations

2.2 New plantations where the composition of the canopy tree species changes over time (semisuccessional plantings)

- Nurse trees (native or exotic species) used to establish commercial tree species plantations option is to simply protect the site from further disturbances (such as recurrent fires, agricultural clearing, logging, firewood collection, or the harvesting of non-timber forest products) and allow natural successional processes to re-establish the forest. These successional processes might involve regeneration from coppice, seeds, or seedlings already present at the site or from seeds of species dispersed into the site from other nearby forest patches. By providing this protection biodiversity is conserved and forest development occurs without further cost. These species-rich forests are then able to supply a variety of goods and ecological services.

But protection can be difficult. Fire exclusion, for example, can be hard to achieve without a well-established fire suppression organization, particularly if wildfire is unchecked in neighboring lands. Nonetheless, there are many examples of where protection of residual forests has allowed substantial forest recovery over large areas. In time selective harvesting of timber or non-timber species can become possible depending on the density of individuals of these species. The primary advantage of this approach is its low cost while the main disadvantage is that recovery may take some time.

Protect and manage forest to encourage favored species A variant of this first option is to intervene silviculturally to promote the regeneration and growth of some of the more commercially attractive species present within the protected forest. Possible interventions may take the form of weeding or tending to remove competing species or thinning to reduce competition between trees of commercial species or to remove individuals with poor form or vigor. Pruning of these target species may also be commercially advantageous.

Protect and enrich with commercially favored species Heavy logging sometimes leaves a residual forest with only a limited stocking of commercially attractive species although many other species may still be present. Under these circumstances the abundance of seedlings or young trees of the more commercially attractive species (e.g., timber trees, fruit trees, medicinal plants in the understory, etc.) may be low. However, it may be possible to accelerate the recovery process by enriching the forest with these species to improve its commercial (or social) value. In tropical forests this usually requires that seedlings of the commercial species are planted as groups in clearings or in lines cut through the forest. In both cases overhead canopy cover must be minimized to avoid seedlings being suppressed. The density of these introduced seedlings is commonly less than 100 trees per hectare. This means the cost of treatment is much lower than clearing the residual forest and replanting with a monoculture.

Experience with enrichment planting in the tropics has been mixed because weed control is often difficult to maintain. Nonetheless, the technique remains an important option because of the large areas of logged-over forest that have accumulated that are depleted in commercially attractive species.

No Existing Natural Forest Remains at Site: Canopy Trees Must Be Replanted

The advantages of the techniques described above are that they conserve plant biodiversity and the ecological services provided by these biota. But different approaches are needed where deforestation is more complete.

New plantations with a more or less constant canopy tree composition

Plantation monocultures of tree species with preference given to native species Most traditional plantation systems are monocultures. Most also involve fast-growing, exotic species chosen because of the attractiveness of their timber properties and their tolerance of a wide range of site conditions. Most of these species also come as a well-developed silvicultural package with seed from seed orchards, a nursery methodology, and a set of postplanting management prescriptions covering fertilizing, thinning, and pruning. These monocultures are highly suited for intensive production and are the favored approach in most large-scale industrial plantation systems.

Some of these monoculture plantations also provide certain ecological services but their capacity to do so may be limited if the species are shallow-rooted or an understory is absent. Some of these disadvantages can be overcome by establishing leguminous groundcovers for nitrogen fixation or to protect surface soils from erosion.

Monocultures of indigenous tree species can offer some advantages over those provided by monocultures of exotic species provided they can still grow at what might have become a rather degraded site. Although they might still make only a minor contribution to regional biodiversity protection compared with, say, a regrowth forest they are still likely to be more attractive to at least some wildlife than plantations of exotic species. This attractiveness may be enhanced by the structural complexity inherent in the different age classes that develop as plantation establishment continues over time. And although native species often grow more slowly than the more common exotic species, they may also have higher market values. This means that timber volume increments may be lower but net value increments may be higher.

Mosaic of tree monocultures across the landscape using mostly native species Additional landscape heterogeneity can be created if a mosaic of monocultures is created across a region using different native species in each plantation wherever this is ecologically possible. In this case, species are matched carefully with their optimal sites. For example, species preferring moist sites are planted in valley floor positions while more hardy species are established on hills or ridges. In this case the silvicultural advantages of monocultures are maintained while landscape diversity is enhanced. Overall productivity may also be enhanced in this way by matching species to their preferred sites. On the other hand, this requires detailed knowledge of the species and their site relationships.

Tree monoculture with inter-row plantings or underplantings of agricultural crops The primary disadvantage of tree crops is the length of the period before any economic benefit is obtained. Rotation lengths for many tree species exceed 30 years. Some landowners or stakeholders need a return before such a time span in order to encourage them to undertake reforestation. One way this might be achieved is by underplanting the tree species with short-lived agricultural crops or medicinal plants. The well-known 'taungya' system that was developed during the colonial period in Burma is just one example of this approach. In this case the crop plants are planted between the rows of trees thereby helping to exclude weeds. Cropping is continued until tree canopy closure occurs and is then abandoned.

This tree-plus-crop combination is commonly referred to as agroforestry and there is a huge number of variants. In some cases, such as the taungya system, the crop is short-lived. In other cases the crop is a more or less permanent component of the plantation system. Many of these systems use only a single species of tree but other agroforestry systems use more than one tree species. The commercial advantages of the system are clear provided the crop species can tolerate their subcanopy position. The system also has some ecological advantages since the more complex canopy structures are likely to provide better ecological services such as watershed protection and wildlife habitats than simple monocultures.

Multispecies tree plantations Plantations involving more than one tree species are more complex silvicultural systems requiring more sophisticated management operations but offering some potential advantages over monocultures. These include the possibility of enhanced productivity, improved nutrition, reduced insect or disease and greater financial security from the spreading of risk (see **Table 3**).

These potential advantages do not invariably occur in every mixture and randomly created mixtures are likely to fail. Great care is needed to ensure that only complementary species are used. Complementary species may be those that minimize competition with their neighbors. Thus they may have differing phenologies (so that their demands on site resources are at different times than their neighbors) or differing root depths (so that roots take resources from different soil horizons). Likewise they may have differing canopy architectures (so that crown and foliar competition is minimized) or differing nutritional requirements (so that resource competition is minimized). Nutritional gains can also occur when nitrogen fixers such as *Acacia* or *Albizzia* are mixed with non nitrogen fixers.

Most mixtures contain only modest numbers of species but these can be planted in various configurations such as in alternate rows of particular species or at random. Alternate rows offer the advantage that a faster-growing species might be removed earlier than a slower-growing species without causing much damage to the residual trees. Random plantings of the trees in the mixture offer the advantage of a more intimate mingling of the species enabling the advantages of complementarity to be more fully expressed.

Table 3 Potential benefits of using more than one species in a plantation

Potential benefit	*Reason*
Competition between trees reduced	Competitors have differing growth phenologies and use site resources at different times
	Competitors have different root or canopy architectures that partition spatially distributed resources and use them differentially
Tree nutrition is enhanced	One of species is a nitrogen fixer that adds N to soil
	Nutrient decomposition and cycling is faster with more than one litter type
Reduced insect or disease problems	Target species for insects are hidden in space; host plants for particular diseases are more widely distributed
Financial outcome is improved	Provides insurance and spreads risk of markets changing during rotation period

Adapted with permission from Lamb D and Gilmour DA (2003) *Rehabilitation and Restoration of Degraded Forest*. Gland, Switzerland: IUCN.

Mixtures obviously have higher levels of plant biodiversity than plantation monocultures although the extent of any biodiversity gain depends on the number of species included in the mixture. In most cases this will still be modest compared with that in a natural forest. But mixtures are also likely to have a greater structural complexity than any monoculture meaning they are likely to be more attractive to some wildlife species. Any gain in species richness is likely to benefit the restoration of key ecological processes and ecological services. The key disadvantage of mixed species plantations is obviously in their greater silvicultural complexity and need for more intensive management.

New plantations where the composition of the canopy tree species changes over time (semisuccessional plantings)

Nurse trees used to establish plantation tree species Some commercially attractive plantation tree species need an overstory canopy of 'nurse' trees to become established. Once they are established this nurse tree cover can be removed. Thus some temperate tree species need protection from frosts when young. Similarly, some tropical tree species are sensitive to full sunlight when at the seedling stage. Nurse crops such as these are also needed for some agricultural crops (e.g., *Erythrina*, *Cordia*, or *Leuceaena* are often used to provide shelter over coffee or cacoa). A forestry example is the requirement by some of the Dipterocarpaceae of Southeast Asia for a temporary overstory cover. Nurse crops can also benefit certain tree species by reducing insect damage, presumably by altering some element of the microclimate affecting the insect. For example, red cedar (Meliaceae) has been found to have greater survival rates when planted below an established cover than when planted in the open. Likewise nurse trees may act to improve soil conditions allowing more valuable species to be established at the site.

These nurse trees facilitate the development and growth of the target species and add to the biological complexity of the new forest. However, they also pose a series of silvicultural dilemmas. These include the question of how tall the nurse trees must be when the target species is planted and how much cover must they provide? How long should this cover be provided before it begins to reduce the growth rates of the commercially attractive species? If the nurse species are short-lived they may disappear around the time when their disadvantages begin to outweigh their advantages. Otherwise they may need to be removed by poisoning or girdling.

While the focus of this silvicultural sequence is the commercial plantation species the added biological and structural complexity of the new forest ensures it has some ecological advantages over simple monocultures as well.

Underplant beneath earlier plantation monoculture A variation on the nurse tree model is when circumstances require that an existing monoculture plantation of one species (perhaps an exotic), be replaced by another (perhaps a native species). This may be because the timber value of the original species has declined or because the environmental or ecological benefits of the current plantation are insufficient and need improvement. In such a situation the best option may be to simply clear the original forest and replant with the preferred species. But in some situations it might be preferable to underplant below the original canopy or plant in strips or corridors cleared through the original plantation and manage a more gradual transition. The choice will obviously depend on the shade tolerances of the various species being added to the site as well as the longevity and current market value of the initial plantation species. The new species might be more valuable timber, nut, or fruit trees or they might simply have greater ecological and conservational value.

The advantage of such an approach is that it avoids rapid changes in wildlife habitat and potentially large soil and nutrient losses caused by erosion after clearing. There is also scope for some financial gain from the harvesting process. The disadvantage is that the shade tolerances of the new species and hence the amount of canopy opening needed must be clearly understood to avoid a lengthy period of trial and error during the transition.

Understory development encouraged beneath tree plantation Many plantations located near intact natural forest can gradually acquire an understory of native species because of natural colonization. The rate at which this occurs will depend on the attributes of the plantation species as well as those of the potential colonists and on the dispersal distances involved. In the tropics greater diversity appears to occur beneath broadleaved plantation trees than beneath conifers. Within the time period of a typical plantation rotation, a very species-rich understory can develop, especially in moist tropical regions. In some cases these colonists can grow up and join the canopy layer.

This phenomenon represents both an opportunity as well as a dilemma. The opportunity is that great biological diversity can be acquired for little cash outlay. This means there may be a significant gain in a variety of ecological services such as watershed protection and nutrient cycling and the restoration of many ecological processes. The dilemma is that there may be an indirect cost in the form of increased competition facing the original plantation trees that will slow their growth. The trade-off will necessarily depend on circumstances. If the site is one where enhanced biodiversity is an advantage then it may be appropriate to tolerate a reduction in timber increment caused by increased competition. On the other hand, if production is the predominant objective then careful management of this competition will be needed.

There are four possible alternative management regimes. One is to harvest the plantation as initially envisaged and to treat the enhanced biodiversity as a temporary benefit that will re-establish again when the second rotation of the plantation is re-established. A second is to regard this biodiversity as now being more socially beneficial than any timber harvest and to not fell the trees as was originally planned. A third is to fell the plantation trees at the end of the rotation as originally planned but to try to protect as much of the new biodiversity as possible while doing this. Subsequently, the primary management objective would then become one of fostering and enhancing this biodiversity rather than re-establishing the plantation timber trees. The final option might be to simply manage the plantation species, together with the new timber species that have joined the canopy, as an uneven-aged forest and to manage this on a selection system. This would recognize that some of the new colonists might have also commercial or social values as food or medicinal plants.

This catalytic role of plantations does not occur everywhere and sometimes the only species that colonize beneath the plantation species are exotic weeds. But provided it is carefully managed, the phenomenon is a cheap means by which monoculture plantations can generate a wider range of ecological services.

Problems in Using These Approaches

This variety of potential alternatives might seem to imply that all are equally available. Unfortunately this is not the case and there are two main reasons. One concerns the biology of native species. Much less is usually known about the ecology or silviculture of most native tree species than is known, for example, about the more common industrial forestry species. This means that species–site relationships and nutritional requirements are uncertain and the competitive abilities or tolerances of these species are mostly unknown. This makes it difficult to develop good mosaics of monocultures or design multispecies plantations using complementary species mixes. A second, even more difficult issue is that of managing the trade-off between production and ecological integrity or authenticity. Different stakeholders will strike different balances because they have differing objectives. This means that reaching a desired balance will probably always involve some degree of trial and error until the basic silviculture and ecology of the several species being used is understood.

The Social–Economic Context for Reforestation

Forest rehabilitation to provide goods and ecological services is more commonly undertaken by farmers and communities rather than by industrial enterprises. This is because of the differing objectives usually being sought by these several groups. But farmers, like industrial enterprises, need some certainty that they will indeed be the ultimate beneficiaries of any reforestation that they undertake. This means that land tenure is a crucial matter. No person is likely to invest time or money in a long-term activity like forestry unless there is some certainty over land ownership or future access. Nor are they likely to protect the young forest from fires or grazing animals unless they can see it to be in their own interest. The irony here, of course, is that many of the most degraded landscapes are also those where rural people's traditional land ownership claims are unrecognized by central governments.

Because ecological services are often distributed far beyond the immediate vicinity of any particular reforestation site there is also the issue of whether these distant beneficiaries of rehabilitation should also contribute to its cost. For example, should a landowner with land affected by salinity contribute to the cost of trees planted in the watershed upstream of his property? These trees will help lower the water table and reduce his salinity problem but will also reduce the area of agricultural land available to his neighbor. If rehabilitation is to be undertaken on a large scale then some way must be found to fund the restoration of these services on degraded lands for the wider public benefit. The current debate over whether the carbon sequestered by tree plantations might be traded in a special market illustrates one approach to this problem.

A related problem is that each forest manager usually makes decisions on a site basis but that many ecological processes operate at a landscape scale. Different land managers will have different goals and therefore use different agricultural and silvicultural approaches. But agricultural sustainability across the landscape as a whole will require collective action by all land managers if optimal outcomes are to be achieved. This will require what might be called forest landscape restoration. Such a landscape may have croplands, patches of remnant forest, and perhaps several of the approaches outlined above. There are few localities where this has been successfully achieved.

See also: **Biological Impacts of Deforestation and Fragmentation**. **Forest Management for Conservation**. **Plant Diversity in Forests**. **Silviculture**: Natural Stand Regeneration; Reclamation of Mining Lands; Sustainability of Forest Plantations. **Sustainable Forest Management**.

Further Reading

Banerjee AK (1995) *Rehabilitation of Degraded Forests in Asia*. World Bank Technical Paper no. 270. Washington, DC: World Bank.

Bradshaw A and Chadwick MJ (1980) *The Restoration of Land: The Ecology and Reclamation of Derelict and Degraded Land*. Berkeley, CA: University of California Press.

Dobson A, Bradshaw A, and Baker A (1997) Hopes for the future: restoration ecology and conservation biology. *Science* 277: 515–522.

ITTO (2002) *ITTO Guidelines for the Restoration, Management and Rehabilitation of Degraded and Secondary Tropical Forests*. ITTO Policy Development Series no. 13, in collaboration with CIFOR, FAO, IUCN, and WWF. Yokohama, Japan: International Tropical Timbers Organization.

Jordan WR, Gilpin ME, and Aber JD (1987) *Restoration Ecology: A Synthetic Approach to Ecological Research*. Cambridge, UK: Cambridge University Press.

Kelty MJ, Larson BC, and Oliver CD (eds) (1992) *The Ecology and Silviculture of Mixed Species Forests*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Kobayashi S, Turnbull JW, Toma T, Mori T, and Majid NMNA (eds) (1999) *Rehabilitation of Degraded Tropical Forest Ecosystems*, Workshop Proceedings, 2–4 November 1999, Bogor, Indonesia.

Lamb D (1998) Large-scale ecological restoration of degraded tropical forest land: the potential role of timber plantations. *Restoration Ecology* 6: 271–279.

Lamb D and Gilmour DA (2003) *Rehabilitation and Restoration of Degraded Forest*. Gland, Switzerland: IUCN.

Parrotta JA, Turnbull JW, and Jones N (1997) Catalysing native forest regeneration on degraded tropical land. *Forest Ecology and Management* 99: 1–8.

Rodwell J and Patterson G (1994) *Creating New Native Woodlands*. Bulletin no. 112. London: HMSO.

Torquebiau E (1984) Man-made dipterocarp forest in Sumatra. *Agroforestry Systems* 2: 103–127.

Wadsworth F (1997) *Forest Production for Tropical America*. US Department of Agriculture Forest Service Agriculture Handbook no. 710. Washington, DC: Department of Agriculture.

Wormald TJ (1992) *Mixed and Pure Forest Plantations in the Tropics and Subtropics*. Rome: Food and Agricultural Organization.

Treatments in Tropical Silviculture

F E Putz, Center for International Forestry Research, Jakarta, Indonesia

Introduction

Silviculture can be defined as the art and science of controlling the composition, structure, and dynamics of forests. Although the traditional focus of silviculture was on timber production, modern silviculturalists are expected to respond to society's often conflicting demands about forests. Sustained yield of timber is still a common goal, but non-timber forest products (NTFPs) such as medicinal plants and wildlife sometime receive as much or more attention from some important forest stakeholders. Forests providing these products and the jobs and revenues they yield are also expected to serve as recreation areas, watersheds, and effective moderators of local and global climates. Foresters are expected to manage forests for these goods and services in ways that avoid losses of genetic, species-level, and landscape-level diversities; sometimes they are expected to manage without apparent disruption of the pristine nature of old-growth forest. With so broad an agenda, the relevant question seems to become what isn't silviculture rather than what is?

This article has a somewhat traditional focus on plants and plant products, how they grow, and how forests can be silviculturally treated so as to increase production of the desired species. Although reference is made to different silvicultural systems that have been utilized in the tropics, the emphasis is on the ecological reasons behind these different methods for increasing the stocking and growth of commercial species and the conditions under which they are likely to be successful.

Treatments to Improve Stocking

General Approach

Securing adequate natural regeneration for future harvests is a central but often hard-won goal for forest managers. Despite the popular perception of forest management as necessarily involving tree planting in tropical forests, natural regeneration has a number of advantages over artificial regeneration (e.g., hand or machine planting of seeds or seedlings). One of these advantages is that because the seed sources for natural regeneration are individuals that successfully reproduced in the stand, it is reasonable to expect that they are genetically well adapted to local biotic and abiotic conditions. For plantation managers, in contrast, mismatches of species, provenances, and genotypes to local site conditions are commonplace. Furthermore, transplanted seedlings often suffer high mortality rates and, if planted poorly, may grow slowly or develop deformed stems even if they do survive. Natural regeneration is also generally less expensive than artificial regeneration, but it is not always 'free.' In any event, where natural regeneration is relied upon, management interventions are generally less drastic than where seeds or seedlings are planted. Lessening the impacts of stand regeneration operations, in addition to saving money, has the advantage of reducing the effects of forest management on biodiversity and ecosystem functioning (e.g., stream sedimentation and nutrient cycling). This is not to say, however, that methods for securing natural regeneration are always gentle. On the contrary, where natural, stand-regenerating disturbances include fires, hurricanes, or other major perturbations, the appropriate regeneration treatments are also likely to be severe.

Successfully regenerating commercial species without causing unnecessary harm to other species or forest processes requires substantial ecological and more specific silvicultural knowledge. For example, the reactions to harvesting and other stand manipulations of commercial species, weeds, and other taxa need to be known. Forest managers thus need to be aware of the intervals between seed crops (e.g., mast year frequencies), the distances to which seeds are dispersed, the probability of seedling establishment and survival, and the relative growth rates of commercial species and the species with which they compete. Due to a variety of factors including destructive harvesting practices, droughts, intense seed predation, herbivory, and the effects of pathogens, natural regeneration may not result in fully stocked stands.

A major challenge for forest managers is developing sufficient understanding of the regeneration mechanisms of the species for which the area is being managed as well as of the other species that influence forest development. Plants regenerate in a variety of ways, both sexually (i.e., by seed), and vegetatively (e.g., from rhizomes or coppicing from cut stumps). Among sexually reproducing species are those that produce seeds that lack dormancy (i.e., they either germinate or die soon after maturing), and others that produce seeds that may remain dormant in the soil for many years. Species that regenerate vegetatively may simply sprout back after being damaged or spread extensively by root sprouts or stem layering. Extensive vegetative expansion is fairly rare among tropical trees, at least those that grow to be large, but is common among other growth forms such as vines, grasses, and ferns. Sprouting of naturally broken or felled trees, in contrast, is commonplace.

Reducing Logging Damage to Advanced Regeneration

The understories of many forests contain substantial populations of seedlings, saplings, and poles of commercial species, which are collectively referred to as 'advanced regeneration,' and subcanopy trees, which are referred to as 'advanced residuals.' Where harvesting is planned to be carried out before completion of a full rotation (i.e., the time required for a germinated seed to grow into a plant of harvestable size), reducing harvesting damage to the future crop trees is critical. Due to limited knowledge about the capacity of most tropical tree species to respond favorably to canopy opening after suffering prolonged suppression, future crop trees should be selected on the basis of stem and crown form, not just by species and stem diameter. In any event, harvesting should be considered to be an intensive silvicultural intervention and not a forest product mining operation.

Promoting Seed Production and Seedling Establishment

Regeneration from seed can fail at any phase of the process of flower production, pollination, seed set, seed dispersal, and seedling establishment. For species that are poorly represented by advanced regeneration or as buried seeds in the soil, retention of seed-producing individuals is generally of the utmost importance. The minimum density of retained seed-bearers is a function of a large number of factors including both propagule and site characteristics. For example, the required density of retained individuals of a dioecious species (i.e., one with separate sexes) that produces large and poorly dispersed seeds is likely greater than for a species with perfect flowers and small, wind-dispersed seeds. The location of seed trees relative to skid trails, felling gaps, and other canopy openings may also be critical. For example, on the Yucatan Peninsula of Mexico, regeneration of *Swietenia macrophylla* is promoted by retention of seed trees upwind from such openings. The timing of harvesting operations can also be critical if the seed-producing trees are cut before their seeds are dispersed. Setting a minimum diameter limit for harvesting that is close to or less than the minimum size at which trees start to reproduce is another obvious cause of regeneration failures. Unfortunately, diameter limits are all too often determined without regard to the biology of the species being harvested.

There is a wide range of harvesting options designed to promote regeneration, ranging from massive clear-cuts to single tree selection, which results in only small gaps in the canopy. In deciding upon the appropriate harvesting system for the forest and species of concern, the silviculturalist needs to determine the minimum canopy opening that promotes the regeneration of the desired species. Where silvicultural treatments other than harvesting are to be applied, the silviculturalist should also know whether mineral soil needs to be exposed to promote seed germination and seedling establishment.

Seeds may be produced in abundance but regeneration nevertheless fail if seed dispersers are absent or limited in abundance due to over-hunting. Although many of the best-known timber trees in the tropics have wind-dispersed seeds, many other timber-producing species, as well as most understory trees and virtually all palms, shrubs, and herbs, produce seeds that require the services of mammals, birds, reptiles, or even fish for their dispersal. Seeds that are not dispersed mostly fall under the parent plant where they suffer greatly from competition, seed and seedling predation, and the impacts of pathogens.

Pre- and postdispersal seed predation can greatly reduce the numbers of seeds available for germination. In some cases, mammals and birds (e.g., parrots and doves) eat large numbers of immature seeds. Similarly, many insects (e.g., some beetles and flies) lay their eggs on flowers or young fruits; the larvae hatch and bore inside where they are nourished at the expense of developing seeds. Many mature seeds are in a sense sacrificed to animals that serve as both dispersers and seed predators. Squirrels and other rodents that scatter-hoard seeds for future consumption are a familiar example of this dual function; the seeds they fail to recover are the most likely to survive and contribute to the next generation.

Dispersed seeds that escape predation may nevertheless fail to germinate or establish as seedlings if the environmental conditions of the places to which they are dispersed are not suitable. For example, seeds that are stimulated to germinate by high red : far red ratios of light will fail to germinate if they land in the forest understory. More commonly, seedling establishment fails because the seedling root fails to find a reliable source of water. Seedlings from small seeds that germinate on top of leaf litter are particularly prone to desiccation. In deep shade, when the reserves of carbohydrates stored in seeds are exhausted, seedlings die if they are not able to photosynthesize enough to balance their respiratory carbon losses. Herbivory and damage from fallen branches and trampling also result in the death of many seedlings, as do nutrient deficiencies, but desiccation and carbon imbalances (often associated with fungal infection) apparently kill the majority of seedlings.

It perhaps goes without saying that most seeds and seedlings fail to survive to maturity, but detailed and long-term studies of population biology are often required to determine whether apparent 'bottlenecks' at the seed or seedling phases actually threaten population maintenance. Nevertheless, silviculturalists need to be careful to avoid inadvertently jeopardizing sustainability by creating conditions favorable to weeds, seed predators, herbivores, and pathogens, or that are unfavorable to pollinators or seed dispersal agents. In some cases, seedling establishment can be enhanced by removing surface litter and near-ground competition with controlled burns, or exposing mineral soil by mechanical scarification with a tractor-drawn plow. Such intensive site preparation treatments are more commonly used in plantations than in managed natural forests, but they should not be disregarded as silvicultural options.

Although traditional forest-dwelling people have successfully enriched forest with useful species for millenia, industrial-scale 'enrichment planting' has generally proven to be a problematic and costly way to increase the stocking of commercial tree species. Despite numerous expensive failures, enrichment planting of nursery-grown seedlings along lines cleared through the forest or in felling gaps continues to be tried in many forests, particularly where uncontrolled logging has left severely depleted stands. While poor planting technique is sometimes the problem, most seedlings die because they do not receive the postplanting tending operations needed to assure their survival. More successful, from a silvicultural perspective, has been a regeneration system referred to by its Burmese name, 'taungya,' in which commercial tree species are planted among food crops plants by farmers who do the necessary weeding. This system was discredited where it was originally used by colonial foresters because once the planted trees were established, the farmers were displaced and their agricultural practices were criminalized. Given the recent substantial devolution of forest management responsibilities back to rural communities from central governments in many tropical countries, some aspects of 'taungya' might prove useful for forest regeneration where the farmers own the land.

Particularly in seasonally dry forests and woodlands, many tree species can be managed for trees that sprout from stumps (i.e., coppicing) or from trees cut off above the reach of browsing animals (i.e., pollarding). Coppice stems of better quality typically emerge from low stools (i.e., stumps), but even the best coppices seldom yield large logs. Nevertheless, coppicing is an excellent way to produce small-dimension timber, poles, firewood, and fiber. Pollarding, in slight contrast, is generally used to provide seasonal shade over crops in agroforestry systems, to produce forage for animals, and for firewood production.

Treatments to Improve Growth

General Approach

Various stand 'improvement' treatments are available to increase light and soil resource availability to commercial species and thereby increase their productivity. In natural forest management in the tropics, these treatments typically involve competition control. Although we are very aware of aboveground competition for light, belowground competition for water and nutrients can also be intense. In this section, weed control and thinning are considered separately even though they are sometimes hard to distinguish.

Weed Control

A 'weed' can be defined as a plant growing where it is not wanted. Depending on the type of weed to be controlled and the ease to which damage to future crop trees can be avoided, silviculturalists can choose from a wide variety of mechanical and chemical treatments or may opt to perform controlled burns.

Among the mechanical weed control methods available, roller chopping, disking, and other tractor-requiring treatments are generally only useful in young stands regenerating after clear-cutting. More often in managed natural forests, weeds interfering with future crop trees are cut with a machete, brush axe, motor-driven weed whacker, or chainsaw. Although many weeds resprout vigorously after cutting, well-timed mechanical treatments can promote growth of future crop trees that may then shade out light-demanding weeds. Generally, mechanical control is most effective early during the season of most active growth when most carbohydrates and other storage materials have been translocated to the aboveground parts that are removed.

When used properly, modern herbicides can be safe, useful, and cost-effective components of a silviculturalist's toolbox. Chemical weed control methods have improved a great deal during the last decade. Compounds used in the 1960s such as sodium arsenite and 2,4,5-trichlorophenoxyacetic acid (2-4-5T) contaminated with dioxins posed serious environmental and health hazards and are now generally banned. In comparison, herbicides such as glyphosate, tryclopyr, hexazinone, and 2,4-dichlorophenoxyacetic acid (2-4D) have low toxicity to animals, brief residence times in the soil, and apparently safe breakdown products. Modern herbicides are all expensive but vary substantially in their modes of action. For example, some are absorbed by roots (e.g., hexazinone) whereas others penetrate leaf cuticles (e.g., glyphosate).

If after weighing the costs and benefits you decide to use herbicides for weed control, there are a number of choices of commercially available products, tank mixtures, dyes, wetting agents (i.e., surfactants), and modes of application.

Suitable ways to apply herbicides vary with the species and size of the target plants, the number of plants you intend to treat, the season, the type of herbicide, and available equipment. Some herbicides, like glyphosate, are often sprayed or wiped on foliage, whereas others, like Garlon 4, are more often squirted around the inside of the bark (i.e., on the vascular cambium) of fresh-cut stumps or into frill girdles cut with a chainsaw or hatchet. To penetrate the waxy coating (cuticle) on leaves, a surfactant is sometimes needed. Because herbicides disrupt metabolic functions, they are best applied when plants are metabolically active. Late growing season applications are often particularly effective because that is when many plants are moving sugars belowground to store for the winter or dry season. Volatile herbicides should be applied when the air is cool and still, lest the fumes escape and kill plants that you were trying to save. And whether herbicides are being applied to bark, stumps, girdles, or leaves, never apply so much that the chemical runs off the surface.

Woody vines, including climbing bamboos, pose serious silvicultural problems in many tropical forests. Vine infestations are especially common in logged forests, particularly those where logging was uncontrolled and carried out by untrained crews. Because many vines survive when their host trees are felled and sprout vigorously from fallen stems, many of the vines in logged areas propagate vegetatively. Prefelling cutting of vines, therefore, can have substantial postfelling advantages in addition to reducing logging damage. Furthermore, due to easier forest interior access prior to logging, prefelling vine cutting is generally more cost effective than trying to control vines in vine-infested logged forests. Finally, because vine leaves may constitute 25% or more of the total forest leaf area, vine cutting is analogous to carrying out a light shelterwood cut; tree seedling densities and growth rates may increase in response to vine removal. Silviculturalists trying to rescue commercial trees in heavily vine-infested forests are generally advised to focus on liberating the crowns of future crop trees rather than trying to cut all of the vines in the entire management area, which is generally too costly.

Thinning

Where future crop trees are crowded by neighbors, thinning can result in substantial increases in growth due to release of soil resources and increased access to light. Thinning treatments can be applied to entire stands or just in the near vicinities of selected future crop trees. Both commercial thinning, in which the thinned trees are extracted and sold, and precommercial thinning are reasonable options in some stands. But before discussing some of the many types of thinning, a few of the silvicultural costs and benefits of thinning need to be considered.

While diameter or volume increments of selected future crop trees can be improved by removing neighbors, heavy stand thinning can lead to retention and growth of lower branches, formation of epicormic branches, increased stem taper, barkscald, abrupt changes in wood properties, and other changes that lead to reductions in stem or wood quality. Thinning stands can also make the remaining trees susceptible to windthrow and weed encroachment. Finally, thinning does not invariably result in the desired growth response. For example, after long periods of suppression, trees of many species do not respond well to thinning; some previously suppressed trees may even die if they are too rapidly exposed to high light intensities, high temperatures, and the consequent water deficits. Where exposure is less rapid and less extreme, formerly suppressed trees that are released from competition may adjust to the new conditions by replacing their shade-adapted leaves with thicker leaves, with thicker cuticles, and other characteristics of 'sun' leaves. Released individuals also adjust their root : shoot ratios so as to increase their water uptake capacities in the more water-demanding conditions of thinned stands.

In silviculturally managed natural forests in the tropics, perhaps the most common thinning operation is the release of selected future crop trees from competition from immediate neighbors. This treatment, often referred to as 'liberation thinning,' has many silvicultural, financial, and environmental advantages in the poorly stocked stands in which tropical foresters generally work. By restricting thinning operations to the near vicinities of future crop trees, portions of most stands remain untreated, which often makes silvicultural sense, saves money, and avoids needless environmental disruption.

Liberation thinning prescriptions generally call for cutting, frill-girdling, or arboriciding trees with crowns above or within some lateral distance (e.g., 2–4 m) of the crowns of future crop trees. The appropriate extent of lateral opening varies with the species and size of the tree to be released. For example, tree species that typically develop broad spreading crowns may require large openings for maximum growth, at least after the selected individual has developed the desired length of branch-free bole.

To maximize the likelihood of increased timber volume increments, future crop trees selected should not have been heavily suppressed for long periods of time. Because stand records are seldom available, the silviculturalist must rely on visible characteristics of trees themselves to determine their histories of suppression. Crown form is generally the best indicator of the conditions under which a tree has been growing. Trees with small, sparse, or poorly formed crowns are likely to have been suppressed for a long time and may not respond well when released from competition. Heavily vine-laden trees may also not be good candidates for liberation treatments. Due to the complexity of liberation thinning operations, tree marking should be carried out by trained staff and the silvicultural responses should be monitored in permanent research plots. Repeated liberation may be required for maximum stand production if the benefits of liberation do not persist for the duration of stand retention.

The primary thinning treatment that most natural forests receive is timber harvesting. All too often logging is not considered to be the silvicultural treatment that it actually represents. In stands with substantial advanced regeneration of commercial species and where some trees have been marked for harvesting and others for retention, timber harvesting is equivalent to heavy thinning and results in similar growth responses of future crop trees.

Environmental Impacts of Silvicultural Treatments

Liberation thinning, vine cutting, soil scarification, and other stand 'improvement' treatments are not improvements at all from the perspective of the vines that are cut, the trees that are girdled, or all the various animal species that depend on the plants selected against. Stands that are intensively managed for timber can be essentially converted into plantations, with all the attendant negative impacts on biodiversity. In most of the tropics the problem is too little, not too much management, but silviculturalists nevertheless should be aware of this concern.

Impatience is a common threat to environmentally, silviculturally, and fiscally sound silviculture. Sometimes the best decision is to let a stand recover slowly on its own, without silvicultural intervention. And some silvicultural treatments may be misapplied. For example, an overstory of fast-growing, short-lived, light-demanding trees may serve as a nurse crop for the slower-growing commercial species that grow up in their sparse shade – removing the cover crop would be wasteful and ineffective. Also, dense stands can be left to self-thin, at no direct cost to the forest manager. And heavily thinned stands may suffer excessive windthrow and other damages. The best overall advice when prescribing and applying timber stand improvement treatments is to be gentle unless the forest indicates otherwise. Silviculturalists need to remember that a noncommercial species today may fetch a high price tomorrow and that today's weed may be tomorrow's wonder crop.

Complicating the challenges faced by tropical silviculturalists is increased awareness of the importance of stand history in determining stand structure and composition. Radical differences between old-growth forests and young (<50 years old) secondary forests developing after abandonment of agricultural clearings are well known. Less widely recognized are the persisting influences of agricultural interventions even several centuries after abandonment. Given the drastic declines in Amerindian populations after European colonization and similar demographic and cultural upheavals elsewhere in the tropics, history cannot be ignored when silvicultural options are being investigated. Similarly, major natural perturbations, such as windstorms and fires, even if they occur at intervals of centuries, can have lasting effects on forests in which trees can live for several hundred years.

It is widely known that well-managed monospecific plantations of fast-growing trees generally out-yield natural forests by up to a factor of 10. Some proponents of plantation forestry argue that given their high productivity, plantations should be established to reduce pressure on natural forests. Although plantations have a substantial role to play in many tropical countries, this argument is weakened by the fact that the wood produced by trees in natural forests is of a quality unlikely ever to be matched in plantations. Furthermore, given the many non-timber benefits derived from tropical forests (e.g., biodiversity protection, carbon sequestration, hydrological functions), it is not reasonable to compare plantations and natural forests solely on the basis of volume yields. Finally, it is critical to remember that forests are more than trees and should be managed accordingly.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Natural Disturbance in Forest Environments. **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Plantation Silviculture**: Tending. **Silviculture**: Managing for Tropical Non-timber Forest Products; Natural Regeneration of Tropical Rain Forests; Natural Stand Regeneration. **Site-Specific Silviculture**: Ecology and Silviculture of Tropical Wetland Forests. **Sustainable Forest Management**: Overview.

Further Reading

Baur GN (1965) *The Ecological Basis of Rainforest Management*. Sydney: Forestry Commission.

Bruenig EF (1996) *Conservation and Management of Tropical Rainforests: An Integrated Approach to Sustainability*. Wallingford, UK: CAB International.

Dawkins HC and Philip MS (1998) *Tropical Moist Forest Silviculture and Management: A History of Success and Failure*. Wallingford, UK: CAB International.

De Graaf NR (1986) *A Silvicultural System for Natural Regeneration of Tropical Rain Forest In Suriname*. Wageningen, The Netherlands: Agricultural University.

Fox JED (1976) Constraints on the natural regeneration of tropical moist forest. *Forest Ecology and Management* 1: 37–65.

Fredericksen TS and Putz FE (2003) Silvicultural intensification for tropical forest conservation. *Biodiversity and Conservation* 12: 1445–1453.

Guariguata MR and Kattan GH (2002) *Ecología y Conservación de Bosques Neotropicales*. Cartago, Costa Rica: Libro Universitario Regional.

Hutchinson ID (1988) Points of departure for silviculture in humid tropical forests. *Commonwealth Forestry Review* 67: 223–230.

Kellman M and Takaberry R (1997) *Tropical Environments: The Functioning and Management of Tropical Ecosystems*. London: Routledge.

Lamprecht H (1989) *Silviculture in the Tropics*. Eschborn, Germany: Deutsche Gesellschaft fur Technische Zusammenarbeit.

Oliver CD and Larson BC (1990) *Forest Stand Dynamics*. New York: McGraw Hill.

Palmer J and Synnott TJ (1992) The management of natural forests. In: Sharma NP (ed.) *Managing the World's Forests*, pp. 337–373. Dubuque, IA: Kendall/Hunt.

Pinard MA, Putz FE, Jardim T, Rumíz D, and Guzman R (1999) Ecological characterization of tree species to guide forest management decisions: an exercise in species classification in semi-deciduous forests of Lomerio, Bolivia. *Forest Ecology and Management* 113: 201–213.

Putz FE, Blate GM, Redford KH, Fimbel R, and Robinson JG (2001) Biodiversity conservation in the context of tropical forest management. *Conservation Biology* 15: 7–20.

Smith DM, Larson BC, Kelty MJ, and Ashton PMS (1997) *The Practice of Silviculture: Applied Forest Ecology*. New York: John Wiley.

Uhl C, Barreto P, Verissimo A, *et al*. (1997) Natural resource management in the Brazilian Amazon: an integrated approach. *BioScience* 47: 160–168.

Wadsworth FH (1997) *Forest Production for Tropical America*. US Department of Agriculture Forestry Service, Agricultural Handbook no. 710. Washington, DC: US Department of Agriculture Forestry Service.

Coppice Silviculture Practiced in Temperate Regions

R Harmer, Forest Research, Farnham, UK

Published by Elsevier Ltd., 2004

Introduction

Coppice is a word that is used by foresters to cover many things including: a type of woodland consisting of trees that are periodically cut; the multistemmed trees that occur in such woodlands; the process of felling the trees; and the production of new shoots by recently cut stools. The management of woodlands as coppice has a long history and archeological evidence indicates that the process was used in prehistoric times. The basic method is simple and relies on the ability of many trees to regrow from the stumps remaining after felling. At its simplest, woodland comprising single-stemmed trees which have grown from seed are clear-felled and allowed to regrow. Repeated felling produces the multistemmed stools typical of coppice woodland. In the developed world elaborate forms of coppice management to control yield, and provide a sustainable supply of small wood and large timber, reached their zenith prior to industrialization when alternative fuels, building materials, and chemicals became more readily available. However, in these regions the art of coppice management has been in decline for 100–200 years and many woodlands have been transformed to high forest. There are still about 50 million ha of coppice within the industrialized nations but only 60% of this is classified as utilizable (**Table 1**). However, during the last two to three decades there has been a resurgence of interest in coppice grown on short rotations, primarily for use as a biofuel although longer rotations are used for the production of pulp woods. In contrast coppice has remained an important system of management in tropical areas where demand for fuel and small-diameter wood, for building purposes is still high. In addition to the use of naturally occurring species and woodland, several million hectares of plantation, often comprising species of eucalyptus, have been established.

Table 1 Estimated areas (ha $\times 10^3$) of coppice woodland[a] in industrialized temperate/boreal countries

Region	*Utilizable*	*Non-utilizable*[b]
Nordic and Baltic	16	0
Central Europe	7687	64
Southern Europe	13 506	4411
Commonwealth of Independent States	12 643	16 071
USA and Canada	0	0
Australasia and Japan	56	0
Total	33 908	20 546

Data adapted from UN-ECE/FAO report ECE/TIM/SP/17, Geneva Timber and Forest Study Paper no. 17 (2000).
[a] Figures are for both simple coppice and coppice with standards.
[b] Non-utilizable, not available for wood supply for a variety of conservation, protection, or economic reasons.

Silvicultural Systems

Three systems of coppice woodland management are generally recognized: simple coppice, coppice with standards, and the coppice selection system. In many areas these idealized systems are probably impracticable at the present time and *ad hoc* systems of irregular cutting are likely to be more typical. Pollarding, which is similar to coppicing and also relies on the ability of the trunk to sprout new shoots, can be used to manage individual trees.

Simple Coppice

In this method the woodland is managed as an even-aged single-story crop grown for fuelwood and small/medium-sized material. The coppice is cut on a regular rotation, the length of which depends not only on the product required but also on species, location, and rate of growth. Theoretically the coppice is managed by sequential cutting of coupes throughout the woodland, with the woodland divided into a number of coupes equal to the number of years in the rotation; one coupe is then cut each year. Coppice woodlands managed in this way, with coupes cut at the appropriate time are said to be 'in-cycle' or 'in-rotation' (**Figure 1**).

Short rotation coppice woodlands are a special example of simple coppice in which the lifespans of any shoots or stools are short in comparison to those of traditional coppice woodlands. For example, typical rotations for clonal stands of *Populus* and *Salix* short rotation coppice are 2–4 years, with the expected lifespan of stools being 10–20 years before they are replaced when yield declines – perhaps four to five rotations in total. In contrast, mixed broadleaved coppice woodlands managed to produce fuel and small-diameter wood, may be cut on 20-year rotations with some stools capable of surviving for centuries.

Coppice with Standards

These woodlands are multistoried with an even-aged lower story of coppice underwood cut regularly to produce small material, and a partial overstory of uneven-aged standard trees which are usually grown

Figure 1 A recently felled coupe of in-cycle, simple sweet chestnut (*Castanea sativa*) coppice approximately 15 years old (Kent, UK). Reproduced with permission from Harmer R and Howe J (2003) *Silviculture and Management of Coppice Woodlands*. Forestry Commission, UK.

from seed and allowed to grow to a sufficient size to produce large timber. This system is more difficult to manage than simple coppice as it is necessary to manage the number, age class distribution, and location of large overstory trees which affect the growth of the understory crop. The underwood is managed as simple coppice, and after cutting each coupe the number and age class distribution of the standards present is adjusted: it is necessary to remove the oldest, reduce numbers of those of intermediate ages, and recruit new standards. This system is rarely used in the tropics.

Coppice Selection System

This method is similar to that for the selection system in high forests. Within the woods managed using this method the stools have populations of stems that are both of different sizes and ages. A target diameter for the product is set, and the age at which the crop achieves this fixes the length of the rotation: this period is divided into a suitable number of felling cycles and the woodland area is divided into a number of annual coupes which equals the number of years in the felling cycle. Harvesting of stems that have reached the target diameter occurs annually within one of the coupes; all smaller stems remain uncut. This is a special system which is rarely applied and is only likely to work well with shade-bearing species; for example, it has been used with *Fagus sylvatica* on poor ground in mountainous areas where the remaining canopy can have advantageous effects protecting both the new shoots and soil from damaging environmental factors such as frost, drought, and erosion.

Pollards

A pollard is a tree that is cut like coppice, but the new shoots grow from a trunk that is several meters long and they are not subjected to browsing damage from animals which can be allowed to graze beneath the trees. The branches are harvested periodically, after one or more year's growth, when the crown is partially or totally removed. Although ancient pollards persist and others managed for ornamental purposes are often seen in urban areas, this method of management is generally unimportant in the developed world. However, in arid regions of the tropics pollarding remains an important method of management to provide products such as fuelwood and animal fodder.

Biology of Coppice Shoots

The ability of trees to resprout is an adaptation that promotes survival after damage to the aboveground parts of the tree by a variety of factors such as fire, storm damage, and pathogens. Not all species of tree will produce coppice shoots and the phenomenon is more common in angiosperms than gymnosperms (**Table 2**). Some species regenerate more readily from

Table 2 Illustrative list[a] of angiosperms and gymnosperms that have been reported to regenerate by coppice shoots

Angiosperms	*Gymnosperms*
Acacia spp.[b]	*Araucaria araucana*
Acer pseudoplatanus[c]	*Cryptomeria japonica*
Aesculus hippocastanum[c]	*Cunninghamia lanceolata*
Albizzia spp.[b]	*Pinus echinata*
Alnus glutinosa	*Pinus rigida*
Betula pendula	*Pinus serotina*
Carpinus betulus[c]	*Sequoia sempervirens*
Castanea sativa	*Taxodium distichum*
Cornus florida	
Corylus avellana	
Eucalyptus spp.[b,c]	
Fagus sylvatica[c]	
Fraxinus excelsior	
Gmelina spp.[b]	
Liquidambar styraciflua	
Nothofagus obliqua	
Platanus occidentalis	
Populus spp.[b,c]	
Prunus serotina	
Quercus spp.[b]	
Salix spp.[b,c]	
Sorbus aria	
Tectonia grandis	
Tilia spp[b,c]	
Ulmus spp[b,c]	

[a] This list is not exhaustive.
[b] Many species or clones in this genus are known to produce coppice shoots.
[c] One or more species in this genus is reported to produce coppice shoots from adventitious buds (i.e., stool sprouts).

stumps than others, for example regrowth of *F. sylvatica* is poor relative to that of *Alnus glutinosa* and *Castanea sativa*. The capability of individuals within a species to regenerate from cut stumps varies with a variety of factors such as the age, size, and vigor of the tree prior to felling.

Origins of Coppice Shoots

Two types of coppice shoot are recognized, these develop from either suppressed or adventitious buds on the stump remaining. In the North American literature these are termed stump and stool sprouts respectively. In addition some species produce root suckers which are new shoots that grow from adventitious buds formed on the tree's roots.

Stump sprouts These are the most common type of coppice shoots found on broadleaved trees. As shoots of broadleaved trees grow they produce lateral buds that are associated with both leaves and bud scales. Most of these newly formed buds are suppressed by the apical meristem and do not grow during the season in which they are formed: they become dormant and will not grow into shoots until their dormancy has been broken by exposure to winter conditions or by other causes. The fates of lateral buds vary: on a typical temperate broadleaved tree some near the shoot tip form branches; many will die; and others, often the smallest, remain suppressed and return to the dormant state growing slowly outwards as the stem increases in diameter. Throughout subsequent annual cycles of growth the suppressed buds remain poorly developed, but they may divide to form large clusters of small buds embedded in the bark. Such suppressed buds are the primary source of most coppice shoots.

Stool sprouts Coppice shoots can also grow from adventitious buds that develop from tissues not closely associated with suppressed buds. Although many woody plants have the potential to form adventitious buds few are formed on stems. When a tree stem is cut adventitious buds and coppice shoots often arise in the ring of callus that develops between the wood and the bark of the stump. Unlike suppressed buds most adventitious buds do not undergo a period of dormancy and they develop into shoots in the season in which they are formed. Whereas suppressed buds are connected to the vascular system via a vascular trace, adventitious buds and shoots must develop a new connection with the plant's vascular system. Adventitious coppice shoots are uncommon, short-lived and generally unimportant in the regeneration of most broadleaved trees (**Figures 2** and **3**).

Silvicultural Factors

The silviculture of traditionally managed coppice woodlands evolved through centuries of practical experience, and there has been relatively little detailed research to investigate and understand the general biology of established coppice stools and shoots. In contrast, considerable effort has been expended during the last 10–20 years studying the growth, physiology, yield, establishment, harvesting, etc., of short rotation coppice crops. Most detailed knowledge on the biology of coppice comes from observations made on regrowth from stumps of single-stemmed trees that have not previously been coppiced, rather than complex multistemmed coppice stools. Many studies have shown that regrowth from such stumps following felling is influenced by age and diameter, but as these are related, their individual effects are difficult to disentangle.

Number and growth of coppice shoots For most species it is not possible to give precise advice about the effect of either stump size, or age, on the probable number of shoots that will be produced

Figure 2 Stump sprouts growing from suppressed buds on an established stool of hazel (*Corylus avellana*). Courtesy of the Forestry Commission.

Figure 3 Stool sprouts growing from adventitious buds formed in the cambium of a recently felled 60-year-old beech tree (*Fagus sylvatica*). Courtesy of the Forestry Commission.

and how they will grow. In general there are relationships between either stump diameter or age, and number of shoots produced and their initial growth. The relationships vary with species and site but overall the number and growth of shoots tend to decline with the size and age of stumps.

Mortality of stumps In general, the mortality of stumps tends to increase with both age and size, but the relationships vary with species. Site quality may influence the success of coppicing by its effect on vigor with slow-growing stools on poor sites re-growing less well than those on good sites. Although several suggestions have been made to explain the decline in shoot numbers and survival of stumps as they become older or larger, there has been little detailed study. The changes may be related to the loss of viable dormant buds from the stem either due to age or reduced vigor; the presence of a thick bark which restricts the growth of deeply embedded buds; and changes that occur when the trees reach the age at which they flower. In productive, managed woodlands dead stools can be replaced by planting or layering (a form of vegetative reproduction using shoots of live stools).

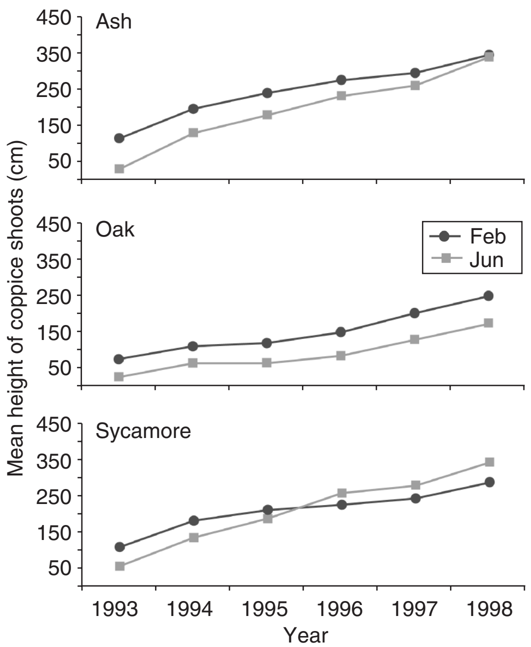


Figure 4 Mean length of the three longest shoots that regrew from stumps of 6-year-old saplings of ash (*Fraxinus excelsior*), oak (*Quercus robur*), and sycamore (*Acer pseudoplatanus*) felled in February or June 1993. The height differences gradually disappeared for *F. excelsior* and *A. pseudoplatanus,* but after six growing seasons the shoots on stumps of *Q. robur* felled in June remained shorter than those cut in February. Reproduced with permisssion from Harmer R and Howe J (2003) *The Silviculture and Management of Coppice Woodlands*. Edinburgh, UK: Forestry Commission.

Seasonal effects Season of felling can influence regrowth and whilst there is some variation between species, it has generally been found that stem survival, and initial numbers and growth of new shoots (**Figure 4**), is usually better when trees are cut during the dormant season. However, this is not necessarily true of all species and in subsequent years the initial differences in numbers and growth of shoots may disappear (**Table 3**). Due to insufficient growth and hardening-off, shoots produced late in the season after summer cutting can suffer more severe winter damage than those that grow early in the season.

Height of the stump The position of the cut and size of the stem remaining can influence subsequent growth. The initial number of shoots produced by some species increases with stump height but differences decline with time. When stumps are cut high the probability of butt rot occurring in the stems that develop is increased. This can have consequences for both the quality of stems in stored coppice, and the longevity of the stool. On some species, the shoots that arise on high-cut stumps develop from buds in areas of thick bark which constricts development of the vascular connection and can affect the stability of the coppice shoot. Shoots that arise at or below ground level can develop their own root systems.

Longevity of Stools

The lifespan of a stool will depend on a variety of factors including species, environment, and management: good growing conditions where soils are fertile, the climate is favorable, and overstory canopy cover is low, will enhance longevity of the stools. Those that are cut on a regular rotation when stems are young and of small diameter will survive longer than those that are cut on less regular, long rotations. Neglected stools can survive for many years with stems attaining large dimensions, but their ability to regrow after cutting will decline with age.

Table 3 Mean number of coppice shoots after 1 and 6 years of regrowth on stumps of three species that were 6-year-old saplings when they were felled in February, April, or June in 1993[a]

	February		*April*		*June*	
	1 year	*6 years*	*1 year*	*6 years*	*1 year*	*6 years*
Fraxinus excelsior	7.8	3.1	10.4	4.2	7.3	3.8
Quercus robur	8.1	4.5	6.7	4.6	7.8	4.2
Acer pseudoplatanus	6.4	3.2	9.0	3.9	11.6	3.6

Reproduced with permission from Harmer R and Howe J (2003) *The Silviculture and Management of Coppice Woodlands*. Edinburgh, UK: Forestry Commission.

[a] Over the period of observation there were, for all species, a reduction in the number of branches present on the stump, and a decline in the relative differences between months of felling.

Browsing Animals

Although coppice shoots can be used as a source of fodder, the browsing of shoots during the early years of regeneration can have an adverse effect on the re-establishment of canopy cover. Prolonged severe browsing can ruin crops, kill stools, and seriously degrade woodland. Provision of adequate protection to the stools from browsing animals is probably the most important operation necessary to ensure successful regrowth of new shoots. Whether the method used is physical exclusion of animals, or control of population size, it must be of sufficient duration to allow re-establishment of robust shoots on stools throughout the woodland. The length of time for which protection is required will vary with a variety of factors including tree species, growing conditions, and type of animals present. Alternatively browsing damage can be avoided by managing trees as pollards.

Management of Stools and Standards

Woodland management by coppicing can play an important role in maintaining biodiversity by providing a wide range of habitats created by variation in both time and space across a range of factors such as structure, light environment, and age of trees. Relative to high forest, traditionally managed coppice woodlands have a large amount of open space and edge habitats, and a range of tree size and age classes, varying from newly regenerating shoots to mature standards. Consequently, the apparent biological interest in a small area of coppice may be greater than for a similar area of high forest. Although coppice woodlands are traditional and provide a sustainable resource, they are managed and have characteristics that differ significantly from natural woodlands including: the size and rate of gap formation; the age structure of trees and compartments; species mixture; amount of dead wood; size; and the flora and fauna present. Many former coppice woodlands have been transformed to high forest and although this trend is likely to continue there are good reasons, both cultural and biological, for the retention of some woodland under traditional systems of coppice management. However, such woodlands must be managed using best available practice otherwise their value may diminish.

Stool Management

Failure to manage stools within a woodland correctly may lead to their death and changes in a number of woodland characteristics; for example, a reduction in stool density and canopy cover, and a change in the structure and species mixture.

Method of cutting The quality of the cut is more important than the tool used. It is important that cuts are clean with no separation of the bark from the remaining stump. Traditionally coppice was cut manually using hand-tools, and whilst these may still be appropriate for young stems with small diameters (e.g., 7–8-year-old *Corylus avellana* stems for hurdle making, or 2-year-old *Betula pendula* for brooms and horse jumps) a chainsaw is probably the only realistic option for cutting most stools (**Figure 5**). The systematic spacing of stools, uniformity of growth, and the easy terrain of sites with young short rotation coppice allows mechanized harvesting. However, efficient use of harvesters within traditional coppices is difficult due to the variable distribution, growth, size, and structure of stools; the terrain; and the need to avoid damage to stools that will regenerate to produce the next crop.

Angle of cut Tradition suggests that stems should be cut to ensure that water drains from the center of the stool; the cut surface of the stump should have a sloping face to shed water, and be south-facing to dry more quickly. Although there is generally little quantitative evidence to support these logical suggestions, young red alder stumps with a flat surface showed greater mortality than those with cut surfaces having southerly or westerly aspects (**Figure 6**). The structure of many coppice stools will make it difficult to fell stems leaving a cut surface with a generally southerly aspect, but all cuts should be clean and wherever possible slope towards the outside of the stool.

Position of cut Maintain the stool at a level close to the ground. When establishing new coppice stools from single-stemmed trees cut as close to the ground as possible, on existing stools fell just above the height of the last cut leaving short stumps from the most recent stems. It is generally inadvisable to cut into old wood below the level of the last cut as successful resprouting is less likely to occur.

Time of felling The best time to cut coppice is during the dormant period: the bark is less likely to tear from the wood; stump mortality will probably be reduced; and new shoots are likely to grow better and suffer less frost/winter damage than shoots formed after a summer cut.

Conversion to High Forest

Many woods that were traditionally managed as coppice have developed a high forest structure following growth after the cessation of regular

Figure 5 Coppice worker using a billhook for felling and trimming 3-year-old *Castanea sativa* stems that will be made into walking sticks. Courtesy of the Forestry Commission.

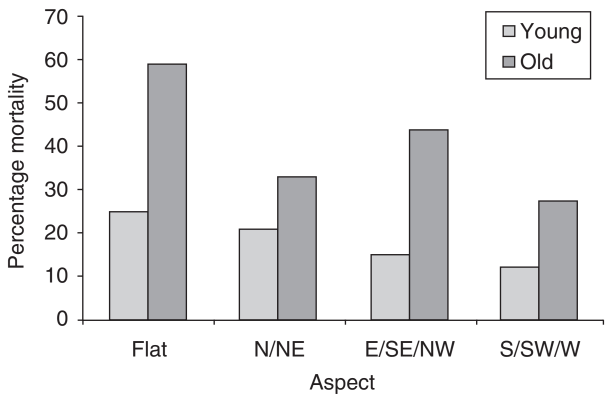


Figure 6 Percentage mortality of young (1–5-year-old) and old (6–16-year-old) red alder stumps in relation to aspect of cut surface. Data adapted from Harrington C (1984) Factors influencing initial sprouting of red alder. *Canadian Journal of Forest Research* 14, 357–361.

cutting. These crops, which comprise trees known as ‘stored coppice,’ are simple to create but may not be appropriate for all sites or species. This is the situation that currently affects many neglected woodlands with overmature coppice stems, on old coppice stools which, if cut, may neither survive nor produce a suitable crop for the future.

Stored coppice Although storing coppice is a simple procedure it has a number of drawbacks which may influence the decision on whether it should be used. In comparison to single-stemmed trees of the same species, growth may be inferior, the stems be of worse form with more butt sweep, and the inclusion of wood from the old stool may cause stem defects. The trees produced are often less stable than single-stemmed trees grown from seed which may cause problems of windthrow after subsequent felling operations. The quality of stored coppice can be improved by thinning to remove from the stool all stems except those which are judged to be the straightest and most vigorous: the stools may be ‘singled,’ leaving only the best stem. Storing coppice is likely to be most successful where stools are young, vigorous, have been cut close to the ground, and are free from decay.

Managing Standards

Well-defined, systematic procedures to control yield from standards have been developed but these have generally fallen into disuse as most large timber is now grown as high forest. The fundamental principle of the method is that number of standard trees in each age-class should be approximately half of that in the next younger class, with about 50–100 standards per hectare of all age-classes, most of which are young: a possible age-class structure is shown in **Table 4**. When the underwood is felled at the end of each rotation the mature trees (age-class IV) are felled, new standards (age-class I) are

Table 4 Possible age-class structure for standards in coppice cut on a rotation of 20 years. Adapted with permission from Harmer R and Howe J (2003) *Silviculture and Management of Coppice Woodlands*. Forestry Commission, UK

Age class of standard	*Rotation number*[a]	*Number of stems to remain*[b] *(ha^{-1})*
I (young)	1	50
II	2–3	30
III	3–4	13
IV (old)	4–6	7
Total		100

[a]The age of the standards defined by the number of coppice rotations for which they have been retained.
[b]Number of standards retained in each age-class.

recruited and intermediate ages thinned. The number of coppice cycles for which a standard is retained depends on species, length of coppice cycle, growth rate, and size of timber required.

The adverse effect of standards on the growth of coppice is well known, and is related to the canopy cover and crown density which influence light, water, and nutrient availability. Silvicultural systems of coppice with standards describe the management of standards in terms of stem numbers, rather than size of individual tree canopies and the amount of shade cast. Under well-managed coppice with standard woodlands, most standards should be young and small, and cast little shade compared with those that are old, large, and cast a lot of shade. Species differ in the amount of shade that they cast, varying in both size of crown produced and the density of leaf cover within the crown. This affects the density of standards of each species that can be maintained with a woodland, and trees such as *F. sylvatica*, *Tilia cordata*, and to a lesser extent *Quercus* spp., which have very dense crowns that can cast heavy shade, should be avoided.

The Future for Coppice Woodlands

In many areas of the world existing coppice woodlands are relics of a bygone age when there was a much greater demand for the crops produced by this simple method of management. Many woodlands have already been converted from coppice to high forest and this trend is likely to continue as the crops produced are more marketable. In contrast, the amount of short rotation coppice may increase if the promises of cost-effectively producing a long-term sustained yield can be turned into reality, and suitable methods of utilization firmly established.

Well-managed coppice woodlands regenerate quickly and the period of time without canopy cover is short relative to that of some high-forest systems where large gaps are made in the canopy. This will have obvious benefits for protection of the physical environment. Similar benefits may be obtained by use of continuous cover forestry, but the temporal and spatial variation in characteristics such as distribution and age-class of crop, and the light environment within the woodland, will differ to that for coppice. Conversion to such high-forest systems is likely to lead to the loss of species that flourish under the routine system of gap creation produced by regular coppicing. The establishment of short rotation coppice plantations may have positive benefits for a variety of characteristics including biodiversity, nutrient capture, and erosion, especially when established on agricultural land.

As traditional coppice woodlands provide a cultural link with the past and can be of important biological interest they are unlikely to disappear completely, but it seems likely that the area of woodland actively managed as coppice will continue to decline.

See also: **Operations**: Small-scale Forestry. **Plantation Silviculture**: Short Rotation Forestry for Biomass Production; Sustainability of Forest Plantations. **Silviculture**: Silvicultural Systems. **Temperate and Mediterranean Forests**: Temperate Broadleaved Deciduous Forest. **Tree Physiology**: Physiology of Vegetative Reproduction; Shoot Growth and Canopy Development.

Further Reading

Buckley GP (1992) *Ecology and Management of Coppice Woodlands*. London: Chapman & Hall.

Evans J (1992) *Plantation Forestry in the Tropics*, 2nd edn. Oxford, UK: Oxford University Press.

Harmer R and Howe J (2003) *The Silviculture and Management of Coppice Woodlands*. Edinburgh, UK: Forestry Commission.

Harrington C (1984) Factors influencing initial sprouting of red alder. *Canadian Journal of Forest Research* 14: 357–361.

Kozlowski TT (1971) *Growth and Development of Trees*, vol. 1, *Seed Germination, Ontogeny, and Shoot Growth*. New York: Academic Press.

Kramer PJ and Kozlowski TT (1979) *Physiology of Woody Plants*. New York: Academic Press.

Macpherson G (1995) *Home-Grown Energy from Short-Rotation Coppice*. Ipswich, UK: Farming Press.

Matthews JD (1989) *Silvicultural Systems*. Oxford, UK: Oxford University Press.

Peterken GF (1996) *Natural Woodland*. Cambridge, UK: Cambridge University Press.

Rackham O (1980) *Ancient Woodland*. London, UK: Edward Arnold.

Forest Dynamics

A E Camp and C D Oliver, Yale University, New Haven, CT, USA

Introduction

Forest stand dynamics (stand dynamics, forest development, forest succession) integrates plant community and population ecology, silvics, physiology, morphology, and knowledge about biotic and abiotic disturbance events and regimes. Forest stand dynamics informs silviculture since it allows predictions of the pathways along which forests could develop given initial conditions, growth, silvicultural operations, natural disturbances, regeneration, and other natural and human influences on the system. Practicing foresters and applied ecologists require a thorough understanding of stand dynamics to predict how stands will change, to determine what values they will provide and when, and to manipulate them as appropriate to ensure they provide the desired flow of values over time. Forest stand dynamics lays the groundwork for landscape management, in which the changes to many stands are coordinated across the landscape and through time.

The defining scale of forest stand dynamics is the individual stand – a relatively homogeneous area of vegetation, soils, climate, and disturbance history that can be easily discerned from an aerial photograph. The primary foci at this scale are the interactions that occur among individual plants and between plants and abiotic factors. Explicit in the term is that these interactions occur in time; forests are dynamic and can be expected to change, albeit in predictable ways. Despite the variety of climates, soils, and evolutionary backgrounds of forests in different parts of the world, they follow remarkably similar patterns of stand dynamics in those temperate, boreal, and tropical forests where stand dynamics have been studied. These similarities probably arise because their physiological similarities leads trees to follow a 'uniformity of processes' in their interactions.

Stand Structures and Development (Silvicultural) Pathways

A useful conceptualization of forest stand dynamics is that, over time, the structure of a stand changes (**Figure 1**). Stand structure refers to the spatial attributes of the living and dead plants and plant components in the stand: the species, sizes, and spatial distributions of living and dead trees and other plants and their components. These structures are helpful in identifying the suitability of the forest for different values – such as habitats for different species, timber quality, and recreation. Stand structure also contributes to risks of fires, insects, and windstorms. The sequence of structures that a particular stand moves among is described as its 'development pathway' or 'silvicultural pathway' (**Figure 2**). The pathway followed by a stand is determined by a number of factors; stands are not predestined to follow a single, specific pathway. Furthermore, pathways are not unidirectional and do not culminate in a fixed endpoint, although a now outdated ecological paradigm previously described forest succession as a fixed, unidirectional pathway towards a stable condition termed the 'climax' forest.

While it is possible – and perhaps sometimes useful – to differentiate many stand structures for a particular forest type, a relatively small number are sufficient to provide a structural overview of a majority of the world's forests. This article refers to five structures commonly encountered as forests develop. Some structures may not occur in some forest types, and more detailed structural classification systems may better explain certain objectives. The five structures used in this article are termed open, dense, understory, complex, and savanna (**Figure 1**). Subsets of these structures can be used to depict the different pathways a stand can follow. As an example of one pathway, a stand initiating after a major (stand-replacing) disturbance and with abundant regeneration would develop from an open structure to one characterized by density-dependent mortality (dense structure). Eventually the stand might develop an understory. Then, a partial disturbance might leave only a few large trees (savanna). As younger trees establish and grow beneath the sparse overstory, the complex structure could result.

One area of expertise that distinguishes professional foresters, especially silviculturists, is the ability to determine the pathway a stand is currently following, predict alternate pathways the stand could follow given various natural disturbances or silvicultural operations, and prescribe silvicultural operations that direct the stand along a desired pathway. The pathways and structural stages are most easily predicted and managed by first understanding the causes of changes in structures along the different pathways.

Ecological Processes Underlying Stand Dynamics

Stands contain a variety of organisms that happen to occur together at the time of observation. Paleoecological research indicates that different trees and

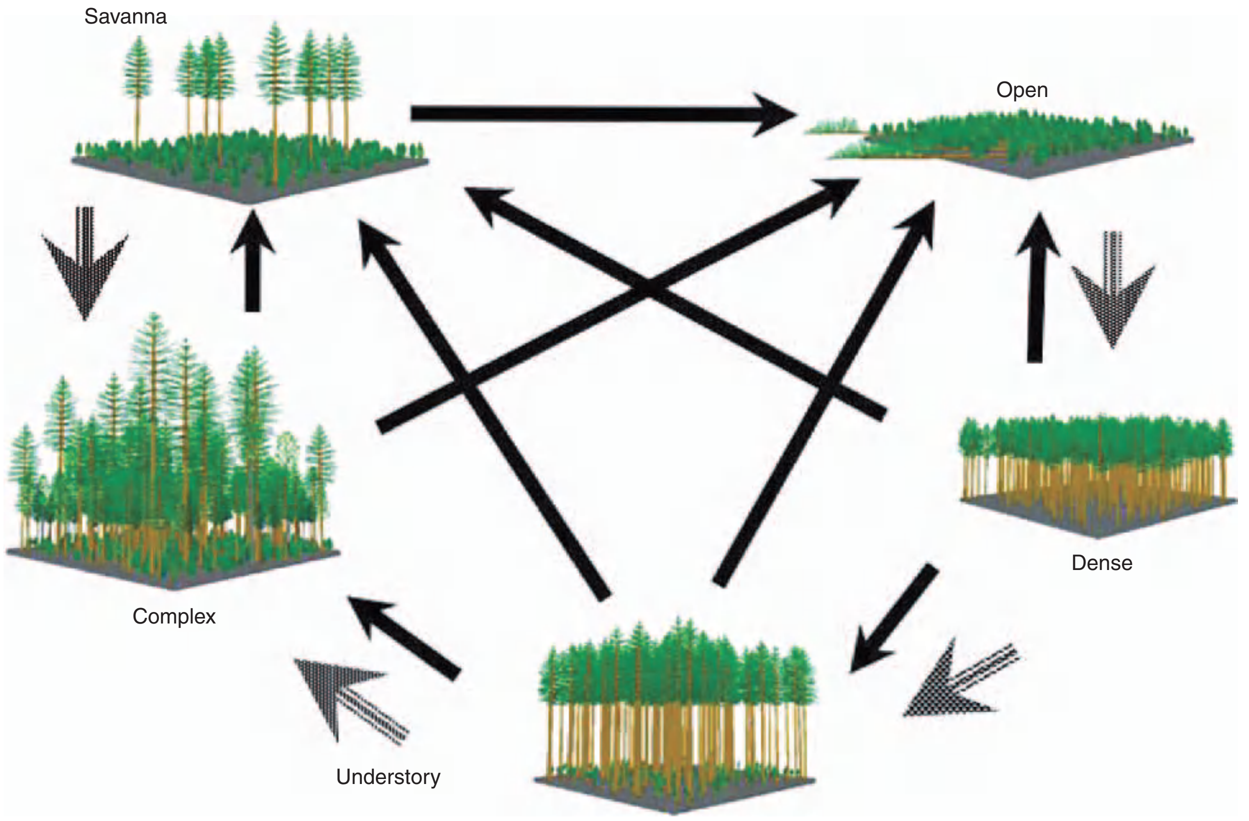


Figure 1 Stands change in structure over time with growth (large, striped arrows) and disturbances (solid black arrows). A robust classification suitable for many forests and purposes are the five structures shown here; however, different structure classifications may be better for certain purposes. © Professor Chadwick Oliver.

other organisms have lived together for only a few hundred or thousand years, have migrated from different locations at different rates, and in many instances are continuing to migrate to new locations. Different organisms evolve at a variety of timescales, with new generations occurring several times each year in insects but only every hundred years or more in trees. Because evolution in trees occurs over very long timescales, trees are slow to evolve mutualistic relationships with their associated species. Most evidence suggests that the dominant interactions among trees are best explained in terms of competition. Trees and other green plants require the same basic factors for survival and growth – light, moisture, nutrients, and warmth. In general, all tree species generally grow best when they receive these factors in the same, relatively narrow ranges of concentration, rather than having diversified into growing best at different ranges. For example, nearly all tree species grow best in full sunlight, under similar soil moisture regimes, and at approximately the same temperatures. A primary difference among species is that various tree species have evolved different abilities to tolerate (survive at) low levels of one or more of these factors. Species that tolerate a wide range of conditions are termed site insensitive and are considered to have wide ecological amplitudes. Species that have a low tolerance for growth factor limitations are termed site sensitive. In general, relative tolerance or intolerance is specified with respect to a particular growth factor, and tolerances such as shade or drought tolerance or intolerance in species are commonly described (**Figure 3**).

Different growth factors, or resources, needed by trees are frequently limited in the natural environment. Trees compete for these limited resources, with different individuals and species gaining a competitive advantage depending on whether they were first to access the growth factors and on whether they can efficiently use the specific range of growth factors found on the site at a given time. Different growth factors become limiting at different times of the day, month, year, and stand development stage. Sometimes it is the interaction of growth factors that determines whether growth is limiting. It is convenient to refer to the net presence of the factors required for growth as the available 'growing space' within a stand. Growing space fluctuates with seasonal variations in rainfall, temperature, and other factors. Growing space is referred to as 'occupied'

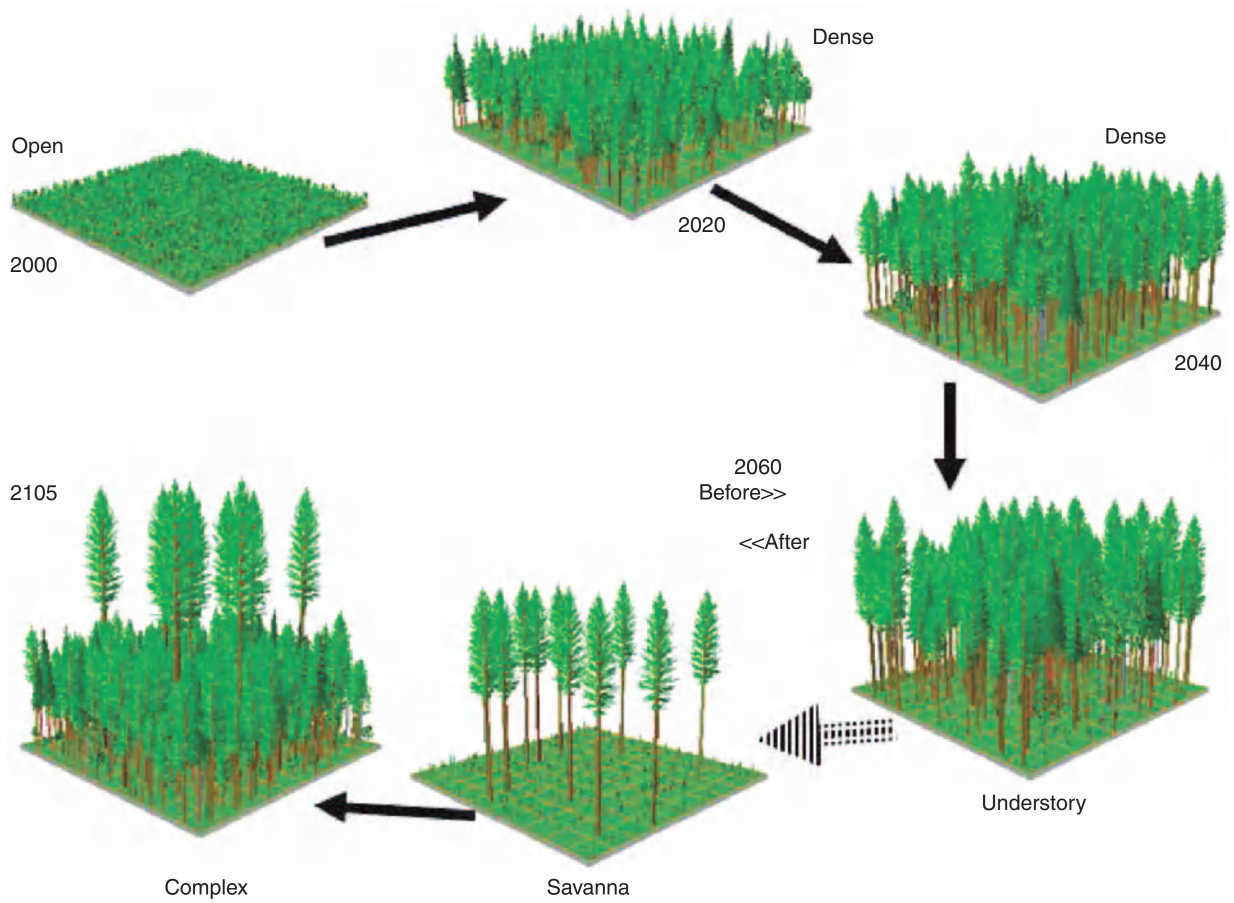


Figure 2 The change in a stand over time caused by growth, natural disturbances, and silvicultural operations is its development pathway or silvicultural pathway. The pathway is depicted here by the stand's changes in structures. This stand modeled here began after a stand-replacing disturbance in 1995, and was shelterwood treated in 2080. A stand can potentially follow many different pathways. © Professor Chadwick Oliver.

when a tree or other plant's roots or leaves are utilizing the moisture or light growing space and excluding other plants from utilizing it. Growing space is available when it is not occupied, such as immediately after a disturbance or during early spring in a field previously occupied by annual plants.

Trees compete with each other over available growing space. The ability to compete successfully is a result of the ability of an individual tree to capture this growing space. Trees that compete successfully become the dominant trees in the stand. Trees that lose the competition for growing space are eliminated or relegated to subordinate positions if they can tolerant less-than-optimal ranges of the growing space. The latter instance is more commonly found where competition for growing space occurs among trees of different species. Competitive ability under a given circumstance integrates species' physiological traits, such as rapid juvenile growth or early germination, with the environment.

Stand dynamics is also concerned with the impacts of natural and human disturbances on the ecological processes, pathways, and structural characteristics of stands. All forests are impacted by disturbances, with different regions of the world characterized by different disturbance regimes. A disturbance regime refers to the integration of the typical kinds, magnitudes, frequencies, and sizes of disturbances impacting a region. In general, disturbances that occur frequently are of less magnitude than disturbances that rarely occur. On one end of the disturbance spectrum are infrequent events such as volcanic eruptions or continental glacial expansions. Other disturbances include hurricanes, landslides, avalanches, fires, ice storms, and insect outbreaks. Some frequent disturbances (at least in some locations) include thunderstorms, windstorms, livestock grazing, and endemic insect and pathogen activity.

Disturbances affect forests by physically deforming or killing trees and other plants and by improving or degrading the soils, depending on specific characteristics of the disturbance. Growing space becomes available when trees are killed; following a disturbance residual and newly initiating trees

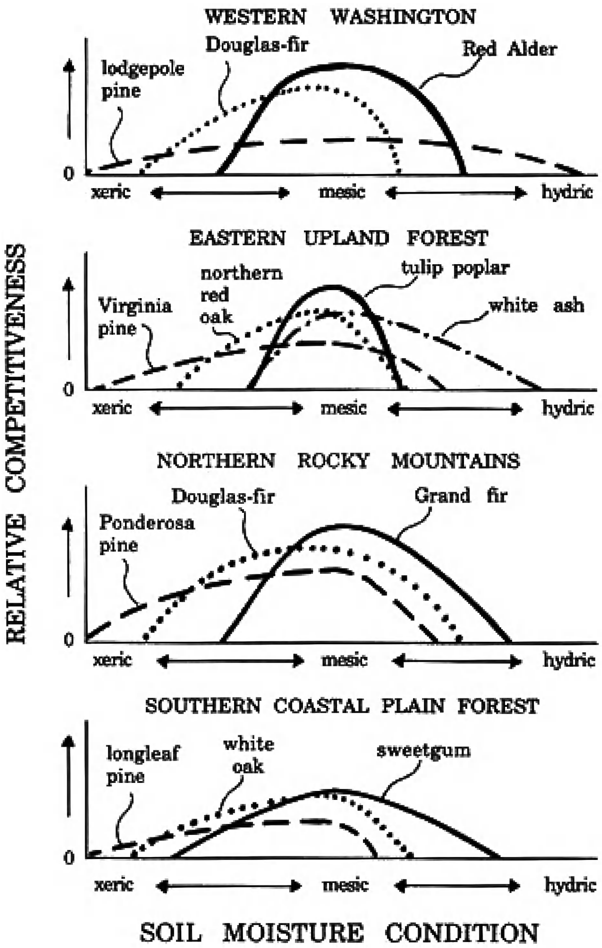


Figure 3 Schematic of relative growth (and competitiveness) of selected species growing together in four forest types found in the USA. All species grow most vigorously under optimum (mesic) conditions, but each species is found where it can outcompete other species, or where other species, cannot grow at all. Reprinted from Oliver CD and Larson BC (1996) *Forest Stand Dynamics*, updated edn, Copyright © John Wiley & Sons Inc. Reprinted by permission of John Wiley & Sons Inc.

reoccupy this growing space. The forest that develops following the disturbance could have a similar or very different structure than the preceding one.

Processes, Stand Development, and Development Stages

As a stand develops, many interactions, or processes, occur among trees and between trees and the environment, with different processes becoming more dominant influences as stands change. It is useful, therefore, to divide the processes of stand dynamics into development stages that reflect the dominance of different processes. Not surprisingly, these development stages are similar to, but not identical with, the stand structures. Four development stages are commonly recognized, but like the stand structures can, if required, be further subdivided. These development stages are shown in **Figure 4** and are discussed below.

Stand initiation Following a stand-replacing (top left, **Figure 4**) or partial (bottom left, **Figure 4**) disturbance, growing space becomes available. Newly initiating trees, other plants, and surviving residual trees can expand to capture this growing space. Where surviving trees are absent, weak, or infrequent, the growing space is primarily occupied by newly initiating plants. Plants, including trees, have a variety of regeneration mechanisms that confer a competitive advantage depending on disturbance type and magnitude. For example, toppling of mature trees by a windstorm can release small advance regeneration of shade-tolerant species growing in the understory. Because this advance regeneration is already established and has a developed root system, species with this regeneration mechanism have a competitive advantage over species that must regenerate from seeds. Fires consume organic matter (and frequently, advance regeneration) on the forest floor, leaving a nutrient-enriched seedbed that favors species with light, windblown seeds or species that can resprout from the root collar or other underground structure. The different regeneration mechanisms can be listed in a gradient according to their relative advantage following disturbances of different magnitudes. This gradient, and examples of species with different regeneration mechanisms, is shown in **Figure 5**. Ages of newly sprouting trees or advance regeneration released by a disturbance are conventionally considered from the time of release (when the stem begins to grow beyond the forest floor level) rather than from the date of germination. Trees that initiate following a specific disturbance are considered a 'cohort,' regardless of whether they initiated from seed germination, sprouts, advance regeneration, or other mechanisms. On very poor sites, or on sites where seedling establishment is slow, there can be a wide range of ages within a single cohort.

Trees and other plants continue to invade during the stand initiation stage until the growing space is refilled with perennial trees, shrubs, and/or herbs. Refilling the growing space can take many decades where the site (soils and climate) is poor and the only regeneration mechanism is primarily from seeds having a distant source. Alternatively, it can take less than 5 years where the site allows rapid growth and preexisting advance regeneration or sprouts are present at the time of the disturbance. During stand initiation, trees compete for growing space with annual and perennial herbs and shrubs, creating a great diversity of potential interactions.

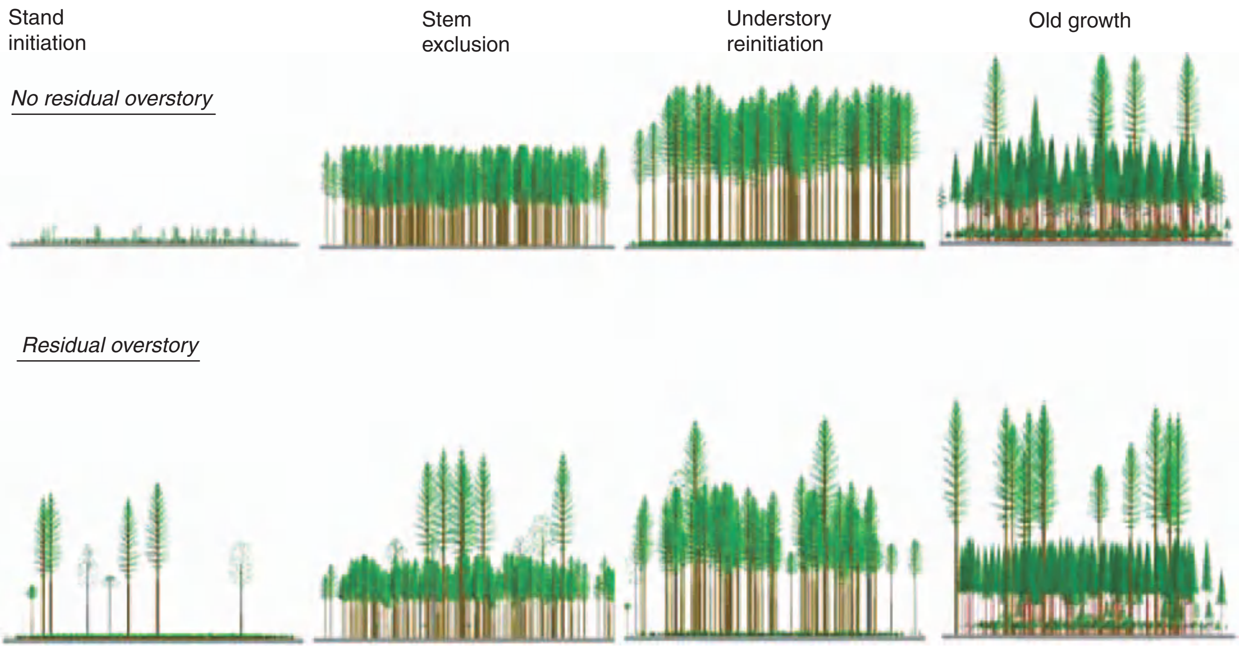


Figure 4 Stages of forest development over time (left to right) when no disturbances occur following the initial one (occurring just before stage at far left). Different ecological processes are dominant during the different stages. Top: the stages when no residual trees were left following the initial disturbance. Bottom: the stages when some residual trees are left following the initial disturbance. © Professor Chadwick Oliver.

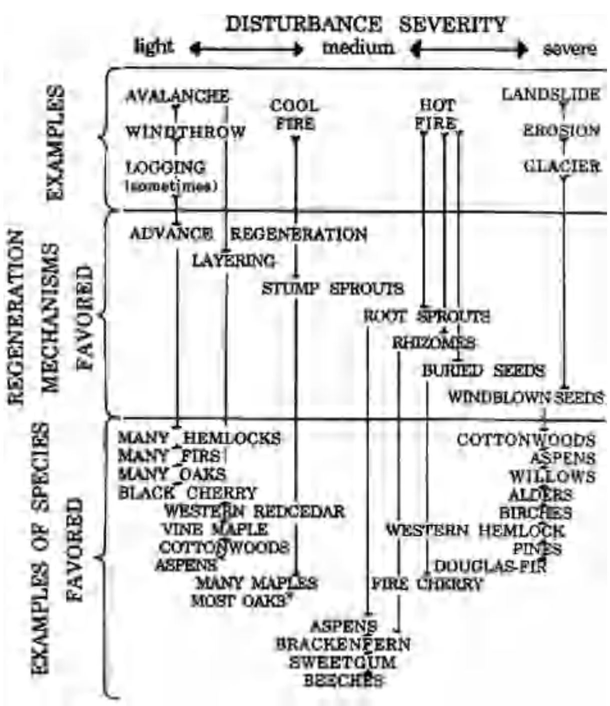


Figure 5 Disturbance 'severity' is here listed as a gradient according to how much of the understory, forest floor, and soil is destroyed. Different forms of sexual and/or asexual regeneration have competitive advantages depending on the severity of the disturbance. Species listed occur in different forest types in the USA. Reprinted from Oliver CD and Larson BC (1996) *Forest Stand Dynamics*, updated edn, Copyright © John Wiley & Sons Inc. Reprinted by permission of John Wiley & Sons Inc.

The species, or groups of species, that gain the competitive advantage during stand initiation can dominate the growing space during the subsequent stem exclusion and understory reinitiation stages, which can last several hundred years. Consequently, a stand can be dominated by a different suite of species than those that previously occupied the site, depending on which species gain a competitive advantage because of regeneration strategies, disturbance type, or stochastic factors such as good seed years.

When no residual trees are present, the stand initiation stage reflects the open structure (**Figure 1**). Because many herbaceous species also initiate following a disturbance, this stage usually contains a high diversity of plants, which attracts a high diversity of animals – butterflies, insects, deer, rabbits, and their predators.

When a partial disturbance leaves residual trees from older cohorts, these trees compete with new regeneration for the released growing space. The influence of the residual trees depends on their vigor and number. If residual trees are numerous and vigorous they can completely reoccupy the growing space, preventing a new cohort from establishing, or outcompeting and eliminating any newly initiating trees. The stand then quickly returns to a dense structure. If a new cohort does establish but is so suppressed that it remains as advance regeneration, the understory structure develops. If the residual trees are few and widely spaced, the savanna structure develops. As in the open structure, the savanna structure contains a great diversity of herbaceous plants and accompanying animals. The savanna structure can also provide habitat for woodpeckers, raptors, and other birds that utilize the relatively isolated trees. In some instances, presence of these trees attracts birds that disseminate the heavy seeds of species that would otherwise have a difficult time moving into open areas.

Partial disturbances during the stand initiation stage can reduce the competitive advantage of established plants, allowing other species to capture and hold growing space. For example, burning newly regenerating conifer forests in arid parts of the United States can convert them to semipermanent brushfields. Frequent surface fires or grazing can maintain a savanna structure by killing new cohorts of trees and promoting the growth of grasses in the growing space between large trees.

Stem exclusion Once growing space is fully occupied, intense competition occurs among existing trees, generally excluding new cohorts. This stage is referred to as the stem exclusion stage and can last between about 40 years for shade-intolerant pine species to over 100 years in mixed species stands that include shade-tolerant species.

Some natural stands and most plantations occur as monocultures of trees that regenerate within relatively short time-frames. Because conspecific trees require an identical set of growth factors, development pathways and resulting structures in monocultures are somewhat limited. Unless moisture or nutrients are limiting, trees will grow vigorously during the stand initiation and early stem exclusion stages until their crowns touch and sunlight becomes limiting. In a uniformly spaced stand with trees of nearly identical ages, the period of vigorous growth will be similar for all trees. In a stand with more irregular spacing and age, some trees will continue to grow vigorously while others will be less competitive, develop small crowns, decline in vigor, and become relegated to subordinant positions. The more vigorous trees in single species stands are generally those that have a competitive advantage because of microsite, age, spacing, and/or genetic makeup. In general, trees in single species stands do not grow well after being relegated to a subordinant position in the stand. Species that are more shade tolerant can sometimes persist, albeit in a condition of low vigor. In a single species, single cohort stand, the canopy will remain as a single layer, with crown differentiation into dominant, codominant, intermediate, and overtopped trees (**Figure 6**).

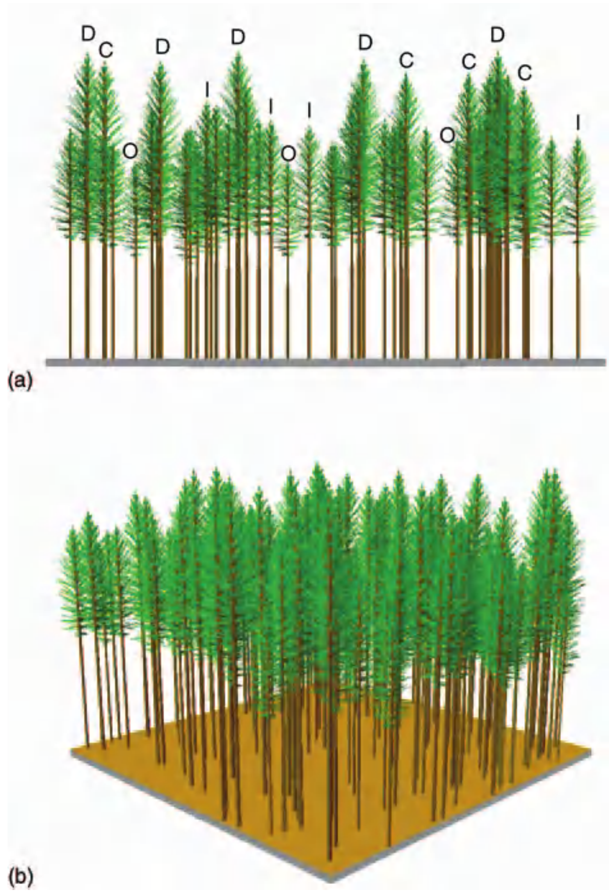


Figure 6 (a) Single species, single cohort stands usually develop in a single stratum; the trees differentiate into crown classes within this stratum. D, dominant; C, codominant; I, intermediate; O, overtopped. (b) The same stand as above, from perspective view. © Professor Chadwick Oliver.

During the stem exclusion stage, dominant trees continue to grow in height and diameter. Subordinant trees continue to grow in height, but diameter growth as well as insect and disease resistance decline considerably. There is less tendency for trees to differentiate in stands that are uniformly spaced, on poor soils, and/or have limited genetic variability. Trees in such stands simultaneously can decline in diameter growth and insect and disease resistance, with the result that entire stands become highly susceptible to wind damage, ice breakage, and insect attacks. In differentiating stands, the number of trees in the stand decreases over time as the average size of the tree (measured in diameter or total volume) increases. The relationships among tree sizes, numbers, and other measures have been quantified and studied.

Multiple tree species regenerating after a disturbance follow a similar pattern of intense competition during the stem exclusion stage. The primary difference between mixed and single species stands is that the different species in mixed stand have different tolerances for growing under conditions where resources are becoming limited. A slower growing species with greater tolerance for light-limited conditions may survive if overtopped by a faster-growing species. Because of these differences among species, the canopy of a mixed species stand can segregate into different strata representing the variety of species' tolerances for growing in shade (**Figure 7**). Trees in lower strata grow very slowly because of the reduced light environment, and eventually are much smaller than upper stratum trees in the same cohort. Small trees in lower strata have been mistakenly assumed to be younger, with the stand considered the result of an uneven or all-age pattern of development. Mixed species, single cohort stands often produce trees of higher timber quality more economically than in pure species or multiple-cohort (uneven-aged) stands. Trees that are eventually relegated to lower strata surround the trees that will eventually form the B-stratum when the stand is young, acting as 'trainers' and keeping the B-stratum crop trees pruned. The B-stratum tree crowns eventually expand above the trainers avoiding the need for a costly thinning.

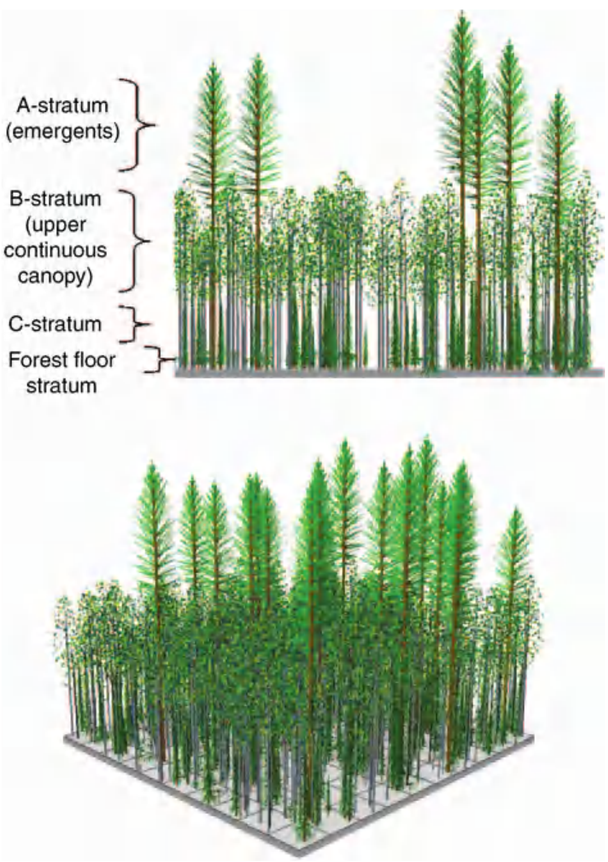


Figure 7 Mixed species, single cohort stands can develop into strata. Nomenclature shown here is common. (a) Within each stratum, the trees can differentiate into crown classes, similar to those in Figure 6. (Multiple cohort stands can develop into similar strata.) (b) The same stand as above, from perspective view. © Professor Chadwick Oliver.

Mixed species stands also differentiate into dominance classes within each canopy stratum. Trees in lower strata will express dominance in essentially the same manner as trees in the upper stratum by retaining a full, deep crown of photosynthetically active tissue (leaves or needles). Dominant trees in lower strata usually do not grow rapidly until released. Upon release these lower stratum dominants are likely to grow more rapidly than the less dominant trees in any stratum, providing they can survive the initial 'shock' of release. While it is possible to have shade-tolerant species in all strata in a stratified, mixed species stand, shade-intolerant species will be found only as emergents (the A-stratum) or in the continuous upper canopy (the B-stratum).

Especially in stands of coniferous species, the forest floor is devoid of vegetation during the stem exclusion stage because most herbaceous plants are eliminated by the vigorous occupation of growing space by the trees. In stands dominated by deciduous trees, shrubs and herbaceous plants that can take advantage of trees' dormant season sometimes are able to persist. Single species stands in the stem exclusion structure commonly create the dense structure. There are generally fewer species of plants and animals in the dense structure than in other structures. Mixed species stands in the stem exclusion stage can assume the dense structure, but are sometimes classified as having the complex structure because of the vertical distribution of their canopies. Mixed and pure species stands in the stem exclusion stage that contain some older, residual trees can be classified as having the complex structure. Such stands may be suitable to more wildlife species than single species, stem exclusion stands lacking residual overstory trees.

Upper and lower strata affect each other's growth in both single and multiple cohort stands. These effects are more pronounced in mixed species stands with more than one cohort. Trees growing immediately beneath an intact canopy experience a light regime that alternates between spots of full sunlight (sunflecks) and shade as the sun moves across the sky. With enough periods of full sunlight, trees in lower strata can retain a full crown and their terminals continue to grow upwards, retaining a single-stemmed form. A light environment that alternates between periods of full sun and shade is termed low shade. A high shade environment develops when trees in the upper canopy grow much taller than trees growing beneath them. Sunlight in this environment is extremely diffuse, with few, if any, sunflecks reaching the understory. Trees growing in high shade develop characteristically flatter tops as the ratio between terminal and lateral branches decreases. These trees die unless they are extremely tolerant of shade, and once released from the effects of this shade, trees may not retain a single terminal leader. Trees in lower strata trees can sometimes affect overstory trees. Especially on sites limited by moisture or nutrients, lower strata trees in the same or younger cohorts can deplete soil moisture and nutrients to such an extent that overstory trees are weakened and invaded by insects and/or pathogens.

Disturbances affect mixed species stands in more complex ways because species differ in their responses to various kinds of disturbances. A fire may selectively kill trees in lower strata because these trees are smaller, have thinner bark, and commonly consist of species more susceptible to fires. Windstorms will generally topple trees in the emergent or upper continuous canopy. Insects and diseases are usually host specific to varying degrees. In this way, disturbances have the potential of reducing the number of species initially present in a stand. Small disturbances in mixed species, single cohort stands can also result in the establishment of new cohorts.

Residual trees of older cohorts can suppress newly initiating cohorts during the stem exclusion stage, depending on the number and vigor of these residual trees. Extreme suppression can kill the younger cohort or relegate it to advance regeneration, as described earlier. Even less extreme suppression will reduce height growth or eventually kill younger trees, with shade-intolerant species killed first. Recent studies suggest that in some instances surprisingly little overstory shade is required to suppress or kill a younger cohort.

The physical appearance of a mixed species, single cohort stand is quite similar to a multiple cohort stand, and the same stratification classification (and crown classes within strata) of **Figure 7** is used in both stand types. Management of these stand types is also similar, recognizing that dominant trees in each stratum are the potentially more vigorous ones and that lower strata trees can become flat-topped, lose their vigor, and possibly die, especially if shade intolerant.

Understory reinitiation Eventually trees grow so large that the death of an individual tree releases enough growing space that adjacent trees cannot rapidly capture all of it, and a new cohort (often a different species that is more tolerant of shade) establishes. The establishment of a new cohort signals the onset of the understory reinitiation development stage. This stage can last for several hundred years because trees in the newly regenerating cohort are commonly so suppressed that they remain in a flat-topped condition near the forest floor as advance regeneration or die within a few years. They are then replaced by more newly germinating seedlings that also may die after a few years. Residual trees of an older cohort can suppress the intermediate cohort and any newly regenerating trees, prolonging their suppression.

The understory reinitiation stage can exhibit the understory structure, although in mixed species stands and in stands with residual older trees it more commonly reflects the complex structure. The understory structure can also result from partial disturbances in the stem exclusion stage that created a new cohort that became suppressed as the forest floor stratum.

Old growth The old growth development stage describes what would happen in the event that no external (autogenic) disturbance event impacted a stand during the lifespan of any of the original initiating trees. The old growth development stage is probably not particularly common in many parts of the world, as fire, wind, insect outbreaks, or other disturbances generally impact a stand before it attains this stage. The old growth stage occurs as overstory trees become increasingly weak and die intermittently, allowing the trees existing near the forest floor in the understory reinitiation stage to grow to the overstory, through a series of suppressions and releases. The resulting stand would consist of shade-tolerant trees in a variety of heights as individual gaps created by senescing overstory trees allowed the released trees to grow at different rates.

Because most tree species live for hundreds of years, a true old growth development stage would not occur until a stand was several hundred years old and had not been impacted by an intermediate disturbance. In some instances of shorter-lived species, this stage might occur much sooner.

The old growth stage would generally take on the attributes of the complex structure; however, most stands identified as having the complex structure are not in the old growth development stage. Instead, they are generally in the stem exclusion or understory reinitiation development stages. These stands are generally made complex by the presence of residual trees and multiple strata (bottom line of **Figure 5**).

These phases of stand development have been observed and documented by foresters and scientists in temperate and tropical forests in many parts of the world. The four phases of stand development are sometimes contrasted with 'gap phase' dynamics, which describes forest development as the ongoing process of recolonization of small openings in the forest that occur upon the death of individual or small groups of trees. The two systems differ mainly in terms of temporal and spatial scales. In some tropical and temperate forests, stand-replacing disturbances occur at longer timescales than the lifespans of individual trees. Senescence and death of individual canopy trees create gaps that are regenerated by seedlings or advance regeneration. As the trees in these gaps grow, they compete with each other for resources. The tree that eventually replaces the gap-forming tree is one that can successfully regenerate and compete in the gap environment. Depending on their geographical location, orientation, and size, gaps can have an abundance or dearth of resources required for tree growth. Trees that can capture resources and/or tolerate lower levels of resources will be favored.

Application of Stand Dynamics to Silviculture

By understanding the processes affecting each development stage and the structures created by the different processes, silviculturists can predict the development pathways that each stand could take and the values that each stand might provide at different times in the future. Moving stands along desired development pathways can be achieved using silvicultural operations as surrogates for natural processes such as disturbances and regeneration. An appropriate silvicultural operation can be prescribed by understanding how the stand will respond. Through understanding the dominant processes occurring within a stand at different development stages, silvicultural operations can be implemented when they will be most effective – at appropriate 'windows of opportunity.' Well-timed silvicultural operations will cause the stand to follow a planned development pathway – a silvicultural pathway.

When in each structure, a stand will provide some values, but not others. For example, an open structure will provide deer and butterfly habitat, but not habitat for 'late successional' species and no opportunity for obtaining timber revenue for a long time. Alternatively, an understory structure will provide some late successional habitat and opportunities for obtaining high-quality timber, but no 'early successional' habitats for deer and butterflies. The full spectrum of forest values can only be obtained when individual stands are managed in concert across a landscape.

Stand Dynamics and the Landscape Scale

Although the primary scalar focus of stand dynamics is the forest stand, knowledge of stand-level processes readily scale up to the landscape. Landscapes are mosaics of individual stands. Landscape vegetation patterns arise from the interactions between vegetation, soils, climate, and disturbances. At the landscape scale, disturbances vary with climate, geomorphology, topography, soils, and vegetation. Some portions of landscapes are very prone to disturbances such that stand development or silvicultural pathways are constrained. Other areas of the landscape are protected from disturbances such as wind and fire and act as 'disturbance refugia' where developmental pathways and structures may differ markedly from those found in the surrounding matrix. At the landscape level, each stand follows developmental pathways and exhibits characteristic structures that reflect its disturbance history and its structure at the time of the disturbance. Like individual stands, landscapes are dynamic, but landscapes still reflect the developmental pathways and forest structures that are possible given the climate, soils, vegetation, and inherent disturbance regimes of the region. Some landscapes are a mosaic of many different structures and development stages, reflecting a history of small disturbance sizes or an underlying patchwork of geological or soil conditions. Other landscapes are structurally and compositionally more homogeneous, indicating large-scale disturbances, homogeneous substrates, and few species; such landscapes typically exhibit a narrow range of structures and pathways.

See also: **Afforestation**: Stand Establishment, Treatment and Promotion - European Experience. **Ecology**: Natural Disturbance in Forest Environments; Plant-Animal Interactions in Forest Ecosystems. **Health and Protection**: Biochemical and Physiological Aspects; Diagnosis, Monitoring and Evaluation. **Landscape and Planning**: Landscape Ecology, the Concepts; Landscape Ecology, Use and Application in Forestry; Spatial Information. **Mensuration**: Yield Tables, Forecasting, Modeling and Simulation. **Plantation Silviculture**: Forest Plantations; Multiple-use Silviculture in Temperate Plantation Forestry. **Silviculture**: Natural Stand Regeneration; Unevenaged Silviculture. **Soil Development and Properties**: The Forest Floor. **Tree Physiology**: A Whole Tree Perspective; Shoot Growth and Canopy Development.

Further Reading

Camp A, Oliver C, Hessburg P, and Everett R (1997) Predicting late successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *Forest Ecology and Management* 95: 63–77.

Frelich LE (2002) *Forest Dynamics and Disturbance Regimes*. New York: Cambridge University Press.

Harper JL (1977) *Population Biology of Plants*. London: Academic Press.

Hunter ML Jr (1990) *Wildlife, Forests and Forestry*. Englewood Cliffs, NJ: Prentice Hall.
Kelty MJ, Larson BC, and Oliver CD (eds) (1992) *The Ecology and Silviculture of Mixed-Species Forests: A Festschrift for David M. Smith*. Boston, MA: Kluwer Academic Publishers.
Oliver CD and Larson BC (1996) *Forest Stand Dynamics*, updated edn. New York: John Wiley.
Oliver CD and O'Hara KL (2003) Effects of restoration at the stand level. In: JA Stanturf and P Marsden (eds) *Restoration of Boreal and Temperate Forests*. Boca Raton, FL: CRC Press.
Smith DM, Larson BC, Kelty MJ, and Ashton PMS (1997) *The Practice of Silviculture*. New York: John Wiley.

Natural Regeneration of Tropical Rain Forests

N Brown, Oxford Forestry Institute, Oxford, UK

Introduction

Natural regeneration is the process by which juvenile plants and coppice that have established naturally replace plants which have died or have been killed. Over time, following a disturbance, the growth of natural regeneration will reestablish canopy trees. This natural recovery process can be exploited in tropical forest management systems to create a new stand after canopy trees have been harvested. This article provides a review of the advantages and problems associated with natural regeneration. The effects of different silvicultural systems on natural regeneration are examined and the causes of success and failure discussed.

Advantages and Disadvantages of Natural Regeneration

Tropical rainforests are well-known for their extraordinarily high diversity of species, including trees. The use of natural regeneration in forest management helps to reduce logging impacts on biodiversity, since the objective is to ensure that exploited trees are replaced by juveniles of tree species characteristic of the natural forest. The diversity of natural regeneration will generally exceed the diversity of species that could be planted on a commercial scale. For example, in a recent large-scale forest rehabilitation project in Borneo many thousands of hectares of logged rainforest were replanted with only 33 commercial tree species. Some of these were not native to the region. Planting replacement trees in sites that are often remote and inaccessible is an expensive operation. Consequently there is little incentive to use species that are of low commercial value or that are relatively slow-growing. Such species are only likely to remain a component of a sustainably managed forest under a natural regeneration system.

Natural regeneration systems exploit existing seed and seedling banks and circumvent the problem of obtaining healthy planting stock. Seed production in many important tropical tree species is erratic and poorly documented and it is often difficult or impossible to obtain a regular supply. Planting stock cannot therefore be produced on demand. Where planting stock is available it is often collected from a narrow range of sites outside the local area and is likely to be of unknown but probably rather narrow genetic composition. Planted seedlings often suffer an initial period of poor growth and high mortality, termed planting shock. Poor initial growth will often put planted trees at a significant competitive disadvantage relative to the regeneration of other plants in disturbed forest sites. In contrast, natural regeneration will often show enhanced survival and vigorous growth in response to canopy disturbance.

In many parts of the world little is known about the ecology of commercially important tree species, including their tolerance of a range of site conditions or their requirements for successful establishment as seedlings. This can make artificial regeneration problematic. Where new trees have been planted extensively in tropical rainforest (typically, enrichment planting of forests with poor natural regeneration of commercially valuable species), seedling mortality has often been high and growth rates disappointing. This has been attributed to poor site–species matching, poor planting and maintenance techniques. The use of natural regeneration increases the chance that seedlings and saplings are of species capable of growing to maturity under local site conditions because they belong to species (and ecotypes) that are already growing in the immediate vicinity.

Under an appropriate silvicultural system the density of seedlings in a naturally regenerating tropical rainforest can be very high. Densities in excess of 75 000 seedlings ha^{-1} of commercial species have been recorded in forests in Borneo. This gives a broad base for the selection of the fastest-growing, best-formed individuals of the most desirable species. In contrast, the costs of replanting a forest are so great that the forester generally aims to make sure that a large proportion of all individuals survive and grow to maturity regardless of their quality. However, a major disadvantage of natural regeneration systems is that the forester has only indirect control over the composition of future forest stands. Although an aim of natural tropical rainforest silviculture is to increase the regeneration of commercially desirable species and enhance their growth, this is constrained by the species and genotypes that are present in the seed and seedling banks. Genetic improvement is unlikely to occur through natural regeneration systems and little or nothing is known about the relative performances of different provenances of climax tropical rainforest trees.

Concern has often been expressed that the 'creaming' or preferential felling of the largest trees or those with the best form from an area of natural tropical rainforest will leave only trees with undesirable genotypes in the forest. Natural regeneration offers a simple method for reducing the risk of such dysgenic selection. Most climax tropical rainforest tree species have populations which are composed of large numbers of seedlings and saplings and progressively fewer larger-sized trees. The largest commercial-sized trees will therefore constitute only a small fraction of the total population (**Figure 1**).

There is also a strong relationship between tree size and fecundity for many tropical trees. This implies that the largest trees are likely to have made a disproportionate contribution to the genetic structure of the seed and seedling bank. As a consequence, if the forest is well-stocked with natural regeneration, harvesting of only the largest individuals is unlikely to result in an immediate loss of genetic variation.

Environmental Control of Regeneration

Foresters and ecologists have been aware for centuries of the importance of forest canopy gaps in the regeneration dynamics of most tropical rainforest trees. Gaps are formed naturally when canopy trees are damaged or die. They can range in size from a tiny patch of light formed by the loss of a branch to several hectares when many trees are lost in a landslide or major blow-down. Most seedlings require the enhanced light levels found in a gap in order to grow to maturity. Only the most shade-tolerant species can survive and grow in the deep shade of a forest understory.

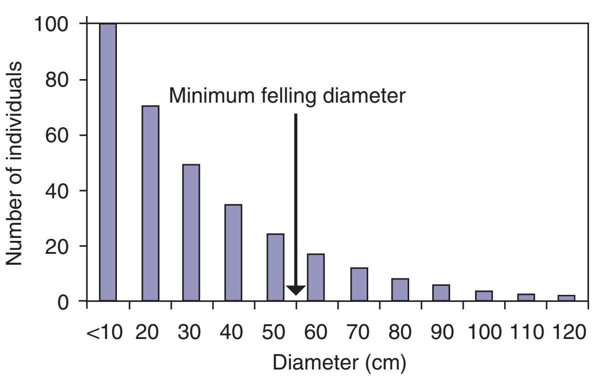


Figure 1 A typical size class distribution for a climax tropical rainforest tree species. Tree size is usually measured as the diameter of the trunk at 1.3 m above the ground.

Measurements of seed germination and rates of photosynthesis by seedlings have shown that species differ in their responses to increasing light levels. Two broad strategies have been described that characterize plant responses to disturbance. Pioneer species show significantly higher levels of seed germination under full sunlight. Their seeds are typically small, widely dispersed, and can remain dormant in the soil seed bank awaiting a disturbance to trigger germination. Once established, pioneer seedlings will grow very rapidly to maturity in a large gap, but they rarely persist for long in the shaded forest understory. In contrast, climax species have the greatest germination success in shade where their seedlings may persist for many years. Even relatively small increases in insolation will increase their growth and survival but they are unable to achieve the very high rates of growth of a pioneer species in the most disturbed conditions. Most species-rich, primary rainforests contain species which fall on a continuum of light response from the most shade-tolerant climax species to the most light-demanding pioneer.

The size of a canopy gap is the principal determinant of the amount and duration of insolation that penetrates the forest, hence different species of tree will find optimum radiation regimes for maximizing their growth in different sizes of gap. As a consequence, forests which are heavily or frequently disturbed will have abundant regeneration of light-demanding species. Pioneer species are often abundant in early successional forest communities such as those found on islands hit by tropical cyclones. Tropical rainforests which are infrequently disturbed are often dominated by more shade-tolerant, slow-growing climax species.

However, competitive superiority is not just determined by which plant has the greatest relative growth rate in response to the ambient light environment. Tall plants are able to capture more light and consequently grow faster and cast shade on the shorter plants beneath them. As the tallest plants in a gap may capture most incoming sunlight they will often dominate the regeneration regardless of their species. When the seedling bank and all advance regeneration is destroyed by a disturbance, the first plants to recolonize a gap will often preempt the light and delay or inhibit further colonization by other species. Furthermore, the species composition of seedling banks and the soil seed bank changes over time, reflecting the fruiting patterns of trees in the vicinity. Only a tiny fraction of the species found in a forest will be represented in the seed or seedling banks at any one place or time. A tree stands a good chance of regenerating if it is simply present as a seed or seedling when a gap forms, irrespective of whether it is well adapted to growing in that particular gap environment. It is salutary to note that in 1930 forest officers in Malaya concluded from practical experience that regeneration was influenced more by chance than by design and that regeneration of any particular species could not be relied on unless it was actually present before or immediately after the felling.

The implication of this for silvicultural systems that depend on natural regeneration is that it is crucial that the forest is already well stocked with abundant seedlings and advance regeneration of desirable species when the forest is logged. It is also important that logging does not destroy these seedlings. If this is not the case then regeneration will be composed primarily of noncommercial species or colonists.

Although many species of tropical rainforest tree have the ability to resprout after damage to the crown, coppicing has rarely, if ever, been used as a means to regenerate tropical rainforest after commercial exploitation. Resprouted stems are known to suffer much higher mortality rates than previously undamaged individuals and resprouts from large-diameter stems are more likely to die than those from small stems. Resprouting has also been found to be more common beneath small canopy gaps than in large ones. This implies that coppicing is unlikely to be a viable silvicultural system in tropical rainforests but may play an important role in forest regeneration after shifting cultivation.

Promoting Seedling Establishment

One of the real challenges in tropical rainforest management is to make sure that there is adequate regeneration before logging. In temperate forest silviculture this can be done by delaying felling operations so that they follow good seed years, by preparing suitable seed beds to enhance seedling establishment and thinning the forest canopy to encourage both seed production and seedling survival. Good seed years can be forecast when production forests consist of only one or a few tree species. However, in tropical rainforests it is much less easy to predict when or where a commercial species is likely to reproduce. Tree species fruit asynchronously in many tropical forests and their fecundity varies in response to very different climatic conditions. For example, the high-value tree Borneo ironwood (*Eusideroxylon zwageri*) has been noted for very poor regeneration for decades, to the point where, exacerbated by overexploitation, the species has become extremely rare. Recent extreme El Niño events which have caused high levels of seedling mortality in many other climax rainforest species seem to have promoted prolific regeneration of *E. zwageri*. Variation in the environment has different effects on the reproductive success of different species. The diversity of most tropical rainforest militates against efficient application of silvicultural treatments to increase the establishment of seedlings of desirable species to the whole forest block. Experience has shown that this only happens for the small number of species that produce abundant seed when the treatment occurs. Otherwise such treatments can promote dense regeneration of unwanted species that can inhibit the establishment of useful seedlings in the future.

The dipterocarp rainforests of South-East Asia are an important exception. Trees in the family Dipterocarpaceae occur in large numbers in these forests, and most provide valuable timber. A large number of dipterocarp species have supraannual, gregarious fruiting across large regions. As a consequence, at intervals varying typically between 3 and 11 years, there is substantial multispecies recruitment to the dipterocarp seedling bank. The density of seedlings can exceed several million ha^{-1} immediately after such a fruiting event, but declines rapidly with time until the next fruiting. These forests were some of the first tropical rainforests to be exploited extensively for timber. In the first half of the twentieth century regeneration of a forest was seen as one of the most important silvicultural tasks. There was a great deal of experimentation in dipterocarp rainforest, with methods for 'releasing' natural regeneration by thinning the canopy above newly established seedlings. A uniform shelterwood silvicultural system was developed that required the removal of all unwanted trees across the entire forest block, resulting in a drastic increase in understory light levels. An essential rule in this system was that felling should 'follow the seed,' meaning that a regeneration improvement felling could not be instigated until there was a substantial crop of newly established seedlings. The Malaysian Uniform System was found to result in a very large increase in the number of high-quality saplings of light-demanding dipterocarps. The success of the system was, however, attributable to the high density of adult trees of desirable species that simultaneously produced heavy seed crops. Similar tropical shelterwood systems, when applied in forests elsewhere in the humid tropics, have been considerably less successful. Either the systems proved too complex to apply reliably or, when applied indiscriminately to a whole forest block, resulted in dense regeneration of unwanted pioneer and light-demanding species.

Promoting Seedling Survival and Growth

Most tropical rainforests are now managed on a selection system, where no silvicultural operations are carried out at all. Some success has been achieved in improving the growth and survival of selected seedlings and saplings by opening the canopy directly above them and cutting back competitors. This type of treatment, known as liberation thinning, is relatively inexpensive and has been shown to increase the number of high-quality crop trees without impacting large areas of forest. Trees of unwanted species that are not impeding the growth of future crop trees are left alone. Concern has often been expressed that older saplings may become moribund and fail to respond to release. However, detailed long-term monitoring of advance regeneration has shown little evidence to endorse this concern. A positive relationship has been found between the height of advance regeneration and its growth response to artificial canopy gaps. Furthermore, it would appear that many canopy trees have experienced repeated periods of rapid growth interspersed with shade suppression in their passage to maturity.

Regrettably, as the costs of silviculture have increased, a view has developed among tropical foresters that logging alone would be sufficient to stimulate adequate regeneration and that silvicultural intervention is expensive and unnecessary. Extraction, rather than regeneration, has become the most important operation. Unlike lowland dipterocarp rainforest, many tropical rainforests have relatively low densities of commercially valuable species and sparse regeneration. Although selective logging has often stimulated vigorous regrowth, it has not been of valuable species. As a result of ‘logging and leaving’ there are now significant areas of secondary forest which have little or no productive potential. The only chance of rehabilitating such forests is through costly and unreliable enrichment planting. Many of these areas are now being converted to more productive nonforest uses, with serious consequences for conservation. An area of logged rainforest of more than 200 000 ha in the Ulu Segama area of Sabah, Malaysia, has recently been cleared and converted to pulpwood plantation because it was judged to be poorly stocked and devoid of natural regeneration and potential crop trees.

Why Does Natural Regeneration Fail?

Some of the most important causes of failure for natural regeneration include:

- Inadequate stocking of seedlings and saplings of desirable species at the time of harvesting. Many species of commercially valuable tropical rainforest tree do not have persistent seed or seedling banks. This is commonly true of more light-demanding climax species, including a number of important timber trees. In the Brazilian Amazon, species such as mahogany (*Swietenia macrophylla*) do produce seedling banks irregularly but these suffer very high rates of mortality in closed forest. Such species are problematic because the logging of large adults removes a significant proportion of the total population and the potential for future seed production. One possible solution is the retention of seed trees; however, experimental studies suggest that seed predation and poor germination limit successful seedling establishment in secondary forest. For many tropical rainforests the period during which recruitment can occur following a disturbance is short, because light and other resources are rapidly preempted by competing vegetation. Consequently the retention of seed trees is unlikely to result in regeneration of these species.
- Excessive damage to natural regeneration caused by harvesting operations. Surveys of logged tropical rainforest frequently report between 30% and 70% of the residual stand damaged. The majority of damage to natural regeneration is caused by careless and unplanned skidding rather than felling. Regeneration in badly damaged areas is either from the soil seed bank or from seed rain and is dominated by pioneer species. Some felling damage is inevitable when harvesting natural tropical rainforest but strict reduced-impact logging guidelines have shown that with care this can be substantially reduced.
- Poor maintenance of the forest following harvesting, resulting in poor growth and high mortality in existing seedlings. Scrambling bamboo and vines such as *Merremia* spp. can infest heavily damaged forest and smother young trees. Surveys in a logged forest in Borneo have shown over three-quarters of all trees to be infested with bamboo or vines. Little is yet known about the ecology of these climbers and the most effective methods for their control.

Long-Term Sustainability of Natural Regeneration

Sustainable use relies on the forest retaining its capacity to regenerate after harvesting. A very large proportion of tropical rainforest trees are dependent on animals for pollination and seed dispersal. Logging can disrupt animal communities in ways which have an impact on tree regeneration. Reduced pollination may lead to reduced seed-set or greater prevalence of inbreeding. Seeds which fall close to a parent tree are often found to suffer greater predation losses than those that are well dispersed. Similarly, seedling survival increases away from the pests and pathogens associated with a parent. Although there are indications that both pollination and dispersal may limit regeneration in forest fragments, there is as yet no clear evidence of impacts on seedling populations in large-production forests. However, seed predation rates have been found to be sufficiently high in logged forest to prevent regeneration of some tree species. Logging removes a significant proportion of the large seed-producing adults of commercial species and the residual seed trees become the focus of all predation.

Fire is becoming an increasing problem in many logged tropical rainforests and has a particularly severe impact on seedling populations. Almost no climax rainforest tree species have fire-tolerant seedlings and even lightly burned forests have been shown to be devoid of natural regeneration of anything other than pioneer species.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Silviculture**: Forest Dynamics; Forest Rehabilitation; Natural Stand Regeneration; Treatments in Tropical Silviculture. **Tropical Ecosystems**: Dipterocarps; Swietenia (American mahogany); Tropical Moist Forests,

Further Reading

de Graaf NR, Poels RLH, and van Rompaey RSAR (1999) Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. *Forest Ecology and Management* 124: 123–135.

Fox JED (1976) Constraints on the natural regeneration of tropical moist forest. *Forest Ecology and Management* 1: 37–65.

Hutchinson ID (1987) Improvement thinning in natural tropical forests: aspects and institutionalization. In: Mergen F and Vincent JR (eds) *Natural Management of Tropical Moist Forests – Silvicultural and Management Prospects of Sustained Utilization*, pp. 113–133. New Haven, Connecticut: Yale University, School of Forestry and Environmental Studies.

Kuusipalo J, Hadengganan S, Adjers G, and Sagala APS (1997) Effect of gap liberation on the performance and growth of dipterocarp trees in a logged-over rainforest. *Forest Ecology and Management* 92: 209–219.

Lowe RG (1978) Experience with the shelterwood system of regeneration in natural forest in Nigeria. *Forest Ecology and Management* 1(3): 193–212.

Nicholson DI (1979) *The Effects of Logging and Treatment on the Mixed Dipterocarp Forests of Southeast Asia*. Report FO: MISC/79/8. Rome: Food and Agriculture Organization of the United Nations.

Webb EL (1998) Gap-phase regeneration in selectively logged lowland swamp forest, northeastern Costa Rica. *Journal of Tropical Ecology* 14: 247–260.

Wyatt-Smith J (1963) *Manual of Malayan Silviculture for Inland Forests*. Malayan Forest Records No. 23. Kepong, Malaysia: Forest Research Institute Malaysia.

Managing for Tropical Non-timber Forest Products

J L G Wong, Wild Resources Ltd, Bangor, UK
J B Hall, University of Wales, Bangor, UK

Introduction

Interest in the management of non-timber forest products (NTFPs) in the tropics has increased dramatically over the past 20 years. This process reflects observations that:

1. Some economically or culturally significant NTFP resources are being overexploited.
2. NTFPs can provide a raw material resource for local enterprise and income development.
3. NTFPs may be the only harvestable commodities left in degraded forests.
4. NTFPs have significant subsistence and cultural values to local peoples.

Although these concerns are most commonly associated with development forestry in the tropics, all of them are increasingly recognized as present and significant in temperate forests and rural economies (e.g., in the Pacific Northwest of the USA, Eastern Europe, and the UK).

Increasing interest in the poverty and development relevance of NTFPs has engendered work on the promotion of income generating enterprises based on them. Because this has a social focus much of this work has been undertaken by socially orientated advisors and hence on management systems based on participatory rural appraisal and other social science techniques. The development of the ecological or autecological basis for species management has only recently become of more concern and suitable protocols for ecological investigation of the multifarious species of NTFPs are only now being developed. Good management should be based on sound ecological knowledge whether this is the result of extended observation and encapsulated in local knowledge or the result of biometric investigations. This article considers how this knowledge has been used to develop NTFP management or silvicultural systems in the tropics.

What is a Non-Timber Forest Product?

For millennia people have used forests as a source of sustenance, raw materials for craft and industry, and as a home. Ethnological surveys demonstrate that roughly 60–70% of any flora and a lower percentage of the fauna are utilized by traditional forest-dwelling societies as food, clothing, shelter, tools, and medicines (**Figure 1**). The advent of sedentary farming, industrialization, and colonialism removed people from the forest, made them less reliant on wild resources and focused attention on the exploitation of forests for timber primarily for export. However, this did not mean that the other products were entirely disregarded. Harvesting of several wild products developed into large-scale export enterprises (e.g., cocoa, coffee, rubber, chicle, and palm oil) though many of the plants from which these were derived were eventually brought into plantation cultivation. By the middle of the twentieth century, the majority of managed tropical forests were a focus for the production of export quality timber. The continued reliance of local people on other products was considered to be insignificant and largely irrelevant and they were termed 'minor,' 'non-timber,' and 'non-wood' and all lumped together – often with less tangible forest 'benefits' and 'services.'

Figure 1 Many NTFPs are used as medicines. This lady is a wholesaler of medicinal plants in the Durban herb market. She is selling parts of wild plants collected from indigenous forest and montane land in South Africa and neighboring countries. Many of these plants are becoming threatened by this trade. Shortages may compromise access to healthcare by poorer members of society. There is an urgent need to institute sustainable management for these resources. Photograph courtesy of Jenny Wong.

Although these terms are in common usage among foresters they do not have currency outside the profession. There is no accepted term for non-timber forest products that is recognized by all disciplines interested in managing forests. This is unfortunate as the successful management of NTFPs by foresters would benefit greatly from cross-disciplinary exchange with wildlife managers (especially as wildlife is considered an NTFP), ethnobotanists, human ecologists, and conservation biologists, none of whom use or recognize the term NTFP.

An examination of the NTFP literature reveals that the term is used to describe wild and semicultivated plants from natural, managed, and modified forests and also semidomesticated forest plants (e.g., trees for fruit or understory plants such as Marantaceae) even where these are not in a forest environment (e.g., in agroforestry systems). Furthermore, some NTFPs are wild products taken from artificial forest environments (e.g., mushrooms from pine plantations in southern Africa and snails from oil palm plantations in Cameroon). The NTFPs themselves may also be cultivated using artificial techniques such as *in vitro* propagation. Careful examination of the actual products and environments covered in the NTFP literature suggests that we can map the area of interest as shown as the shaded areas in **Figure 2**.

Although the rhetoric suggests that animals should be considered as NTFPs there is very little evidence that foresters have done much work in this area. However, there is substantial work on sustainable management of animals in the conservation world especially in Latin America which is not often referenced in the forestry literature.

In a further complication, the term NTFP has been more literally interpreted as including products made from wood but which cannot be classed as 'timber' including the derivation of chemical feedstock from

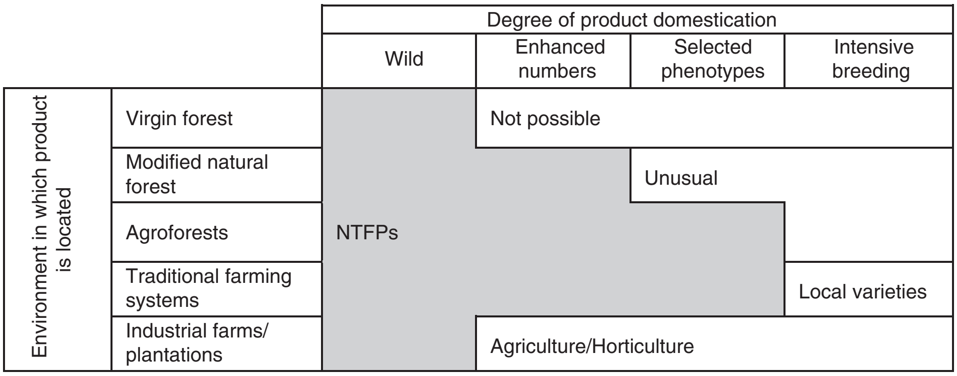


Figure 2 Map of products termed NTFPs.

wood. This latter interpretation is ignored for the remainder of this article as silviculture for wood-based products is the same as for maximizing wood volume which is dealt with elsewhere (*see* **Silviculture**: Silvicultural Systems).

What is NTFP Silviculture?

Before answering this question we have first to consider what is meant by silviculture. Silviculture is the art and science of controlling the establishment, growth, composition, health, and quality of forests and woodlands. Silviculture entails the manipulation of forest and woodland vegetation in stands and landscapes to meet the diverse needs and values of landowners and society on a sustainable basis.

In principle this definition includes the proactive management of NTFPs. However, silvics is the study of the life history and dynamics of forest trees. Although including other forest plants seems reasonable, stretching it to include animals seems unreasonable. However, the principle of developing an understanding of a species and then manipulating its environment to produce desirable products is one that applies to sustainable management of any NTFPs.

Proactive manipulation of a species to increase the quantity or quality of a product often begins with harvesting regulations and ends in the domestication of the species with production in monoculture far from the forests which were its original home. Cocoa and oil palm were both once harvested from the wild and ended as highly modified plants in monocultures. Other products such as locust bean (*Parkia biglobosa*) are halfway along this road and although not yet extensively modified by selective breeding are hardly present in the wild. Yet others, such as Brazil nuts (*Bertholettia excelsa*), are closer to the beginning and have properties that make them difficult to domesticate. Once a species has been recognized as an NTFP it seems to retain this title as it becomes progressively domesticated and increasingly characteristic of farmland. The line between NTFP silviculture and horticulture is indistinct.

Identifying a product as an NTFPs depends on the plant or animal being found in a forest or being produced by a tree more or less regardless of location. The only exceptions are orchards or fruit tree plantations. This means that wild-harvested products from different habitats, such as veld or desert, are not included. However, the similarities between the management systems required by these products are such that they are increasingly classed as NTFPs in the literature even though they have little to do with 'forests' (e.g., devil's claw (*Harpagophytum procumbens*) in Botswana).

So a pragmatic definition of NTFP silviculture would need to include the development of cultural systems for all wild and semidomesticated non-timber tree products, regardless of where they are located, and anything found in a forest environment.

Although the issues included in NTFP silviculture represent a continuum which is rather poorly defined, it is possible to recognize three areas that have distinct silvicultural and management features. The regulation of harvesting from wild populations has a very long history and is known in the Americas as 'extractivism.' The semidomestication of trees in traditional farming systems across the tropics likewise has a long history, and has resulted in distinct anthropogenic landscapes such as the African savanna parklands, the agroforests of Indonesia, and the home gardens of Nigeria. A third trend is for cultivation of wild products leading eventually to full domestication, this being a more recent phenomenon.

Harvesting Natural Forests

This section describes the silvicultural systems that are used to harvest 'wild' products, i.e., those in the third column of **Figure 1**. Most silviculture for wild products in natural forest takes the form of harvesting rules. These are most often concerned with one or more of the following:

- prescribed harvesting methods
- exploitation of only a portion of the species range in any year (coupes)
- a fixed harvesting interval.

Wild products are also exploited from farm and plantation habitats where they often occur as weeds or by serendipity. Silviculture in such environments may be the same as for natural forests but, in these anthropogenic situations, there is much more scope for proactive intervention such as the tending of plants and the promotion of suitable habitats for wildlife.

Traditional Systems

Local people who have depended on NTFPs for many generations have a vast repository of knowledge of the plants, animals, and ecosystems in their locales. This experience is very often encoded into myths, taboos, rules, and decision-making processes which maintain a balance between exploitation and productivity.

NTFP protection and harvesting restrictions feature in many cultures. In some African parklands, for example, anyone felling the soil-improving *Faidherbia albida* could traditionally face execution! In other instances, all a community's trees of a key species might be owned by the chief, regardless of who farmed beneath them (*Parkia biglobosa*), or the community could harvest fruit only when the chief declared the season open (*Sclerocarya birrea*).

The use of traditional management practices has in many cases provided a sustainable resource for local use for many generations. However, as the market economy takes hold, favored products enter commercial trade and the equilibrium between traditional rules, expectations, and market demand is disrupted. Almost inevitably unchecked, these processes lead to either overexploitation or the domestication of the species, both to the detriment of the local economy.

The advent of participatory forest management initiatives such as Joint Forest Management in Nepal has provided a basis for the integration of traditional knowledge with modern forest management planning. The silvicultural elements of this exchange are exemplified in Oaxaca in Mexcio with the development of what has been termed 'barefoot silviculture.' The origins of such systems is indigenous knowledge which can give rise to systems which can be recognized as conforming to single and multicohort stand management. Within such systems NTFPs are managed alongside the trees as an integral part of the silvicultural system.

Extractivism

Extractivism is a term used, mostly in the Americas, to describe any gathering of natural products, whether of mineral (mining), animal (skins, meat, fats), or plant (woods, leaves, fruits etc.) origin. In the forests of Amazonia, large stocks of nuts and rubber resulted in the establishment of a harvesting system based on wild collection using indentured labor. In time this system collapsed but the nut collectors and tappers remained and have found themselves in conflict with forest clearance for large-scale ranching. The outcome has been the formal recognition of extractive reserves in Brazilian law. By April 1994, nine extractive reserves had been established for harvesting of babaçu (*Orbignya phalerata* – fruit), açai (*Euterpe oleracea* – fruit), rubber (*Hevea brasiliensis* – latex), Brazil nuts (*Bertholletia excelsa*), and copaiba (*Copaifera langsdorffii* – oil) though each reserve is managed for multiple use.

An example of the type of silviculture proposed in the utilization plans is that for babaçu in the Frexal Extractive Reserve. Babaçu is a palm which grows in dense monospecific stands in which fruit productivity can be restricted by overcrowding. It is therefore suggested that unproductive trees should be removed and the density of immature plants controlled by thinning. It is also suggested that the babaçu forests could be combined with perennial crops adapted to the region. In effect, this is a move towards a more managed landscape with the wild trees treated as a plantation crop.

The management planning and social elements of extractive reserves make them uniquely suitable for the Forest Strewardship Council type of certification. Recently Brazil nuts and chicle (edible tree latex) have been successfully certified as being derived from sustainably managed forests.

Sustainable Harvesting Plans

The development of a management system for NTFPs is basically the same as that for timber with the following recommended sequence of activities:

- inventory
- growth and yield determination
- determination of harvesting methods and yields (perhaps using some form of growth modeling)
- monitoring.

Although much of this information is often available as local knowledge, there is increasing interest in the scientific appraisal of such knowledge and biometric approaches to data collection. A review of the available biometric methods for NTFPs revealed a dearth of tried and tested protocols. However, in many cases the use of conventional forest inventory techniques is prohibitively expensive for use with NTFPs. There is a need to develop cheaper, statistically efficient means of inventoring NTFPs.

The scarcity of good resource and growth data for many NTFPs means that taking an adaptive management approach is desirable. Adaptive management accepts that decisions have to be based on imperfect information. Management prescriptions are therefore based on the precautionary principle and monitoring systems put in place to learn from experience. The monitoring itself therefore becomes both an instrument for research and feedback to ensure that management improves with each reiteration which should therefore take place at regular intervals.

Wild Products from Farmed Landscapes

Farmed landscapes with trees retained from the natural ecosystems originally cleared, sometimes as much as 200 years earlier, cover millions of square kilometers of the tropics. They support tens of millions of people in Africa alone and supply a wide range of NTFPs produced under varying degrees of management. These environments constitute an outstanding example of the way that NTFPs are integrated into the daily life and vital needs of rural communities on an extensive scale, primarily from indigenous trees.

Parkland Systems

Since the 1960s the farmed landscapes of the savanna regions of sub-Saharan Africa, especially, have been described and studied in some detail. The farmed landscape with trees (widely called 'parkland') is a refinement of the natural vegetation of the area. Tree removal is effected to enable annual crops to be grown but the removal is highly selective. Impact is less on the populations of species valued for NTFPs and, favored by measures taken to tend crops, the individual trees retained commonly display enhanced growth and vigor. Products sought from the trees have significance as dietary essentials (e.g., vitamin C in the fruit flesh of *Sclerocarya birrea* and *Ziziphus mauritiana*), positive seasonal impact as nutrient rich fruit pulp and seeds in the mid- and late dry season when alternatives are few (e.g., *Adansonia digitata*), and options for making cash income (e.g., tapped sap from the palm *Borassus aethiopum* or the fresh fruits of *Lannea microcarpa*). Complementing these rewarding but routine uses of the most highly regarded species is the availability of others with food security roles exploited when circumstances dictate. Among these 'famine' foods are proteinaceous meal from the kernels of *Balanites aegyptiaca*, palm kernels (*Hyphaene thebaica*), foliage of *Ficus* spp., and young shoots of *Borassus aethiopum*.

Keystone Species

Particularly significant NTFP tree species retained in farmed landscapes are the keystone species – those which are so abundant that the ecosystems are named from them. Parklands of *Faidherbia albida* (fodder, including fruit for livestock), *Vitellaria paradoxa* (edible oil from fruit), *Parkia biglobosa* (seeds for seasoning), and *Adansonia digitata* (leaves as a vegetable) are examples (**Figure 3**). Tendencies towards gregariousness are reinforced by selective removal of unwanted species, and a high proportion of the trees left may be of the keystone species. Thus, *Vitellaria paradoxa* (the shea butter tree) commonly accounts for 70–90% of the mature trees in large areas of farmed landscapes but under 20% of those in natural woodland.

Because of their significant nutritional values, dominant among the NTFP tree species of farmed landscapes are the fruit trees. Some of these are the basis of considerable specialized activity involving restricted sections of the local communities, generally defined by gender and/or age. Those NTFPs of outstanding local importance ultimately result in processed output. The cooking oil (shea butter) extracted from the seeds of *Vitellaria paradoxa* and the fermented seed meal (soumbala) of *Parkia biglobosa* are the best-known West African examples, and in many parts of southern Africa fermented drinks are processed from the fruit pulp of *Sclerocarya birrea*.

Management

In an established farming setting, the tree cover is the product of considerable conscious selection when individuals for retention are identified, as well as management actions at system and tree level. Selection goes well beyond choice of species and removal of moribund or unhealthy individuals. Over a period of several years as the farming system is introduced, the farmer also applies a wealth of indigenous knowledge equivalent to infraspecific taxonomy, with varieties recognized within the local culture being valued differently and individuals of the less attractive ones likely to be removed. In central Burkina Faso, for example, several varieties of *Parkia biglobosa* are locally distinguished, the so-called 'black' type (dark bark; black seed coat) being favored as superior for seeds used in cooking.

Figure 3 The dry season aspect of typical agroforestry parkland in northern Nigeria. Prominent in the foreground is the spreading, heavily branched crown of a large *Parkia biglobosa* tree. To the right, further back, is a baobab tree (*Adansonia digitata*), the pale bole a consequence of bark removal for fiber. Photograph courtesy of Fergus Sinclair.

Other than undertaking selection, the principle thrust of the management of farmed landscape NTFPs is the imposition of pruning practices. Despite the impression of stability given by scattered large trees in crop land the system is highly dynamic. The enhanced growth rates arising in the favorable environment of a well-tended crop brings a need to prune trees which progress to a widely spreading form in old age (such as *Ficus* spp. and *Parkia biglobosa*), which would otherwise cast excessive shade. An alternative, used more to compensate for the growth in species with more compact crowns (e.g., *Vitellaria paradoxa*) is thinning of the tree population. With increasing demand for fodder and wood products, particularly fuelwood, poles, and wood for tool handles, pruning tends to meet more than one need. Nevertheless unless pruning intensity is modest (with half or more of the crown left in place) fruit production may be severely depressed for several seasons – to a mere 5–10% of a mature tree's full fruit crop in *Faidherbia albida* (typical yield 125 kg), *Parkia biglobosa* (typical yield 70 kg), and *Vitellaria paradoxa* (typical yield 50 kg).

Whilst presently minor elements of management, two further measures, fire protection and planting, merit comment. Fire protection is mainly achieved opportunistically because after crops are harvested, and livestock brought to feed on the residues, there is no fuel bed at the period when fire risk is high. However, in many farmed landscapes fallow phases remain an integral part of the land use system and are associated with increasing frequencies and intensities of wildfire. It is traditionally recognized that NTFP yields from trees exposed to intense fire are lowered (e.g., with *Parkia biglobosa*), and that smoke and other particulate matter released in an untimely fire will reduce pollination efficiency in species with dry season flowering (e.g., *Vitellaria paradoxa*). Individual trees considered of exceptional value may be protected with a firebreak, usually an area of cleared ground. Assuming wildfires will become increasingly problematic, active fire protection will be routinely needed in farmed landscapes for efficient NTFP production.

Much attention has been drawn to the lack of planting of indigenous NTFP trees in farmed areas and the population structures of NTFP tree species emphasizes this and has prompted forestry extension services to address the problem. There are two main difficulties. The first is complacency, since in most tree populations there is a vigorous core of mature trees with a projected productive life of decades. Nevertheless, the combined impact of natural mortality, removal of trees of declining productivity and of further trees to create crop space and emergency fellings for fuelwood indicate accelerating change and a need for the reinvigoration of the populations. The second difficulty is opposition to planting indigenous trees based on cultural beliefs which have been reported for various societies. It does not apply everywhere, nor to all species, however, and there are also traditions which encourage planting, as with

Adansonia digitata. The *Sclerocarya birrea* population in Namibia has also been attributed to planting germplasm brought from what is now Angola, and suggestions have also been made that planting and introduction could explain aspects of the regional variation of *Vitellaria paradoxa*.

Commerce

There has been a long history of trade in more easily handled NTFPs from farmed landscapes, where processing is relatively simple and storage difficulties are minor. Foremost among these are exudates tapped directly from the trees (e.g., gum arabic, *Acacia senegal*) or collected from insects, such as lac, from, for example, *Butea monosperma* in India. Another significant NTFP from farmed landscapes is the leaf of *Diospyros melanoxylon*, used to wrap cheroots, through which upwards of 1 million people find employment even though serving the internal market of India rather than international consumers.

Today, commercial interests based on NTFPs from farmed landscapes are expanding and diversifying as technological advance has created opportunities to utilize the qualities of fruit products in the cosmetics and food sectors, notably with *Sclerocarya birrea* and *Vitellaria paradoxa*. There is also growing willingness to support processed and packaged products from these species released in local markets, together with those from other keystone species (e.g., food seasoning cubes from *Parkia biglobosa*; cosmetics and drinks based on *Adansonia digitata*).

The Road to Domestication

All domesticated plants and animals were at one time wild. Presumably some proved so useful or amenable that they were domesticated and eventually rendered dependent on cultivation. This process of taming, and later modifying, species for more intimate use by humans is a continuous one and there are many species presently in the process of being domesticated. However, there are several forms that such a transformation can take as shown in columns four and five of **Figure 1**, a few of these are described below.

Farming the Forest

The first stage in domestication is often the manipulation of a wild species *in situ* to improve productivity. This often involves an increase in the number and density of the target species either by protecting juveniles, creating conditions for enhance recruitment or transplanting wild plants to create gardens of the species. In America this process of 'farming' wild plants *in situ* is termed 'woods grown' and is applied to understory herbs such as American ginseng and goldenseal. In Japan similar techniques are used to grow indigenous saprophytic mushrooms (e.g., shi-take) using stacks of cut logs as a substrate within the forest.

Rescue from Extinction

For a great variety of reasons many NTFP species end up being overharvested to the extent that they are at risk of becoming locally extirpated and perhaps even threatened with extinction. In these circumstances the only option is to undertake *ex situ* conservation and if market demand remains high to proactively domesticate the species. An example of such a process for a tropical species is that for eru (*Gnetum africanum*) in Cameroon. This is a climbing plant from which the leaves are harvested, for use as a vegetable. It is becoming increasingly rare in the wild and has been the subject of intensive cultivation trials at the Limbe Botantical Gardens in Cameroon.

Figure 4 This is a wild coffee (*Coffea* sp.) that grows in the forests of Uganda. In the past young plants were collected and used to establish coffee farms outside the forest. Since the introduction of cultivars this practice has all but ceased. The world coffee market is swamped with large volumes of cultivated coffee but the speciality market is always receptive to additional varieties. Wild coffee could potentially be sold to the speciality market and its reintroduction into coffee farms in Uganda could bolster farm incomes. Photograph courtesy of Jenny Wong.

Trials have been successful and local communities and farmers' groups are now successfully cultivating the plant and obtaining a good income from sales locally and export to Nigeria. Silviculture in these cases is synonymous with horticulture.

The Market Takes Over

When market demand is for consistent quality, reliable large volumes, and a product which is a profitable export, it is often only a matter of time before production becomes industrialized (**Figure 4**). At this point market forces take over and capital is invested in large-scale or at least farm-scale production which almost inevitably takes the production process away from small-scale farmers, gatherers, and the poor. This is the end of the road to domestication; from this point onwards agriculture and horticulture take over. However, through long association, the tag NTFP may still remain as evidenced by articles in the *Journal of Non-Timber Forest Products* covering *in vitro* propagation of trees and provenance trials for common farm trees (e.g., neem).

Although often advocated, and in many instances necessary, captive production or cultivation (*ex situ*) is not without its conservation risks. Domestication can lead to environmental degradation, pollution, and reduction in genetic diversity as well as loss of incentives to conserve wild populations.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Human Influences on Tropical Forest Wildlife. **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest; Forest Biodiversity Prospecting; Medicinal and Aromatic Plants: Ethnobotany and Conservation Status; Medicinal Plants and Human Health; Tribal Medicine and Medicinal Plants. **Non-wood Products**: Resins, Latex and Palm Oil; Rubber Trees. **Sustainable Forest Management**: Definitions, Good Practices and Certification.

Further Reading

Boffa J-M (1999) *Agroforestry Parklands in Sub-Saharan Africa*. Rome: FAO.

Booth FEM and Wickens GE (1988) *Non-Timber Uses of Selected Arid Zone Trees and Shrubs in Africa*. Rome: FAO.

Cunningham A (2000) *Applied Ethnobotany*. London: Earthscan.

Falconer J (1990) *The Major Significance of 'Minor' Forest Products*. Rome: FAO.

Murrieta JR and Rueda RP (1995) *Extractive Reserves*. Gland, Switzerland: IUCN.

Oyen LPA and Lemmens RHMJ (2002) *Plant Resources of Tropical Africa: Precursor*. Wageningen, The Netherlands: Plant Resources of Tropical Africa.

Robinson JG and Bennett EL (1999) *Hunting for Sustainability in Tropical Forests*. New York: Columbia University Press.

Russo L, Vantomme P, Ndeckere-Ziangba F, and Walter S (2001) Non-wood forest products. *FAO Forestry Paper* 140: 81–98.

Sequeira V and Bezkorowajnyj PG (1998) Improved management of *Butea monosperma* (Lam.) Taub. for lac production. *Forest Ecology and Management* 102: 225–234.

Verheij EWM and Coronel RE (1991) *Plant Resources of Southeast Asia: Edible Fruits and Nuts*. Wageningen, The Netherlands: Pudoc.

Wong JLG, Thornber K, and Baker N (2001) *Resource Assessment of Non-Wood Forest Products*. Rome: FAO.

Unevenaged Silviculture

R Helliwell, West End, Wirksworth, Derbyshire, UK

Introduction

Uneven-aged silviculture may be defined as the tending and regeneration of woodlands or forests which contain trees of several age classes in intimate mixture. In terms of silvicultural systems (*see* **Silviculture**: Silvicultural Systems) this would, strictly speaking, include only selection and group selection systems. A looser interpretation might include stands of trees with only two or three age classes, such as coppice-with-standards or even-aged crops which have been underplanted with younger trees. However, these will either be managed as overlapping even-aged crops, which will be maintained as such, or as the first stage towards a truly multiaged stand.

Stands of trees which are basically even-aged may also go through a period when some of the older trees are retained while younger trees become established, as in shelterwood systems, so that the stand will be temporarily uneven-aged to some degree, but the silviculture which is involved will remain essentially even-aged. Similarly, areas of forest may, for various reasons, be divided into smaller units, but the silviculture of these units would still be described as even-aged if each is managed with reference to its age and area, even if each unit is very small. The essential difference, in silvicultural terms, between even- and uneven-aged silviculture is that the latter does not take any direct account of the age of the trees or the area which is occupied by each age class. Age and area, as such, are ignored. This involves a fundamentally different approach, both in theory and in practice.

History of Uneven-Aged Silviculture

In many parts of the world there have been periods when forests have been managed on an uneven-aged basis. Often, this was carried out without sufficient understanding, consistency, or care, and led to the removal of the best timber trees and/or inadequate regeneration of young trees, leaving the forest inadequately stocked or containing few trees of value. This led to a desire to adopt more organized forms of silviculture, and even-aged silvicultural systems with clearfelling came to be regarded as the best way to manage forests. This was most notably so in Germany in the latter part of the eighteenth century, and forests managed in that way were certainly easier to organize and control.

Towards the end of the nineteenth century a few foresters, most notably in Switzerland, became unhappy with the even-aged approach and developed systems of selection, whereby individual trees or small groups of trees were selected for removal and the forest was never subjected to clearfelling. Recording and management of the growing stock were by periodic measurement of all trees above a minimum size, enabling productivity and changes in growing stock to be assessed over time. These forests typically included spruce (*Picea abies*), silver fir (*Abies alba*), and beech (*Fagus sylvatica*) growing in their natural habitat, and management in this way was seen as being fairly natural or ‘close to nature.’ Other advantages were perceived, including reduced risk of soil erosion and avalanches of snow, greater emphasis on the production of large stems, and reduced costs of planting. This approach became more widespread in some areas and, from early in the twentieth century, Swiss law has forbidden felling of any areas greater than 2 ha without special consent. Slovenia followed suit in 1950, and state-owned forests in a number of German provinces have been managed without clearfelling since the 1980s.

Elsewhere, experience was less satisfactory. Methods which may have been successful in spruce/silver fir/beech forests in Switzerland did not always transfer readily to conditions in Scandinavia, North America, or other parts of the world, and uneven-aged silviculture fell out of favor in such countries during most of the second half of the twentieth century.

In Germany, an organization called Arbeitsgemeinschaft Naturgemässe Waldwirtschaft (Working Group on Woodland Management Using Natural Methods) was formed around 1950 to promote forestry which utilized natural processes as far as possible, and this eventually provided a catalyst for the creation of Pro Silva (a pan-European organization with similar objectives) in 1989. This now has national groups in most European countries, and there has been a considerable resurgence of interest in uneven-aged silviculture or ‘continuous cover’ forestry in many parts of Europe and North America. Elsewhere in the world, in places such as New Zealand and many tropical countries, there has in recent years been a dichotomy of silviculture, with even-aged plantations of timber species on the one hand and conservation of what remains of the natural forest, in the form of nature reserves, on the other. Harvesting of timber on a sustainable basis from natural tropical forests has been attempted in a number of places, but has not had a generally good track record. This has often been due to a combination of political, social, and economic problems rather than to any intrinsic silvicultural difficulties.

Felling and Regeneration

For management purposes, forests are usually divided into compartments (typically between 5 and 50 ha in temperate forests, but often much larger in tropical regions) which are relatively uniform in terms of physical attributes such as soil type and slope, and which are of a convenient size to be dealt with as part of an annual program of thinning or felling. In uneven-aged forest, each compartment will be visited every few years (usually between 5 and 12 years, depending mainly on the rate of growth) and selected trees removed.

The selection of trees for removal needs to be undertaken with several objectives in mind, and demands a degree of skill and experience. Where timber production is a main object of management there will be an emphasis on favoring trees of good form and growth potential by the removal of trees which are coarsely branched or which have already reached their maximum potential value. The removal of any one tree should, in theory, maximize the value of the forest, in terms of current and future income combined. The forester will be constantly striving to improve the quality of the trees and the overall value of the forest at minimum cost.

At the same time, the removal of trees should not be carried out in such a way as to cause instability of the forest. In particular, in places where there is a high risk of damage from wind, only a limited proportion of the timber volume should be removed at any one time and it may be necessary to leave some big trees to provide stability, if their removal would leave other trees vulnerable to being uprooted or broken by the wind. However, uneven-aged forests are, in general, less likely to suffer catastrophic damage from wind than vulnerable stages of even-aged forests. In vulnerable areas, removal of more than about one-sixth (15–17%) of the standing volume of timber at any one time might be inadvisable. If, on a highly productive site in a vulnerable area, annual increment were equal to 5% of the standing volume, that would imply a felling cycle of only 3 years in such areas, whereas if increment is equal to only 2% of the growing stock a felling cycle of 8 years would be appropriate.

There is a viewpoint which considers that the best way to manage forests in areas where gale-force winds are frequent and soils are wet and anaerobic is to grow trees with an even-aged unthinned canopy and then to clearfell them before they start to be blown down. If conditions are not so severe, then it is likely that an irregular structure will be less subject to catastrophic windthrow than an even-aged structure and will, in the long term, be more sustainable and more economic.

If a greater proportion of the standing volume can be removed without causing instability or other problems, a longer felling cycle may be appropriate. This will improve the economics of the harvesting operation, and may favor the regeneration of light-demanding species, but shorter felling cycles will allow better stand management and will tend to favor shade-tolerant species. In some instances removal of more than 50% of the standing volume may be possible. However, such heavy felling is likely to reduce the range of size classes and the productivity of the stand for several years and removal of more than 30% at any one time would be unusual.

Trees of unwanted species will be preferentially removed, while maintaining a reasonable diversity of species, and mature trees of desired tree species may be retained for longer than normal in order to ensure an adequate supply of seed.

In uneven-aged stands, a mixture of tree species is nearly always easier to manage than a single species, and also tends to have greater biodiversity and fewer problems with pest species.

Wherever possible, regeneration will be by natural seeding rather than planting, as this will be cheaper and easier to manage on an extensive basis. The selection of trees for felling will take into account the need to allow space for some seedlings and saplings of desired tree species to survive and grow, although these will not normally occupy more than 15% of the forest area at any one time. Too many saplings can be a problem, as they may require costly thinning or respacing to prevent them becoming overcrowded and spindly. With shade-tolerant species, in particular, there will often be seedlings present which are growing very slowly in shaded conditions and are 'waiting' for an opportunity to grow. If some of the mature trees are removed in that area, these established seedlings are then likely to make more rapid growth, due to the additional light and a reduction in competition for soil moisture and nutrients, even if there is some increase in the growth of herbs and shrubs, or other tree species. Ideally, individuals or small groups of saplings should then be able to grow rapidly into the upper canopy; and, ideally, these should require little or no tending until they reach a useful size and thinning can be done at no net cost.

The balance between the various factors can be critical, and obtaining natural regeneration is not always easy. However, it should be only one of several considerations in the mind of the person who is deciding which trees to remove, and should not be allowed to dominate the system.

Other factors (**Figure 1**) also influence the success or failure of natural regeneration, including the numbers of grazing or browsing animals such as deer, sheep, goats, cattle, rabbits, and hares. If these are too numerous there may be no successful regeneration, either planted or natural, unless fencing or other methods of control or protection are implemented.

Structure of the Growing Stock

The growing stock of uneven-aged forests often tends to follow a negative exponential curve, when numbers of trees are plotted against their stem diameters (**Figure 2**). This curve is frequently referred to as a reverse-J or simply a J-curve. It can be expressed mathematically, and an 'ideal' curve can be produced for any particular area of forest, but the mathematical formula requires the input of data on the required ratio between the numbers of trees in one diameter class and the next, and the 'ideal' basal

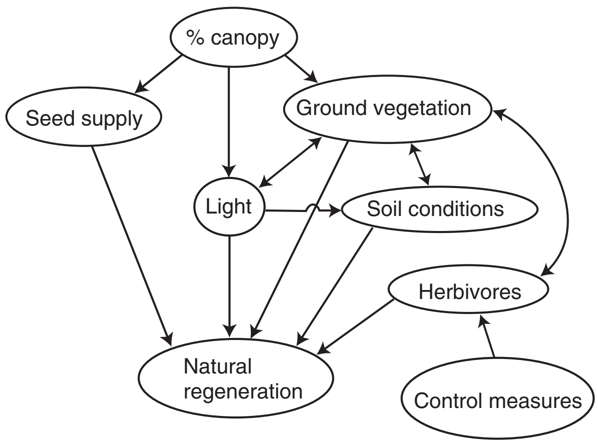


Figure 1 Factors affecting natural regeneration. © R Helliwell.

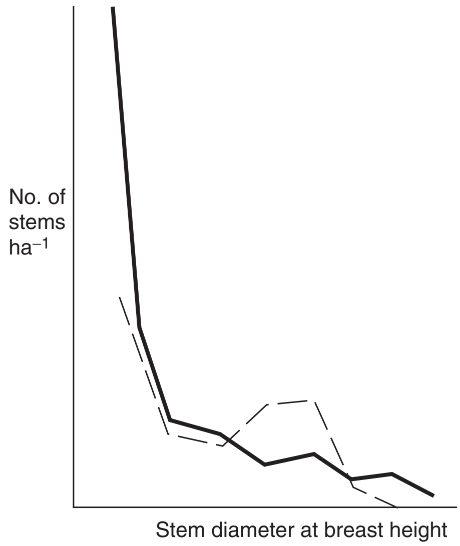


Figure 2 Typical distribution of stem sizes and numbers. (The dashed line indicates an abnormal distribution.)

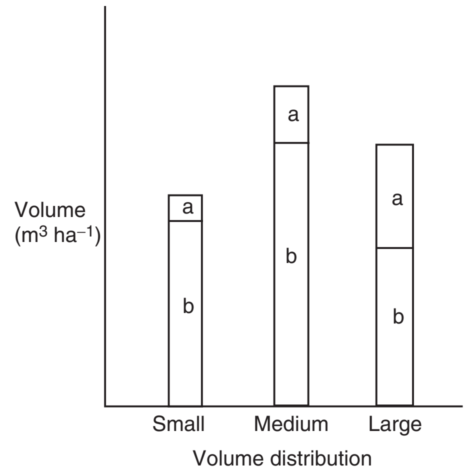


Figure 3 Typical distribution of size classes, by volume. a = species a; b = other species.

area of the stand. Neither of these can be known until a period of management experience has been obtained and data collected from several periodic measurements. It tends, therefore, to be something of a circular process, and it is probably better to regard the J-curve simply as an expression of what is happening, rather than as a prescriptive tool. Its exact form is probably not important, although any major difference from the general negative exponential form (such as a large hump in the middle: **Figure 2**) may indicate that all is not as it should be. Slavish attempts to make the forest conform to such a curve are not likely to be necessary, and may result in unnecessary expense.

One alternative to plotting stem numbers against diameters is to plot the volume of different size classes of tree, usually in three classes: small, medium, and large. The relative volumes in each class will depend to some extent on the size categories which are selected, but this method can provide a better visual impression, as significant changes in the volume of large trees may scarcely be visible on a J-curve, but will be quite clear if presented as volumes (**Figure 3**). As with J-curves, however, there is no easy way to determine the 'ideal' distribution of size classes.

Yield Prediction

Under even-aged systems there will usually be published yield tables available, which tabulate the rate of growth of trees of a given species against volume production, based on data from sample plots. If the age of the trees is known and the height of the dominant trees is measured, such yield tables can then be applied to predict future timber production by establishing a site index or yield class.

There are no such yield tables for uneven-aged stands, as the age of the trees is not known (and younger trees can sometimes spend several decades 'waiting' to grow, so their actual age is not of any particular relevance). The volume of timber which is likely to be produced from an uneven-aged stand can only be assessed by reference to the site type (i.e., the soil and climate) and tree species, or to previous records of production from the site or similar sites in the locality.

Control of the Growing Stock

If periodic measurements are taken of the growing trees (usually by the use of sample plots) and of any trees that are blown down or harvested, a picture will be built up of the growth of the forest and any changes in the growing stock. It is usual for managers to adopt tentative targets for the appropriate volume or basal area of the standing crop, which they think will give optimum timber production and regeneration. If the volume of the growing stock becomes too large, there is likely to be inadequate recruitment of smaller trees and it is possible that the larger trees will be so overcrowded that useful timber increment will stagnate and the individual trees lack stability and vigor, and they may even suffer outbreaks of diseases or pests as a result of the stresses which result from this. On the other hand, if the growing stock is too small, there may be an excess growth of troublesome herbs, shrubs, or climbers, and timber volume production will be reduced, as there will be fewer trees on which volume can accrue.

Control of regeneration by measuring the size of gaps or the amount of daylight at ground level is not a part of normal practice in uneven-aged silviculture. Reliance is placed on adjusting the intensity of felling according to the perceived response to previous fellings. This is more a matter of judgment than following a set formula.

Shade-Intolerant Species

Uneven-aged silviculture is particularly well suited to shade-tolerant tree species, such as beech and silver fir, which can regenerate in the relatively shaded conditions which are created by the removal of a small percentage of the standing volume. Other species, such as pines and oak in north temperate countries, or the various species of mahogany (e.g., *Swietenia* and *Khaya*) in the tropics, which require more light for regeneration and growth, are sometimes perceived as being less well suited. It is, however, possible to manage such species on an uneven-aged basis if they are well matched to the site and if there are no other more shade-tolerant species that would tend to replace them. In marginal cases, a shift from single stem selection to a group selection system may allow sufficient regeneration of the less shade-tolerant species to maintain an adequate percentage of those species in the stand.

Nature Conservation

There appear to have been few direct studies of the relative merits of different forms of silviculture for nature conservation. Uneven-aged silviculture may not provide suitable conditions for mobile or ephemeral species that utilize clear-felled areas, and if all the forest in a region is managed in this way it may be necessary to have some clear-felled areas (which would include any coppiced areas) or permanent open space, in order to allow such species to survive. However, uneven-aged forest provides a much greater degree of stability and continuity for the many species which require this. It is also easier to leave some trees to grow to senescence, and to provide a continuity of deadwood for species of fungi, insects, and birds which make use of this. The greater structural complexity of uneven-aged forest provides a greater variety of ecological niches at a local scale than do even-aged stands (and should be more ecologically stable as a result).

See also: **Biodiversity**: Biodiversity in Forests. **Plantation Silviculture**: Sustainability of Forest Plantations. **Silviculture**: Coppice Silviculture Practiced in Temperate Regions; Silvicultural Systems.

Further Reading

Dawkins HC and Philip MS (1998) *Tropical Moist Forest Silviculture and Management*. Wallingford, UK: CAB International.

Hagner M (ed.) (1992) *Silvicultural Alternatives. Proceedings from an Internordic Workshop*, June 22–25, 1992. Report 35. Umeå, Sweden: Sveriges Lantbruksuniversitet, Institutionen för Skogsskötsel.

Hart C (1995) *Alternative Silvicultural Systems to Clear-Cutting in Britain: A Review*. Forestry Commission bulletin no. 115. London, UK: HMSO.

Kelty MJ, Lawson BC, and Oliver CD (eds) (1992) *The ecology of mixed-species forests. dordrecht*. The Netherlands: Kluwer Academic Publishers.

Kuper JH and Maessen PPThM (eds) (1998) *Proceedings of the Second International Congress of Pro Silva (1997) Apeldoorn, The Netherlands* (in English, French, or German). Apeldoorn, The Netherlands: Dutch Pro Silva Congress Foundation.

Matthews JD (1989) *Silvicultural Systems*. Oxford, UK: Clarendon Press.

O'Hara KL (1998) Silviculture for structural diversity. A new look at multiaged systems. *Journal of Forestry* 96(7): 4–10.

O'Hara KL (2001) The silviculture of transformation – a commentary. *Forest Ecology and Management* 151: 81–86.

O'Hara KL (2002) The historical development of uneven-aged silviculture in North America. *Forestry* 75: 339–346.

Otto H-J (ed.) (2000) *Third International Congress of Pro Silva, Fallingbostel, Germany* (in English, French, or German). Langenhagen, (Hanover), Germany: Poppdruck.

Peterken GF (1996) *Natural Woodland. Ecology and Conservation in Northern Temperate Regions*. Cambridge, UK: Cambridge University Press.

Pro Silva (1993) *Proceedings of First European Congress, Besançon, France* (in English, French, or German). Besançon, France: Centre Régional de la Propriété Forestière de Franche Comté.

SITE-SPECIFIC SILVICULTURE

Contents

Reclamation of Mining Lands

A J Moffat, Forest Research, Farnham, UK

Introduction

Worldwide, land has been significantly, and in some areas drastically, affected by mineral extraction. Societal pressures in most parts of the world now demand that after mining has ceased, someone (usually the mineral companies) should restore the affected land back to beneficial use, and this is controlled by legislation of various kinds and severity. Depending on a variety of factors including geology and landform, regional land use and ecology, climate and the views of community and landowner, the post-mining landscape may take a number of forms. Increasingly, the disturbance to the land caused by mining is used to advantage to regenerate the economic potential of the region or locality, increase the diversity of the landscape, and to enhance biodiversity and recreational value. In many parts of the world, trees, woodland, and forests are an essential part of this new landscape, following mining for materials that include lignite and coal, bauxite and other metal ores, aggregates, clays, and limestones.

The success of forestry schemes has not been assured – there has been considerable effort to improve reclamation standards by a growing understanding of the environmental and silvicultural issues involved. Even today, after several decades of modern research, forestry schemes can and do fail. This article will examine the main factors that must be considered in order to achieve the aims and objectives set for a woodland or forest planted on land previously used for mining.

Basic Principles

Trees have similar requirements on a post-mining site as they do in a forest: below ground, the provision of a nontoxic soil (or soillike) substrate to provide water, nutrients, air and anchorage, together with adequate climatic conditions above ground. The main issue for silviculturalists is that mined land often fails to meet these basic needs, so it is necessary for reclamation to take place according to their advocacy of the tree's requirements. Thus, the silviculturalist must have a reasonable understanding of basic biological tree needs, coupled with an appreciation of proper site and substrate characterization, and the ability to find a 'best fit' solution given inevitable constraints on substrate and site improvement. It can also be an advantage to think laterally in order to secure the best reclamation solution that will suit forestry planting. In addition to basic silvicultural concerns, forest establishment on often unstable and certainly fragile sites will require particular attention to the risk of soil erosion and surface water pollution. These needs usually require a team approach to land reclamation and tree establishment, and may include civil engineering and soil science in addition to silviculture. Other inputs may involve landscape architects and wildlife ecologists, as well as community consultation.

Reclamation of mined land is very dependent upon the manner of site preparation for mineral extraction, and subsequent site management (**Figure 1**). The most important factor determining the success of the forest re-established on the site is whether soil resources are identified, stripped, and stored sensitively. For sites to be mined, there should be no reason why soils are not stored for future re-use, but unfortunately many mined sites suffer from a paucity of soil or its damaged state through misuse. It is therefore vital that the silviculturalist gets involved in the process that will lead to forest establishment, preferably before any mineral has been extracted from the site.

Plans for the reclamation of the site should ideally be drawn up and agreed before mineral extraction. A soil resource survey and plans for final topography should enable an evaluation of the potential for the site. The actual plans for the site will be adjusted by the needs and wishes of the landowner, as modified

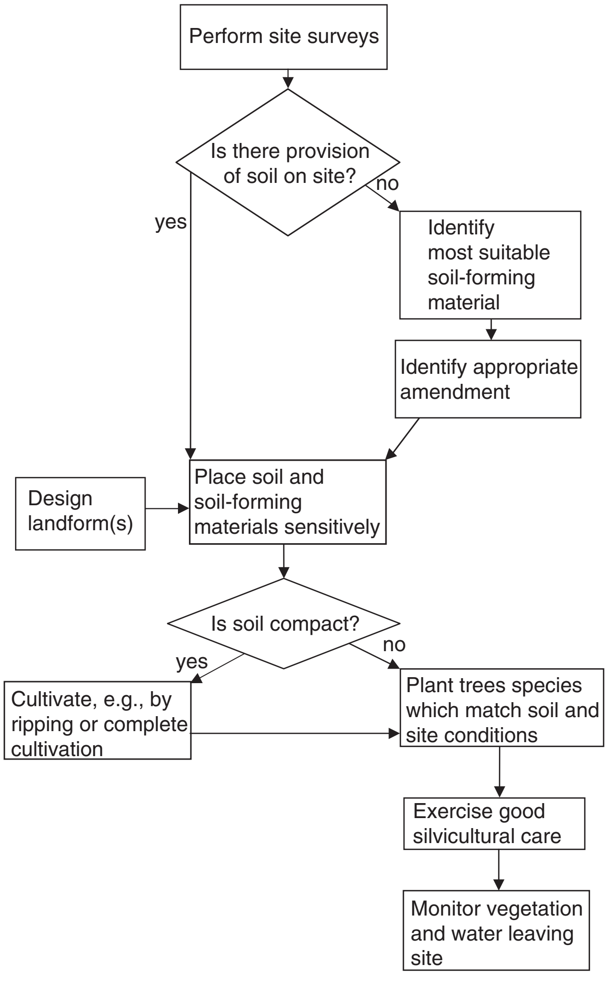


Figure 1 Basic stages of reclamation of mining land to forestry.

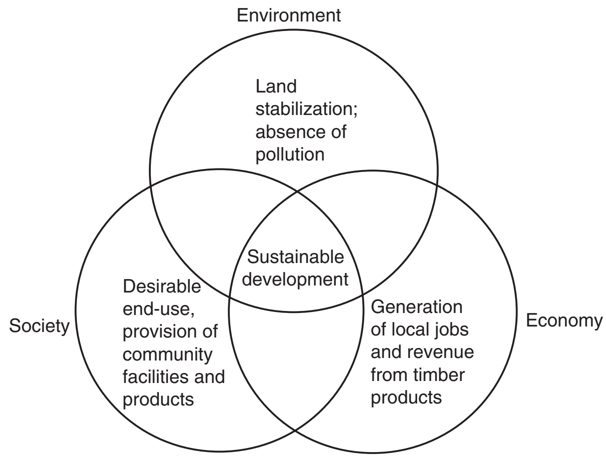


Figure 2 Mining reclamation to forestry and sustainable development.

by community expectations, usually expressed through the planning process. In all these deliberations, it is important that the aims and objectives for any woodland established on the reclaimed site should marry with natural soil and ecological processes. In other words, the direction of reclamation and tree establishment should be similar to that which naturally occurs, or might be predicted to occur. In addition, it is desirable to trim expectations for the forest according to realistic assessment of the resources available to support it, and not to strive for forestry objectives, for example an expectation of high wood quality, that cannot be met without inordinate inputs of engineering, raw materials, and continual site maintenance.

Mineral extraction per se will pose a certain risk of environmental pollution, but technologies at the mining site for mineral concentration and processing and mineral waste disposal usually pose far greater risks which must be managed upon reclamation. Mineral tailings are a particular type of waste which results from mineral processing, and may form a significant area of the site, usually in lagoons of mineral material of small particle size (e.g., fine sand, silt, and clay). Depending on mineral industry, tailings can contain elevated concentrations of heavy metals or potentially toxic elements (PTEs) and are often very acidic due to the presence of pyrites (FeS_2). Such areas may require significant remediation (see below) if they are to support forest, though trees may be amongst the most suitable vegetation types as they are generally relatively tolerant of elevated metal concentrations. Furthermore, forests and woodland can act to phytostabilize these areas, significantly reducing both wind and water transport and redistribution of pollutants. Phytoremediation, the abstraction or destruction of pollutants, may also be a realistic goal in some cases, because tree metal uptake and rhizosphere activity can both help to decontaminate some sites. For example, some poplars and willows enjoy a reputation for metal uptake, and in intensive silvicultural systems such as short rotation coppice, site pollutant remediation may be possible in the long term. Nevertheless, decontamination will only occur within the depth of the root zone.

An important principle is to plan a reclamation solution which is genuinely sustainable (**Figure 2**). From an environmental viewpoint, this is one that does not require repeated inputs of fertilizer, or continuing remedial attention to prevent water pollution. After trees are planted, it is difficult and cost-ineffective to right wrongs, and these should be scoped, predicted, and dealt with during the reclamation phase when earth-moving equipment is on site. From an economic point of view, the forest, if successful, should fully meet the aims set for it, and preferably generate income to support the silvicultural management inevitably required. Finally, the forest should meet societal aspirations and needs, whether for timber production, wildlife habitat, landscape stabilization or improvement, sport and recreation, or some or all of these. Forestry schemes that fail in some of these are likely to falter before they reach maturity. The management needs of the forest must be built into the plans for site reclamation, even though the responsibility for these may fall to agencies other than those responsible for the actual engineered reclamation solution.

Although satisfying the demands briefly described above may be a complex task, many examples worldwide indicate that successful woodland and forest reclamation can take place, testifying to the ability to avoid the weakest links in the reclamation chain.

Because mining technologies vary considerably according to geological circumstance and economic ability, there is a large range in the type of site and substrate presented for the silviculturalist to consider establishing forest on. It is therefore difficult to generalize effectively with broad reclamation guidance so that risk of failure is reduced adequately. It is essential that scientific (and other) literature relating to a particular mineral extraction and physiographic region is used effectively to build understanding of the local problems to be overcome. Nevertheless, there are some issues common to most mine sites which should be addressed, and these are discussed in broad terms below.

Landform and Drainage

The final landform of the mined site is usually partly determined by the nature of the geological obstacles to be overcome, and the original topography. Nevertheless, there are usually opportunities to input design into the final landform, and silvicultural needs should be included. For all sites, slope plays a part in affecting soil water drainage, and may be used to advantage in slowly permeable soil materials to reduce the likelihood of waterlogging. Slope angle, length, and form are also important in the control of soil erosion, and this should be dealt with by suitable engineering input. For relatively large sites where mechanical timber harvesting is in prospect, landform should be planned to facilitate this, and drainage located with due regard for the need for vehicular access. Roads should be designed at the same time as surface drainage, again by an appropriate engineering authority.

Surface water features are often sought on reclaimed sites. From an engineering viewpoint, these may serve as settling facilities to remove sediment before discharge of site waters into the main land drains and surface water system off-site. Suitably vegetated, e.g., with willows (*Salix* spp.) or reeds (*Phagmites* spp.), they may also help to remove water contaminants such as sulfates from the oxidation of pyrites. Water features can be attractive components of a reclaimed forest site, and will usually enrich its biodiversity and recreation potential.

Soil

Soil Selection

If soil materials are inadequate for forest establishment because of loss or degradation, there are two main options: (1) importation of substitute soil, or (2) soil manufacture using geological and/or waste materials. Option 1 is likely to be comparatively expensive if materials require purchasing, and there remains a need for strict quality control to prevent accidental importation of unsuitable (e.g., toxic) materials. For forestry schemes around the world, option 2 has been a mainstay in the absence of soil provision, and through considerable experience there is now strong guidance on this aspect of reclamation. There are usually good opportunities to select quarry wastes or reject materials, and possibilities to mix and blend to produce a desirable particle size range of soil-forming material. Reclamation of some mineral sites, e.g., after opencast coaling, will allow a wide choice of material due to the range of overburden materials, and it is important to characterize these fully with chemical and physical laboratory tests in order to select the most suitable for use. Here, the silviculturalist has a vital part to play by stipulating the kind of soil-forming material that will support the proposed forest. Sometimes, geological prospecting cores can be used to establish the range of possibilities before mineral extraction begins, but usually soil-forming materials will be identified during mineral extraction. It is important to have prepared guidance for machine operators so that they can select and store appropriate materials.

Some mineral substrates are intrinsically toxic and will not support satisfactory tree survival and growth without considerable treatment, for example some metalliferous mine tailings. If possible, such materials should be rejected as potential soil-forming materials in favor of less hostile materials rather than attempt to treat them. If there is little alternative but to attempt to establish vegetation, opportunities should be taken to cover these materials with whatever benign materials are available, even if these will not provide the full rooting depth of the trees and other vegetation types chosen. Of course, the underlying materials should be treated to minimize phytotoxicity before covering them, usually by controlling pH with lime or organic materials (see below).

Soil Placement

If original soil materials exist or can be saved before mineral extraction, reclamation can proceed routinely once final landform has been engineered. In hard rock quarries where a large void is created with steep sides, there will be limited opportunities for tree planting except in the bottom of the quarry. In soft rock quarries or opencast quarries where the product to overburden ratio is small, restoration to final landform involves the manipulation of overburden materials. Soils are then simply spread over them, provided slopes have been suitably engineered to allow this to take place and erosion risk has been assessed.

Soil (and soil-forming material) placement is at the center of good reclamation practice. Tree performance is severely hindered by soil compaction, which is often caused during reclamation by careless or misguided placement, or subsequent trafficking over newly laid soil. Compaction prevents deep rooting and therefore restricts the tree's ability to abstract moisture and nutrients. It can also cause surface waterlogging and ultimately lead to premature death or windthrow. Prevention is more certain than cure, and methods that spread soil without trafficking such as loose tipping are infinitely preferable to methods using earthscrapers or dozer tractors. The final configuration of the ground surface should be influenced by the climatic limitations of the site, and whether moisture retention against drought, or water shedding against waterlogging is the most important issue.

Soil Amendment

The principal difference between soil and soil-forming materials is the presence of soil organic matter in the former. This is the substrate which allows biological soil processes which in turn support and sustain plant life. In the absence of organic matter, soil-forming materials usually struggle to provide adequate nutrients to planted trees, especially nitrogen but also usually phosphorus. Soil materials put in storage often suffer from a loss of organic matter and a reduction in biological activity, but they generally recover if spread sensitively. In contrast, soil-forming materials may take decades or centuries to acquire organic matter levels comparable to those of normal soil. Research around the world has shown conclusively that it is extremely beneficial to amend soil-forming materials with organic matter at the time they are placed on the reclaimed land surface and awaits vegetation establishment. Materials such as sewage sludges or composted wastes are often used for this purpose, and **Table 1** gives more examples. Organic amendment can significantly improve the physical, hydrological, and nutritional qualities of the soil materials to be used. It may also reduce effects of acidity and metal toxicity, for example produced by the oxidation of pyrites. Soil placement methodologies using loose tipping can easily be developed to include the placement and incorporation of organic amendments, though for other technologies it may be necessary to consider premixing before the amended soil-forming material is finally placed on site.

Table 1 Examples of organic rich materials used as amendments in land reclamation to woodland

Raw sewage sludge
Digested sewage sludge
Thermally dried sewage sludge
Farmyard manure
Sugar mill waste
Paper mill sludge
Fish mort compost
Spent mushroom compost
Green (yard) waste compost
Municipal solid waste (MSW) compost
Wood residue

The size of organic material addition will depend on its chemistry, physical, and hydrological behavior, the evaluation of the amount required to produce a sustained supply of nutrients to the growing plantation, and the degree of risk posed to other receptors such as water bodies or humans who may visit the reclaimed site. It has been proposed that as a general rule, a reclaimed site requires between 1000 to 1500 kg N ha^{-1}, and this can usually be supplied by a manageable amount of organic material. It is desirable to achieve the addition of an amount that will supply tree nutrient needs until nutrient cycling via leaf fall and litter mineralization can provide the major source. A balance may have to be struck between this aim and managing the risk of water pollution from leaching and runoff. In some cases, it may be necessary to consider mixing more than one material, e.g., sewage sludge and papermill sludge, in order to achieve a more controlled nutrient supply.

Cultivation

It is still commonplace to require remedial cultivation in order to decompact soil (or soil-forming) materials prior to planting. This can be avoided completely if soils are loose tipped, but this may not be possible. Nevertheless, decompaction remains a vital operation – the comparative failure or poor performance of many tree planting schemes on land reclaimed after mineral extraction is due to lack of effort in achieving this. Techniques for decompaction will vary depending on available technology, ground conditions, and climate. In temperate countries, 'ripping' is commonly deployed, using a set of tines pulled by a crawler tractor. Fitted with 'wings,' these can be effective in loosening the ground, and ripping to depths of 1.5 m has been achieved in Australia, though depths of about 0.75 m are more common. Ripping is comparatively inexpensive, but it is prone to abuse by poor operator control, and loosened soil can recompact quite quickly. It must take place when the soil is dryer than the liquid limit to be effective in creating fissures and porosity. Ripping has been carried out both parallel and perpendicular to the contour.

Ripping is most suitable when a full soil sequence has been replaced on site because the operation generally keeps the soil horizons unmixed. It is not effective for mixing and incorporating organic amendments. Here, soil loosening with an excavator bucket also allows the incorporation process to take place with the same machinery, and 'complete cultivation' has proved very successful, if a little expensive.

It is obvious that, once decompacted, the ground so treated should not be trafficked by machinery if possible. Ripping can cause large stones to emerge at the soil surface, but stone picking and removal should only take place if such material will form a genuine impediment to tree planting.

Silvicultural Issues

Tree Stock and Planting

It is difficult to give useful generalizations because decisions about tree stock size, species, and density of planting will depend to a large extent on local environmental limitations and the particular objectives for the forest when mature. Experience in the UK has shown that it is important to be flexible in approach. There is a widespread belief that 'native' or 'indigenous' species are the most suitable for newly created sites such as those coming out of mineral reclamation, but this is challenged by considerable research. It seems sensible to choose species from those known to perform well on such substrates (including nonnatives), and to consider removing the least desirable species as thinnings when the forest matures, or to replant with more desirable species in a following rotation once the site has stabilized and nutrient cycling has commenced. Certainly, it is useful insurance to plant several species in group mixtures, so that some failures will not cause instability in the plantation as a whole. So-called pioneer species, such as willows (*Salix* spp.), poplars (*Populus* spp.), and alders (*Alnus* spp.) in the UK, tend to do well in the early stages of forest growth, and it is wise to use a significant proportion of these unless the site has been restored with original soil resources. These pioneers can tolerate the relative infertility that is usually associated with reclamation using soil-forming materials, and some are also able to withstand elevated concentrations of potentially toxic elements such as heavy metals.

Establishing forest blocks on post-mining land by application of tree seed is increasing in popularity. Seemingly ecologically more acceptable, especially if local seed sources are used, this technique has a place if carried out with due regard to seed dormancy (and seed is duly treated), and animal predation. The degree of silvicultural input is probably larger than with conventional planting, and the risk of failure is greater, but the results may look more naturalistic. Nevertheless, attention must still be given to the preparation of a suitable thickness of soil or soil-forming material during the engineering phase of reclamation.

Mycorrhizae and *Frankia* Inoculation

Initially, mineral sites restored using soil-forming materials can be almost microbiologically sterile unless organic amendments have been added. There has been considerable interest in the potential for purposefully introducing mycorrhizal fungi with tree stock in order to encourage survival and early performance on mined land. Several outlets now exist for the supply of material supposedly suitable for this purpose, but tree response is by no means assured, and local advice should be taken before embarking on a program of inoculation as a matter of course. In contrast, there is good evidence that when planting actinorhizal species such as *Acacia* spp., *Casuarina* spp., *Alnus* spp., *Elaeagnus* spp. or *Shepherdia* spp., only plants with Mycorrhizae and *Frankia* inoculation should be used.

Ground Vegetation

Although the importance of weed control is obvious, it is also the case that reclaimed post-mining sites often benefit from the establishment of a ground vegetation cover at the same time that trees are planted. For sites restored using soil-forming materials this vegetation will act immediately to facilitate the processes of soil formation which will benefit the site and the trees planted on it. While the trees are small, it will also 'green up' the site, improving its visual appearance and demonstrating commitment to the reclamation process. For sites restored using original topsoil, or amended with organic wastes, the correct choice of vegetation will permit effective control using selective herbicides – the alternative is to see a wide spectrum of weeds establish themselves that can be very difficult or expensive to control. For example, nonvigorous grass species are often chosen on reclamation sites in the UK, in order to hinder broadleaved weed germination while being susceptible to graminocide weedkillers. There has been considerable interest in the use of leguminous or actinorhizal plants as a significant component of a low ground cover, in order to provide or enrich the nitrogen capital of the site, and thus of the trees established on it. Choice will depend upon circumstance. However, it is important to ensure that such types of vegetation are truly infected with the requisite microorganism (usually confirmed visually by the presence of nodules on the plant roots).

Forestry objectives to increase biodiversity may demand that a ground flora of native plants be established, or vegetation similar to that which would be found under mature, seminatural woodland on neighboring undisturbed land. Nevertheless, these objectives should not obstruct the need to protect the tree seedlings from weed competition. In addition, the risk of fire should always be considered in the choice of ground vegetation cover.

Tree Protection

Tree protection is an important issue in all forest establishment, but imperative for forest planted on post-mining land. Unless reclamation operations have been exemplary, the site will still pose considerable problems for the newly planted tree, and silvicultural care must be first class. Weed control is usually vital but practice will depend on available technology and the size of the problem. Droughty sites, for example where stone content is high and organic matter content is low, should be given particular attention. So, too, should sites where organic amendment has taken place. Such materials usually promote rapid and large weed growth which can outcompete the planted trees for moisture, space, and light. Weed control may be necessary for several years on sites where tree growth is comparatively slow. Protection from animal browsing can also be important on reclaimed sites, and again, the form of protection will depend on the particular threat or threats. It may include fencing or individual tree protection; animal culling or control may also be necessary. Illegal grazing can be a significant problem in some parts of the world, requiring more severe measures if it is to be kept to tolerable levels.

Fertilizer Application

Infertility will require attention, and is commonplace when soil materials are not used for reclamation. Nevertheless, if organic amendments are used to improve both the physical and nutritional behavior of the soil-forming material, the use of mineral fertilizers may be unnecessary. And because funding for reclamation is usually more certain than that for maintenance, this approach is preferable to a reliance on one (or more) fertilizer applications during tree establishment. Fertilizers should be used with care, especially if soil materials contain little organic matter, because risk of leaching can be high. Fertilizer prescription should be based on soil or foliar analysis, or both. Local experience will guide interpretation, and, if limited, nursery or field experimentation may be warranted.

Site Monitoring and Maintenance

A forest established on sites reclaimed after mineral extraction is usually more susceptible to destructive agents such as drought, insect attack, or infertility than that on undisturbed land. It is therefore vital that attention be paid to the performance of the forest as it develops, especially in its early years. Regular site visits are necessary to check protective measures and the efficacy of operations such as weed control. Tree failure should be investigated and remedies put in place in case of significant loss. In addition, monitoring of water quality may be necessary for those sites where there is a risk of degradation of water quality, and consequent pollution to surface or groundwaters supplied from the site.

Conclusions

The principles of sustainability demand that land used for mineral extraction is brought back to beneficial use, and legislation around the world has been progressively tightened to ensure that this occurs. The largest responsibility for reclamation usually falls on the mineral operator. From an ecological viewpoint, a forestry after-use is often a serious candidate following mineral reclamation, though economic and social issues must also be taken into account. There is sufficient known about the science behind land reclamation to forest to suggest that high standards of reclamation practice are realistically attainable, and **Figure 3** shows examples of some successful schemes. Reclamation methodology is not overdemanding intellectually or economically. However, it is important for silvicultural issues to be put forward at the beginning of any

Figure 3 Examples of successful reclamation practice. (a) Bauxite mine in Australia during mineral extraction and about 15 years after reclamation (photographs by P. Garside). (b) China clay waste tip in Cornwall, UK before and 10 years after woodland establishment (photographs by A. Moffat). (c) Afan Argoed Country Park, Wales, UK during coal extraction and after reclamation (Forestry Commission). (d) Sand and gravel workings in southern UK before and after reclamation to woodland and wildlife habitat (photographs by A. Moffat).

reclamation project, understood, and then adhered to. There are many stages in the reclamation process, and failure at any of them will compromise forest performance. Effective management is therefore essential.

See also: **Afforestation**: Species Choice. **Landscape and Planning**: Forest Amenity Planning Approaches. **Site-Specific Silviculture**: Silviculture in Polluted Areas. **Social and Collaborative Forestry**: Social and Community Forestry. **Soil Development and Properties**: Nutrient Cycling. **Temperate Ecosystems**: Alders, Birches and Willows. **Tree Physiology**: A Whole Tree Perspective.

Further Reading

Ashby WC and Vogel WG (1993) *Tree Planting on Minelands in the Midwest: A Handbook*. Carbondale, IL: Coal Research Center, Southern Illinois University.

Barnhisel RI, Darmody RG, and Daniels WL (2000) *Reclamation of Drastically Disturbed Lands*. Madison, WI: American Society of Agronomy.

Bending NAD, McRae SG, and Moffat AJ (1999) *Soil-Forming Materials: Their Use in Land Reclamation*. London: Stationery Office.

Bradshaw AD (1983) The reconstruction of ecosystems. *Journal of Applied Ecology* 20: 1–17.

Bradshaw AD and Chadwick MJ (1980) *The Restoration of Land: The Ecology and Reclamation of Derelict and Degraded Land*. Oxford: Blackwell Scientific Publications.

Cooke JA and Johnson MS (2002) Ecological restoration of land with particular reference to the mining of metals and industrial minerals: a review of theory and practice. *Environmental Reviews* 10: 41–71.

Gardner J (2001) Rehabilitating mines to meet land use objectives: bauxite mining in the jarrah forest of Western Australia. *Unasylva 207* 52: 3–8.

Griffith JJ and Toy TJ (2001) Evolution in revegetation of iron-ore mines in Minas Gerais State, Brazil. *Unasylva 207* 52: 9–15.

Hüttl RF, Heinkele T, and Wisniewski J (eds) (1996) *Minesite Recultivation*, *International Symposium*, 6–8 June 1994, Cottbus, Germany. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Kendle AD (1997) Natural versus artificial methods of woodland establishment. In: Moffat AJ (ed.) *Recycling Land for Forestry*, pp. 26–35. Edinburgh: Forestry Commission.

Malajczuk N, Reddell P, and Brundrett M (1994) Role of ectomycorrhizal fungi in minesite reclamation. In: Pfleger FL and Linderman RG (eds) *Mycorrhizae and Plant Health*, pp. 83–100. St. Paul, MN: American Phytopathological Society Press.

Sarrailh JM and Ayrault N (2001) Rehabilitation of nickel mining sites in New Caledonia. *Unasylva 207* 52: 16–20.

Sopper WE (1993) *Municipal Sludge Use in Land Reclamation*. Boca Raton, FL: Lewis Publishers.

Torbert JL and Burger JA (2000) Forest land reclamation. In: Barnhisel RI, Darmody RG, and Daniels WL (eds) *Reclamation of Drastically Disturbed Lands*, pp. 371–398. Madison, WI: American Society of Agronomy.

Silviculture in Mountain Forests

W Schönenberger and P Brang, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

Mountain Forests are of Global Importance

What is a mountain forest? Definitions are, to a certain extent, arbitrary. Defining criteria usually include altitude, slope, and local elevation range (**Table 1**). Thus, steep mountain forests can also occur in the lowlands. Mountain regions cover 24% of the earth's land surface and contain 28% of the world's closed forests. Fifty-five percent of these mountain forests occur below altitudes of 1000 m above sea level. Mountain forests are found in areas with tropical, subtropical, temperate, and boreal climates. While only one in 10 people live in mountain regions, what happens in these regions affects many more people living in the lowlands. For example, deforestation in mountain forests may have an impact on climates and contribute to flooding in lower regions. Mountain forests are therefore globally important.

Rather than adopting a definition based on arbitrarily chosen ranges of altitude and slope, we take a silvicultural perspective in this article. Our focus is on those forests that require specific silvicultural treatments due to particular characteristics, or because they provide forest products and services associated with high altitudes and/or steep slopes. We therefore exclude, e.g., forests on flat highlands that are primarily used for timber production. We also exclude mountain forests in nature reserves since these are not silviculturally treated.

We first describe the characteristics of mountain forests, and then outline the silvicultural systems used in them. Since our areas of expertise focus on temperate mountain forests of the northern hemisphere, this article makes most reference to this forest type.

Mountain Forests are Different from Lowland Forests

Mountain forests of the montane and subalpine zones differ from lowland forests with regard to physical

Table 1 Areas (km^2) of mountain forest types in different mountain classes

Forest type according to altitude, slope, and elevation range	*≥ 4500 m*	*3500–4500 m*	*2500–3500 m*	*1500–2500 m and slope ≥ 2°*	*1000–1500 m and slope ≥ 5° or local elevation range > 300 m*	*300–1000 m and local elevation range > 300 m*	*Total*	*%*
Tropical (and subtropical) moist forests	19 359	83 597	139 607	399 656	482 061	1 197 610	2 321 890	24.5
Tropical (and subtropical) dry forests	183	15 054	35 293	50 565	107 267	343 390	551 752	5.8
Temperate and boreal evergreen conifer forests	2008	22 954	151 809	547 984	788 684	1 377 105	2 890 544	30.5
Temperate and boreal deciduous conifer forests			1241	76 209	313 908	985 600	1 376 958	14.5
Temperate and boreal deciduous broadleaf and mixed forests	1713	19 832	122 858	476 865	441 055	1 275 723	2 338 046	24.7
Total	23 263	141 437	450 808	1 551 279	2 132 975	5 179 428	9 479 190	100
%	0.2	1.5	4.8	16.4	22.5	54.6	100	

Reproduced with permission from Kapos V, Rhind J, Edwards M, *et al.* (2000) In: Price MN and Butt N (eds) *Forests in Sustainable Mountain Development. A State of Knowledge Report for 2000.* IUFRO Research Series 5. Oxford, UK: CABI Publishing http://www.wcmc.org.uk/habitats/mountains/statistics/htm.

conditions, species composition, stand structure, disturbance regimes, and the products and services they provide. Forest management must take into account the characteristics of mountain forests and the fact that the range of silvicultural options becomes smaller with increasing altitude or steepness.

Physical Environment of Mountain Forests

Many mountain forests at lower elevations are among the most productive in the world. However, the physical conditions of mountains change and usually deteriorate with increasing altitude. Mountains are exposed to excessive solar radiation. At 1800 m above sea level solar radiation is doubled compared to sea level. In contrast to lower altitudes, soil and vegetation absorb most heat from direct insolation, not from warm air currents. Wind speeds increase, and between 500 and 2500 m above sea level precipitations increase by about 100 mm per 100 m. Moreover, soil and air temperatures decrease, in the case of air temperature by about 0.55°C per 100 m in the free atmosphere. Precipitations fall partly as snow, and the duration of the snow cover increases by about 10 days per 100 m. Correspondingly, the growing seasons are shorter (about 1 week per 100 m), especially for young trees covered by snow. Tree growth is slow, seed production rare, and seedling establishment threatened by browsing ungulates, pathogenic fungi, snow movement, and climatic injuries. A unique feature of mountains is the Foehn, a frequent strong, warm, dry, falling wind, which in some regions can raise the temperature considerably above the usual values, but also cause severe windthrows.

On steep terrain in higher altitudes pronounced variations in slope and aspect give rise to steep gradients in site factors and a high variability in mesoclimate and small-scale microhabitat patterns. Here surface erosion and rockfalls may have considerable impact on the forest and vice versa.

The harsher climate at higher altitudes affects tree growth and forest dynamics. Snow cover and snow movements, ranging from creeping and gliding to avalanches, damage trees mechanically, and can uproot and kill seedlings. The growth and regeneration dynamics of trees are slowed down, reducing productivity and tree size. Regeneration is often scarce since seed years are infrequent; the harsh climate impedes the reestablishment of trees after logging or natural disturbances, and successful establishment is confined to favorable microsites. Moreover, established seedlings at high altitudes grow slowly and may therefore be potentially affected by competing vegetation, pathogenic fungi, and browsing ungulates for several years or decades.

Timberline

With increasing altitude the trees become gradually smaller. Finally, above the upper or alpine timberline (treeline), regeneration and growth of trees are no longer possible. The timberline can vary from sea level in polar up to about 4500 m in tropical regions. The current location of the timberline can have climatic, orographic, edaphic, or anthropogenic causes. In many parts of the world it has been considerably lowered by human activities, mainly by livestock grazing over the centuries. A variety of factors may locally be responsible for the timberline: low air and soil temperatures, negative CO_2 balance, frost damage, winter desiccation, wind abrasion, short growing season due to long-lasting snow cover, pathogenic fungi, or mechanical damage by moving snow. The transition between the forest and alpine meadows is often not a line but a zigzag ecotone. Trees growing in the timberline ecotone are often restricted to the most favorable microsites and are forced to adjust their growth forms to the respective conditions (e.g., tree islands, flag shape, carpets). Near the timberline many tree species almost exclusively regenerate by layering. In some arid regions of the world, mountain forests not only have an upper, but also a lower timberline, which grades into grasslands.

Species Composition of Mountain Forests

The number of tree species that are able to cope with the increasingly harsh environment at higher altitudes decreases from the montane to the subalpine zone. The lower elevations of the wet tropics are often covered with very complex montane rainforests, whereas the upper parts carry cloud forests, which are extremely rich in endemic species. On the medium and high mountains of the temperate zone and on the high mountains of the tropics needle-bearing genera such as *Abies, Cedrus, Juniperus, Larix, Picea, Pinus, Tsuga,* and *Dacrycarpus* prevail, often accompanied by *Betula* and *Alnus*. In the southern hemisphere the genera *Nothofagus, Libocedrus, Podocarpus, Dacrydium,* and *Eucalyptus* are prominent. Important timberline species in the tropics are *Senecio*, *Polylepis*, and many others. In the subalpine zone, the resulting stands are typically rather poor in species, sometimes even almost monospecific.

Structure of Mountain Forests

The northern coniferous mountain forests at lower and medium altitudes usually have a rather homogeneous stand structure, similar to many lowland forests. Towards the subalpine zone near the timberline, the horizontal stand structure is increasingly open, with single trees or tree clusters alternating with gaps of different sizes (**Figure 1**). The open texture is often accentuated by human activities, such as livestock pasturing or tree cuttings. The upper parts of these forests grade into tree islands and then into the alpine environment above the timberline. Avalanche tracks or screes often interrupt the forest canopy. Open stands have extensive internal margins and green crowns reaching close to the ground. Such forests are referred to as 'mountain selection forests' or 'group selection forests.' However, not all subalpine forests are open. *Nothofagus* forests in the southern hemisphere can form completely closed canopies near the timberline.

Disturbance Regimes in Mountain Forests

Mountain forests are subject to most of the well-known natural disturbance agents, such as fires, wind storms, droughts, insect and pathogen outbreaks (**Figure 2**). Human disturbance occurs as a result of road construction, timber harvesting, fire, or livestock grazing. Some disturbance agents are specific features of high-altitude mountain environments: for example, snow gliding can cause stem deformations, avalanches are capable of destroying whole stands, while rock and ice fall often injure stems or break trees.

The establishment and growth of seedlings and saplings may be hampered by livestock or browsing wild ungulates, by pathogenic fungi developing in the snow pack, or by frost injuries and winter desiccation. These agents may reduce growth or sometimes even kill regeneration established over decades. While mountain forests are not generally less resistant to most disturbance agents than lowland forests, their recovery after disturbance (resilience) becomes increasingly slow the closer the timberline is. This special feature of mountain forests must be considered in any silvicultural operations.

The Value of Mountain Forests

People use forest products and services in a variety of ways: for protection, for cultural and leisure activities, and as sources of timber and food. Some of these are specific to mountain forests.

The protection of the human environment against natural hazards is nowadays often regarded as the most important economic value of forests in mountain regions with high population densities. Most such hazards primarily pose risks on steep slopes, and some occur only at high altitudes. Steep slopes are prone to all sorts of mass movements, such as soil erosion, debris flows, mud- and landslides, rockfall, torrents, and snow avalanches (**Figure 3**). Many mountain forests provide the people or objects of value beneath them with direct protection. The

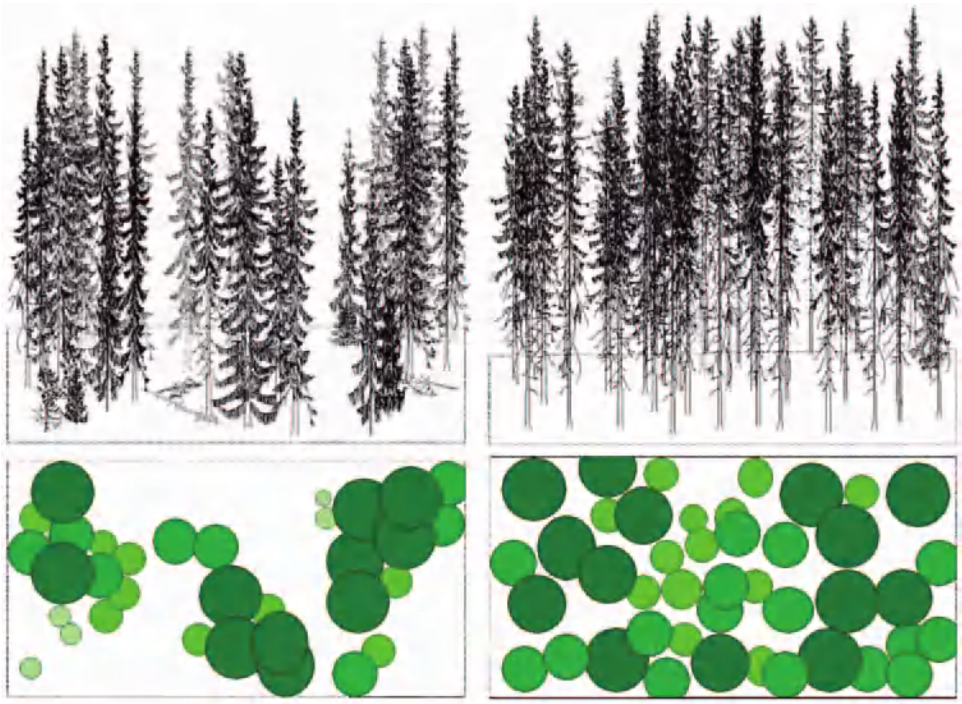


Figure 1 Cluster structure in a natural spruce mountain forest (left) in contrast to the typical uniform and homogeneous structure of a forest originating from afforestation (right). The clustered stand allows enough light and warmth to penetrate to the ground, thus creating good microsites for regeneration. The trees within a cluster maintain a common crown reaching almost to the ground. In the uniform stand there is not enough light for long crowns and forest regeneration. Reproduced with permission from Price MF and Butt (eds) (2000) *Forests in Sustainable Mountain Development. A State of Knowledge Report for 2000*. IUFRO Research Series 5. CABI Publishing.

Figure 2 Windthrow is an important disturbance agent in mountain forests. In protection forests natural hazards, such as rockfall, avalanches, and surface erosion, are matters of concern. Windthrow area near Disentis, Switzerland, caused by the winterstorm Vivian in 1990.

protective effect must be maintained continuously at the stand level, and not just at the landscape scale. If such a stand is destroyed, it must be replaced by expensive technical defense constructions. In direct protection forests the silvicultural options are therefore limited. Other protection forests provide only indirect protection, i.e., their effect is regional or at the scale of a whole landscape. Examples of indirect protection are forests that help to mitigate floods, or forested water catchments that ensure continuing

Figure 3 Mountain forests are capable of preventing natural hazards, in this case avalanche release, and of protecting people and assets. Andermatt, Swiss Alps.

Figure 4 Steep slopes hamper timber harvesting. Cable crane logging is a suitable technology developed for mountain forests. Photo courtesy of F Frutig.

supply of clean water and protect against soil erosion. In such cases, the exact location of the protection forest is not the important factor, but rather the proportion of the area stocked. In indirect protection forests more silvicultural options are available.

Timber production is not easy in mountain forests. Steep slopes and high altitude complicate timber harvesting operations (**Figure 4**). Access to the forests is usually difficult, so that logging is expensive and may be impossible in winter. Road construction is often costly if the roads are not to lead to more landslides. The potential for rationalization is limited in mountain forests. Most harvesting and planting technologies have been developed for lowland forests and cannot be used on steep terrain. But cable crane logging is one technological development that is suitable for harvesting in mountain forests. Another factor is that slow tree growth at high altitudes also means low forest productivity. This makes investing in a permanent infrastructure in mountain forests unattractive. It will only pay off if large enough quantities of timber are harvested; this may be excessive and unsustainable.

In less developed regions mountain people still depend directly on their local forests to satisfy many needs. However, timber production for fuel and construction wood has lost much of its former importance in industrialized regions during recent decades because cheaper fuel and imported timber mean it is no longer economically competitive.

With regard to nontimber products and uses mountain forests perform important functions as wildlife habitats, hunting areas, and livestock pastures. Forest products include fodder from forest trees, forest litter, fruits, mushrooms, fibers, resins, gums, medicinal plants, and agricultural crops in agroforests. These products are of variable importance over the world. In addition, the social, ecological, and amenity functions of forests are becoming increasingly valuable. For example, forests are essential for preserving biodiversity, for nature and soil conservation, for storing CO_2, as sources of fresh water, as recreation areas, and as areas of scenic beauty with spiritual or sacred values. Mountain regions play a special role in providing areas where these services can be performed because many mountain forests are still relatively uninfluenced by human activities.

While all mountain forests are multifunctional and provide several products and services, one function often dominates and guides silvicultural decision-making in a particular case. In some stands, silvicultural operations may not be required since either there is no specific local requirement for forest products or services, or a natural forest development is unlikely to impair the forest's ability to fulfill existing demands.

Silvicultural Systems for Mountain Forests

Historically, many mountain forests have been subject to severe degradation followed by erosion, which has caused loss of soil and site productivity. Large parts of the European Alps, for instance, were destroyed by excessive felling, burning, and grazing, before their restoration during the last 150 years. Most of the bushlands that cover the eroded mountains surrounding the Mediterranean today were once forest. Such silvicultural treatments – or maltreatments – have shaped many forests ('silvae' in Latin), but certainly not in the sense of a 'culture.' And the degradation continues today: silvicultural practices in mountain forests still deviate greatly, in some regions of the world, from recommended practice. Silviculture as a scientific discipline and wide-ranging practice only has a history of about 200 years. During this time several silvicultural systems, i.e., planned series of treatments for tending, harvesting, and reestablishing stands, have been developed for managing forests in a sustainable way.

Silvicultural systems vary in their ability to handle the management constraints in mountain forests. These constraints are related to the steep terrain, difficult forest access, harsh climate, slow tree growth, and natural hazards. Taking these constraints into account is part of a preventive silvicultural practice which strives to avoid costly restoration measures, regardless of whether they are biological (e.g., planting) or technical (e.g., erosion control).

Below we describe those silvicultural systems that are especially important and useful for managing mountain forests and make recommendations for how they should be applied. They include clearcutting, shelterwood, border cutting, selection, and coppice systems. Other systems that can be successfully practiced in mountain forests are agroforestry and variable retention systems (*see* **Silviculture**: Silvicultural Systems).

Clear-Cutting

Clear-cutting is a silvicultural system that removes an entire stand of trees from an area of 1 ha or more, and greater than two tree heights in width, in a single harvesting operation (**Figure 5**). It can be highly profitable. However, its application in mountain forests often involves unacceptable risks, or impairs landscape values.

Clear-cutting mountain forests can initiate erosion processes which may result in a complete loss of the soil. On a regional scale, higher altitudes in mountain areas usually receive higher precipitation. Steep slopes are prone to surface erosion (gullying, rill erosion),

Figure 5 A clear-cut and subsequent planting in Austria. On steep slopes clearcutting may lead to serious erosion problems.

nutrient leaching, landslides, and debris flows. Clear-cutting often contributes to reductions in root strength and soil water-holding capacity, due to soil compaction and reduced transpiration. Moreover, the removal of the forest cover exposes the soil surface to heavy precipitation and large variations in temperature. If natural hazards are to be prevented, the size of clear-cut areas in protection forests must be kept small. Thus, clear-cutting is often not an option.

Unstocked, even slopes steeper than about 30° at high altitudes are prone to avalanche release. If a slope exceeds 45°, snow avalanches can start in canopy gaps exceeding 30 m perpendicular to the contour line. Any rough surface structure, such as a rock, trunk, or tree, reduces the risk of snow movement by creating heterogeneity in the snow layer and 'nailing' the snow to the ground. While forests can rarely stop flowing snow avalanches, they are highly effective in preventing avalanche release. Surface roughness is also important for impeding rockfalls. However, in this case, forests serve not to prevent rockfall starting, but rather stop falling rocks.

If clear-cutting is not properly applied as a silvicultural system and is the first step to permanent deforestation, it usually has a negative impact on the fresh water supply. More than half of the world's population relies on clean water from mountains. While the demand is increasing, the supply is endangered. Mountains are the sources of most rivers, and mountain forests help to ensure that the water supply is seasonally balanced and that the water is of high quality. Clear-cutting large mountain forests without restoration cannot, therefore, be considered at all sustainable.

The impact of clear-cutting will obviously depend on the size of the clear-cut area. Large clear cuts in environments with pronounced climatic extremes, where tree regeneration depends on the beneficial effects of adult trees, must be avoided. This means that clear-cutting is not appropriate on very dry, very cold, or very wet sites, as it can lead to failures in stand renewal, even with repeated plantings. A system of small patch cuts is similar to the selection system, whereas leaving seed-dispersing trees to facilitate natural regeneration (the seed tree system) is comparable to the shelterwood system.

Not all damage attributed to clear-cutting is caused by the unwanted side-effects of the silvicultural system itself. The damage may actually be the result of inadequate road construction, of inappropriate site preparation treatments such as burning, or of careless logging practices, which damage the advance regeneration. However, even careful clear-cutting should not be used in those mountain forests where protection from natural hazards is needed, where erosion is a matter of major concern, and where the sites do not restock easily.

Shelterwood System

The shelterwood system is a silvicultural system in which trees are removed in a series of cuts designed to achieve a new stand under the shelter of remaining trees (**Figure 6**). In contrast to clear-cutting, it avoids having time periods where there are no trees to give shelter and to protect the soil, and thus reduces the associated risks. This system, therefore, has potential in mountain forests. However, it involves more costly

Figure 6 A shelterwood area with larch (*Larix occidentalis*) retained to provide seeds and to shade the regeneration. British Columbia, Canada.

timber harvesting than the clear-cutting system, and careful logging is required to avoid damage to the remaining stand and to the regeneration, particularly on steep slopes. If the individual trees in a protection forest are vulnerable to wind damage, shelterwood cuts will destabilize the stand and are therefore not advisable. The final cut can only be carried out when the regeneration has grown up sufficiently to ensure the protective effect is maintained.

Border-Cutting System

The border-cutting system (or strip-cut system) may also be appropriate in mountain forests (**Figure** 7). It involves successive cuttings in narrow strips, which combine the advantages of concentrated harvesting operations (one cut in one area) with limited harvesting damage. It does not create an open-land climate that impedes natural regeneration. In avalanche protection forests, the borders need to be sufficiently narrow to prevent avalanche release and must not be parallel to the slope. The borders can be laid out in the direction of cable crane lines.

Selection System

Selection systems remove mature timber either as single scattered trees or small groups at short, repeated intervals. Selection systems can be applied in a highly variable manner. They can range from small-scale patch cuts, shelterwood cuts and border cuts, to the single-tree selection system where only single trees are harvested. Selection systems are based on a heterogeneous stand structure and are therefore most suitable for ensuring continuous cover on steep slopes. A patchwork of tree groups of variable sizes and gaps is most efficient in structuring snow deposition, and can thus prevent, or at least reduce, avalanche release. Natural disturbance regimes can create this structural diversity, in particular in forests in extreme edaphic or climatic environments. However, on more productive sites, natural disturbances often lead to rather uniform stands, which then require conversion treatments.

Limited accessibility often makes the selection system too costly since the timber to be harvested is distributed over large areas, and very careful logging practices are required to avoid damage to the remaining stand. In some cases, cable cranes or even helicopters need to be used.

Group selection (or patch-cut) systems create openings narrower than twice the height of mature trees in the stand, and leave groups of up to about 20 trees in a cluster (**Figure** 8). They can be flexibly designed to fulfill potentially conflicting requirements in protection forests, namely high stand density in tree groups to ensure effective protection against avalanches and rockfall, and open canopy patches to allow sufficient regeneration and thus ensure continuous protection. Group selection, with special focus on the retention of small tree clusters and gaps, is referred to as 'mountain group selection.'

Selection systems also facilitate advance regeneration and thus ensure high resilience after disturbances. In subalpine forests, the gaps created with single-tree selection systems may be too small to ensure sufficient regeneration. Examples are the numerous dense, uniform Norway spruce stands in the European Alps, which are often the result of

Figure 7 An example of a border cutting in a Norway spruce–larch forest with narrow strips and replanting in Austria.

Figure 8 Tending in a regular thicket of Norway spruce to create clusters and gaps in Switzerland.

Figure 9 An example of a slit opening in a Norway spruce stand to stimulate forest regeneration in Switzerland.

untended regular plantings or of natural regeneration after large-scale disturbance. They can be opened up with slit-shaped openings to stimulate natural regeneration (**Figure 9**). Leaving 'nurse logs' is a good long-term means of encouraging future regeneration on decaying wood.

Coppice System

Coppice systems lead to a high stem density and can therefore be recommended for rockfall protection forests if the areas cut are sufficiently small. This system is highly appropriate if there is need for fuel wood. Collecting fuel wood does not require heavy machinery and therefore is less of an erosion hazard than commercial timber harvesting.

Afforestation

The restoration of degraded mountain forests on pastures by means of afforestation is not a silvicultural system, but requires great silvicultural expertise. For afforestation at high altitudes, suitable species and provenances from similar environments need to be carefully selected. Damage due to grazing by wild or domestic animals needs to be limited to acceptable levels. In environments with extreme climates, planted seedlings may need further management interventions for decades, e.g., planting a forest of pioneer trees to reduce frost damage, watering during drought periods, or setting up temporary barriers to prevent snow gliding.

In contrast to the open structure of natural stands described above, many planted stands tend to become single-storyed, even-aged, uniform, monospecific, and short-crowned. In protection forests, new plantings should be arranged in an irregular, grouped pattern over the terrain, corresponding to the distinct microsite variations found at this altitude. Favorable microsites, such as locally raised areas, are planted, while unfavorable ones, such as gullies or patches with well-established tall forbs, are left unplanted. This minimizes losses among planted trees and prevents the formation of uniform thickets. Planting should take place over a long time span to create uneven-aged structures of different sizes.

Conclusions

Mountain forests provide goods and services that are vital for people's well-being throughout the globe. They are, however, notoriously difficult to manage: their special topographic and climatic features mean that they are highly susceptible to degradation. To sustain mountain forests, careful and sometimes very sophisticated silvicultural approaches are required.

Careful silvicultural practices alone, however, will not ensure a sustainable future for the mountain forests of the world. A silvicultural system might be biologically perfect, but totally inappropriate if it fails to take into account the wider social context. Moreover, attempts must be made to anticipate the effects of changes in human demand, economic constraints, and ecological changes, such as global climate warming. Existing silvicultural systems must then be refined accordingly, or new innovative systems developed. Approaches such as the mountain group selection system, and their use on a large scale, are quite recent. Testing the real merits of these systems on an operational scale is a challenge that forest managers and scientists will have to face.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging; Forest Operations under Mountainous Conditions. **Plantation Silviculture**: Multiple-use Silviculture in Temperate Plantation Forestry. **Silviculture**: Coppice Silviculture Practiced in Temperate Regions; Forest Rehabilitation; Silvicultural Systems. **Windbreaks and Shelterbelts**.

Further Reading

Brang P, Schönenberger W, Ott E, and Gardner B (2001) Forests as protection from natural hazards. In: Evans J (ed.) *The Forests Handbook*, vol. 2, pp. 53–81. Oxford: Blackwell Science.

Evans J (ed.) (2001) *The Forests Handbook*. Oxford: Blackwell Science.

Garfitt JE (1995) *Natural Management of Woods – Continuous Cover Forestry*. Taunton, UK: Research Studies Press.

Glück P and Weber M (eds) (1998) *Mountain Forestry in Europe–Evaluation of Silvicultural and Political Means*. Publication Series of the Institute for Forest Sector Policy and Economics. Vienna: Universität für Bodenkultur.

Hamilton LS, Gilmour DA, and Cassells DS (1997) Montane forests and forestry. In: Messerli B and Ives JD (eds) *Mountains of the World. A Global Priority*, pp. 281–311. New York: Parthenon.

Helms JA (ed.) (1998) *The Dictionary of Forestry*. Bethesda, MD: The Society of American Foresters, CABI Publishing.

Holtmeier FK (2003) *Mountain Timberlines. Ecology, Patchiness, and Dynamics*. Dordrecht: Kluwer Academic.

Matthews JD (1989) *Silvicultural Systems*. Oxford: Oxford Science Publications.

Messerli B and Ives JD (eds) (1997) *Mountains of the World. A Global Priority*, pp. 281–311. New York: Parthenon.

Ott E, Frehener M, Frey H-U, and Lüscher P (1997) *Gebirgsnadelwälder*. Haupt, 287 S. Bern, Switzerland: Verlag Paul Haupt.

Peterken GF (1996) *Natural Woodland. Ecology and Conservation in Northern Temperate Regions*. Cambridge: Cambridge University Press.

Price MF and Butt N (eds) (2000) *Forests in Sustainable Mountain Development. A State of Knowledge Report for 2000*. IUFRO Research Series 5. Oxford, UK: CABI Publishing.

Ecology and Silviculture of Tropical Wetland Forests

P Hogarth, University of York, York, UK

Introduction

Tropical wetland forests comprise a highly diverse group of habitats scattered throughout the humid or coastal tropical regions of Africa, Asia, the Americas, and Australia. They include inland riverine and swamp forests and coastal mangroves. Depending on definition, the total area of tropical wetland forest is probably in the range $160–180 \times 10^6$ ha worldwide. The tree species of inland forests are often of poor quality as timber, and are difficult to extract: forest management and silviculture are therefore often rudimentary. Nevertheless, some trees, and many secondary products, are of economic value. Mangroves, or tidal forests, in contrast are often of high value, and may be intensively and efficiently managed for timber, as well as providing a range of other goods and services.

The defining character of a tropical wetland forest is that the soil in which the trees stand is submerged or waterlogged, either permanently or intermittently. Intermittent flooding may be seasonal, for months at a stretch or for shorter periods, with the forest sometimes reverting to virtually dry land conditions between inundations. In the case of coastal mangrove forests, flooding is tidal and typically occurs twice daily for hours at a time, with the soil remaining waterlogged between high tides.

The topology and hydrology of wetland forests profoundly affect their ecology and relationship with adjoining ecosystems. Basin forests, with net inflow of water into a depression, are net accumulators of silt, nutrients, and suspended organic matter. Forests fringing rivers may trap sediment, hence may also be net accumulators, or, depending on flow patterns and other factors, they may be net exporters. Tidal forests are exposed in addition to fluctuating salinity as well as to fluctuating water levels, and have special adaptations to cope with salt as well as with waterlogging.

Adaptations to the Wetland Environment

Waterlogged ecosystems present particular challenges to plants growing in them. The underground roots must acquire oxygen for respiration and eliminate carbon dioxide. In a normal soil, gas exchange presents few problems. The atmosphere comprises 20% O_2, and, since much of the soil volume consists of air space, rapid diffusion is possible. In contrast, diffusion of O_2 and CO_2 through water occurs at a fraction of the rate through air. Moreover, even at saturation the concentration of O_2 in water is low: in the richly organic waters of many wetland forests microbial action is likely to reduce it further, creating virtually anoxic conditions.

Wetland forest trees have therefore evolved adaptations to their waterlogged environment. The ratio of root-to-shoot biomass is often lower in wetland trees: relatively less of the tree structure is in the anoxic waterlogged soil, and underground roots are in general restricted to the upper, partially aerated layers of the soil. The relatively high stem density of some basin wetland forests, a response to poor soil aeration, may also result in a relatively increased stem surface area available for gas exchange. In many species, the roots themselves leave the main trunk well above ground (or water) level. Such aerial roots take many forms, and are often described as buttress or knee roots. They have numerous lenticels to allow gas exchange with the atmosphere, and spongy aerenchyma tissue to allow gas movement by diffusion within the root mass. The most striking forms of aerial or buttress root occur in mangrove trees, such as *Rhizophora* species, where the roots may separate from the trunk several meters above ground level (**Figure 1**). Freshwater wetland trees such as *Pterocarpus* (**Figure 2**), *Casuarina*, and *Myristica* produce similar aerial roots, and are sometimes known as freshwater mangrove.

Figure 1 A mature mangrove (*Rhizophora*) with aerial roots (Merbok, Malaysia).

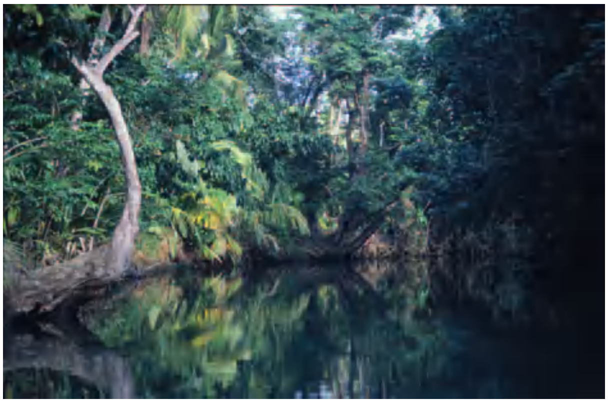


Figure 2 The bloodwood or freshwater mangrove, *Pterocarpus officinalis*, in Dominica. Photograph courtesy of Lance Leonhardt.

Aerial roots supply adequate anchorage and support. The absorptive function of roots is carried out by the reduced underground components: as these lie close to the soil surface they benefit from close proximity to the leaf litter layer in which inorganic nutrients are released by microbial decomposition.

Mangroves (*Avicennia* and *Sonneratia* species) and some freshwater wetland trees (*Dactylocladus* in

Southeast Asia, *Mitragina* in Africa) facultatively produce another specialized respiratory structure, the pneumatophore. Pneumatophores are vertical peg-like columns of aerenchyma that grow from horizontal underground roots and protrude from the soil surface. One tree may be served by many thousands. In *Avicennia*, these are typically 10–15 cm in height, but in *Sonneratia* may be more than 3 m, suggesting that their role is to maintain contact with the atmosphere even at high tide, rather than merely to avoid anoxic soil.

Tidally inundated mangroves are also exposed to high and fluctuating salinity: significantly raised salinity also occurs in some other wetland forests in coastal plains. Several methods of coping with high salinity have evolved. The proximity of horizontal roots to the surface enables them selectively to exploit less saline water in the surface layers of soil, avoiding the sea water itself and the deeper soil water, which may be of higher salinity. In some mangrove species, such as *Aegiceras* and *Avicennia*, up to 90% of salt is excluded at the root surface, by a poorly understood selective physical process.

Inevitably, some salt does accompany water uptake. *Avicennia* and other mangrove species (*Rhizophora*, *Sonneratia*) tolerate high internal salt levels by sequestration within vacuoles and exclusion from cell cytoplasm. Finally, salt may be either deposited in bark or in senescent leaves that are then shed (*Xylocarpus*, *Excoecaria*) or actively secreted from leaf salt glands (*Avicennia*, *Aegiceras*, *Sonneratia*).

Reproduction in a flooded environment presents particular problems. Mangroves typically show vivipary, and the release of large floating propagules. Those of *Rhizophora*, for example, may be 0.5 m long (**Figure 3**). Flotation provides a means of dispersal, with the size and robustness of the propagule conferring resistance to current and wave damage, and its advanced stage and the lack of a quiescent stage and the need to germinate enhancing its prospects of successful settlement. Freshwater wetland trees show fewer obvious reproductive adaptations, but the Central American *Pterocarpus officinalis* has a buoyant fruit 5 cm in diameter which can be dispersed by water currents.

Figure 3 Propagules of *Rhizophora*. Reprinted from Encyclopedia of Biodiversity, Vol. 3, P. Hogarth, Mangrove ecosystems, pp. 853–870, 2001, with permission from Elsevier.

Meaningful comparisons between wetland and dry tropical forests are not easy, and there are exceptions to all generalizations, but in general wetland forests are slower-growing and lower in above-ground biomass, and show simpler physical structure and reduced understorey vegetation. Tree species diversity is generally lower than in dry forests, decreasing with increasing frequency or duration of inundation: wetland forests have a tendency towards domination by a small number of tree species. In mangroves, and some fresh or brackish water coastal plain forests, there may be virtually monospecific zones within a forest. Offsetting relatively low tree species diversity, canopy epiphytes may be abundant. Riverine wetland forests tend to have greater productivity than those with stagnant water. Within the mangroves, increasing salinity is associated with lower growth rates and biomass, and towards the northern limits of mangrove distribution the combination of adverse physical circumstances results in dwarf forests, where the maximum height attained by mature trees may be as little as 1 m.

Wetland Forest Communities

The fauna of wetland forests falls into two more or less distinct categories: the terrestrial or arboreal, and the aquatic. Animals associated with the trunk, leaves, and canopy of wetland forests are in general similar to those in dry forests and other adjacent habitats. They are usually highly mobile, and individuals may move freely between the wetland forest and its surroundings. Most ground-living vertebrates such as deer, rodents, and lizards retreat from seasonal or tidal wetland forests as the water rises, and reenter as it falls: flying animals such as many bird, bat, and insect species can exploit wetland forests even when the ground is submerged, and may even benefit from the scarcity of predators.

Few species of bird, mammal, or insect are restricted to wetland forests: in Australia, for instance, of more than 200 species of passerine bird recorded from mangroves, only 14 are virtually confined to this habitat. The relatively small number of mangrove-specific bird species may reflect the simplified physical structure of the forest, with little scope for niche specialization. Similarly, although many monkey species forage within Southeast Asian mangrove forests, only the proboscis monkey (*Nasalis*) is found exclusively in mangroves and adjacent riverine forests. Among the invertebrates, many insect species occur in mangroves – any mangrove biologist can testify to the abundance of biting midges and mosquitoes – but only a single truly mangrove-specific species of ant has been reported, the Australian *Polyrachis sokolova*, which lives intertidally under the mud surface.

The aquatic components of wetland forest faunas are also largely the same as in adjoining habitats with few endemic species. In freshwater forests the dominant aquatic groups are mollusks (gastropod and bivalve mollusks) and fish. Mangrove faunas are dominated by marine fish and crustaceans. Among the fish, mudskippers are largely restricted to mangroves: the remaining species, often commuters, also occur in other habitats. The most abundant and diverse crustacea in Indo-Pacific mangroves are crabs, most notably fiddler crabs (*Uca*: family Ocypodidae) and leaf- or detritus-eating sesarmids (family Grapsidae). Fiddler crabs are deposit feeders, favoring sandy and muddy habitats which often coincide with mangroves. Sesarmids are more strongly associated with mangroves, at least in the Indo-Pacific region where some species have been recorded only from mangrove habitats: in the neotropics the association is less exclusive.

Freshwater forests are less well understood, but the general situation is likely to be similar to mangroves, with the majority of the forest fauna derived from adjacent terrestrial and aquatic habitats. The lack of a characteristic fauna does not, however, mean that the fauna is not important in the distinctive ecosystems of tropical wetland forests. In mangroves the role of sesarmid crabs, for example, is often crucial: by selectively predating seedlings, they influence the distribution of mangrove species, hence forest structure; by eating fallen leaves they facilitate energy flow through the ecosystem; by burying leaves they retain primary production locally; and by their labyrinthine burrows they aerate the soil and increase productivity of the trees. Fish that enter mangrove forests to forage at high tide represent a major channel of energy flow between mangroves and other habitats.

Similarly, in the freshwater forests of Amazonia, many species of fish seasonally occupy flooded forests. Amazonia has the most diverse freshwater fish fauna in the world: more than 1300 species have been described, and perhaps around 2500–3000 species exist, representing one of the most extreme cases of evolutionary radiation known. With the seasonal rise in river level, the adjacent forests are flooded for several months at a time, to a depth of up to 15 m. During this period many fish invade the forest. These range from predators such as piranhas (family Characidae) and small blood-sucking siluroid catfish to leaf-, fruit-, and seed-eating fish which have no clear ecological parallel elsewhere in the world. The characid *Colossoma macropomum*, for instance, has molar- and incisor-like teeth which have evolved to crush hard nuts. The gut of a single fish can contain up to 1 kg of seeds of the rubber tree *Seringa*, comprising a total of about 150 seeds. A single tree may carry only 100–200 seeds at a time. Many other fish species (including, despite their reputation, species of piranha) also eat seeds and fruit. Although it is hard to evaluate the importance of seed-eating fish, it is likely that, among other impacts, they contribute to the maintenance of tree diversity within the forest. They may also assist in seed dispersal.

Tropical wetland forests are therefore ecologically diverse, notwithstanding the common features of trees adapted to inundated habitats, and contain a fauna that comprises both aquatic and terrestrial components.

Silviculture and Management of Tropical Wetland Forests

Freshwater Wetland Forests

In the neotropics, wetland forests are often inaccessible for much of the year, and inhospitable because of the hosts of biting insects. Many of the tree species are of little commercial value, and the species richness that delights biologists means that, to foresters, the few economically valuable species tend to be sparsely distributed. Exploitation of neotropical wetland forests is generally minimal and management virtually nonexistent. Secondary forest products, such as fisheries, may be significant, but timber extraction is sporadic.

***Pterocarpus* forests** An example is the *Pterocarpus* forested wetlands of Central America and islands of the Caribbean (**Figure 2**). These are dominated by *P. officinalis* (Leguminosae), the bloodwood or dragon's blood tree. In coastal forests, for example in Puerto Rico, *Pterocarpus* forms monospecific stands, but it is more typical for it to comprise perhaps 70% of the basal area in a mixed forest which may contain scores, or even hundreds, of other tree species.

Pterocarpus is a species well adapted to the swamp environment. It grows to a height of 30 m, with buttress roots arising from up to 5 m above soil level. The subterranean roots are shallow, with nodules of symbiotic nitrogen-fixing bacteria, giving an advantage in a (presumably) nitrogen-depleted environment. A further, probably major, factor contributing to its dominance is the propensity to develop secondary sprouts (suckers) from the roots following damage or rotting of the primary trunk. This may enable reproduction in permanently flooded conditions, as the floating seeds of *Pterocarpus* cannot root in water deeper than 3–4 cm, but it is also highly advantageous in recovery following hurricane damage. Much of Central America and the Caribbean is subject to frequent hurricanes.

Unfortunately, given the relative abundance of the species, *Pterocarpus* wood is of poor quality, being weak, light (with a specific gravity of 0.3–0.6), and lacking resistance to termite and fungal attack. It is therefore of use chiefly for the manufacture of boxes and plywood, in the production of charcoal, and as fuelwood. More than 90% of the rural population of Central America depend on fuelwood for cooking. The blood-red resin that seeps out when the bark is damaged, and which gave the tree its common names, was formerly exported as an astringent and hemostatic, but is now of very limited pharmacological interest. Harvesting involves much waste, because *Pterocarpus* must be cut above the buttress roots: this further reduces its economic value.

Most attention is currently being given to enhancing the economic value of the swamp ecosystem so that *Pterocarpus* and other low-value species are replaced, where appropriate, by more valuable species. In Guyana and Surinam, for instance, swamp forests include the decay-resistant *Triplaris surinamensis,* the very hard *Eschweilera longipes* and *Ceiba pentandra*, and species of medicinal interest such as *Bonafousia tetratstachya*; other favored species in the region include *Symphonia globulifera*, *Calophyllum calaba*, *Carapa guianensis*, and *Virola surinamensis*.

In Guadeloupe, there are plans to cultivate *Calophyllum* and *Symphonia* at the expense of *Pterocarpus* where these species are already well established, to maintain monospecific *Pterocarpus* plantations where this species has virtual dominance, and to introduce, on an experimental basis, valuable nonnative species such as *Carapa* and *Virola*. Cultivation of economically desirable tree species will depend on successful harvesting and germination of seeds, and mastering effective planting techniques.

The Acai palm (*Euterpe*) One of the most successful manipulations of forest composition is of the multistemmed Acai palm *Euterpe oleracea* (**Figure 4**). This is widespread throughout parts of Latin America in *Pterocarpus* and other wetland forests, and is the source of several products of major economic importance. The fruits, of which a single tree produces about 20 kg per year, are used to produce a refreshing drink (acai) which is the most important nonwood product of the Amazon river delta, amounting to more than 100 000 t $year^{-1}$, valued at more than US$40 million.

Figure 4 The palm *Euterpe oleracea*, near Belem, Brazil. Photograph courtesy of Rolf Kyburz.

The other major *Euterpe* product is palm heart, a popular gourmet food in North America and Europe. In one region of Amazonian Brazil, harvesting of palm hearts employs 30 000 people and generates US$300 million annually. As the palm heart or 'cabbage' is the terminal bud of the palm, its removal kills the stem, and traditionally, Acai palm trees were simply cut down to harvest hearts. The relative ease of replanting in the middle of the forest and rapid growth, made this a reasonably viable process. A recent and more sustainable approach is to harvest stems from an individual palm by rotation, so new stems continually appear and a single tree can be cropped for decades. Regular cropping in this way also increases fruit yield.

Euterpe depends on the organic matter supplied by trees of the surrounding forest, so its successful cultivation depends on a balance being maintained with other species. Manipulation of wetland forest ecosystems, rather than single-species cultivation, can undoubtedly enhance the economic value of the forest resource. The success of this strategy depends on an understanding of the interactions between species. Due regard must also be had to other goods and services supplied by wetland forests, such as fishing, hunting, and ecotourism.

Mangroves

In contrast to the situation with freshwater wetland forests, mangrove forests are often intensively and efficiently exploited, using relatively sophisticated management strategies and techniques. This is particularly true in Asia, where large numbers of people depend directly or indirectly on mangrove forests. In addition to the use of mangrove wood as timber, fuelwood, and in charcoal production, mangrove leaves are used in fodder and medicinally, and the forests are the basis of local and nearshore finfish and shrimp fisheries and a productivity base for aquaculture; the protective value of mangroves against typhoons and coastal erosion generally is increasingly recognized.

There are many reasons why the exploitation and management of mangrove forests is so different from that of freshwater swamp forests. Mangroves almost always occur on the coast, or in the estuaries of large rivers. They are thus intrinsically more accessible than inland swamp forests. The number of species of mangrove tree is low: only around 50 true mangrove species are recognized worldwide, and an individual forest may be dominated by only two or three species. These generally grow in more or less single-specific zones, rather than being intermingled, so efficient extraction of a preferred species is relatively straightforward. And, finally, several mangrove species provide valuable timber which is resistant to insect attack and fungal decay.

An important factor in the management of mangrove forests is the typical mode of mangrove reproduction: vivipary, with the release of large, robust propagules. These can be collected either from the tree or after release, and either used directly or reared in nurseries for subsequent replanting (**Figure 5**).

The potential for ecosystem modification, and the effective management of the mangrove forest resource, is therefore greater than for freshwater forests. In countries such as Thailand and Malaysia, recognition of the economic importance has led to the development of long-term strategies for the sustainable management of mangrove forests, which in some cases have been in place for many decades.

Figure 5 Replanted mangrove, *Rhizophora mucronata* in the Indus delta, Pakistan (Korangi creek). The established trees are mixed *Avicennia marina* and *Rhizophora*.

The Matang forest, Malaysia One of the best examples of intense exploitation of a mangrove forest is that of the Matang forest of western peninsular Malaysia. The present sustainable management regime, accommodating timber extraction and other uses, has been running in more or less its present form for around a century.

The managed area of the Matang comprises an estuarine complex of streams, creeks, and inlets, amounting to more than 40 000 hectares. Around 2000 hectares are left untouched as virgin jungle reserve, a biodiversity reservoir which helps to sustain the surrounding managed area. Further patches are set aside for research, or protected as archeological, ecotourism, educational, or bird sanctuary forests.

The principal harvest from the Matang is wood for charcoal, the major domestic fuel of the local rural population. The management routine currently operates on the basis of a 30-year rotation period. The exploited forest is divided into blocks of a few hectares, allocated to charcoal companies by the Forestry Department, which manages the whole forest. Each block is clear-felled: workers move in by boat and demolish every tree with chainsaws, cutting the timber into logs of standard length. Where a cleared area abuts a river or tidal creek, a band of trees 3 m wide is left on the shoreward side of the block to prevent erosion of the bank. The logs are ferried to charcoal kilns in a nearby village.

No two adjacent blocks are cleared simultaneously, so that the forest is a mosaic of patches of different ages and newly cleared areas are always surrounded by mature trees. Spontaneous colonization and repopulation with incoming mangrove propagules are therefore rapid. The debris from the clearing operation takes about 2 years to decompose. A year after clearance, each site is inspected. If the area then covered by natural regeneration is less than 90%, repopulation is assisted by artificial planting, mainly with the dominant, and preferred, species *Rhizophora apiculata*. Local villagers rear seedlings in small nurseries for this purpose. At this time, weed species can also be removed by hand, or with weedkillers. The mangrove fern *Acrostichum* can be a particular problem (**Figure 6**). It is well adapted to occupying sunlit spaces in the forest, so rapidly occupies a cleared site, and prevents successful rooting of mangrove propagules. Destruction of seedlings by crabs and monkeys can also be a problem. The following year, the site is again inspected, and any parts where seedling survival has been less than 75% successful are again replanted.

Figure 6 *Rhizophora* in the intensively managed mangroves of Matang, Malaysia. All trees shown are of the same age, hence similar diameter. Much of the understorey vegetation is the mangrove fern *Acrostichum*, a significant weed species that may prevent the establishment of mangrove propagules.

Some 15 years later, the site is revisited, and the young trees thinned out to a distance of 1.2 m apart (based on a premetric distance of 4 feet, unchanged since). The thinnings – all the same age, hence a standard thickness – are valuable as fishing poles. When the stand is 20 years old, it is again thinned, this time to a distance between trees of 1.8 m (6 feet): this time the thinnings (still of uniform thickness) are of a size suitable for the construction of village houses. Because the previous thinning means that the trees are not crowded, these grow straight and are ideal for their purpose. Finally, after 30 years, the block is again clear-felled for charcoal.

Since management began, there has been a trend towards virtual monoculture of *Rhizophora apiculata* in the intensively managed areas of the Matang. During this time, there is some equivocal evidence of a slight decline in productivity, but overall the Matang is a model of sustainable management of a natural resource – a depressingly rare situation.

In 1992, wood extraction amounted to more than 450 000 t and was worth a little over US$4 300 000. In recent years, declining demand for charcoal, and a shortage of workers for the labor-intensive business of timber extraction and charcoal-burning suggest that the future value of the Matang may lie in other products. Although the management is largely directed towards timber extraction, this accounts for only around 12% of the total economic value. The area supports thriving fisheries: the offshore waters annually yield more than 50 000 tonnes of fish, valued at US$29 million, and supporting nearly 2000 people. Much of this probably depends on the productivity of the mangroves. Farming of the blood cockle (*Anadara*) currently runs at more than 34 000 tonnes a year, worth US$3 million, and could be further developed. The Matang also has considerable potential for tourism, being rich in wildlife, including otters, monitor lizards, and a wide range of birds, including the rare milky stork (*Mycteria cinerea*). At present, with virtually no infrastructure, tourism probably brings in around US$430 000 annually to the local economy.

Sustainable forest management is therefore of importance beyond the production of wood and other direct forest products. Even if the market for charcoal disappears, managed mangrove forests such as the Matang should therefore have good long-term prospects, provided the connections between mangrove production and other activities are fully recognized.

See also: **Plantation Silviculture**: Multiple-use Silviculture in Temperate Plantation Forestry; Sustainability of Forest Plantations. **Silviculture**: Managing for Tropical Non-timber Forest Products; Treatments in Tropical Silviculture. **Tropical Ecosystems**: Mangroves.

Further Reading

Beadle LC (1974) *The Inland Waters of Tropical Africa: An Introduction to Tropical Limnology*. Harlow, UK: Longman.

Field C (1995) *Journey Amongst Mangroves*. Okinawa: International Tropical Timber Organization, and Institute for the Study of Mangrove Ecosystems.

Goulding M (1980) *The Fishes and the Forest: Explorations in Amazonian Natural History*. Berkeley: University of California Press.

Hogarth PJ (1999) *The Biology of Mangroves*. Oxford: Oxford University Press.

Hunter ML (ed.) (1999) *Maintaining Biodiversity in Forested Wetlands*. Cambridge: Cambridge University Press.

Kathiresan K and Bingham BL (2001) Biology of mangroves and mangrove ecosystems. *Advances in Marine Biology* 40: 85–254.

Lacerda LD (ed.) (1993) Conservation and sustainable utilization of mangrove forests in Latin America and Africa regions. *ISME/ITTO: ITTO Technical Series* 13.1: 1–42.

Lacerda LD de (ed.) (2002) *Mangrove Ecosystems. Function and Management*. Berlin: Springer.

Lugo AE and Bayle B (eds) *Wetlands Management in the Caribbean and the Role of Forestry and Wetlands in the Economy*. Puerto Rico: USDA Forest Service.

Lugo AE, Brinson M, and Brown S (eds) *Ecosystems of the World*, vol. 15, *Forested Wetlands*. Amsterdam: Elsevier.

Whigham D, Dykyjová D, and Hejnŷ S (eds) (1992) *Wetlands of the World: Inventory, Ecology and Management*, vol. 1. *Handbook of Vegetation Science*, vol. 15/2. New York: Kluwer.

Silviculture and Management in Arid and Semi-arid Regions

E-H M Sène, Food and Agriculture Organization, Rome, Italy

Introduction

Drylands cover 41% of the earth and are represented in all the continents. Insufficient water quantity and in particular inadequate moisture to support plant growth during most of the year characterize these drylands.

Forests and tree formations play important economic, social, and environmental roles in these regions through a variety of functions including:

1. Conservation of soils through the buffering of erosion processes and land degradation control.
2. Conservation and improvement of the quality of water and regulation of the water regime.
3. Reduction of wind velocity, control of wind erosion, and buffering of water and moisture depletion.
4. Influencing local rainfall and condensation.

All these functions are essential and of high value in drylands and for the communities living therein.

The management and silviculture techniques and other human activities essential to the conservation and sustainable development of forests and trees are important but insufficiently documented in drylands. They promote efficient ecological and environmental buffering, and help to mitigate the harsh climatic conditions that characterize drylands. Biological diversity of forests and woodlands in drylands and the physiological functioning that allows their survival under the harsh conditions are conducive to a number of adaptations and processes. These need to be understood so that they may be used as tools underpinning sound silvicultural practices and good management of dry forests.

Arid and Semi-Arid Regions

Drylands 'experience during all or part of the year a period when evaporation exceeds precipitation, a period when all life in such lands must adapt in some way to reduced supplies of water or face death from dehydration.' They are understood generally as being in regions of the earth where the availability of water is deemed unsufficient to respond to the needs of living organisms. In particular, the water supply is insufficient to respond to the needs of human development including all the production activities that transform natural resources into goods and services. Drylands are generally marked by seasonality of rainfall, translating into an unsatisfactory distribution of water and moisture through the year. These elements affect the nature, quality, and distribution of plant life and of forests in particular.

Drylands are defined in terms of water related stress where mean annual rainfall (P) over potential evapotranspiration (PET) is less that the unity: $P/PET < 1$. Drylands are divided into various categories depending on the value of this equation. The greater the difference from 1, the greater the saturation deficit and the greater the stress plant communities are submitted to. The various subdivisions are shown in **Table 1**.

The Food and Agriculture Organization of the United Nations, with concerns mostly related to an effective growth period of vegetation used definitions based on the length of growing period (LGP). The growing period starts once rainfall exceeds half of the potential evapotranspiration. Areas are classified as follows:

- hyperarid (true deserts): LGP less than 1 day
- arid lands LGP less than 75 days,
- (dry) semi-arid LGP 75 to 120 days,
- (moist) semi-arid 120 to less than 180 days.

Overall, drylands cover 61 million km^2 or 40.7% of the total land area of the earth.

Forest Resources in Arid and Semi-Arid Regions: Categories, Location, Extent, State, and Evolution

The *Forest Resources Assessment 2000* estimated the extent of dry forests, mostly in arid and semi-arid areas, at 676 million ha, or 17% of the world's forested area. This covers a variety of formations from woodlands to steppe formations of various

Table 1 Subdivisions of the drylands of the world

Category	*P/PET*	*Percentage of global land area*
Hyperarid lands (usually known as deserts where vegetation is absent or discrete)	<0.05	8%
Arid lands	0.05–0.20	12%
Semi-arid lands	0.20–0.50	18%
Dry subhumid lands	>0.50	10%

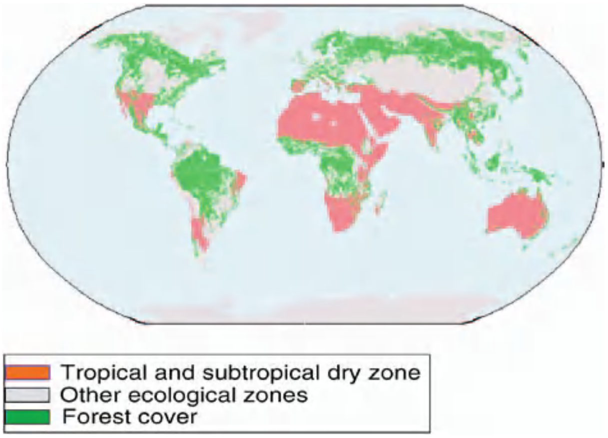


Figure 1 World distribution of dry zones and forest cover. From *Forest Resources Assessment 2000*.

structures and composition, but they occur mostly in the intertropical zones and subtropics (**Figure 1**). (Forests that are dry owing to the unavailability of water because of frost processes are not covered in this section.) Subtropical or Mediterranean forests have the same main characteristics as tropical arid and semi-arid forests: seasonal rainfall with frequent drought periods; structuring and biological influences of forest/bush fires; strong interactions with and mutual influences of agriculture and livestock raising; and the multifarious social and human functions they fulfil.

Categories of Forests and other Wooded Lands in Arid and Semi-Arid Areas

Most of the intertropical dry forests change according to rain and temperature/ecological gradients that run parallel to the equator. Although they share a number of characteristics due to the adaptation of local vegetation (vegetative cycles around and in the warmer and rainy seasons, presence of spines in arid areas, brilliant or velvety foliage, staged and deep rooting, stunted shapes under extreme conditions), these forests differ according to regions and continents. In general, tree presence, cover, and density decrease while grass cover increases regularly from higher to lower rainfall areas and increasing areas of stress. The typological gradient goes from dry deciduous forests to thickets, to open woodlands and savanna woodlands and then to tree savanna, shrub savanna with mixed trees, to thorny shrub steppes. **Figure 2** gives an overview of the arid and semi-arid woody plant formations of the world.

In the forest or woodland formations of arid and semi-arid areas, woody species play important and various functions. They produce small-dimensioned timber of specific and valued characteristics in density, grain, coloration, and resistance, suitable for various uses and applications from luxury wood handicrafts, saw timber to fuelwood and charcoal. Such forests also produce a great amount and diversity of non-wood goods including material for handicrafts, food, gums, resins, honey and wax, feed and fodder which help in the livelihoods of the local communities. Thus they provide vital support, directly or indirectly, for food production, security, health, and amenity.

Extent of Arid and Semi-Arid Forests in the World

Forests of arid and semi-arid areas are designated dry forests in this section. Dry forests occur in the dry, semi-arid, and arid ecological zones in tropical and subtropical regions. Most of them are found in the dry tropics and subtropics (83%). A low percentage of dry forest (17%) is found in the areas characterized by shrubs, steppes and desert formations (**Table 2**).

Economic and Social Importance of Forests in Arid and Semi-Arid Areas

The importance and central role of forest and tree formations in the well-being of populations in dry areas and specifically in arid and semi-arid areas cannot be overemphasized. Populations in arid and semi-arid areas have technologies and practices that use tree and forest resources in many aspects of their livelihoods: dwelling, food supply, clothing, comfort and amenity. In this, timber is a secondary product compared to non-wood forest products.

Direct Food Production

Shrubs and trees provide many food items. These include fruits, nuts, gums, roots and more rarely tubers, an innumerable array of leaves, and flowers. A number of species of particular interest have become internationally traded products such as gum arabic from *Acacia senegal*, setigera gum from the mbep tree *Sterculia setigera* occurring in the African Sudano-Sahelian woodlands and tree savannas, tamarind from *Tamarindus indica* of the tree savannas and woodlands of Africa, Southern America and tropical Asia, the butter from the renowned shea butter tree *Vitellaria paradoxa*, and the various products from the genus *Prosopis* particularly *Prosopis juliflora* of Central and South America. Flowers in dry forests yield excellent honey, pollen, and wax. A host of beverages are brewed from leaves and grasses, e.g., *Combretum* spp., *Vitex*, *Lippia*, and *Vetiveria*.

Dry deciduous forests These formations are at the fringe of semi-arid forests. They derive from subhumid forests with trees around 20 m tall over an understory of smaller trees and shrubs. The grass layer is discontinuous except in openings or clearings.

Thickets These are low formations of shrubs and small trees of 8 m or less. Generally they include shrubby acacias other stunted evergreen species.

Open woodlands As rainfall decreases formations of tall trees (around 20 m) scattered over an understory of smaller trees and shrubs appear in the landscapes of open woodlands. These are strongly wooded formations neither as tall nor as densely populated as forests but whose overall multistory stands cover the soil.

Savannas Dry forests and woodlands generally respond to the agreed definition of forest: 'land with tree crown cover (or equivalent stocking level) of more than 10% and area of more than 0.5 ha. The trees should be able to reach a minimum height of 5 m at maturity.' When woodlands evolve to savannas, grass cover becomes nearly dominant to exclusive. These formations are common in Africa and in the Brazilian *cerrados* and *campos* in South America.

Steppes The steppes have an even more modest tree cover and a discontinuous grass cover. They are however the domain of some woody species of high ecological, economic, and social relevance.

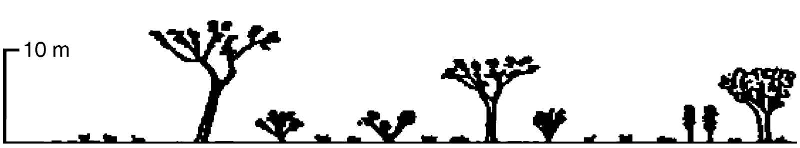


Figure 2 An overview of dry forest and tree formations. After Tropical Forest Botany, CTFT, Tome I, p. 135–139.

Table 2 Extent and distribution of dry forests

Region	*Tropical dry forest ($ha \times 10^6$)*	*Subtropical dry forest ($ha \times 10^6$)*	*Total dry forest ($ha \times 10^6$)*	*Percentage of total regional forest*	*Percentage of total world dry forest*
Africa	215 560	7 176	222 736	34	33
Asia	98 178	5 938	104 116	19	15
Oceania	78 535	47 881	126 416	64	19
Europe	0	41 748	41 748	4	6
North and Central America	8 861	15 267	24 129	4	4
South America	147 404	9 850	157 254	18	23
Total	548 539	127 861	676 399	17	100

Data from Forest Resources Assessment 2000 (FAO).

Medicinal and Related Products

Some of the species mentioned above provide medicinal preparations, but many other species of the arid and semi-arid lands produce the active ingredients for medical and cosmetic uses. These products bring cash income into the communities living in the forest and savanna. Many countries in the dry zones of Africa have organized the traditional practitioners and their activities in the formulation and presentation of local medicines. Cooperation has been established with modern medical and health institutions. Species such as *Vitellaria paradoxa*, *Jatropha curcas*, the jojoba (*Schimondsia chinensis*), and many other species exemplify the contribution of plants of dry areas to the production of medicinal ingredients.

Figure 3 Various locally manufactured products from non-wood forest products in a dry region of West Africa. Courtesy of FAO.

Timber, Fuelwood, and Charcoal

Forests and trees of dry areas yield important timber resources but only in limited quantities; hence their sustainable management is important. Due to the heat and water stresses, growth of timber is usually slow. This results in high-value timber in terms of texture, grain, and coloration. Most of the timber is of precious wood for cabinet-making or art handicrafts. Examples include the *Pterocarpus* species such *P. erinaceus* producing the precious Venn timber, the dry-area mahogany (*Khaya senegalensis*), and the ironwood produced by *Dalbergia melanoxylon*.

Wood for various local services (poles, building materials) is also important. But the most pressing use of wood is for energy. In all arid and semi-arid areas the processing and transport of fuelwood or charcoal is an active sector of the local and national economies. The first initiatives in the management of dry forests are aimed at organizing and regulating the supply of fuelwood to consumers, mostly in cities.

Miscellaneous Products for Small Industry Opportunities

Dry forests and other wooded lands of arid and semi-arid areas are sources of various products which play key roles in the livelihoods of local communities. A rich and diversified set of traditional technologies have made use of them. Today they are often the basis of small family enterprises contributing to fighting poverty. Processing of nuts, drupes, and beans (e.g. of *Balanites*, *Ziziphus*, *Parinari*, *Parkia*, and *Borassus*, to note some examples from dry West Africa), provides trade opportunities beyond village consumption to medium and large cities and to regional and international markets (**Figure 3**).

Wildlife, Game, and Recreation

Arid and semi-arid zones are rich in wildlife and spectacular landscapes. This is an interesting area that forest management cannot ignore but which has not up till now been appropriately taken into account. It has been dealt with in protected areas and game reserves, but in terms of international tourism and hunting. However, in the African woodlands and savannas antelopes and gazelles, (e.g., *Tragelaphus scriptus*, *Gazella rufifrons*, and *Cephalophus* spp.), as well as many small rodents, can provide protein for the diet of the local population. Warthogs and larger antelopes in the more subhumid areas offer opportunities for hunting and tourism. The spectacles of myriad of birds local or migratory in wet areas and water points are also excellent features, which benefit conservation and tourism activities. The criteria for sustainable forest management developed in all dry forest zones include conservation of biological diversity and it is expected that greater attention will be devoted to this in future.

Support for Agriculture

Dry forests are areas of major human development. Agriculture has had maximum development in semi-arid tropical and subtropical regions and at present they continue to play major roles in providing food in these areas. Forests and tree formations are a ready source of agricultural lands, and countries where rates of deforestation have remained high have lost these forests to agriculture. In the Sudan, hundreds of thousands of hectares of *Acacia seyal* forests have been lost to extensive sorghum cultivation; most of the annual loss of 900 000 ha of forest and other wooded land in this country between 1990 and 2000 was from the semi-arid and arid areas. The same situation prevails in all dry tropical countries. In the Mediterranean region pressures on forests for agriculture are very limited, except where irrigation systems can be extended. Indeed most suitable dry lands have been already occupied. Pressures may remain high in Asia and Latin America.

Fodder Production and Animal Husbandry in Pastoral Communities

Arid and semi-arid lands provide range areas *par excellence*. Throughout the world, people in these areas have built their livelihoods on the intimate knowledge and use of plant communities. A substantial corpus of traditional knowledge on the multifaceted role of the woody and grass vegetation of drylands has been developed. Very specialized modes of utilization have been developed, as shown in the example in **Table 3**.

Amenity

Species of arid and semi-arid areas are usually slender, with symmetrical canopies and often beautiful flowers. Some offer much needed shade in hot areas or may constitute efficient windbreaks to buffer heat and check dust. Some *Acacia* species, *Bauhinia*, *Cassia*, *Combretum*, and *Prosopis* are beautiful trees with magnificent flowers (**Figure 4**). Some species of worldwide importance include *Dichrostachys* spp., *Bauhinia*, some *Cassia* (e.g., *C. sieberiana*); and a number of *Cactus* species. The development of urban and peri-urban forestry has used species such as

Figure 4 A blooming *Combretum lecardii* in the dry season in the Sudano–Sahelian zone. Photograph by E Sène.

Table 3 Species utilization in the livelihood systems of dryland communities in the Sahel of Senegal

Objective	*Species used*
Animal nutrition	
For lactation	*Grewia bicolor*, *Acacia radiana*, *Acacia albida*, *Adansonia digitata*
For fattening	*Acacia radiana*, *Acacia albida*, *Acacia senegal*
Medicinal/veterinarian purposes	*Adansonia digitata*, *Adenium obesum*, *Acacia nilotica*, *Combretum glutinosum*, *Combretum micranthum*, *Combretum aculeatum*, *Crataeva religiosa*, *Bauhinia rufescens*, *Grewia bicolor*, *Dichrostachys cinerea*, *Cadaba farinosa*, *Balanites aegyptiaca*, *Sclerocarya birrea*, *Salvadora persica*
Construction	*Balanites aegyptiaca*, *Acacia nilotica*, *Prosopis africana*, *Hyphaena thebaica*, *Borassus aethiopum*

Parkinsonia spp., *Prosopis*, *Tamarindus indica*, and a number of Australian species including dry-area eucalyptus and acacias (e.g., *Acacia bivenosa*, *A. holosericea*, and *A. tumida*), *Prosopis*, in particular *P. juliflora* and *P. chilensis*, *Tamarix* spp., etc.

Biology of Dry Forests, and their Silviculture

Ecology of Arid and Semi-Arid Areas

The biological and physiological characteristics of the vegetation of arid and semi-arid areas guarantee adaptation to great heat and light, the inadequate availability of water, and, in a number of cases, salinity. In many cases the highest temperatures correspond to periods when availability of water is lowest which significantly increases stress in plant communities. A number of characteristics and attributes of these plant communities will be strong tools for the silvicultural treatment of forest and tree formations. The following should be particularly retained:

1. Protection and mobility of seeds. Most seeds are efficiently protected either by a long dormancy or a physical barrier to moisture, comprising a cuticle which needs to be altered chemically or mechanically before germination. Thus, seeds eaten by animals may benefit from partial modification of the cuticle, which later facilitates germination far from their origin. Other seeds (e.g., *Pterocarpus*) have wings or light tufts that facilitates transportation by wind.
2. Structure and functioning of the root system. The root systems of plants in arid and semi-arid areas are the strongest tools for their adaptation, survival, and regeneration. Most of them are deep with a taproot, which can extend to more than 10 m below ground. They have, in addition, extremely well-developed superficial horizontal roots (**Figure 5**), which can explore both for nutrients and moisture from the upper layers of the soil. Often roots develop suckers when they are slightly damaged or after fires.
3. Sprouting and protection of shoots. Many arid area species sprout vigorously and abundantly. The initial vitality of the shoots may facilitate survival through part of the dry season. These shoots have a number of adaptative options (stunting, early formation of thick bark, survival through shedding the aboveground part of the stem, and strengthening of underground organs) that guarantee final survival.
4. Reduction of leaf surface area. A relatively small leaf surface area helps dry-zone species overcome stress and maintain limited functions during the dry season.

Figure 5 Rooting system of *Acacia*. Photograph by E Sène.

5. Other flexible biological adaptations. Grasses and some shrubs develop a number of other adaptations, producing, e.g., bulbs, voluminous rootstock (*Guiera senegalensis, Icacina* spp.) which not only guarantee survival but also facilitate dissemination.
6. Adaptation to salinity. Many species are able to grow on saline soils or resist rising salinity. They adapt through evaporation and deposition of the salt on the leaves which are protected by leaves becoming succulent (*Dodonea* spp.) or very thin (*Tamarix* spp.).

It is only through these various adaptive strategies that plant formations succeed in living nearly unnoticed during dry periods and indeed are able to bounce back with speed and vigor as soon as rains occur. The silviculturist will use these adaptative strategies to trigger and manage regeneration.

Silviculture and Dry Forests

The corpus of knowledge supporting silviculture in arid and semi-arid forests is still to be largely completed. Some of the elements on which silviculture of these ecosystems are based are reviewed below.

Climate and seasonality The general pattern in drylands features the existence of strongly marked seasons. The dry season, of variable length according to the region, subjects living organisms to strong stresses. They are usually accompanied by the loss of foliage, to reduce evapotranspiration. Species adapt in a number of ways: spines, coated or velvety leaves, thick bark. This period is also marked by fires which debilitate the forests, kill seedlings, and when occurring late in the cycle destroy flowers and fruits. This may influence the livelihoods of populations as their strategy includes the use of fruits that mature in dry seasons (e.g., *Cordyla*, *Parkia*, *Ziziphus*) for lean periods. It may, by contrast, facilitate germination when the rainy season comes. Managing forest fires is then a potent tool in the management of dryland forests.

The unpredictability of the onset of the rains, the occurrence of large spells of drought during the rainy season itself or its precocious end are factors that strongly affect the growth and vitality of the forest in drylands and which make more difficult the silviculture of these forests. Fire hazards and the spread of insects will be highly dependent on such factors.

Heat and moisture are other important factors affecting the vitality of the forest. Temperatures in drylands may reach very high levels. In the Africa Sudano-Sahelian and Sahelian zones they are over 30°C for most of the year. In some periods high temperature and low humidity combine to produce high stress. These periods are the ones that most influence survival and the physiognomy of arid and semi-arid formations. When biological activity is at its lowest logging and other silvicultural operations may best be carried out.

Land and soils In most semi-arid regions, the most valuable land is devoted to agriculture. Forestry is reserved for poorer lands. In arid areas livestock rearing is dominant. But forests and tree formations have other important roles to play. Organic matter is in short supply in dryland soils. In forests and other wooded lands, which should play important roles in producing organic matter, mineralization is extremely quick. The grass biomass, however, contributes much to the process and should be incorporated into soils as early as possible. This prevents the export of much of the moisture when the climate dries up. Plantation silviculture needs to take this into account through well-planned seedling production campaigns, thorough soil preparation practices optimizing the relatively small amount of rainfall, adequate timing of planting operations, and weeding.

Human and social environment The dependence of local communities on the forest and tree resources is very high in arid and semi-arid areas. Stabilized agriculture takes place mostly in valleys and other topographically suitable areas with a high water table. Rain-fed agriculture is linked to the removal of the forests where some organic material has been accumulated under fallow or as new land. Pastoral land use is pervasive and forests and other wooded lands are the main resources supporting livestock. Silviculture as well as agriculture withstands competition with animal husbandry, but the control of livestock movements will be an important prerequisite in any forest management option. The utilization of a host of non-wood forest products is characteristic of dry forest use. This entails an intimate interaction of people and forests which can have a strong impact on silviculture and forest management.

Options for Silvicultural Models in Arid and Semi-Arid Forests

Silvicultural operations have a number of major functions, including structuring the stands; boosting growth and favoring selected stems; enhancing non-wood production, in particular fodder; securing health and vitality; and assisting regeneration. Generally, dry formations include separate or combined grass layers, bush and thicket, and intermediate small trees between taller trees. Silvicultural operations will aim at:

- controlling grass for proper use and avoiding its unplanned burning
- clearing or structuring the thicket to make it 'user friendly' and easy to enter
- maintaining the intermediate trees as a balanced filling to respond to needs for wood for fuel and service (usually by coppicing)
- dealing with biotic interferences, especially protecting regeneration from browsing by livestock or wild animals
- maintaining at long rotations the 'high forest' component often made up of species of high value.

Objectives usually cover (1) conservation and protection; (2) multipurpose production; (3) fuelwood production; and (4) timber production. As in all silvicultural regimes the regeneration methods and objectives govern options in dry forest silviculture. Dry forest formations can be regenerated through seeding and planting and through a series of vegetative regeneration practices. The regeneration methods are summarized below.

Natural regeneration Natural regeneration is constrained by many factors. Most fruits and seeds mature at the end of the rainy season or just before it. Seeds are very difficult to conserve when they are fleshy or if they are difficult to germinate. Fleshy seeds germinate very easily with the rains (e.g., *Sclerocarya birrea*, *Cordyla africana*) provided the soil is not hard or glazed. Unfortunately the seedlings have to face immediate competition from grass and other plants and the difficult survival conditions of the dry season. The risk of fire is high and most probably with no particular protection a very limited number of seedlings survives. There is also the risk of seedlings being eaten by wild or domesticated animals. Seeds with hard coats may lie dormant and resistant to mild natural processes and germinate only under particular natural processes or guided assistance provided by the silviculturist. The ingestion of fruits and seeds by animals including birds is important in the natural regeneration process. The digestion process alters the seed coat and facilitates germination (this explains the clustered nature of trees in *Acacia* savannas and steppes.)

Assisted natural regeneration Silvicultural interventions to assist and enhance natural regeneration are indispensable. They will aim at (1) easing water percolation and storage through subsoiling, ridging, and creation of structures where seeds and water preferentially accumulate; (2) reducing competition from grasses and shrubs with timely weeding; and (3) protection from fire either through complete weeding, partial weeding around the seedlings, and establishment of fire breaks.

Vegetative regeneration Usually species of dry areas react well to vegetative stimuli through sprouting, layering, cutting, and suckering. Vegetative regeneration is the most common basis of silviculture. Stands are regenerated after logging as most species sprout very strongly, thus providing stems that are appropriate for fuelwood or for making posts. Medium to superficial subsoiling may be used to scar roots and enhance regeneration through sucker inducement (e.g., most *Acacia* species, *Balanites aegyptica*, *Daniella olivieri*, *Cordyla pinnata*, and a number of miombo species).

Silvicultural Regimes

The coppice system Production of fuelwood and posts is the major objective of dry forest management. In West Africa it is in the production of fuelwood from the mix of Combretaceae and Leguminosae (mostly *Acacia*), with a filling of *Detarium macrocarpum* that management has evolved. These constitute the bulk of woodland stands. Pure stands sprout after logging. Cases in point are stands of *Combretum* and *Anogeissus*; pure stands of *Acacia seyal*; and partially inundated valley stands of *Acacia nilotica*.

Coppice and standard system In many types of dry forests and woodlands dominant trees are species of high value that are not used for fuel but for timber (*Khaya senegalensis*, *Pterocarpus erinaceus*, *Detarium* spp.) or fruit production (*Parkia biglobosa*, *Cola cordifolia*, *Sclerocarya birrea*). The same approach is valid for the miombo woodlands. Smaller trees and shrubs are periodically clear-cut, mostly for fuelwood and charcoal. This treatment is a coppice-with-standard system with different objectives pursued through the two components.

High forest system Pure high forests originating from seedlings are seldom established in dry regions. However under some special stand conditions pure stands can exist and naturally regenerate. A number of *Acacia* species are gregarious and may develop sizeable pure stands. Examples are *A. seyal*, *A. senegal*, and *A. nilotica* associated with floodplains or low-lying lands. In Central and southern America, *Prosopis juliflora* and *P. tamarugo* grow usually in thick pure stands, naturally regenerated. With the potential of abundantly producing suckers, some species produce pure stands with the appearance of seedling originated natural regeneration. *Daniella oliveri* in West Africa is an example. Silvicultural operations may choose to take advantage of these special situations, but then sprouts and suckers may overtake seedlings and most of apparently seed generated communities may well have derived from vegetative propagation.

Plantations Plantations in arid lands raise many problems but may be the only option when needs are urgent, or when rehabilitation and restoration are essential. Considerable efforts have been made in creating new forest plantations in some countries. There are 14 countries in the dry zones that have large planted forests. They include India, Thailand, Iran, Turkey, South Africa, Australia, Pakistan, Algeria, Sudan, Argentina, Chile, and Spain. These countries account for around one-third of the world's planted forests as estimated in the FAO's *Forest Resources Assessment 2000*.

Economic considerations Silviculture and management of forests succeed only if the operations engaged are sustained throughout the cycle of the forests. The initial investment in partitioning the forest and the subsequent operations of maintenance, thinning, and intermediate cutting call for financial resources. These are not always readily available with neither national forestry institutions nor local or private entities and individuals as investors. Options should be low in external and capital inputs and reasonably labor intensive. Foresters in many dry areas have promoted community-driven forest management and efforts on efficient marketing of products from managed forests (*see* **Social and Collaborative Forestry:** Joint and Collaborative Forest Management).

Managing Dry Forests for Various Objectives

Specificity and General Objectives of the Management of Dry Forests

Dry forests have to meet diversified economic, social, and ecological needs. The management of dry forests aims at (1) assessing societal needs; (2) measuring the resources and their potential, and (3) prescribing programs and operations to satisfy the needs, while securing conservation of the major characteristics of the resources. This is common to all types of forests, but dry forests are strongly constrained by low water availability, drought spells, forest fires, and strong human needs and expectations. Managing dry forests will respond to the needs for timber, wood for energy, a host of non-wood forest products, conservation and utilization of wildlife, recreation and overall conservation of the unique genetic and biological diversity present in them. Management includes a range of options corresponding to: (1) conserving and using sustainably naturally occurring formations; (2) cultivating coppice and high forest trees for differentiated production; (3) planning, organizing, and effecting active renovation of stands through reforestation; and (4) planning and effecting afforestation on bare land. A number of activities where trees are mixed with other land uses can be associated with forest.

History in the Management of Dry Forests

Until the early 1950s in many dry areas forestry was focused on conservation. Then initiatives for plantations started to grow, initially with no clear set objectives. Forest management started with very simple goals in many cases, aiming at securing fuelwood supplies for rail companies or for small industries such as brickmaking or cane alcohol distillation. But by the early 1980s, overconsumption of fuelwood and initiatives concerning renewable energy resources had brought attention to the potential of forest management to secure sustained supplies and conservation of resources. Programs of management of native forests instead of plantations were later promoted by aid donors, and by the early 1990s a number of demonstration projects had been completed allowing lessons to be drawn and targeted extension work to be developed. Countries such as Burkina Faso, Niger, and Madagascar in Africa began to develop national programs of forest management.

Promoting Sustainable Management of Dry Forests

The Intergovernmental Panel on Forests/Intergovernmental Forum on Forests program of action has addressed the issue of criteria and indicators for sustainable management of dry forests in Africa, Asia, and Latin America. A set of internationally accepted thematic areas corresponding to the following seven criteria for sustainable forest management have been agreed upon:

1. The extent of forest resources.
2. Biological diversity of the forests.
3. Forest health and vitality.
4. Productive functions of forests.
5. Protective functions of forests.
6. Socioeconomic functions of forests.
7. Legal, policy and institutional framework.

Forest management and silviculture should aim for the realization of these criteria that cater for the new paradigms of sustainable development.

Defining and protecting forest status/extent in arid and semi-arid areas At international level, FAO estimated that in developing countries dry forests, which covered 238.3 million ha in 1990, were being lost at the rate of 2.2 million ha per year in the period 1980–1990. This represented 1.1 million ha in Africa, 0.5 million ha in Asia, and 0.6 million ha in Latin America. *Forest Resource Assessment 2000*, estimated dry (tropical and subtropical) forests at 374 million ha. At national level maintaining the forests is a great challenge for dryland countries with growing populations and rampant poverty. Many countries now encourage the populace to get organized and engage in forest management as full partners.

Conserving the biological diversity of dry forests The multifunctional characters of vegetation from arid and semi-arid areas underlines the need for the conservation of the genetic resources they contain. Many efforts have been devoted to this and the multipurpose woody species of arid and semi-arid regions have been the subject of many projects on forest genetic resources. The Convention on Biological Diversity has reserved particular efforts to defining a program on the biological diversity of drylands, Mediterranean, arid, semi-arid, grassland, and savanna ecosystems. FAO has promoted national and regional projects for the conservation and use of the genetic resources of woody species of arid and semi-arid zones in Africa, Asia, and South America. A number of countries from the arid and semi-arid regions have recently developed national forest seed centers supporting growing afforestation programs. Ecosystem conservation is active in arid and semi-arid regions in response to their rich animal biological diversity, but more efforts are certainly needed.

Health and vitality of semi-arid and arid forests The greatest challenge to the management and protection of forests and woodlands of arid and semi-arid areas is the prevention and control of forest fires. Forest and/or range management should intimately encompass fire management. This will entail where possible methods of early burning in semi-arid forests, forest protection work in areas with high asset values, and population sensitization, training, and organization. The most efficient measures are those that create assets for people in and close to the forests through sustainable use of pasture, wood, bee-keeping operations, etc. Pests and diseases may cyclically break out and careful monitoring is essential.

Maintaining and heightening the protective functions of forests in arid and semi-arid areas It is essential that the management models of forests enhance the role of forests, trees, and grass formations in controlling land degradation, especially through limiting water loss, controlling wind erosion, and improving nutrient intake in soils. A number of species such as *Acacia albida* and *Prosopis procera* are known to improve and maintain soil fertility and moisture content of soils. The ability of, e.g., *A. albida* to conserve its foliage during the dry season and hence attract livestock and other animals under its shade is used in the agroforestry parklands and farming systems in dry regions. Efforts are being made to manage woodlands in watersheds (Guinea, Fouta Djallon, the Volta watershed in Ghana, etc.) to protect headwaters and secure steady flow to the major rivers in West Africa.

Productive and socioeconomic functions of forests The productive and socioeconomic functions of dry forests are closely linked (**Figure 6**). Silviculture and forest management should enhance them. The productive capacity of the resource is however limited. While some woodland and wooded savanna could yield wood products up to $8\,m^3\,ha^{-1}\,year^{-1}$, dry shrub savanna and steppes yield less $1\,m^3\,ha^{-1}\,year^{-1}$. Information on yield is fragmented and of various reliability; it needs to be further documented.

Legal, policy, and institutional framework of dry forest management Forest management needs continuity and monitoring to learn the lessons of experience and to consolidate options, techniques, and practices. In most arid and semi-arid areas the institutional framework for forestry is weak or strongly dependent on other sectors. Laws and regulations may be obsolete. During the last decade, however, sustained efforts have been made to strengthen national institutions and to update legislation and regulations. Efforts to involve local communities in forest management and the work of a number of networks have advanced decentralized models of participatory forest management, mostly in dry areas. The post-Rio Conventions, in particular the Convention to Combat Desertification, have provided new opportunities for institutional strengthening for overall natural resources management in dry areas.

Figure 6 A women's cooperative group in Nazinon forest, Burkina Faso.

Practical Experience

Experiences at country level have closely followed international developments in incorporating progressively current and emerging paradigms in forest management. Among those most important are (1) the devolution of the resources to people and putting forest at the service of local community development; (2) developing and disseminating the concept around the link of forests, trees, and people; (3) managing forest to enhance the multiple functions they support and following agreed-upon criteria and indicators for sustainable forest management in dry areas.

At the start of the twenty-first century, it is difficult to assess overall progress in effective forest management. The *Forest Resources Assessment 2000* of the FAO showed that for developing countries engaged in forest management, out of a total of 2139 millions ha, at least 123 millions ha or about 6% were covered by 'a formal, nationally approved forest management plan.' This shows that efforts are still inadequate. The situation is not much worse in arid and semi-arid areas taking into account the greater involvement of populations in participatory forest management in those areas. In Africa 4% of the dry forests of countries covered by the *Forest Resources Assessment 2000* study on forest management are under some management plan; in South America only 2% are under a management plan.

Challenges Ahead

There are daunting challenges in the management of forests in arid and semi-arid areas which will need to be faced in a sustained and continued way. They include, among others, the following:

1. Raising awareness on the many functions goods and services provided by dry forest resources, to communities that are among the poorest in the world.
2. Strengthening institutions that deal with dryland ecosystems, in particular research and policy institutions at national and regional levels.
3. Increasing knowledge and expanding technologies about assessment, management, conservation, and use of arid and semi-arid forest and tree resources.
4. Continuing work and strengthening cooperation on the assessment of the social, economic, and environmental services of dry forests.
5. Further focusing work on criteria and indicators for sustainable management of dry forests towards effective application and development on the field including considerations of wood and non-wood products of forests of arid and semi-arid zones.
6. Supporting effective action on the field so as to apply the wealth of knowledge acquired and paradigms developed to the sustainable management of forest and tree resources of dry areas.

See also: **Genetics and Genetic Resources**: Forest Management for Conservation. **Medicinal, Food and Aromatic Plants**: Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Silviculture**: Managing for Tropical Non-timber Forest Products. **Social and Collaborative Forestry**: Common Property Forest Management; Forest and Tree Tenure and Ownership; Joint and Collaborative Forest Management; Public Participation in Forest Decision Making; Social and Community Forestry; Social Values of Forests. **Tree Physiology**: Stress. **Tropical Forests**: Tropical Dry Forests.

Further Reading

Arnold JEM (1991) *Community Forestry: Ten Years in Review*. Rome, Italy: Food and Agriculture Organization.

Association Internationale Forêt Méditerranéenne (2002) Problématique de la forêt méditerranéenne. *Journal Forêt Méditerranéenne* 1: (Special Issue).

Bellefontaine R, Petit S, Pain-Orcet M, Deleporte P, and Bertault J-G (2002) *Trees outside Forests: Towards Better Awareness*. Conservation Guide no. 35. Rome, Italy: Food and Agriculture Organization.

Boffa JM (1999) *Agroforestry Parklands in Sub-Saharan Africa*. Conservation Guide no. 34. Rome, Italy: Food and Agriculture Organization.

Booth FEM and Wickens GE (1988) *Non Timber Uses of Selected Arid Zone Trees and Shrubs in Africa*. Conservation Guide no. 19. Rome, Italy: Food and Agriculture Organization.

Center for International Forestry Research (2002) Africa's tropical dry forests: time to re-engage an agenda for priority research. CIFOR & SIDA.

De Montgolfier J (2002) *Les Espaces Boisés Méditerranéens: Situation et Perspectives*. Montpellier, France: UNEP.

FAO (1984) *Études sur les Volumes et la Productivité des Peuplements Forestiers Tropicaux*, vol. 1, *Formations forestières sèches*. Rome, Italy: Food and Agriculture Organization.

FAO (1989) *Role of Forestry in Combating Desertification*. Conservation Guide no. 21. Rome, Italy: Food and Agriculture Organization.

FAO (1992) *Forestry in Arid Zones: A Guide for Field Technicians*. Conservation Guide no. 20. Rome, Italy: Food and Agriculture Organization.

FAO (1993) *The Challenge of Sustainable Forest Management: What Future for the World's Forests*. Rome, Italy: Food and Agriculture Organization.

FAO (2000a) *Fodder Shrub Development in Arid and Semi-Arid Zones*. Rome, Italy: Food and Agriculture Organization.

FAO (2000b) *Management of Natural Forests in Dry Zones*. Conservation Guide no. 32. Rome, Italy: Food and Agriculture Organization.

Hopkins ST and Jones DE (1983) *Research Guide to the Arid Lands of the World*. Phoenix, AZ: Onyx Press.
UNESCO (1961) *Histoire de l'Utilisation des Terres des Regions Arides*. Nancy, France: Berger-Levrault.

Silviculture in Polluted Areas

M V Kozlov, University of Turku, Turku, Finland

Introduction

The influence of industrial pollution on forest health has long been recognized as a serious applied and scientific problem. Although numerous field experiments have been established to determine practical measures for both the alleviation of pollution impacts on stand vitality and the rehabilitation of damaged forests, a general strategy has not emerged, and 'silviculture in polluted areas' is still in the incipient stages of development. Maintenance of forests in polluted areas requires more intensive management than in unpolluted areas, involving 'soft' techniques and highly skilled manual labor.

The prescriptions that form the basis of silviculture in polluted areas should be preventive, aimed at improving the ecological stability of stands in such a way that they will better resist pollution impacts. In many cases the vitality and productivity of forests affected by chronic acidification and heavy-metal contamination can be maintained by chemical amelioration. However, to be successful, the revitalization strategy should first aim at identification of nutritional disturbances and then apply diagnostic fertilization to alleviate these disturbances, balancing the anticipated beneficial and adverse effects. Suggested silvicultural measures include the creation of substitute stands, maintenance of stand integrity, a decrease in rotation time, avoidance of monocultures, and replacement of clear-cuts by selective logging and gap-oriented regeneration. The practical application of silvicultural measures, with successful amelioration of pollution impacts, is still limited to a very few areas of boreal and temperate forests.

Polluted Forests: Past, Present, and Future

Pollution, Polluters, and Pollutants

Historically, sulfur dioxide was the first pollutant to cause local but severe forest deterioration. This is the best-studied pollutant, under both experimental and natural conditions. In high concentrations it causes acute foliar damage, which weakens and then kills the trees; in low concentrations it contributes to regional acidification. Conifers are generally more sensitive to SO_2 than broadleaved species.

Fluorine emissions to the atmosphere started to increase in the late 1930s, reaching peak values in the late 1960s. These emissions were primarily associated with aluminum production, and they caused severe but local forest damage. However, fluorine emissions strongly decreased between 1970 and 1980 due to effective measures taken to minimize the release of fluoride from aluminum smelters to the atmosphere.

Heavy metals are very common pollutants but in general do not spread far from smelters. Only some of the largest polluters have caused detectable contamination of soils and vegetation at distances exceeding 50 km from the emission source. Heavy metals emitted by Monchegorsk and Norilsk can be detected (in atmospheric aerosols) and identified (e.g., attributed to the specific polluter) at distances up to 2000 km from the polluter. However, these long-transported metals have never been said to cause any biotic effects, especially in forests. Although most heavy metals are extremely toxic, they have rarely been reported as a cause of forest death. However, heavy metals adversely affect seedling establishment, thus hampering the natural revegetation of contaminated areas long after any decline in atmospheric pollution levels.

Increased deposition of nitrogen started to play an important role in European forests several decades ago. Although this pollutant does not create the dramatic landscapes of some other pollutants, its effects are insidious and long-lasting. In some countries, such as the Netherlands, annual deposition of nitrogen in the late 1980s reached $200\,Kg\,N\,ha^{-1}$, making eutrophication more important than the impact of 'traditional' pollutants. Increases in N deposition are also a big issue in some parts of North America, such as the San Bernardino Mountains of California.

Finally, ozone was recently identified as a possible contributor to forest damage in Europe and North America. Although unequivocal evidence for O_3-induced foliar injury on woody species under field conditions has only been found in a few places, mostly in regions with a warm and sunny climate (the Mediterranean, south California), and in alpine areas, including Sierra Nevada and the Appalachian mountain chains, ozone obviously weakens the trees leaving them vulnerable to other assaults and stresses. Overall, the quantitative risk assessment of O_3 impact on mature trees and forests is uncertain at the

European scale. Research suggests that risks exist, but these need to be validated for stand conditions.

Extent and Severity of Impacts

Local scale Extensive forest mortality around large sources of pollution has sometimes transformed forests to barren 'industrial deserts', and – despite the relatively small areas affected – has attracted considerable public and scientific attention in recent decades. The most striking examples of severe local pollution have long been associated with the Canadian smelters (Trail, Sudbury, Wawa). However, after implementation of strong emission controls in most industrial countries during the 1970s, the largest individual polluters are now located in Western Europe and Russia, with the Norilsk smelter in Northern Siberia being the largest globally: forest damage had been observed at distances over 150 km from this smelter. The largest point sources of fluorine-containing emissions are also situated in Siberia (Bratsk, Shelekhov, Irkutsk). The most extensive scientific information concerning both severe pollution impact on forest ecosystems and experimental remediation measures has been collected around the Monchegorsk smelter (Kola Peninsula, northwest Russia).

Regional scale Large areas of forest require rehabilitation as a result of the impacts of acidic deposition and other forms of pollution. The problem is particularly apparent in central Europe, with the most striking example being the 'Black Triangle,' an area along the German–Czech–Polish border. This region has been heavily affected by industrial pollution over the past 50 years, with severe consequences for the forests, landscapes, environment, and public health. Model calculations demonstrate that by 2050 severe regional problems will also occur in Southeast Asia, South Africa, Central America, and along the Atlantic coast of South America. However, almost no relevant research had been conducted in these regions, which may pose a serious problem for sustainable silviculture in the near future, when local foresters are faced with the need to mitigate pollution impacts.

Global scale In 1985, 8% of the forested areas of the world received annually $>1\,\mathrm{kg\ H^+\,ha^{-1}}$ as sulfur, and it is estimated that 17% of the forested areas of the world will receive this pollution load by 2050 (**Figure 1**). Similarly, 24% of the global forest was exposed to O_3 concentrations exceeding 60 ppb in 1990, and this proportion is expected to increase to 50% of global forest by 2100. These model calculations, however, should be treated with caution, as they are based on a number of assumptions and simplifications; however, it seems more likely that more and more extensive areas will require specific management that accounts for pollution impacts. Moreover, current predictions of forest responses to global climate change do not consider important physiological changes induced by air pollutants that may amplify climatic stress.

Forestry Facing Pollution: History, Theory, and Practice

Silviculture in Polluted Areas: An Operational Field

The impact of pollutants in concentrations exceeding critical levels (or permissible loads) results in the deterioration of forest ecosystems, and they move from their original state towards industrial barrens (secondary open landscapes with $<10\%$ vegetation cover and extensive soil erosion) with the rate proportional to both the severity and the longevity of the pollution impacts.

In two-dimensional space, with canopy closure along the horizontal axis and pollution load along the vertical axis (**Figure 2**), industrial barrens occupy the upper left-hand corner (low canopy closure, intolerable pollution load) as opposed to undisturbed forests in the lower right-hand corner (high canopy closure, low pollution load). Clear-cuts occupy the space along the left vertical axis (low to zero canopy closure, low to intolerable pollution load).

The costly measures aimed at changing the landscape appearance in areas affected by very high levels of pollution are called 'regreening'; these changes do not lead to forest formation. Forest restoration can be attempted only following a decrease in pollution loads; it results in the formation of semistable forests on previously deforested contaminated (acidified) landscapes. Restored forests, as well as existing forests subjected to pollution, need to be managed differently from unpolluted forests. This practice, accounting for environmental changes caused by pollution, can be called 'silviculture in polluted areas.' The lower part of **Figure 2** represents traditional silviculture, or 'silviculture in unpolluted areas.'

As forest regeneration is very sensitive to pollution, and dense forests better sustain pollution impacts than sparse forests, silvicultural practices involving clear-cutting should be adjusted at lower pollution loads than practices based on selective logging and gap-oriented regeneration.

Silviculture in Polluted Areas: Myth or Reality?

The practical measures applied in some of polluted forests are still too intuitive to be called 'silviculture';

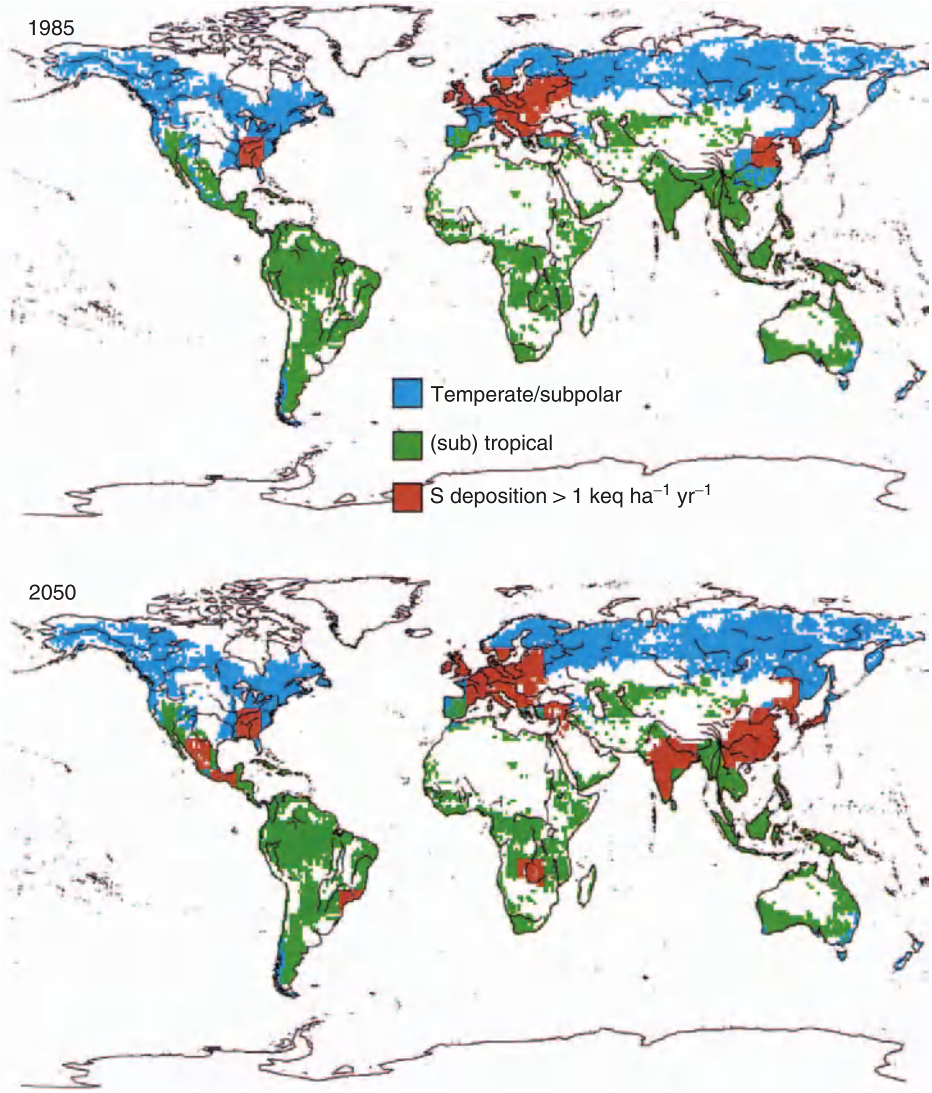


Figure 1 The global distribution of forest cover where total sulfur deposition exceeds 1 keq ha^{-1} year^{-1}, for 1985 and 2050. Reproduced with permission from Fowler D, Cape JN, Coyle M, *et al.* (1999) The global exposure of forests to air pollutants. *Water Air Soil Pollution* 116: 5–32.

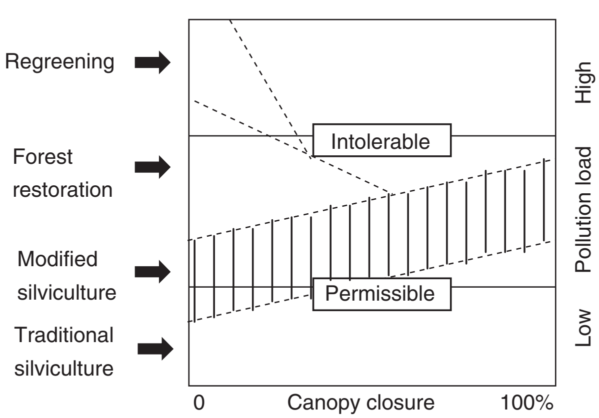


Figure 2 The operational field of silviculture in polluted areas in relation to traditional silviculture, forest restoration, and regreening of heavily contaminated barren landscapes.

optimistically, the silviculture in polluted areas, which can be seen as a specific branch of silviculture, is now *in statu nascendi*. It will need to develop for several decades at least to become 'the science of managing a polluted forest,' and even more time is necessary before 'the art of managing a polluted forest' is evident. This delay is partly related to the long time, measured in decades, that is necessary to evaluate the consequences of modified forestry practices and hence recommend (or not recommend) these practices for wide-scale application.

The International Union of Forest Research Organizations (IUFRO) Working Group on silviculture in polluted areas was established in 1951, and existed in the IUFRO structure until 1996. Activities of this group were mainly experimental, but they steadily declined in the mid-1990s due to a loss of scientific interest and (presumably) an absence of social or industrial demands for results. Not surprisingly, publications in this field are scarce and mainly restricted to reports on small-scale and usually short-term experiments. No general overview has ever been attempted, and silvicultural textbooks usually ignore the existence of polluted areas.

On a few occasions, specific silvicultural practices have not only been developed but also applied in polluted areas. These practices have resulted from the extensive and long-term efforts of scientists, and are largely based on site-specific information. Adjustment of these practices for other polluted areas would require extensive research; direct application of existing methods could easily result in adverse consequences.

What Can Be Done with a Polluted Forest?

The decision on what to do with a polluted forest naturally depends on the primary objectives of a stand at a given site. Any decisions will obviously differ between commercial forests and ecologically important forests that have a role in, for example, watershed regulation, erosion control, or nature protection.

When commercial forests started to die due to pollution impact, the first reaction of foresters was often to cut down the damaged stands in order to prevent further losses of timber. This practice was widely applied in central Europe until at least the mid-1970s, when it became obvious that the cost of harvested timber was minor in relation to the costs of rehabilitation measures required after clear-cutting. Despite this knowledge, some local regulations (such as in Russia) still require the immediate felling of pollution-damaged forest in order to make use of the timber, regardless of what happens after the clearcutting. This emphasis on short-term economic values of the forest can be highly detrimental to longer-term values, as illustrated by the difficulties in reforesting areas such as the Ore Mountains of the Czech Republic.

The polluted forest never dies completely, and even the dead trees maintain some climatic and biotic stability for the contaminated habitats, in particular preventing soil erosion. The old clear-cuts under severe pollution impact can be rapidly transformed into industrial barrens, while some vegetation in the adjacent uncut areas remains alive (**Figure 3**). Therefore stand integrity should be maintained as long as possible, allowing some time for the development of pollution control technologies and the application of rehabilitation strategies.

It might sometimes be possible to plan different forms of timber production for different levels of pollution, but in practice this has been done only exceptionally. If a pollution impact had not been expected when a forest was established, or no preventive measures had been taken despite an obvious danger of pollution impact, the forestry practices are best modified when the process of forest degradation is at its initial stages. Whenever possible, the modified management strategy should allow an optimal balance between timber production and long-term sustainability of forest ecosystems. In some countries, modification of silvicultural practice in polluted areas is obligatory, but in most cases the

Figure 3 The former Scots pine forest 1.5 km north of the nickel–copper smelter at Nikel, Russia. Pictures are taken from the same position: uncut area (left) and former clear-cutting (right). Photographs by M. Kozlov.

recommendations developed by scientists are implemented only rarely, either because of the high cost of the suggested measures or through ignorance or negligence. In many areas, there is a recognition that severely polluted forests should not be used for timber production, especially in the ecosystems that have been badly damaged. Instead, the emphasis is on regaining ecosystem stability and integrity, and preventing any further deterioration of the forest. This is the approach often adopted in North America, with the reforestation of slopes around the Trail smelter in British Columbia, Canada, being an example.

Suggested Silvicultural Measures

Maintenance of Existing Forests

General strategy As the visible symptoms of forest damage appear long after ecosystem stability has become affected, and after a long period of invisible or latent damage, emergency measures are needed to help declining stands. Regular restorative measures, forming the basis of silviculture in polluted areas, should be preventive, aimed at an improvement of the ecological stability of stands in such a way that they will better resist future pollution impacts. The maintenance of forests in polluted areas requires more intensive management than in unpolluted areas, involving 'soft' techniques and highly skilled manual labor.

The health of forests depends not only on pollutant toxicity or soil nutritional quality but also on a number of other environmental factors, including climate, water supply, stand density and composition, weeds, pests, and pathogens. Therefore, the direct mitigation of pollution effects is only one of several options; any technically possible and economically feasible measure to improve forest growth could be used to maintain and improve the stability of forests suffering from pollution.

This article describes restorative measures that are likely to prevent or at least slow down forest deterioration in polluted areas. For commercial forests it is also important to promote the vigor of stands as well as to attempt to produce larger trees in a shorter time, as the stands may need to be cut prematurely. Shortening the rotation time is recommended so that trees are cut before they start to die from pollution, and also to minimize soil acidification, which increases with stand age; the latter is especially important for stands of Norway spruce (*Picea abies*). In the most polluted temperate forests, rotation times may be reduced by 20–40 years, and in moderately polluted forests by 10–20 years; forests subjected to low pollution load can be cut at the same interval as unpolluted forests. Large-scale curative measure should only be applied if they are likely to mitigate the expected adverse consequences of pollution impact for at least 20 years.

Stand integrity management The maintenance of continuous canopy (closure >80%) is especially important in polluted boreal forests, because it not only maintains a favorable microclimate near the ground but also provides some shelter for individual trees. Intentional or accidental increases in crown exposure of healthy trees often results in severe crown damage. In nitrogen-polluted forests, any disturbance of stand structure may have even more dramatic consequences, because it leads to nitrate mobilization, implying high risks of water contamination. Disturbances caused by silvicultural management should therefore be minimized, and a gap-oriented natural regeneration is preferable to clear-cuts.

Silvicultural systems based on the maintenance of diverse forests (both in terms of species composition and distribution of age classes) often need almost no adjustment when pollution increases. The continuous cover method prescribes the removal of individual trees and tree groups weakened or damaged by pollution, thereby maintaining integrity of the stand. This approach is ecologically sound, although in the long term it can result in the conversion of a predominantly coniferous forest to one dominated by broadleaved trees, simply due to the higher sensitivity of conifers to pollution.

If cutting is considered in polluted areas, the forest should not be felled until adequate regeneration is established. This is especially true of mountain areas, where the forests have important soil and climate protective roles. Large, uninterrupted clear-cuts should be avoided; instead, a two-pass system with initial cuts of 15–30 m wide strips has been recommended as facilitating the reconstruction of damaged forests. The remaining forest strips can be harvested in a second pass after 7–10 years, when young forest has established in the cleared strips.

Liming No other silvicultural method is so debatable as the liming of polluted forests. Its principle is based on the idea that soil acidification due to the uptake of weak acids not only results in modification of nutrient availability but may cause toxic damage of fine roots of trees. An alternative theory attributes some forms of forest decline primarily to the leaching of magnesium and calcium directly from needles, giving less importance to nutrient deficiency in soil.

The main objective of older liming trials and practices was to enhance the mobilization of nutritional elements in acidic forest soils and thus increase stand productivity. However, the majority of German liming trials indicate either insignificant or no growth increase. In both Finland and Sweden, liming of Norway spruce and Scots pine (*Pinus sylvestris*) stands actually resulted in slight growth reductions. As expectations of increased tree growth were not met, and important questions about the ecological side effects of liming arose, widespread liming was discontinued in the mid-1970s. However, with the appearance of symptoms of magnesium deficiency in many forests, liming was reconsidered as a means of stabilizing stands affected by acidic deposition. Over the past two decades, dolomite lime or easily soluble neutral salts such as magnesium sulfate have been applied to many forests in central and northern Europe, the United Kingdom and the USA.

Diagnostic liming trials conducted in Germany suggest that Mg-containing lime improves the Mg status of soils, although the effect is considerably slower compared with rapidly soluble Mg fertilizers. Some of the trials conducted in the Bohemian Mountains have demonstrated a positive effect of Mg-containing lime on the growth of Norway spruce. More recently, the application of granulated magnesium-rich limestone to Scots pine stands growing on soils heavily contaminated with Ni and Cu in southwest Finland enhanced both the aboveground volume increment and the fine root production. However, the stimulation of fine root growth in the uppermost soil layers may not always be beneficial to the stand as it increases the risk of damage by drought, frost, and windthrow.

Fertilization Fertilization has long been used in forestry both to improve forest health and to enhance the productivity of stands, including forests suffering from excesses of sulfur dioxide and fluorine. As many forest ecosystems developed under conditions in which nitrogen supply is the limiting factor for tree growth, N-containing mineral fertilizers were widely applied between 1950 and the 1970s, also to aid the recovery of degraded forests.

A change has occurred in recent decades, as N inputs in polluted areas now exceed the demand of some forest ecosystems. As a result, elements such as Mg have become limiting factors for tree growth on acidic substrates. In such circumstances, application of rapidly soluble mineral NPK fertilizers in acidified stands, even those with a high soil Mg content, induced Mg deficiencies and led to nutritional imbalances in Norway spruce, as well as to NO_3^- contamination of seepage water. Conversely, an organic slow-release fertilizer amended with magnesite-derived fertilizers led to balanced nutrition and a fast recovery of tree health.

Following the widespread appearance of Mg deficiency in central Europe in the 1980s, a large number of diagnostic Mg fertilizer trials were established. These trials demonstrated that Mg deficiency in Norway spruce, silver fir (*Abies alba*), Scots pine, Douglas-fir (*Pseudotsuga menziesii*), and beech (*Fagus sylvatica*) could be corrected through the application of soluble Mg fertilizers. Although nearly any source of Mg is able to improve the nutrition of trees, in some cases an improvement in stand vitality and growth was only recorded following the application of dolomite lime or magnesite; for example, the fertilization of forests on acidified soils was particularly efficient when the supply of nutrients was combined with pH stabilization measures. Site- and stand-specific K and Mg fertilization led to the successful recovery of affected deciduous and coniferous stands of all ages (**Figure 4**) and resulted in a long-lasting improvement in soil nutritional status, aboveground biomass production and fine root vitality.

Figure 4 Scots pine in a heavily polluted site, 10 km south of Monchegorsk smelter, 3 years after application of dolomite and NPK fertilizer. Note the condition of control trees in the background. Photograph courtesy of N. Lukina.

Removal of excess nutrients In northern boreal forests, growing on infertile soils, increases in nitrogen deposition have increased forest growth. This effect may appear beneficial for commercial forests in a short-term perspective, but it can be damaging for ecologically important forests, mainly due to changes in species composition and general loss of biodiversity. Moreover, from a long-term perspective the increased N availability may lead to the economically undesirable replacement of coniferous stands by broadleaved forests.

Reduction of the accumulated nutrients can be achieved by removal of the litter and humus layer, usually by mechanical sod-cutting; the experimental removal of litter in oak forests was once carried out by a powerful litter-blower. Grass mowing with subsequent removal, intensive grazing, and prescribed burning have also been suggested, although such techniques have rarely been applied, even at the experimental scale. Mechanical removal of litter and humus should be combined with intensive thinning, which reduces the litter production and increases the decomposition rate by changing the microclimate near the forest floor. As a palliative, measures enhancing the medium-term storage capacity of forest ecosystems for nitrogen should be applied before the nitrogen deposition levels are reduced, and nitrogen-releasing disturbances should be strongly avoided.

Protection against co-occurring stressors Forests damaged by pollution may be subjected to increased attacks of pests and pathogens, implying a need for careful monitoring and possibly for the application of protective measures at lower levels of infestations than recommended for unpolluted forests. Moreover, silvicultural measures, especially the application of N-containing fertilizers, may enhance forest damage by some herbivores.

Regeneration of Polluted Forests

General strategy The regeneration procedure that is adopted will obviously depend on the scale of disturbance and the site conditions, primarily microclimate, soil toxicity, and soil nutritional quality. If neighboring stands ameliorate the microclimate sufficiently, target forest stands with the original or an adjusted species composition can be established directly. On large clear-cuts, where the forest microclimate has been severely disrupted, substitute forest stands should first be established. This may be with a nurse crop of trees that will not necessarily be a component of the final forest, mainly due to change in species composition and general loss of biodiversity. For example, in the Ore Mountains, rowan (*Sorbus aucuparia*) has been used as a nurse crop for beech, enabling the beech seedlings to become established.

In the most severely affected areas, where soil toxicity inhibits the growth of seedlings, soil detoxification by liming should be undertaken, followed by the establishment of a herbaceous grass cover before trees and shrubs can be successfully established. Monospecific stands should be avoided, as these are unstable.

Site preparation Soil ploughing after clear-cutting is a common forestry practice, which has positive effects on the first phases of forest regeneration. In the Upper Silesian Industrial Region, full tillage of the sandy soil promoted better growth of nearly all tree species in their juvenile period than other methods of soil preparation (plowing or disk cultivation). Full tillage decreased soil acidity, reduced metal contents, enhanced microbiological activity, and decreased infections of young trees by root-rot fungi (*Heterobasidion annosum*). However, plowing also decreased mycorrhyzal infestation of Scots pine roots and the soil content of N, K, and Mg, requiring compensatory measures.

During the reforestation of clear-cuts exposed to acidic deposition, diagnostic fertilization and liming were applied in the same way as for the revitalization of damaged stands in Germany and the Czech Republic. Current recommendations are that liming be conducted at least twice, before the mechanical preparation of soils and after planting of seedlings. Fertilization should be restricted to planting holes or planting rows so as to minimize competition from weeds. Herbicide application may enhance seedling establishment in habitats covered by grasses (*Calamagrostis villosa* or *Agropyron repens*) but others recommend that herbicides be avoided during site preparation in polluted regions. Bulldozing of areas covered by *C. villosa*, the grass species that makes the replanting of forest trees extremely difficult or even impossible, promoted the establishment of pioneer trees and therefore accelerated the natural succession leading to the establishment of a full forest cover.

Selection of tree species In some cases, forest stands that are unable to fulfil their production, protection, or recreation functions as a result of recent or expected damage by pollution should be gradually converted. In particular, dense stands of Norway spruce trap more pollutants than broadleaved forests, and therefore a change to beech stands has a potential to reduce the impact of further deposition on forest soil to about half the value in spruce stands. Conversion may also be unintentional, resulting from subjective (partially economic) reasons, when trees requiring greater cultivation skills and continuous care, such as beech and silver fir (*Abies alba*), are replaced by less demanding tree species, primarily birches (*Betula pendula* Roth and *B. pubescens* Ehrh.) and mountain ash (*Sorbus aucuparia* L.), which simply occupy the clear-cuts when recultivation measures are insufficient or neglected. After 10–20 years, these substitute forests can be gradually converted by planting the seedlings of target species.

Substitute tree species should assure the environmental and, to a certain extent, also the production functions of forest ecosystems. The choice of tree species for the conversion depends primarily on the site conditions, but it is always advisable to allow the development of a forest with a tree composition typical for the region, and seed material should preferably represent a local ecotype.

Selection of resistant genotypes Conspecific plant individuals differ greatly in their sensitivities to both pollutant toxicity and the impact of co-occurring stressors. Some individuals of generally sensitive species, such as Scots pine and Norway spruce, can sustain extreme pollution loads for decades after their neighbors have been killed by pollution. Selection for pollution resistance has been demonstrated for trembling aspen (*Populus tremuloides*), birches, and willows, and several researchers have recommended the planting of the progenies of the resistant individuals in polluted areas. However, it seems that this recommendation had never been applied, nor have recommendations arising from several provenance experiments that demonstrated different pollution tolerances amongst geographical strains.

In view of the co-occurrence of numerous stressors in polluted areas, as well as the long production time of trees, it seems inadvisable to select genotypes on the basis of their resistance to a single stressor, even if this stressor is currently believed to be the most important. Sufficient genetic variation should therefore be maintained in the cultivated populations to allow for the distribution of risks.

Planting, tending, and thinning The reforestation measures to be adopted in clearcuts subjected to acidic deposition do not differ from those applied under normal forestry practices. Direct sowing is mostly used for birches (*Betula pendula* and *B. pubescens*) and *rowan*, provided that conditions permit. When using the seedlings, container-grown plants (normally with a bigger root-ball volume) are preferable to bare-root stock because they increase the chances of successful establishment. The best-growing seedlings and saplings should be selected with the assumption that their vigor will potentially assure relatively higher performance in contaminated habitats.

Stand density is linked to tree health via competition with neighbors, resistance to wind and snow, and the ability to regulate microclimate. It has long been suggested that young stands in areas affected by acidic deposition should be established with a low density, which would allow plants to develop large symmetrical crowns. However, recent recommendations have been to the effect that the number of seedlings planted in the polluted areas should be 15–20% higher than in unpolluted areas. This compensates for higher mortality and also offers more opportunities for selecting the trees with the best crown vitality during precommercial and commercial thinning.

Silvicultural measures in young stands growing in polluted areas should begin earlier and be more frequent but less intensive than in unpolluted areas. From the earliest stages of the stand, i.e., from the thicket stage onwards, care should be taken to ensure the optimal development of crowns but at the same time avoid disruption of the canopy. An additional problem is stand resistance to wind breakage, which is generally lowered by pollution; it can be increased by manipulation of the crown cover, specifically encouraging the growth of long crowns.

Forest Restoration

The full restoration of forests differs from the restoration of other types of vegetation, mostly in relation to the time required to complete the process, and there is no known example of a successfully completed restoration (*sensu stricto*) of the forest communities on lands contaminated by industrial pollution. The land reclamation program in Sudbury, Canada, the only practical example of a large-scale restoration of an area impacted by an extreme pollution conditions, has only been in operation for a relatively short period compared to the time required for successional processes to form forest ecosystems. However, this example (**Figure 5**) shows that it is possible to convert heavily contaminated barrens into forests over a period of about two decades, assuming that there is the social demand for such a conversion and sufficient financial support is granted.

Forest restoration in Sudbury started with liming and seeding of barren land, followed by planting tree seedlings, mostly of species that were dominant in the previous forest. The original motivation was to improve Sudbury's image as a treeless wasteland, but gradually the revegetation philosophy became increasingly based on landscape and ecosystem. New perspectives include assistance in the establishment

Figure 5 Revegetation of the Camberian Heights site in Sudbury, Canada. (a) 29 July 1981; (b) 20 May 1982, following liming and grass sowing; (c) 6 July 1988; (d) 28 April 2003. (a, b, c – reproduced with permission from Winterhalder K (1995) Natural recovery of vascular plant communities on the industrial barrens of the Sudbury area. In: Gunn J (ed.) *Environmental Restoration and Recovery of an Industrial Region*, pp. 93–102. New York: Springer-Verlag. d, photograph courtesy of K Winterhalder.)

of an appropriate understory in the re-established pine 'forests.'

When the Sudbury Environmental Enhancement program started in 1969, it was specifically stated that the intention was not to create a commercial forest. The main motive was aesthetic, which means that there was no plan to harvest these forests in the future, although they are not formally protected like a nature reserve.

Conclusion

As forests cover some 30% of the earth's land surface, account for some 70% of terrestrial net primary production, and are being bartered for carbon mitigation, it is critically important that we continue to develop the strategies aimed at sustainable forestry in the industrialized world. Forests were disturbed or destroyed by pollution for a quite long time, as an inevitable part of civilization. We inherit a large area from the past and the destruction continues to the present, in spite of efficient pollution control and advanced mitigation measures.

The key to the sustainable management of forests under pollution stress is the knowledge of the biological processes that are affected by pollution, as well as on basic forest ecology, and substantial progress in obtaining relevant knowledge was achieved during recent decades. However, the knowledge that a certain input may stress certain type of forests is of little use unless those forests can be identified reliably and treated accordingly. Identification of forest damage is progressing better than the mechanisms for making management decisions, most of which are currently based on empirical field trial results. More generally, silviculture in polluted areas, seen as a specific branch of silviculture, is still in the process of development. However, in spite of the limited theoretical framework, silviculture in polluted areas has already produced valuable practical results, showing that both forest restoration and sustainable forest management in polluted areas are possible – although costly – as they usually require highly skilled manual labor and intensive application of lime and fertilizers.

See also: **Afforestation**: Stand Establishment, Treatment and Promotion - European Experience. **Environment**: Environmental Impacts; Impacts of Air Pollution on Forest Ecosystems. **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Silviculture**: Forest Rehabilitation.

Further Reading

Evers FH and Hüttl RF (1990) A new fertilization strategy in declining forests. *Water Air Soil Pollution* 54: 495–508.

Gunn J (ed.) (1995) *Environmental Restoration and Recovery of an Industrial Region*. New York: Springer-Verlag.

Hüttl RF and Schneider BU (1998) Forest ecosystem degradation and rehabilitation. *Ecological Engineering* 10: 19–31.

Hüttl RF and Wisniewski J (1987) Fertilization as a tool to mitigate forest decline associated with nutrient deficiencies. *Water Air Soil Pollution* 33: 265–276.

Kozlov MV, Haukioja E, Niemelä P, Zvereva E, and Kytö M (1999) Revitalization and restoration of boreal and temperate forests damaged by aerial pollution. In: Innes JL and Oleksyn J (eds) *Forest Dynamics in Heavily Polluted Regions*, (IUFRO Research Series no. 1), pp. 193–218. Wallingford, UK: CAB International.

Malkonen E, Derome J, Fritze H, *et al*. (1999) Compensatory fertilization of Scots pine stands polluted by heavy metals. *Nutrient Cycling in Agroecosystems* 55: 239–268.

Schütz J-Ph (1985) Forest decay in a continental-wide polluted environment: control by silvicultural measures. *Experientia* 41: 320–325.

Sheppard LJ and Cape JN (eds) (1999) *Forest Growth Responses to the Pollution Climate of the 21st Century.* Dordrecht, The Netherlands: Kluwer.

Slodičák M and Novák J (eds) (2002) *Results of Forestry Research in the Ore Mountains in 2001*, Proceedings from the National Workshop, 14 March 2002, Teplice, Czech Republic. Prague: Forestry and Game Management Research Institute.

Tesař V (ed.) (1994) *Management of Forests Damaged by Air Pollution*, Proceedings of 'Silviculture in Polluted Areas' Working Party, 5–9 June 1994, Trutnov, Czech Republic, Brno, Czech Republic: University of Agriculture.

SOCIAL AND COLLABORATIVE FORESTRY

Contents

Forest Functions

A Blum, Wageningen University
Wageningen, The Netherlands

Introduction

The term 'forest functions' is often used to describe a set of functional relations between forest and humans. Despite its descriptive and pragmatic advantages, the term offers some analytical shortcomings: these can be overcome, if the functional relations are separated into two classes: the effects of forests and the specific performance of forestry. This can offer a sound analytical base for forest policy and forest management.

Functions

A Descriptive and Pragmatic Concept

Trees and forests have always provided goods and services for individual or societal use. The term 'function' refers to the relation between forest and humans that is constituted by the process of offering and obtaining goods and services. Similar to the way in which the term is used in mathematics, forestry tries to encapsulate human–forest relationships by means of the term 'forest function.' It is not known when the term 'function' was used first in forestry but in 1953 Viktor Dieterich stated in his forest policy textbook a system of functional relations and described a so-called theory of forest functions (*Funktionentheorie*). Since the second half of the twentieth century forestry has been, and still is, influenced by this theory of forest functions, but the triad of Dieterich's forest functions, namely 'use,' 'protection,' and 'recreation' (in German: *Nutz-*, *Schutz-*, *Erholungsfunktion*) has been extended and modified over several decades. One example for a list of forest functions is shown in **Table 1**.

Whether developed by practitioners or scientists, most of the tables enumerating functions have been pragmatically constructed after seeking the existing or potential use of forests. Intuitive answers or empirical findings were then transformed into abstract classification systems, which in general can be seen as groupings according to the main types of forest use. Main functional categories refer to 'commodity functions' for timber and nontimber forest products, 'protective functions' against natural hazards, 'social functions,' which are mainly related to recreational use of forest areas, and 'conservation and cultural functions.' Nowadays the various classification schemes for forest functions, which are described in literature or used in forestry practice, are innumerable.

Multifunctional Forestry

There is constant debate about whether a separation or an integration principle for the management of the various forest functions should be used as a guiding principle. A central European perspective, developed on the basis of the natural potentials of temperate zone forests, favors the multifunctional integration of different forest uses in the same forest area. The Anglo-Saxon and American management approach seems to favor a separation of uses, thus defining areas mainly to be used for wood production, while dedicating other forest areas for nature conservation purposes or recreational use. For both of the approaches some good arguments from the natural sciences do exist. However, in essence, the main reason for accepting or rejecting separation or integration can be traced back to some ideological and normative aspects, rooted in the realm of social sciences.

The separation or integration of forest uses is directly related to the political and economic question of what type of ownership should be responsible for guaranteeing appropriate levels of function provision. The separation approach allows private forest owners to concentrate on the production function, while community- or state-owned forest land is to be used to provide recreational or conservation functions.

In contrast, the integration approach served for a long time as the standard for good central European forest stewardship and led, irrespective of ownership, to a concept of multifunctional forestry. This option for a harmonious coexistence of different uses on the same forest land is based on the assumption that sustainable timber production and all other nonproductive functions could be supplied at suitable levels. Statements that all other functions of forest follow in the wake of the production function have been used in forest policy debates especially since the 1970s in order to avoid restrictions on forest management, potentially imposed by societal concerns for the recreational and natural protection functions.

Currently, new approaches to nature conservation, in particular to the protection of evolutionary and self-regulated processes, increasingly pose questions about the multifunctional concept. The separation concept also increasingly comes under pressure as acceptance of pure production from at least parts of the forest area is vanishing. Regardless of whether the ongoing developments will lead to forest management concepts beyond separation or integration, the central European idea of being able to perform simultaneously various, if not all, forest functions at the same place and time generated the term multifunctional forestry, which has a striking appeal and has become accepted worldwide.

Political Merits of the Term Functions

The forest functions offer exceptional potential as container terms in political debates. On the agendas of these debates forestry communities seek to legitimize their claims in a changing society and to be approved for using existing forest resources according to their own needs as free as possible from unwanted outside influences. A 'functions' perspective always ranks the forest first and somewhat overshadows the user: forests offer functions that can be obtained provided forest management is appropriate. The ideology of forest-centrism (*Silvazentrismus*) therefore can restrict societal attempts to misuse forests and to restrain forest community infighting, which undoubtedly exist, if only subliminally, as the respective forest managers represent different types of forest ownership.

Be it a standard functional or a more sophisticated multifunctional perspective the term 'function' can be used to emphasize the societal importance of the interconnected unit of both forests and foresters. According to traditional self-perception and external communications there is a cooperative supply chain, as forestry transmits and administers forest functions to society. Forestry is located in the center of the exchange system between forest functions and contributes to societal welfare (**Figure 1**).

Table 1 Example of a classification scheme for forest function: reference model for variety, importance and interactions of forest functions of the European Parliament (1997)

Social functions				*Economic functions*		*Ecological functions*					
Cultural	*Education*	*Recreation*	*Landscape*	*Activities and services*	*Production*	*Preservation*		*Protection*		*Regulation*	
History	Information and sensitizing	Leisure (relaxation, culture)	Rural landscape	Environment for recreation	Wood (industrial wood, fuelwood)	Biological diversity	Maintenance of current diversity	Against natural risks	Avalanches	Climate	Temperature
Myths	Ecocitizenship education	Eco-tourism	Urban landscape (Trees and green areas)	Reserve of land	Game/fowl		Preservation of future diversity at local level		Rock-slides		Humidity
Aesthetic and spiritual values				Hunting	Cork and bark		Preservation of future diversity in land-use planning	Against noise			Atmospheric composition
				Leisure activities and tourism	Decorative plants						Rainfall
				Land use planning							Wind
										Air quality	Refinement
											Purification
										Water systems	Controlling rising water levels
											Maintenance of low levels
										Water quality	Purification
											Protecting water-catchments and supply areas
											Reduction of sediment content in water flows
										Soil maintenance	Reduction of diffuse erosion
											Reduction of erosion in fragile areas
											Soil reconstitution

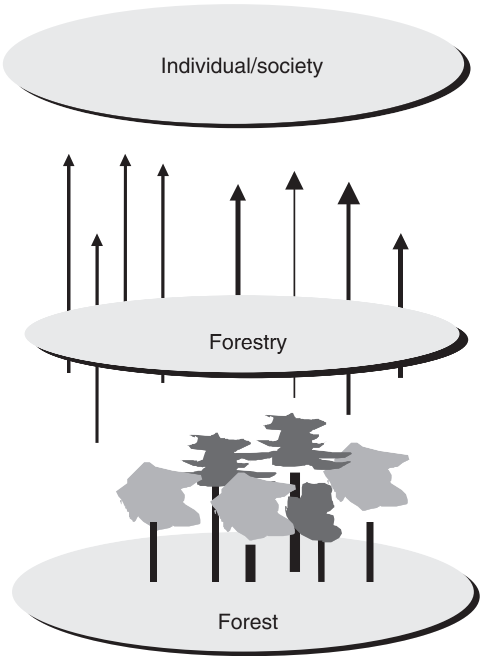


Figure 1 A classical perspective on the various functions of forests and multifunctional forestry as a transmitter of forest functions to society.

Analytical Shortcomings

Regardless of the merits of the functions term in political discussions, there are some basic analytical shortcomings that need to be mentioned. From a scientific point of view, the quality of all descriptive approaches to collecting and enumerating existing or potential forest functions is restricted by the completeness of the enumeration of individual functions and the logical consistency of the ordering system employed. A collection, enumeration, or classificatory system can itself never serve as a sound explanatory system, which provides deeper insights or better understanding of the object of interest. For example, the German discussion on the intrinsic content of the term use-function (*Nutzfunktion*) can be mentioned; is there reason to distinguish the mainly timber-related use-function from the nature protection-function, as both are inevitable of societal use? A pure classification system, offering definitions only, was mistaken for an explanatory system to be employed for directing processes and influencing actual political developments.

Nowadays, forest policy research therefore rejects the uncritical use of the concept of forest functions, which never met the demands of a theory. Instead the interest approach of the social sciences is employed in order to describe, analyze, and explain processes in forestry and activities of forest-related stakeholders.

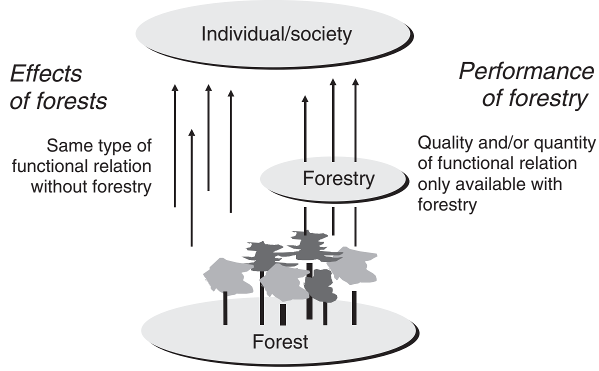


Figure 2 Distinction between effects of forests and the performance of forestry.

Beyond Functions

Effects of Forests vs. Performance of Forestry

Traditional forest economics has some problems with the concept of forest functions; this can be linked to the fact that the concept fails to describe forestry adequately, as the main object of interest of forest economics, in its role as a transmitter of benefits between forest and humans (**Figure 2**).

Analyzing the list of forest functions shown in **Table 1** it must acknowledged that only parts of the beneficial stream of goods and services from forest to humans can be improved or even influenced by forestry. At least for some of the functions of forests, there is no need for forestry (by means of any kind of human influence on natural processes) to safeguard given levels of individual or societal well-being. One can make a thought-experiment to envisage the future development of existing forests or even bare land in the absence of any kind of forestry and to analyze the hypothetical outcome, for all ecotypes and geographic zones that are naturally covered with forests. There is evidence that for all regional conditions a distinction can be made between functions or forest–human relations, which will remain unchanged or continue to exist only slightly changed without forestry, while other functions immediately or in the mid-term will cease to exist, if forestry activities should be stopped.

Managing for Performance

According to a standard definition, sustainable forest management aims to ensure that the goods and services derived from the forest meet present-day needs while at the same time securing their continued availability and contribution to long-term development. The clear distinction between effects and performances will help forestry to focus its activities efficiently. Some of the functional relations deserve and require intensive forest management, while other functional relations between forest and humans do exist, even without any kind of forestry intervention. Forestry activities therefore may be ordered according to a tripartite classification system (see **Figure 3**):

I. Functional relations are described as the effects of forests that exist without human interaction through forest management. There is no way to manage forests efficiently to improve the benefit. All forestry resources dedicated to influence these pure effects of forests may result, at best, in an alteration, but not in an improvement of the respective functional relation.

II. The performance of forestry can be understood as the ability to alter quality and quantity of existing functional relations between forest and humans through forest management. Pristine forests may provide a base level of goods and services that will meet present-day individual or societal needs, but there is an option to increase the quantitative or qualitative level of these 'functional flows' by active management (IIa). Some other functional flows may not be provided by nature herself and so do inevitably require forestry to be practiced (IIb).

III. A basic precondition for the clear distinction between effects and performance is the assumption of an enduring existence of forests. All over the world situations may be found where forests naturally could exist and even could recover easily from disturbances, but are currently threatened by destructive human influences. All forestry activities that result in a reduction of harmful human influence and increase the preservation of natural forests and their effects must be acknowledged as important measures of the performance of forestry in safeguarding the functional relations between forest and humans. This is true even if the intrinsic relation must be classified as a pure effect of forests.

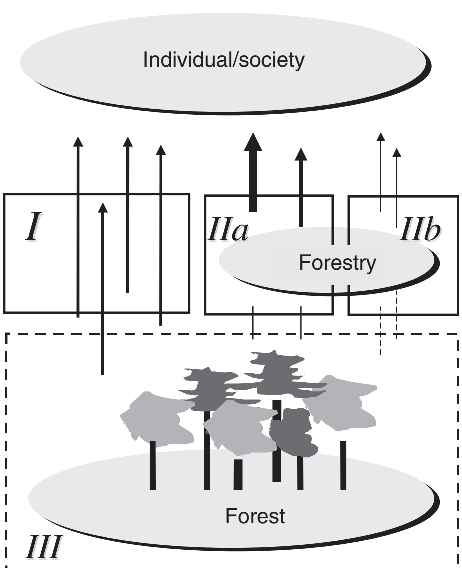


Figure 3 Distinction between effects of forests and the performance of forestry.

Social Conditionality of Forest Effects and Forestry Performance

At first glance, the distinction between the effects of forests and the performance of forestry seems to be a straightforward result of a thorough analysis employing data and information mainly of natural sciences.

The amount of, e.g., carbon sequestered in trees may completely be described on the basis of information delivered by the natural sciences. However, the question of whether or not carbon sequestration is an effect of forests or a specific performance of forestry has to be seen in direct relation to its social conditionality.

The property rights of forest management are a direct result of the social conditions and legal framework in which forest management takes place. If, for example, the property right of forest management includes the explicit right to permanently eradicate forest cover, all functional relations between forest and humans inevitably must be classified as in the forestry performance category. The permission to decide freely whether a forest is kept or cleared offers the broadest set of options for forest management, while, in contrast, strict standards of forest stewardship, including obligations to safeguard specific functional relations, will reduce the options available for forest management.

Implications and Outlook

As the functions of forests often justify financial and other public support of forestry, there is good reason for the intensity of debates on the meaning of functions, effects, and performances. The term forest functions offers a nebulous concept, which might be of specific value in political debates. In contrast, the terms effects and performance require a clear statement of whether something is delivered by nature without additional need to spend forestry resources, or whether something has to be delivered by forestry under given legal conditions, or, lastly, something can be offered as beneficial good or service by forestry. Under given societal and market conditions, for most countries the distinction will result accordingly in no financial streams, in compensatory payments, which at best will cover the related expenses, or in the option to actively market and sell functional relations and to gain profits, if expected income exceeds related expenses.

The term forest functions (as well as its predecessors and its successors) served and will serve an important function itself, as it enables foresters and society to discuss forestry in a broader perspective than primary production alone. The constant change of relative dominance of particular functional relations (production, recreation, conservation) has characterized the history of forestry and probably will characterize its future development; time will show, for which functional relations societies will appreciate forests in future.

See also: **Landscape and Planning**: Perceptions of Forest Landscapes; Perceptions of Nature by Indigenous Communities. **Social and Collaborative Forestry**: Canadian Model Forest Experience; Common Property Forest Management; Forest and Tree Tenure and Ownership; Joint and Collaborative Forest Management; Social and Community Forestry; Social Values of Forests.

Further Reading

Blum A and Schanz H (2002) From input-oriented to output-oriented subsidies and beyond–theoretical implications of subsidy schemes in forestry. In: Ottitsch A, Tikkanen I, and Rieva P (eds) *Financial Instruments of Forestry Policy, Rovaniemi, Finland 2001*. Joensuu, Finland: European Forest Institute.

Blum A, Brandl H, Oesten G, *et al*. (1996) Wohlfahrtsökonomische Betrachtungen zu den Wirkungen des Waldes und den Leistungen der Forstwirtschaft. *Allgemeine Forst- und Jagdzeitung* 167(5): 89–95. (English and French summaries.)

Dieterich V (1953) *Forstwirtschaftspolitik*. Hamburg, Germany: Parey Verlag.

European Parliament (1997) *Europe and the Forest/L'Europe et la Fôret*, vol. 3. DG IV Publication, Series AGRI. www.europarl.eu.int/workingpapers/forest/eurfo_en.htm.

Ferguson IS (1996) *Sustainable Forest Management*. Melbourne, Australia: Oxford University Press.

Göttle A and Séne E-HM (1997) Protective and environmental functions of forests. In *Proceedings of the 11th World Forestry Congress*, 13–22 October 1997, Antalya, Turkey, vol. 2, pp. 233–243.

Leibundgut H (1985) *Der Wald in der Kulturlandschaft*. Bem, Switzerland: Haupt-Verlag.

Social Values of Forests

A Lawrence, University of Oxford, Oxford, UK

Introduction

Amongst all the environmental sciences, forestry is perhaps the one that has to recognize and work with the values of the widest range of social groups. Forests affect the interests of everyone, but are often the property or responsibility of a few. Even the definition of a forest is a value-laden exercise, in what has been termed the 'social construction of forests.' There is however a difference between the postmodernist view that forests are the projections of each observer, and the more pragmatic philosophy that forests are real systems with definite contents and boundaries – but that the importance of the contents, boundaries, and whole varies according to the observer. The last consideration has been much discussed during the last 20 years, following the famous statement by Jack Westoby in 1968 that 'Forestry is not about trees, it is about people'.

This article explores the many ways in which social values have been defined and applied, and looks at how such values are formed, recognized by forest managers, and incorporated into forest management – and what happens when they are not. Issues of consensus and conflict are considered, and the article concludes with a discussion of the evolving demands on the modern forester who needs to be able to balance social sensitivity with technical and management skills.

Definitions

The value of a forest refers to its 'worth, desirability or utility,' while the values held by people regarding the forest refer to their principles, or judgments about what is important in life. Values are implicitly subjective, and forestry, which has always held itself to be a science, sits uneasily with subjectivity. Economics has evolved its own ways of dealing with the economic value of a forest in the face of environmental concerns. However, forestry is not only about environmental values, but also about social values, a phrase which has come to be used frequently in relation to forests, but often only in passing and without explanation.

The term 'social values of forests' can best be understood as referring to the basic worth and utility of forests as are experienced by people. A distinction can be made between material utilitarian values, nonmaterial utilitarian values (such as soil conservation, climate regulation), cultural and spiritual values, and aesthetic values. These terms all relate to values of forest with respect to human use and perception. In addition, the term 'intrinsic value' is used, to denote that value related not specifically to human use and benefit, but an unchanging value outside the human sphere of influence and perception.

Another approach towards defining social values of forests is derived from environmental economics. Here a distinction is made between direct use values, indirect use values, option values (options for use in the future), bequest values (value of leaving use values for coming generations), and existence values (value from knowledge of continued existence).

Both the social values of forests and the environmental economics approach basically focus on the role of forests for human benefits. Such values do not include all forest–people relations. For instance, social values regarding forests may also include perspectives on the appropriate relation of people to forests, with, for instance, a distinction between dominion or guardianship.

The term social values has a more general connotation, referring implicitly to 'values held by people other than foresters.' In democratic, post-industrial countries the phrase might perhaps be synonymous with public values but the notion of a public that is unanimous in its desires and behavior, is transparently a problematic one.

Whilst in industrialized countries the social values of forests can seem largely related to enhancing the quality of life, in developing countries the phrase can refer to much more tangible benefits. Poor rural communities are often highly dependent on forests as part of their resource use system, for animal fodder, fuelwood, soil nutrients, medicinal supplies, and also in emergencies (times of famine, drought, war) as their sole source of food. Where forests are so essential to livelihoods, their use is often controlled by other social values as well, such as the need to maintain good social relations or one's place in the social hierarchy; and in the expression of cultural values which hold the community together. For example, the presence of sacred groves in India, Laos, and Ghana continue (to varying extents) to represent persistence of culture and to symbolize a nonutilitarian importance of the forest.

Other values held by society, or groups of people, affect their attitude to forest less directly. Spiritual beliefs, or an ecocentric philosophy, can affect people's stance on whether a forest and its species have intrinsic value, or whether aspects that benefit only humans should be valued. In the same way, some social values also have a negative impact on forests. The spiraling desire to consume, and the search for satisfaction in material goods, which underpins so much deforestation, urbanization and environmental degradation, is a much more powerful force than that based on conservation and aesthetic values.

One definition cannot cover all of these uses. 'Social' refers to society, its organization, and the relationships between groups of people. We might summarize by describing social values of forests as those that are beneficial to society as a whole, or to particular sections of society, or that are held dear in particular cultures, or that contribute to the development of human organization in a sustainable way. They may or may not be freely available, measurable, and/or accessible to all who desire them. Furthermore, they do not exist independently of people, so they evolve as society evolves – and forest management that takes account of social values will therefore be a dynamic, adaptive enterprise.

The Evolution of Social Values in Forestry

Both society, and forestry, have changed radically over the centuries of forest management, and both have affected ways in which social values are recognized. Social values change as society's organization, beliefs, affluence, level of education, and spare time change. The rise of pluralistic forestry is often attributed to the surplus income and spare time of people in post-industrial parts of the world, and it is true that the social value of forests is referred to increasingly in industrialized countries. But there has always been a social value or function of forests, in that forests have always provided benefits for people other than foresters or forest owners; and it is interesting to note that much of the early discussion of social values in forestry publications comes from Romania, Bulgaria, Poland, Hungary, and (the then) Czechoslovakia, while donors and policy-makers emphasize the value of forests for the poor, in developing countries.

There is an element of positive feedback here, in that the recognition of social values stimulates study of them, leading to further recognition. Some of the stimulus has come from within forestry: the rise of approaches such as community forestry, urban forestry, and adaptive management, and the recognition of non-timber forest products in rural communities' lives has opened the way to foresters listening to a wider range of people. But these approaches have in turn been prompted by wider movements: the global sustainability debate, and the rise of interdisciplinarity. To foresters, sustainability has in the past meant sustainable timber production, but the enormous amount of global discussion, while sometimes appearing inconclusive, at least highlights the need for attention to social as well as ecological and economic factors.

Attempts to bridge the natural and social sciences have also affected forestry. The door has opened to anthropology, which has provided a number of insights into the cultural construction of nature, the recognition of a conservation ethic among some cultures, and the documentation of indigenous knowledge and practices with potential importance for forest management. Environmental psychology has also contributed understanding of the meaning of nature, wilderness, and beauty, among other factors, to forest management. At the same time, science itself is increasingly recognized as a political and value-laden activity, where conservation values are not objective. These changes are affecting the way in which the relationship between society and nature is mediated by policy and research, and forestry is not alone in having to adapt to the new agenda.

Social values, or the values held by society, are particularly evident in the choice of species to be planted, for example on farms and common land, as well as in more conventional plantations. In making such choices, foresters, farmers, and planners reveal and reflect a wider set of values. In particular, the importance attached to the use of native or exotic species varies widely. In postindustrial society, there is often a strong public demand for native trees, resulting from awareness of threats to wildlife depending on those species, as well as perhaps a nostalgia for wilderness and more 'natural' appearance of the landscape. By contrast, foresters in many countries continue to favor exotics which grow fast and reliably, and have established markets. Exotic species can also have social value. In Ghana, rural people can associate foreign with modern and successful, and hence favor exotic trees; in contrast, in India, introduced species represent colonialism and can inspire political protests and moves to uproot plantations. A sense of aesthetic in forestry is also affected by society's stage of 'development'; in Cameroon the forest landscapes considered most beautiful include modern houses and electricity wires, a view which provides a sharp contrast to the aesthetic sense of the overurbanized, jaded, European.

Values and Stakeholders

Value Formation

In order to understand the wide range of perspectives held by society in relation to forests, we must look at the process by which values are formed. Values are strongly linked to culture, or the set of practices and beliefs which holds a community together; but they are also affected by individual circumstances, education, and experience.

Forests feature in the mythology of many cultures, and have deep-rooted associations with nature, magic, religion, safety, or evil. Consequently, they mean something to almost everyone. Religious beliefs can also influence value formation with respect to the environment, though in a wide range of ways: there are numerous studies of the proto-environmentalist messages in religious texts, but Christianity at least has in the past nurtured a view of humankind as lord of creation, which arguably has supported the exploitation and destruction of nature.

Societal change obviously affects such values, and disillusionment with consumer culture is reportedly causing a decline in materialist values among the young, in Western Europe. The global debate about biodiversity has brought a new term, and arguably a new concept, into the forest debate: to a wide range of people, forests are no longer just utilitarian storehouses of trees and forest products, but the embodiment of biodiversity, a more holistic, intangible concept. And of course the changing environment, loss of forests, and loss of contact with wilderness, as society becomes more urbanized, leads to greater interest in nature as it becomes scarcer. But the increasing emphasis placed on social choice means the public often have influence over decisions for which they are not equipped to understand the ecological consequences.

At a more individual level, education and personal experience deeply affect values. People who have experience of the negative effects of deforestation are more cautious about further damage to forests, and value forest more highly. Contact with nature is also relevant; longstanding visitors to national parks often have stronger conservation values than short-term and new visitors.

Stakeholders, Conflict, and Consensus

The existence of different values for forests among different sectors of society requires an approach that analyzes the perspectives of stakeholders. 'Stakeholders' are defined as groups and organizations that have an interest or are active players in a system, such as a forest. A methodology known as stakeholder analysis for exploring the goals, values, and influence of such groups has become widely used since the early 1990s. Stakeholder analysis begins by defining the system boundaries, in order to then define groups of people who may have an interest. Direct and indirect research methods are then used to analyze the perspectives of each stakeholder. The tool is a powerful one for pointing to potential conflicts of interest, based on conflicting goals, beliefs, or values; and also for providing a starting point for building consensus or trade-off of costs and benefits between different stakeholders.

Some differences of values are broadly predictable. For example, communities living close to forests are likely to be more economically dependent on them and to value the products accordingly, while those traveling from further away tend to be seeking the 'wilderness experience' or landscape beauty values. Forests with high economic value may have low social and ecological value; and conversely, wild, wet, irregular and twisted trees may fill the imaginations of myth-starved urbanites and provide them with the high social value that the foresters' forest fails to. At a global level, those with most influence over international policy-making may value the rarity of particular kinds of forests or species (e.g., montane cloud forest in Costa Rica, or elephants in Namibia) which contrast directly with the values of local people who depend on alternative ecosystems or species for their livelihoods.

Hence, pluralistic, democratic decision-making needs to take into account not only the different values of different stakeholders, but also the potential for distortion by the greater power and louder voices of some stakeholders. A new and challenging role for foresters requires them to see through this clamor and balance the multiple desires and goals of forest users, with the need to maintain an ecologically healthy forest.

Eliciting and Measuring Social Values

Defining the stakeholders is one important step in understanding social values, but the most challenging methodologically is that of finding out (or eliciting) and comparing the values held by the different stakeholders. Economists are expert in comparing values, particularly where a financial value can be attached to them, and their expertise has certainly provided a starting point for the measurement of social values for forests. Many of the values termed 'social' are what economists would consider to be externalities, i.e., not values accounted for within the forest production system, and not accruing to the forest owner. Many are also 'intangibles,' in other words not directly amenable to measurement. Both provide a challenge in terms of observation and measurement – because the stakeholders need first to be accessed, and then indirect methods need to be used to measure their values. Still worse, as we have seen, social values can be strongly affected by personal experience, and hence be subjective, highly variable between individuals, and even unmeasurable.

Many clever methods have been devised to measure social values indirectly, under what is generally termed 'contingent valuation' using indicators such as 'willingness-to-pay.' Such values are then added or subtracted, in a process known as cost–benefit analysis, which produces an overall value for the forest.

Criticism of such approaches has focused on the hypothetical nature of such responses, their vulnerability to the phrasing of the questions, and the essentially consumerist assumptions underlying such approaches. The reaction against the economist's desire to quantify all values has asked questions such as, 'How are we to attach a number to the beauty, uniqueness, or spiritual importance of a forest or a place in a forest? How are we to account for the subjectivity of personal experience, and how do we add together the variety of personal experience?' And to some stakeholders, values of nature are absolute and cannot be discussed; for example, the Paiute Indians of Michigan, USA, cannot rank one species over another, because they consider them all to be sacred.

Experience suggests that quantitative valuation may in any case be fallacious because the resulting numbers do not represent 'reality.' The value of valuation may lie more in the process, i.e., in the scope that the activity provides for helping different stakeholders to understand each others' goals and objectives. The use of participatory methods, semi-structured interviews, focus group discussions, and storytelling may help people to express their values in ways that they can later communicate to foresters and forest planners, so that they are taken into account.

Combining the quantitative and qualitative approaches, a range of visualization tools has been developed recently that helps stakeholders interact in discussing their preferences for forest management. An approach known as multicriteria analysis (MCA) can be used to define a set of criteria that are weighted after consultation with experts, after which stakeholders are invited to score each criterion. The quantification process can itself provoke questions about the meaningfulness of such numbers, and stimulate reflection on the usefulness of instead making values explicit in debate amongst stakeholders.

A similar approach is used in the many attempts to define criteria and indicators for sustainable forest management, epitomized by a large research program conducted throughout the 1990s by the Centre for International Forestry Research (CIFOR). This enterprise has recognized that indicators of social values need to be more widely developed and applied than they currently are, and must be able to respond to change in those values. Attempts so far have proved particularly difficult – largely because the results are so different in different cultures, ecosystems, and stakeholder groups.

A different approach may be taken by psychologists, who seek to understand the attitudes and values that affect people's behavior, both in order to understand what 'the public' wants, and to consider effective communication methods to encourage the public to interact with forests in a sustainable way. Psychologists may use both quantitative and qualitative approaches in their research, but conduct their analysis and communicate their results on their own behalf. They can also help foresters to understand how they are perceived, and to change their public image.

Implications

Implications for Forest-Based Trade and Certification

The values that consumers hold in relation to forests can be powerfully expressed through their purchasing behavior. The ethics of consumption choices has increasingly been expressed through various certification schemes, in the case of forestry since the early 1990s. Most certification schemes allow consumers to choose timber which has been sourced from forests deemed to be managed sustainably – a definition which in the last few years has sought to include social sustainability by responding to the concerns of forest-dwelling communities. In so choosing, the consumer rarely knows the forest in question and is in fact expressing a value for the forest's existence and for the philosophy of ethical consumption; he or she is valuing an idea as much as a product. The premium for certified forest products might be held to represent the social value of sustainability, and reflect the increasing concern about sustainability in general.

The timber certification movement has taken off surprisingly quickly, but its representation of social concerns responds more to the beliefs of consumers about how forests should be managed, than to their knowledge.

Implications for Forest Training and Practice

The rise of pluralistic and adaptive forest management requires a revolution in forestry planning, management, and evaluation. The forester can no longer be the manager of a biological resource with economic value, but must acquire skills in communication, consultation, facilitation, and conflict-management participation. The forester has evolved from regulator to facilitator, from harvest planner to intermediary, channeling communication and perspectives between community and government.

Foresters continue to be on the receiving end of criticism that they fail to understand the values and needs of the urbanized or forest-dependent communities that they serve, both in postindustrial countries and in developing countries. Several studies and surveys indicate contrasts between the values of foresters (favoring nature conservation and/or timber production) and their constituency (villagers needing sustainable production of food and medicine; urban public wanting landscape beauty and recreation, or a wilderness experience). To a large extent, diplomas and undergraduate training in forestry tend to be a biological and industry-based education, focusing on timber production; the social skills are acquired (if at all) during MSc courses and vocational or in-service training programs.

Foresters can feel threatened by the changes in values and expectation, but on the other hand there is little currency in the argument that there is no longer room for professional foresters who can ensure biological sustainability. Instead, foresters need their ecological training, and must also be able to listen to the public and balance publicly defined goals with the demands of biology.

Implications for Policy and Governance

Amongst forest users, the single factor that most directly affects values for the forest is tenure; and in industrialized countries, recreational access. It is widely recognized that the forest with highest value to society is not private forest. Both ownership and access rights are factors which are directly affected by policy and its implementation.

Finally of course the vast range of social values and stakeholders in forestry require attention to the processes by which forest-related decisions are taken. Deliberative, inclusive, and reflective policy-making processes help people to recognize and develop their values. The fact that pluralistic, values-based forest management involves moral and political questions, has in many countries moved forestry decisions out of the relevant department of the civil service, to a higher, or more intersectoral, or more participatory, arena.

See also: **Landscape and Planning**: Perceptions of Forest Landscapes; Perceptions of Nature by Indigenous Communities; Visual Resource Management Approaches. **Social and Collaborative Forestry**: Canadian Model Forest Experience; Common Property Forest Management; Joint and Collaborative Forest Management; Social and Community Forestry

Further Reading

Adamowicz WL (ed.) (1996) *Forestry, economics and the environment*. Wallingford, UK: CAB International.

Buckles D (ed.) (1999) *Cultivating Peace: Conflict and Collaboration in Natural Resource Management*. Ottawa, Canada: International Development Research Centre and World Bank.

Colfer CJP and Byron Y (eds) (2001) *People Managing Forests: The Links Between Human Well-Being and Sustainability.* Washington, DC: Resources for the Future.

List PC (ed.) (2000) *Environmental Ethics and Forestry: A Reader.* Radnor, PA: Temple University Press.

Lockwood M (1999) Humans valuing nature: synthesising insights from philosophy, psychology and economics. *Environmental Values* 8(3): 381–401.

Raison RJ, Brown AG, and Flinn DW (eds) (2001) *Criteria and Indicators for Sustainable Forest Management.* Wallingford, UK: CAB International.

Richards M, Davies J, and Yaron G (2003) *Stakeholder Incentives in Participatory Forest Management: A Manual for Economic Analysis*. London, UK: Immediate Technology Publishing.
Sheil D and Wunder S (2002) The value of tropical forest to local communities: complications, caveats and cautions. *Conservation Ecology* 6(2).
Sheppard SRJ and Harshaw HW (eds) (2000) *Forests and Landscapes: Linking Ecology, Sustainability and Aesthetics*. Vancouver, Canada: University of British Columbia.
Vermeulen S and Koziell I (2002) *Integrating Global and Local Biodiversity Values: A Review of Biodiversity Assessment*. London, UK: IIED.
Westoby J (1989) *Introduction to World Forestry*. Oxford, UK: Blackwell.

Common Property Forest Management

J E M Arnold, Oxford, UK

Concepts, Definitions, and Terms

A 'common-property' regime is a regulated form of joint control and management of a resource by a group of users, with powers to define membership of the group, to exclude those who are not members, and to set rules governing use of the resource. It contrasts with unregulated 'open access' use of such resources when they are available to all and consequently not owned or managed by anyone, or with private or state control.

In the past a resource used in this manner has often been termed a 'common-property resource.' However, the use of the term 'common property' for both a resource that can be used in a managed or unmanaged fashion, and for a form of management regime that is limited to a specific group that holds rights in common, has proved to be confusing. A resource used in common is therefore now termed a 'common-pool resource.' Such a resource is usually characterized as one where exclusion of users from the resource is costly, one person's use subtracts from what is available to others, and overuse leads to degradation.

A common-pool forest resource may be the forest as a whole, or part of it. Or it may relate just to the product flows from that resource, or to individual product flows, such as timber, or fuelwood, or grazing. It is thus necessary to distinguish between rights to use a resource and the rights related to the resource itself. A common-property regime does not necessarily require ownership of the forest resource, just rights to control usage.

This is particularly important in understanding uses in forests, where much of the resource is owned by the state, but most usage is by individual, collective or industrial entities, frequently with multiple users exercising rights to different products or to use at different times of the year. There can therefore be several different common-property regimes governing different outputs of a particular forest, and involving different groups of users. Similarly, the institutional arrangements for producing and selling forest products (flow units) are quite likely to be different from those controlling and managing the forest itself (the stock). Common-property use of particular forest products can also be found on private property.

Most management of forest resources as common property involves extractive outputs such as wood, nonwood products, and forage. However, it can also involve nonextractive uses, such as flood control.

Common-Property Versus Alternative Forms of Forest Tenure

Historically, common-property regimes have evolved where the demand on a resource has become too great to tolerate open access use any longer, so that property rights in the resource have to be created, and other factors make it impossible or undesirable to allocate the resource to individuals, or to the state. A common-property regime can also emerge as a way of securing control over a territory or a resource, to exclude outsiders, or to regulate the individual use by members of the community. Collective management has historically been particularly prevalent where forests have provided critically important inputs into agriculture (e.g., providing replenishment of soil nutrients through green mulch or tree fallow), where livestock management depends on access to woodland or forest (as in arid Africa and Asia), or where forests provide important dietary inputs (e.g., in high forest regions without livestock).

As pressures on the resource increase over time, common-property regimes may be replaced by private property or state management, or revert to unregulated open access use, or, as is found in many forest situations, to some combination of rights and regimes. However, forest resources can continue to be managed as common property for long periods, where this continues to be the most appropriate form of management. For instance, it is still an active system of forest management in parts of the European Alps.

Historically, however, common-property forest management regimes have been widely reduced. Much of the decline has come about because of economic, demographic and social change, e.g., increasing pressures to privatize a resource or product in order to benefit from new market opportunities, the option of purchasing rather than producing certain goods earlier sourced from a common-pool resource, and changes in rural labor availability and allocation. The share of forest resources controlled as common property has also been much reduced by expropriation by governments of forest and woodland as forest or nature reserves or some other form of state property, or as part of moves by colonial and postcolonial governments to increase their control over local activities.

Government policies and strategies that eroded common property have been widely influenced by arguments that it is inefficient, and unsustainable, by comparison with private property or state ownership. Such arguments stem from an assumption that, as user pressures build up, the cohesion and discipline necessary for effective collective management cannot be sustained and will break down, and that it will become increasingly difficult to exclude outsiders, resulting in unregulated, open access overuse of the resource. This thesis, given prominence through a very influential 1968 article by G. Hardin in *Science* entitled 'The tragedy of the commons,' contributed to pursuit of land distribution policies that favored individual private land holdings, and state control of forest resources.

Since the mid-1980s, evidence has accumulated to show that, while this thesis can and often does apply, it should not be held to be of general application. In appropriate situations users often prove to be able to create and sustain collective arrangements that avoid overuse. In addition, it has been demonstrated that private and state alternatives to common-property management can also fail to prevent overuse of forest resources.

Recently there have been major shifts in development thinking and policy that have begun to reverse some of the tendencies to centralize control. Structural adjustment policies in favor of devolution and decentralization, and greater local participation, have seen the emergence in forestry of a much greater focus on local forest management. Much of social or community forestry has been taking forms that are derived to some extent from concepts and practices of common-property management.

Conditions Favoring Common-Property Forest Management

A considerable amount of research attention has been directed towards identifying the conditions in which common property is likely to be viable and stable. **Table 1** summarizes the main variables that have been identified as being critical to the sustainable functioning of common-property systems across

Table 1 Critical enabling conditions for sustainability on the commons

(1) Resource system characteristics
- Small size
- Well-defined boundaries
- Low levels of mobility
- Possibilities of storage of benefits from the resource
- Predictability

(2) Group characteristics
- Small size
- Clearly defined boundaries
- Past successful experiences – social capital
- Appropriate leadership – young, familiar with changing external environments, connected to local traditional elite
- Interdependence among group members
- Heterogeneity of endowments, homogeneity of identity and interests
- Low levels of poverty

(1 and 2) Relationship between resource system characteristics and group characteristics
- Overlap between user group residential location and resource location
- High levels of dependence by group members on resource system
- Fairness in allocation of benefits from common resources
- Low levels of user demand
- Gradual changes in levels of demand

(3) Institutional arrangements
- Rules are simple and easy to understand
- Locally devised access and management rules
- Ease in enforcement of rules
- Graduated sanctions
- Availability of low-cost adjudication
- Accountability of monitors and other officials to users

(1 and 3) Relationship between resource system and institutional arrangements
- Match restrictions on harvests to regeneration of resources

(4) External environment
- Technology
  - Low-cost exclusion technology
  - Time for adaptation to new technologies related to the commons
- Low levels of articulation with external markets
- Gradual change in articulation with external markets
- State:
  - Central governments should not undermine local authority
  - Supportive external sanctioning institutions
  - Appropriate levels of external aid to compensate local users for conservation activities
  - Nested levels of appropriation, provision, enforcement, governance

Adapted with permission from Agrawal A (2002) Common resources and institutional sustainability. In: Ostrom E *et al.* (eds) National Research Council, *The Drama of the Commons*, pp. 62–63. Washington, DC: National Academics Press.

a range of different common-pool resources. All four of the areas identified – characteristics of the resource, characteristics of the user group, institutional arrangements, and external factors – have application to common-pool forest resources.

Characteristics of the Resource

Physical characteristics Collective management is more likely to succeed if the resource has definable boundaries and can be shown to be linked with the user community. For instance, proximity to the user community facilitates protection of the resource for the exclusive use of the controlling group, and monitoring of its use by its members.

A forest resource that needs to be managed in its entirety, in order to maintain the interactive environment necessary to maintain some of the desired outputs, is more likely to induce collective management than tree stocks that could be split up into individually managed units. This is also the case with some large resource systems, such as woodland in arid areas, where the location of productive zones can vary from year to year. Group management will also be favored where there are multiple uses and users, and coordination among them is necessary.

Productivity and capacity to meet user needs The incentive for users to invest in collective management is likely to be greater if the resource is capable of meeting a substantial part of users' needs, and if these benefits can be obtained rapidly and regularly. An existing forest that is already producing is consequently more likely to be suited to local management than one that has to be planted up and will yield benefits only after several years.

The resource also needs to have the potential to yield benefits commensurate with the costs the group are likely to incur in bringing it under management. Failure of common-property forest management can often be linked to the shrinking size or degraded nature of the available local resources. Similarly, if only low-grade forest or low-value components of a forest are made available for local use, the incentive for users to manage them as common property is likely to be weak.

Ease of management The ease with which the resource can be managed by the user group is also important. Most functioning local collective systems in practice involve easily managed products such as fodder and fuel (which are also products from which members of the user group are likely to be able to benefit in an equitable manner). Managing a wider range of forest products, or more intensive use, can introduce levels of complexity and skills that groups may find difficult to take on.

This reflects the high costs of obtaining information on which to establish more intensive management and use practices, and the risk that lack of knowledge or skills could lead to overuse of the resource on which they depend. Ease of enforcement of rules governing use by members can also be an important factor.

Characteristics of the Group of Users

A number of group characteristics may affect the capacity of a group of users to collaborate effectively in the control and management of a local forest resource.

Shared or conflicting interests One is the presence of more than one set of users, each with different interests and objectives. While some among multiple demands on a forest may be complementary (e.g., for products obtained from different component species, or for using the forest at different times of the year), others may be more competitive or incompatible. For instance, the continued dependence of the poor on local common-pool forest resources for outputs to meet their subsistence needs frequently conflicts with the interest of the wealthier within the community in privatizing the resource, or some of its product flows, in order to take advantage of growing market demand for forest products. A consequence of such competing pressures is likely to be a need for more complex control and management measures. This increases the transaction costs associated with maintaining a common-property system, sometimes to the point where such management is no longer possible without external support.

Creation of a common-property system, by excluding those who are not members of the group from further use of the resource, can also lead to conflict between the group and outsiders who previously had access to it. In addition, there can be disputes within a group over collective choice processes, or over rules for resource management and enforcement of these rules on members.

Size and composition It has been widely argued that some of these difficulties and constraints can best be minimized by organizing collective management around small homogeneous groups, with membership of each confined just to those with similar views about the use of the resource. There is considerable evidence that such small uniform groups do find it easier to establish and maintain collective control.

However, the thesis that smallness is invariably desirable is being increasingly challenged. Although the task of dividing responsibilities and benefits may favor small and cohesive user groups, the task of managing and exercising control over the resource may call for a larger body that encompasses all those with a claim on the resource. Larger bodies are likely to be able to generate more funds with which to hire watchers to protect the resource, or to buy in outside advice or assistance. Bigger groups are also likely to have more leverage in accessing public support services, and in other dealings with government departments.

Similarly, though homogeneity of interest, needs, etc., among users can have obvious benefits in terms of internal cohesion, the thesis that this is necessary in order to manage collectively is also being questioned. Although cultural differences, or differences in the nature of the interests of participants, can make collaboration difficult, differences in economic endowment need not necessarily be an impediment, for instance if rich and poor in communities have common use patterns, and consequently a shared interest in how local forest areas should be managed. Alternatively, component subgroups may have complementary interests, e.g., with poorer members able to draw on the subsistence goods they need, and wealthier members able to generate income from other parts of the resource.

Active involvement of the more powerful within the community can also provide it with effective leadership, and increase the chances that the common-property regime will work. Lack of trust in their leaders has proved to be one of the main reasons for failure of common-property systems.

Local Institutional Arrangements

The rules relating to control and management of common property, and the local institutions to develop, apply, and enforce these rules, lie at the heart of any common-property management system. It is only a self-governed form of forest management if it rests primarily on the decisions and actions of the user group. This in turn requires that it encompass a mechanism that enables members to communicate with each other about its functioning.

Freedom to set, modify, and enforce group rules Few common-property forest management regimes are governed entirely by participants. In most situations local and central government regulations also affect what can be done. Some measure of external regulation is usually also necessary in order to establish the rights of the group to control and use the resource, to protect it against unauthorized uses by those who are not members of the group, and to enable it to access government support services.

However, overly tightly formulated government rules for the operation of common-property systems can create problems. The very process of imposing rules itself undermines a basic principle of self-governance – namely, that the local body needs to be able to create rules appropriate to its own situation, and to modify these rules as the need to do so arises. Rules that cannot be altered by a group can freeze a constantly evolving relationship between people and the resource they draw upon at a particular point in time, preventing its adaptation to further change.

If the ability to determine and implement its own rules becomes undermined to the point that the user group is no longer the principal source of decisions and enforcement, the system is likely to have become one that is more accurately categorized as a form of shared management with the state, or industry, or whatever other entity has also acquired rights or authority to participate in the control and use of the forest resource.

For rules to be effective they need to apportion benefits in proportion to the costs that participants incur through participation in the common-property regime, which can vary across a user group. Groups in the middle hills of Nepal, for instance, recognize that households living further away from the resource are less able to benefit from it and should therefore not be expected to bear as much of the burden of protecting and tending it as those living nearer to it. There need to be incentives to cooperate, and an effective system for monitoring to ensure adherence to the rules, with agreed sanctions to be imposed on offenders, and a mechanism for resolving conflicts among users. Rules need to be accepted as being fair and legitimate by all participants.

Functional and representative institutions A wide variety of different forms of local institution, both informal and formal, can take responsibility for a common-property forest management regime. Some comprise just the group of users themselves, acting as an independent body. These will usually need to be recognized by formal government bodies in order to get access to government resources, services, and authority. Many user group institutions are in practice affiliated to, or are a subbody of, a higher-echelon community or local government institution. However, issues arise when such parent bodies, with predominantly political and bureaucratic agendas, have priorities that conflict with the interests of the forest user group.

Difficulties can also arise for long-established local common-property institutions, which reflect social values and practices from an earlier period when they came into existence, in accommodating to changes in the broader framework of local governance, for instance male-dominated forest management groups that may not adequately reflect current requirements for equitable participation by women.

External Environment

The capacity of common-property forest management regimes to function, and their continued relevance by comparison with alternative forms of tenure and management, can be affected by change in a number of external factors, for instance introduction of new technology that permits agricultural use of land previously left as commons. However, the two most important factors are usually increasing exposure to market forces, and the impact of actions by the state.

Articulation with external markets As households become more integrated into the market economy, and seek to generate more income with which to purchase goods, the task of managing forest as common property becomes more complex. Wage employment becomes more rewarding than gathering activities. The potential to sell products of the forest is likely to increase pressures to privatize the resource, and to overharvest. If the interests of those within a user group able to exploit such market opportunities, and those needing continued access to it to meet their subsistence needs, diverge, the potential for dispute and conflict is increased. Exposure to market forces can therefore put pressures on existing mechanisms for exclusion and control, and increase the costs of maintaining a resource as common property. This can be a major factor in moving management from common property to shared control involving other categories of stakeholder as well.

It has consequently been argued that management of forests as common property is usually better suited to meeting subsistence demand rather than production for the market. Though there are many instances where this form of management has handled commercial production successfully, one factor that may need to be taken into account in assessing whether a resource is suited to management as common property can therefore be the extent to which its output is likely to attract commercial rather than local use.

Interactions with the state The environment within which local common-property forest management systems are located is likely to be shaped by broader government actions in a number of ways. For the rights of a user community to control and manage a local forest resource to be recognized outside that community, they need to be supported in a manner that records this transfer of rights from the state. Ideally, there need to be legislation and regulations that provide authority both to communities and government agencies to generate the necessary rules, regulations, and operational measures, and that give them authority to implement and enforce them.

Lack of enabling legislation does not necessarily mean that local self-governance of forest resources cannot happen. In its absence, forest departments can still arrive at extralegal working arrangements with communities that enable them to continue to manage the forest areas from which they draw supplies. However, without a legal base, community-based rights can be challenged in terms of national law, and local groups can encounter difficulty in using the law to assert their rights. Without secure legal backing, local people are also left in a weak position in negotiating change with government, and can be left exposed to risk by even the best-intentioned initiatives introduced by the government.

Such problems are often aggravated because the legal base is weak and confused. In most developing countries western tenure, and more recent systems designed to transfer control over land to the new political elites, coexist with community systems, undermining the latter systems but seldom providing a satisfactory alternative because they are not enforced. This causes confusion, because the legal status of land and forest resources becomes unclear, and people can be faced with different fora for settling a dispute under the different legal systems.

The other main way in which the state impacts on common-property forest management is through broader national policies and strategies, and in the way these are implemented by government agencies. Recent trends towards liberalization and privatization, and towards structural adjustment and downsizing of the presence of central governments, have had a number of profound impacts. Liberalization has tended to reinforce pressures to privatize land and other resources, to the detriment of the often informal common-property practices that provided the poor in many places with their fuelwood, grazing, and other forest products. Structural adjustment, on the other hand, has given impetus to policies to devolve and decentralize control over forest resources, thereby encouraging local participation in forest governance and management. This has been reinforced by the growing focus of development policies on poverty alleviation.

With community forestry having become a major component of forestry over the past quarter-century, forms of local management which contain elements of common-property management have become widespread, particularly in developing countries. However, this has often evolved in ways that entail quite close involvement of government forest departments in their organization and operation. Local forest management institutions frequently have to operate within a framework of quite restrictive regulations laid down by forest departments. Forest departments often also have a presence in local management structures, and retain rights over some of the income-generating components of the forest, such as commercial timber. In practice, though there is no clearly defined border between them, many of these systems have more of the character of forms of control that are jointly managed by local people and the state, than of common-property regimes governed exclusively or primarily by the group of users.

See also: **Landscape and Planning**: Perceptions of Nature by Indigenous Communities. **Social and Collaborative Forestry**: Canadian Model Forest Experience; Forest and Tree Tenure and Ownership; Joint and Collaborative Forest Management; Public Participation in Forest Decision Making; Social and Community Forestry.

Further Reading

Arnold JEM (1998) *Managing Forests as Common Property*. Forestry Paper no. 136. Rome: FAO.

Baland J-M and Platteau J-P (1996) *Halting Degradation of Natural Resources: Is There a Role for Rural Communities?*. Oxford: Clarendon Press.

Hardin G (1968) The tragedy of the commons. *Science* 162(3859): 1243–1248.

McKean MA (2000) Common property: what is it, what is it good for, and what makes it work? In: Gibson CC, McKean MA, and Ostrom E (eds) *People and Forests: Communities, Institutions, and Governance*, pp. 27–55. Cambridge, MA: MIT Press.

Messerschmidt DA (ed.) (1993) *Common Forest Resource Management: annotated Bibliography of Asia, Africa and Latin Americ*a. Community Forestry Note no. 11. Rome: FAO.

Ostrom E (1999) *Self-Governance and Forest Resources*. Occasional Paper no. 20. Bogor, Indonesia: CIFOR.

Ostrom E, Dietz T, Dolsak N, Stern PC, Stonich S, and Weber EU (eds) (2002) *The Drama of the Commons*. Committee on the Human Dimensions of Global Change. Division of Behavioral and Social Sciences and Education. National Research Council. Washington, DC: National Academy Press.

Social and Community Forestry

K F Wiersum, Wageningen University, Wageningen, The Netherlands

Introduction

Traditionally, in tropical countries forest management strategies have been based on the premise that sustainable forest management is best secured by state custody over forests, with management being the responsibility of a professional forest service, and by focusing forest production measures predominantly on commercial timber production. In the mid-1970s it became recognized that this strategy was too top-down-oriented and that it focused predominantly on national interests rather than on the needs of local communities. Therefore it did not contribute much towards improving the welfare and well-being of large segments of the population living in or near forests. Consequently, a new strategy for forest management was proposed, in which explicit attention was given to the forest-related needs of rural communities and to community participation in the sustainable management of forest resources. This new strategy was termed social forestry or community forestry. This strategy has become widely accepted, and in the last decades of the twentieth century much experience has been gained about how to involve local communities actively in forest management. Although many local interpretations of the meaning of the terms social forestry and community forestry exist, at present often a conceptual differentiation between the terms is made. Social forestry relates to the planning and implementation by professional foresters and other development organizations of programs to stimulate the active involvement of local people in small-scale, diversified forest management activities as a means to improve the livelihood conditions of these people. Community forestry refers to the forest conservation and management activities that are carried out by people living within rural communities, who are not trained as professional foresters, and who carry out management activities on the basis of local norms and interests. In contrast to the traditional professional approach to forest management, community forestry is not based on standard models, but on adaptation to site-specific conditions in respect to both type and conditions of forests, local livelihood strategies, and community institutions. Two main community-based forest management systems exist: community forestry in the form of the management of forest resources on any lands within a local territory by the community inhabitants, and collaborative management in the form of the collaboration of community groups in the management of state forest lands as the result of (partial) delegation of the management responsibility by professional forestry organizations. By the beginning of the twenty-first century community-based forest management had reached a significant scale, and has been accepted as a genuine strategy for forest management in tropical countries. Gradually this approach to forest management is also gaining prominence in the more economically advanced countries in Europe, northern America and Australia.

History

Changes in Thinking on Forestry and Development

In the second half of the 1970s changes in thinking about the concept of rural development as well as increasing concerns about the ongoing process of deforestation contributed to a reappraisal of traditional forestry policies and a search for new forest management systems, which would contribute better towards rural development.

Changing concepts of rural development Since the start of international programs to assist the development of the newly independent tropical countries in the 1950s, concepts of development have changed. In the early development strategies, economic growth through the creation of a modern economic sector was a major objective. Subsequently, it was realized that an increase in production does not automatically result in a proper distribution of the products. In several cases the one-sided attention to the creation of a modern economic sector resulted in a growing gap between the modern and traditional economic sectors and marginalization of various groups of people. To counter the effects of this growing inequality, more attention was then given to the distribution of economic assets, focusing specifically on provision of basic human needs and poverty alleviation. The main objective of this basic needs strategy was to fulfill the needs of underdeveloped groups of the population for food, clothing, education, and health. This strategy was based not only on humanitarian objectives, but also on the theory that economic growth will be stimulated once basic needs are met. Later still, a third aspect received attention, i.e., the possibility for rural people to participate actively in their own development process rather than being a subject of development. The objective of such local participation is to stimulate the emancipation and self-reliance of the local people. Self-reliance is not only a development objective in itself, but it also enables a more efficient use of development efforts and funds.

This evolution in thinking on the meaning of development has influenced ideas about the role of forestry in rural development in several ways:

- In line with the critical assessment of the results of the modernization approach, it was recognized that the traditional approach to forestry development, in which it was supposed that forestry would contribute to economic development through the creation of employment and income from timber plantations and wood-working industries, is often not effective. The supposed forward and backward linkages of such enterprises were mostly smaller than originally anticipated. Too often, local people hardly profited from such enterprises and, if realized, profits were siphoned off to urban elites and/or foreign investors.
- In conformity with the basic needs development strategy, it was recognized that wood products such as fuelwood for cooking and heating and timber for house construction are essential for human survival. The concerns in the early 1970s about an energy crisis contributed towards increased attention for the critical fuelwood situation in many tropical regions.
- The growing interest in providing basic needs for rural people increased awareness about the need to improve food production on marginal lands. On these lands forests and/or trees have important protective functions in moderating climatic and soil conditions. They also provide a wide range of forest products which are essential for the livelihoods of local people, not only fuelwood and timber for construction, but also wood for agricultural implements, fodder, and a multitude of non-wood forest products such as edible leaves and fruits, edible and oil-bearing seeds and nuts, honey, medicinal plants, gums and tannins, and bark products.
- As a result of the growing interest in stimulating participation, it was recognized that, rather than restricting local people's access to the forest resources, their involvement in forest management should be stimulated. Forest benefits for local people can best be assured when they can manage the forests themselves.

Impacts of deforestation, desertification, and forest degradation Simultaneously with the changes in thinking about the role of forests in rural development, concern also grew about the rate of uncontrolled deforestation and forest degradation in tropical countries. The loss of forest resources results in many undesirable ecological and environmental effects and influences the livelihood of many rural people in a negative way. In the humid tropics deforestation has resulted in land degradation and the advent of waste lands, in mountainous areas in erosion and increasing flood damage, and in the arid tropics in desertification. Especially after the disastrous drought years of the 1960s in the Sahel, these degradation processes received increasing international attention. It was recognized that the prevailing forestry policies had not been able to control the process of deforestation, and that the state forest services had often been unable to deal with the various pressures on forest which induce overexploitation or conversion to other types of (often marginal) land use. In many tropical regions the local population is dependent on forests for their livelihoods, and consequently they often bore the brunt of deforestation. It was suggested that, in view of their forest-related needs, local communities should have a stake in maintaining forest resources and could contribute towards forest conservation.

Reappraisal of forestry policies The new insights on alternative approaches to rural development and forest conservation reinforced each other as regards the development of forest policy. Increasingly it was recognized that important discrepancies exist between the claims for sustainable forest management for multiple human benefits and the actual situation with respect to the conservation and utilization of tropical forest resources. Consequently, during the 1970s a reevaluation of the relation of forestry to rural development took place. The assumption that forest protection and management should be based on central policy and planning within an authoritative and hierarchical forest service, having important territorial and policing functions, was reappraised. A need was identified to complement the strategy of forestry development based on national interest and industrial growth with new strategies focusing on basic needs, equity, and popular participation. It was proposed that a dualistic forestry development strategy should be pursued, in which the emphasis on developing modern forest industries with their related industrial wood production areas is matched by efforts to develop forestry for rural development by focusing on the needs of the local communities and their active involvement in forest management. The new approach for forestry serving rural development was labeled as social forestry.

Gaining Practical Experience

Since the identification of the need for a new social forestry strategy, much attention has been given to formulating and implementing social forestry programs. In 1978 both the Food and Agriculture Organization and the World Bank indicated their intent to stimulate such programs. An important stimulus was also provided by the deliberations at the Eighth World Forestry Congress held in 1978 at Jakarta under the theme 'forests for people.' Many international donor agencies quickly accepted the new strategy and, since the early 1980s, an increasing number of social forestry projects have been implemented. Three phases in social forestry development can be distinguished: an experimental phase, a consolidation phase, and a diversification phase. During this evolution a gradual diversification in approach took place (**Table 1**).

The diversification in social forestry strategies concerned both technical and organizational aspects. Regarding the technical aspects, at first most attention was directed at reforestation of degraded lands,

Table 1 Phases in social forestry development

Period	*Social forestry development approach*
Experimental phase (late 1970s to mid-1980s)	Emphasis on establishing village woodlots and individual tree growing based on scaling-down of conventional forestry practices as a means to address fuelwood and desertification problems
Consolidation phase (second part of 1980s)	Increased understanding about the role of trees in livelihood strategies of villagers
	Less emphasis on firewood, more on multiproduct systems and integration of tree-growing with agriculture
	Increased recognition of significance of indigenous forestry practices
	Growing attention to village-level manufacturing of forest/tree products
Diversification phase (early 1990s)	Increased emphasis on conservation and management of existing forests, including controlled utilization of nonwood forest products
	New understanding about the role of common property
	Recognition of the need to conserve the cultural integrity of tribal forest dwellers
	Development of joint and collaborative forest management

but increasingly the focus became enlarged to involve natural forest conservation and management as well as agroforestry development. Several social forestry programs still focus on rehabilitating degraded lands, but increasingly also well-stocked forests are brought under community management. Concurrently, a change in product orientation took place. At first most attention was focused on the provision of products for subsistence needs. However, gradually it was recognized that appropriate forms of commercial production are also of importance for improving rural livelihoods, and that communities should have access to increased benefits from markets rather than focus on subsistence production only. Also regarding the local organization of forest management a gradual change in policy took place. Originally, social forestry projects were mainly based on the involvement of village organizations in managing village lands. In the first instance, this approach was not very effective, and consequently the emphasis changed to schemes on private lands. However, with increased understanding of the nature of common pool resources, a renewed interest in involving user-group organizations in forest management developed. Moreover, the scope of social forestry projects gradually became enlarged from either communal or private village lands to officially gazetted state forest lands. Whereas on village lands, management is under the authority of the local organizations, on the public lands the final authority still rests with the official forestry service. In this case, local organizations and professional forestry organizations enter into a collaborative program. This collaborative forestry strategy has gained prominence since the mid-1990s.

Thus, during the first phases of social forestry development it was considered that forestry development should be based on a dualistic model in which professional forest management on state lands and community forest management on village and private lands should coexist. As demonstrated by the advent of collaborative forest management schemes, at the start of the twenty-first century increased attention is given to the integration of professional and community-based forest management.

By the beginning of the twenty-first century community forest management had reached a significant scale. In tropical countries 23% of forests are either owned or managed by indigenous people and local communities. In several tropical countries an impressive number of local communities have become involved in community-based forest management. For instance, in India 63 000 village forest committees have been formed under the Joint Forest Management program, and in Nepal over 4 million people are represented in the Federation of Forest User Groups. In Mexico in less than 15 years between 7000 and 9000 communities have moved from merely owning land to community-based timber production and have started local manufacturing of wood products.

Definitions of Social and Community Forestry

During the advent of the social forestry strategy, various terms were used to represent it: not only 'social forestry' but also 'community forestry.' Originally, these terms were often considered as synonyms. Both terms were used to refer to any forestry policies and activities that closely involved local people in forest management and tree-growing, for which rural people assumed (part of) the management responsibility, and from which they derived a direct benefit. Gradually, however, the terms were differentiated on the basis of either normative commitments or management systems. In respect to normative commitments it has been suggested that the term social forestry should primarily be understood as a reaction to the conventional approaches to forestry, which were dominated by the ideology of forest conservation and production forestry under state stewardship, which legitimized forest service control over forest lands and tree species. It was suggested that social forestry involves the development of new forestry professionals who can work within a rural development context rather than a bureaucratic context. The motives of local people for being involved in forest management are not related to such considerations regarding the nature of professional activities. Rather, the community interests are to maintain forest resources as part of the local livelihood strategies. Community forestry can best be used in relation to such local interests. Alternatively, it was also suggested that the term social forestry is often used in an implicitly narrower sense than community forestry. Social forestry would refer to activities that aim at the fulfillment of subsistence needs of the poor people, and thus refer predominantly to a basic welfare function of forests, whereas community forestry would refer to a more diversified set of activities, including more commercially oriented ones.

In respect to management arrangements, it was suggested that the term social forestry could be defined as an umbrella term for various schemes aiming at forest and tree management on private and village lands aimed to produce local needs. Community forestry could be used as a broad term which includes indigenous forest management systems and government-initiated programs in which specific community forest users protect and manage state forests in some form of partnership with the government.

Thus, the term social forestry has a strong policy connotation, and is mainly related to activities of professional foresters. In contrast, the term community forestry has a more descriptive connotation, and is mainly related to activities of rural communities. The two terms can logically be differentiated on the basis of whether the terms relate to policy development activities or forest management practices and whether these activities are carried out by professional foresters or local communities.

Social forestry can be defined as a development strategy of professional foresters and other development organizations with the aim of stimulating active involvement of local people in small-scale, diversified forest management activities as a means to improve the livelihood conditions of these people.

Community forestry can be defined as any forest management activities undertaken by rural people as part of their livelihood strategies. Such activities may be self-initiated or proposed by external development programs.

The differentiation between social forestry and community forestry can further be clarified by the identification of social forestry as a development strategy aimed at the stimulation of more effective community forestry.

Social Forestry as Development Strategy

Social forestry policies encompass the process of formulation and implementation of measures to stimulate community involvement in the management of forest resources. It refers on the one hand to activities of professional foresters or development organizations aimed at stimulating the forest and tree management activities that are under the control of local people. On the other hand it refers to activities aimed at adapting the professional management practices in official (public) forest reserves, in order that this management becomes more explicitly directed towards an improvement of the welfare of rural communities. The development measures to stimulate local communities to intensify forest management may consist of the provision of external inputs, such as secure access to land, financial incentives, technical support, or extension. Also they may include arrangements for proper institutional and organizational frameworks, including legal codes, tenure policies, forestry extension organization, in order that community forestry can proceed.

Organizations which plan and implement social forestry programs do so for different reasons. The rationale for social forestry development is based either on assumptions regarding the contribution of social forestry measures to improved forest conservation and management, or on assumptions concerning its contribution to socioeconomic development (**Table 2**). Due to the different assumptions regarding how social forestry can contribute to solving either forest management or rural development problems, there is not just one objective for stimulating social forestry, but rather a group of objectives:

- To improve livelihoods of rural people by linking rural development and environmental conservation by ensuring that rural people can produce, or have better access to, certain basic needs in the form of essential forest and tree products and

Table 2 Assumptions on the rationale for social forestry development

Assumptions with respect to forest conservation and management

- Small-scale forest exploitation by local community groups better ensures sustainable forest management and forest conservation than large-scale commercial timber exploitation by concessionaries, because of the lower ecological impact of such small-scale activities and because, in contrast to large companies, local people cannot shift their activities to other areas in case of forest degradation resulting from overexploitation
- Allowing local forest utilization in certain concentrated areas can take the utilization pressure away from essential conservation areas, and therefore ensures better forest and nature conservation
- Ensures optimal use of human resources in forest management and therefore provides better prevention of forest degradation and improved rates of forest rehabilitation
- Changing open-access forest exploitation to community-controlled forest exploitation ensures more effective forest conservation
- Active participation of local communities in forest management lowers the costs of the state for forest conservation

Assumptions with respect to social development

- Local people should be legitimized to use and manage forest resources for their own needs and encouraged to apply their own indigenous knowledge in doing so
- Community forest management contributes towards the increased self-reliance of local people in producing valuable forest products, and allows equitable distribution of those products
- Community management of natural forests allows the preservation of the cultural integrity of tribal people and contributes to the empowerment of tribal communities to gain control over their own traditional resources
- Underprivileged rural groups should be empowered to gain control over the resources needed to improve their livelihood

services, and by promoting sustainable use of natural resource, employment generation and local institution building

- To honor the principles of democracy and social justice by devolving power and authority from state bureaucracies to local groups, increasing the participation of rural people in the management of forest and tree resources as a means of stimulating their self-reliance, and by addressing the needs and aspirations of specific underprivileged groups within the rural population, such as subsistence farmers, landless families, or other sectors of the rural poor
- To make forest conservation and management more efficient by involving local communities in the management of forest and the rehabilitation of degraded and marginal lands, thus reducing the state's costs for forest conservation

Some of these objectives may be congruent or may reinforce each other. Others are broadly divergent:

- Much attention has been given to the role of social forestry for meeting subsistence needs of poor people. However, activities to optimize subsistence production for poor people do not contribute towards the economic development of rural households which are incorporated in a commercial economy. For such households attention should be given towards improved options for production, local manufacturing, and marketing of commercially valuable forest products.
- In schemes to stimulate farmers to grow trees to meet specific market demands, it may be difficult to achieve democratic participation, especially of poor, landless people. In this case, equity objectives and distributive benefits may have inconsistent impacts among different sectors of the rural population.
- The provision of specific tree products (such as wood, fodder, or fruits) to local people may be assured by individual trees, even if standing alone or scattered in backyards or agricultural lands. These needs could be met by stimulating agroforestry practices on private lands. However, for securing other forest-related benefits (e.g., environmental services) it is often necessary to maintain forest reserves as complete and well-functioning ecosystems.

Thus, when formulating social forestry programs it is essential to specify what the precise objectives of the program are and to relate those objectives to the specific characteristics of different community forestry management schemes.

Community Forest Management

Variation in Community Forestry Arrangements

Community forestry refers to forest and tree management activities undertaken either individually or cooperatively by the local people, either on their own or on leased private lands, on communal lands or on state lands. It involves the process of making and implementing decisions with regard to the use and conservation of forest resources within a local community, with the organization of the activities being based on shared norms and the interests of the people living in that local community. Community forestry is a generic term as different forms of community forest management exist. This variation reflects the various meanings of the term 'community.' A community may be either a locality in the sense of a human settlement with a fixed and bounded local territory, a local social system involving interrelationships among people living in the same geographic area, or a type of relationship characterized by a sense of shared identity. Consequently, different community forestry arrangements are possible depending on the type of territory and the type of social relations being considered. In respect of such institutional arrangements, three main types of community forestry may be distinguished:

1. Management of any woody resources on lands which are located within a local territory, irrespective of whether these resources are privately, communally or *de facto* state-owned
2. Management of common pool resources, such as communal forest or grazing lands, which are shared or held in common and jointly used by people who are formally or informally organized in a forest user group
3. Collaborative management of state forest lands under cooperative arrangements with a public forest administration

The term community forestry is often used in reference to any local arrangements for managing forest resources within a village territory, irrespective of the land tenure conditions. In this case community forestry involves both forest or tree management on private lands (often labeled as farm forestry), on village lands, or on state lands which are used by local people. However, the term is also used in reference to specific forest management arrangements on either communal or public lands.

Community forest management arrangements may also be differentiated on the basis of the type of the community organization which bears responsibility for forest management. Such organizations may range from specific user groups and family lineages, to village organizations or tribal organizations. Thus, community forestry is not restricted to village territories, but may also involve the ancestral territories of indigenous tribal groups.

Community Forestry Activities

In community forest management the main responsibility for making arrangements for forest management rests primarily with rural people. The local people do so on the basis of their own specific management objectives, rather than on the basis of the policy objectives of forestry development organizations. The local objectives for forest management involve not only fulfillment of basic household needs and the provision of marketable products, but also include the provision of forest products to be used as inputs for agricultural and livestock production. Moreover, forests may also be maintained because of cultural and religious values. Community forest management is not a specialized activity, as in the case of professional forest management, but rather forms an integrated component of the local land-use strategies. Local communities often not only attribute utilitarian values to forests, but also cultural and spiritual values. Their multiple values concerning forests may be reflected in location-specific indigenous forest management systems. Such indigenous forest-related practices include not only regeneration and maintenance of trees in either forests or agroforestry systems, but also conscious conservation of forests, controlled harvesting of forest products, and local manufacturing of these products. In many rural communities such indigenous management activities have existed for a long time. Due to the advent of modern state bureaucracy and the belief in the progressive value of professional forest management, these practices have often been overlooked in traditional forestry development programs, and have even been marginalized. However, the advent of interest in community forestry development has brought renewed interest in using such indigenous systems as a starting point for further community forest management. Thus, regarding the evolution of community forestry, a distinction can be made between indigenously evolved systems and externally sponsored systems.

Conclusion

In the late 1970s the concepts of social and community forestry emerged as a focus for addressing the linkages between forestry and rural development. Different interest groups stimulated community forest management for different reasons:

- As a component of strategies to enhance rural livelihoods, in particular the livelihoods of the poor, and/or to maintain the cultural integrity of tribal people
- As a means to manage forest resources sustainably so as to conserve both forests and their biodiversity
- As a component of government strategies to devolve and decentralize responsibilities, and to reduce the budgetary costs of state governments for forest management

Since the advent of social and community forestry considerable experience has been gained with these strategies. Experience has shown that it is not always possible to fulfill all different expectations regarding the outcomes of social and community forestry at the same time. It was also found that the original approach to social and community forestry was rather limited; consequently the approaches became gradually more diversified. At the start of the twenty-first century it is clear that social forestry policies and project approaches should be carefully harmonized with the realities of local communities. In view of the various interpretations regarding the scope of community forest management, the objectives for social forestry development should be clearly specified and related to the specific characteristics of different community forestry schemes.

Another important lesson learned is the need not to limit social forestry to a strategy for meeting subsistence needs and alleviating poverty of the poor. Rather, social forestry should be focused on a large array of social development issues, notably aspects of provision of land rights, reclaiming of indigenous territories, and access to markets. Gradually also collaborative management schemes are developing between local communities and commercial forestry enterprises. To stimulate such trends, attention also needs to be given to networking of community forestry organizations and improvement of the skills of community organizations to negotiate with external organizations. As a result of such developments, community forestry will increasingly become a multifaceted component of a pluriform system of forest management rather than a complement to professional forest management.

See also: **Landscape and Planning**: Perceptions of Nature by Indigenous Communities. **Operations**: Small-scale Forestry. **Silviculture**: Managing for Tropical Non-timber Forest Products. **Social and Collaborative**

Forestry: Canadian Model Forest Experience; Common Property Forest Management; Forest and Tree Tenure and Ownership; Joint and Collaborative Forest Management; Public Participation in Forest Decision Making; Social Values of Forests.

Further Reading

Arnold JEM (2001) *Forests and People: 25 Years of Community Forestry*. Rome: Food and Agriculture Organization of the United Nations.

Fisher RJ (1995) *Collaborative Management of Forests for Conservation and Development*. Gland, Switzerland: IUCN/World Wide Fund for Nature (WWF). Issues in Forest Conservation.

Hobley M (1996) *Participatory Forestry: The Process of Change in India and Nepal*. Rural Development Forestry Study Guide no. 3. London: Overseas Development Institute.

Mayers J and Bass S (1999) *Policy that Works for Forest and People*. London: International Institute for Environment and Development.

Peluso NL, Turner M, and Fortmann L (1994) Introducing community forestry; annotated listing of topics and readings. Community Forestry Note no. 12. Rome: FAO.

Wiersum KF (1999) *Social Forestry: Changing Perspectives in Forestry Science or Practice?*. Wageningen, The Netherlands: Wageningen Agricultural University.

Working Group on Community Involvement in Forest Management (1999–2002). *Communities and Forest Management*. Regional profiles series. Gland, Switzerland: IUCN World Conservation Union.

Joint and Collaborative Forest Management

A Lawrence and S Gillett, University of Oxford, Oxford, UK

Introduction

With the increasing recognition over the last 30 years that forestry is a pluralistic enterprise with a wide range of legitimate stakeholders, new arrangements for sharing management decisions among local forest users and professional forestry services are emerging under various titles including 'participatory forest management,' 'collaborative forest management' (CFM), and 'joint forest management' (JFM).

In many parts of the world CFM is a relatively new idea. Despite widespread use of the term, and 20 years since its inauguration in India and Nepal, CFM in many ways remains an experimental process. Consequently, CFM often takes the form of adaptive management with objectives and activities gradually being adjusted to both the experiences learned as well as the evolving needs of the resource and the stakeholders.

Since the 1990s many countries have introduced CFM programs and policies (**Table 1**), usually with strong donor support, and encouraged by international post-Rio forest dialog supporting National Forest Programs. There are high expectations for CFM. Different stakeholders hope that it will:

- benefit the rural poor who depend on forests for their livelihoods
- contribute to sustainable resource use and reduced forest degradation (through strengthened ownership)
- reduce the cost of forest management by the state.

The diversity of CFM models, stakeholders, objectives, forms of community organization, and partnerships with professional forestry organizations makes it hard to generalize about the impact of CFM, particularly in relation to forest conservation and social aspects factors. Similarly, the factors contributing to success are open to interpretation. Whilst tenure, institutional arrangements, and local organizational strengthening have often been highlighted, the effects as experienced by forest users are rarely considered.

In this article we first look more closely at the various terms used, and take an overview of the way CFM has developed around the world, before discussing the issues that are implicated in its success or failure.

Definitions and Main Characteristics

The involvement of nonforesters in forest management has taken off to such an extent that there is now a plethora of terms to describe it (**Table 2**).

'Collaborative forest management' refers to an explicit partnership between professional forestry organizations and communities or defined groups of local forest users. The objective of this strategy is to manage forests to provide sustainable benefits for a range of stakeholders. It has been emphasized that CFM is an intervention by outsiders (public forest services, donors, and nongovernmental organizations (NGOs)), and therefore contrasts with traditional forest management practices.

The term 'participatory' has become so widely used that there is a risk of its being misunderstood. Participatory is understood to refer to a range of relationships between professionals and local people,

Table 1 Examples of countries implementing CFM to a significant level

Region/country	*Policy and date introduced (with amendments in parentheses)*	*Type of partnership*	*Estimated numbers of communities involved*	*Area of forest under CFM (ha)*
South Asia				
Nepal	**1976 – National Forestry Plan**. Allowed land to be handed over to local users, with technical assistance provided by the forest department.[b,o] **1978 – Panchayat Forest and Panchayat Protected Forest Regulations**. (1980) CFM enacted.[o,u] (1988 – Adopted concept of Forest User Group, 1990 – Panchayats replaced by Village Development Committees.[o]) **1982 – Decentralization Act**.[o,u] Formalized duties and responsibilities of village panchayats and ward committees, empowering them to form people committees for forest conservation and management.[u] (1984) **1987 – Decentralization Act**.[u] Introduced the concept of User Groups for local administration. **1988 – Community Forestry By-Laws**.[o] (1989) **1989 – Master Plan for Forestry Sector**.[b,o] **1993 – Forest Act**.[b] FUGs clearly defined, and clear implementation guidelines produced. Provides the legal basis for CFM implementation.[u] (1999 – provisions for FD to impose penalties on offenders at request of FUG if they are unable to enforce themselves.) **1995 – Forest Regulations**.[b] Procedural guidelines for implementing the Forest Act of 1993. **2001 – Forest (Second Amendments) Bill**.[u]	Forest User Groups supported by District Forest Office	6022[b] to 13 000[a] Forest User Groups	400 719[b]–850 000[a] ~12% of Nepal's forest lands
India	**1988 – Forest Policy**. The launch of JFM. Followed by State JFM Resolutions.[e] **1990 – Guidelines for JFM** issued by Ministry of Environment and Forests.[e,o] **1994 – Draft Forest Act**.[e] **1998** – Formation of **JFM Standing Committee** by the Ministry of Environment and Forests.[o] **2000 – Guidelines for JFM revised** to include forests with over 40% canopy cover.[v] **2002 – Guidelines for JFM revised**.[v]	State forest department with village forest committees or forest protection committees	30 000–35 000[o] (2000)	10.24 million ha in 22 states[d]
Pakistan	**1996 – Hazara Protected Forests Rules**[o] (modification of the Forest Act of 1927). Mandates the formation of JFM committees, including operational guidelines and production sharing arrangements with provincial FD.[o]	Provincial Forest Departments with Forest Management Committees		

Southeast Asia				
Philippines	**1982 – Integrated Social Forestry Programme** established.[p]	Villagers and local government representatives work together.[p]	550[c]	700 000 ha (potential area 1.5 million ha)[c]
	1987 – Constitution. Recognized the importance of the environment and rights of indigenous people.[p]			
	1990 – Indigenous people's rights to ancestral lands and domains recognized.[p]			
	1994 – Social Reform Agenda.[p]			
	1996 – Community Based Forest Management Program formulated.[c,p] Guidelines included community mapping.			
	1997 – Indigenous Peoples' Rights Act. Gave indigenous communities title to ancestral domain and land claims.[c,p]			
	1999 – CBFM program put on hold.[p]			
Laos	**1994 – National Leading Committee** for Decentralized Rural Development (1996, 1998).[c]	Forest departments and villages		
	Village forestry is a key element in the **National Forestry Action Plan**, and policies are being adopted that foster local people's participation in forest management, including the allocation of access and use rights of forest resources.[c]			
Thailand	**1993 – Forestry Master Plan**.[p] Extends forest areas under conservation.			
	1992 – Tambon Administration Organization Act (TAO). Strengthens role of village governments in forest use and planning decision-making.[p]			
	1997 – Constitution. Traditional communities granted the right and duty to manage resources where they live. However, without enabling CFM laws, current conservation policies are at odds with the community rights provisions listed in the Constitution.[p]			
	Pending – New **Ministry of Natural Resources Bill**, formalizing CFM. Deferred for approval to 2003.[f]			
Vietnam	**1991 – Tropical Forestry Action Plan**, the Forest Resources Protection Act, the National Forest Policy. Private households replace state forest enterprises as new units for forest management, with appropriate guidance from the state.[p]	Private households with state guidance.[p]	1203 communes[c]	
	1993 – Land Law gives local inhabitants extensive user rights over agricultural and forest land.[p]			
	Recent amendments restrict rights and limit role of local people as forest custodians.[p]			
Meso-America				Over 2 602 425 ha (14.5% of forest cover)[g]

continued

Table 1 Continued

Region/country	*Policy and date introduced (with amendments in parentheses)*	*Type of partnership*	*Estimated numbers of communities involved*	*Area of forest under CFM (ha)*
Mexico	**1917 – Constitution**. Ancient land use customs clarified and applied to land tenure. The reforms enabled indigenous communities to obtain property titles for their lands via presidential decree, and to reclaim usurped land if they could legally show when and how it was taken.[s] **1992 – Ejido property laws** were reformed. Allow lands to be rented by ejidos to anyone from farmers to multinationals. Ownership assigned to ejidos already managed communally, allowing them to be sold for the first time.[s] The National Forest Commission developed the **New Community Forestry Plans**. This provides loans for development and management of non-timber resources in Community and Ejido Forests.[s]		Approximately 8 000 ejido village communities.[s]	80% of Mexican forests owned by ejidos.[s]
South America				
Bolivia	**1996 – Forestry Law** recognizes that communities may be better stewards of the land than large, private concessionaires. Communities given preferential rights to use forest areas on properties that they possess.[h]	State forest department and communities		
Brazil	**1965 – Forestry Code**, Law No. 4.771/65 (the Code). Establishes woodland zones that are subject to 'permanent preservation management.'[r] **1988 – Federal Constitution** clearly recognizes indigenous rights over lands that they have traditionally occupied. Extraction is allowed, but only after zoning and an inventory of exploitable land has been done.[r]			
Africa		State forest department and communities[i]	45 000 rural communities in 30 countries[i]	At least 3 million, 1% of forest area of Africa.[i]
Cameroon	**1994** – Community forests can be formed from National Forests by a community official entering into an agreement with the Ministry of Environment and Forests. Forest products from those forests are the exclusive property of the community for the duration of the agreement, but the forest is not owned by the community.[j]	Ministry of Environment and Forests and communities	35[k] to 40[i] community forests allocated	1 000 000[l]
Tanzania	**1998 Changes in Forest Policy**. Include Guidelines on the development of CBFM and JFM.[l]	Forest departments and villages or communities	500 village forest reserves; 100 community forest reserves (groups); 30 pilot comanagement of forest reserves[i]	500 000[l]

The Gambia	**1990 – The Forest Department introduce Community Forestry**	Between the local community and the forest department on behalf of the government.[m]	300[m] to 500[i] villages involved	39 000[i] to 50 000[n]
	1994 – The Gambian Forest Management Concept.[m] Forest park management and CFM merged into one framework. **1995–2005 – New Forest Policy**. Aims to transfer ownership thus encouraging local participation for sustainable forest management as well as advancing decentralization within the country.			
Europe	International policy frameworks supporting CFM in Europe: **1992 – Agenda 21** **1992 (in force 1995) – Convention on Biological Diversity** **1992 – The UNCED Forest Principles** **1999 – The Forest Stewardship Council's Principles and Criteria** **1998 (in force 2001) – European Aarhus Convention on Access to Information, Public Participation in Decision Making and Access to Justice in Environmental Matters**.[q]			
Belgium	**1990 (1999) – The Government of Flanders Act on Forest**. Requires local forest managers to consult the local people when drafting management plans.[q]	Forest Department and local stakeholders		
Finland	**1997 – new Forest Act**. Requires public participation in forest planning and management. Usufruct rights of the Saami people have not been recognized.[q]	Forest Service and local stakeholders		
Ireland	**1996 – Strategic Plan for Forestry**. Involves a broadly based consultation procedure.[q]	Forest Service and forest owners, farmers and local communities		
Portugal	**1996 – new National Forest Act**. Participatory planning required at regional levels.[q]	National Forest Service and forest owners, local community-owned forests, forest industries, and hunters		
Spain	**2000 – National Forest Strategy**. Based on a public participation process lasting several years.[q]			
UK	Clear policy statement on multiple use forestry. **1995 – Rural White Paper**. The government wish to enhance the contribution forestry can make to sustainable communities	Forest Commission and rural communities		

continued

Table 1 Continued

Region/country	*Policy and date introduced (with amendments in parentheses)*	*Type of partnership*	*Estimated numbers of communities involved*	*Area of forest under CFM (ha)*
North America				
USA	**1994 – Federal Advisory Committee Act**. This law has thwarted many CFM initiatives, and remains a barrier.			
Canada	**1992 – Canada Model Forest Programme**. Funds given to local communities, and all rights devolved to them as a pilot study.[t]	Between Forest Industry and local communities, environmental NGOs and First Nations Groups		
	Different provinces have different laws. Quebec has the richest history of CFM in Canada.[t]			

[a]Ojha ZW and Bhattarai B (2003) Learning to manage a complex resource: a case of NTFP assessment in Nepal. International Forestry Review 5(2).
[b]http://www.panasia.org.sg/nepalnet/forestry/comm_forestry.htm
[c]http://www.recoftc.org/01country/home.html
[d]Sharma RC (2000) *Indian Forester* 126(5): 463–476.
[e]Hobley M (1996) *Participatory Forestry: The Process of Change in India and Nepal*. London: Overseas Development Institute.
[f]Daniel R (2002) Thailand: Forests communities to renew struggle for rights. *World Rainforest Movement Bulletin* 63: 24–25.
[g]http://www.forestsandcommunities.org/central-south-america.html
[h]http://www.forestsandcommunities.org/Country_Profiles/bolivia.html
[i]Alden Wiley L (2002) The political economy of community forestry in Africa: getting the power relations right. *Forests, Trees and People Newsletter* 46: 4–12.
[j]Watts J (1994) Developments towards participatory forest management on Mount Cameroon (The Limbe Botanic Garden and Rainforest Genetic Conservation Project 1988–1994). *Rural Development Network Paper* 17(d): 1–19.
[k]Research and Action Centre for Sustainable Development in Central Africa (2002) Cameroon: developments of community forests. *World Rainforest Movement Bulletin* 63: 14–16.
[l]Moshi E, Burgess N, Enos E, *et al*. (2002) Tanzania: joint and community-based forest management in the Uluguru Mountains. *World Rainforest Movement Bulletin* 63: 16–17.
[m]http://www.dfs-online.de/cfo.htm
[n]http://www.statehouse.gm/budget2002/9.htm
[o]Poffenberger M (ed.) (2000) *Communities and Forest Management in South Asia*. Gland, Switzerland: IUCN.
[p]Poffenberger M (ed.) (1999) *Communities and Forest Management in South East Asia*. Gland, Switzerland: IUCN.
[q]Jeanrenaud S (2001) *Communities and Forest Management in Western Europe*. Gland, Switzerland: IUCN.
[r]http://www.forestsandcommunities.org/Country_Profiles/brasil.html
[s]http://www.forestsandcommunities.org/Country_Profiles/mexico.html
[t]http://www.forestsandcommunities.org/Country_Profiles/canada.html
[u]Springate-Baginski O, Blaikie P, Dev O, *et al*. (2001) Community forestry in Nepal: a policy review. http://www.york.ac.uk/inst/sei/prp/pdfdocs/nepalpolicy.pdf
[v]http://www.rupfor.org/jfm_india.htm

Table 2 Different terms for joint and collaborative forest management

Abbreviation	*Term in full*
CBF(R)M	Community-based forest (resource) management
CF	Community forestry
CFM	Community forest management or collaborative forest management or collective forest management or community involvement in forest management
JFM	Joint forest management
PFM	Participatory forest management
VJFM	Village joint forest management

Table 3 Typology of meanings of 'participation'

Type of participation	*Characteristics*
1. Passive	Participants are treated as sources of information, and/or are told about decisions already taken. Information being shared belongs only to external professionals.
2. Consultative	Participants are consulted about their opinion, but does not necessarily lead to those views being taken into account when decisions are made, usually by non-participants.
3. Functional	Participants contribute knowledge and skills to meet predetermined objectives (such as forest management goals). Often seen as helping to reduce costs of outside agents.
4. Collaborative	Although the initiative is usually taken from outside, participants share goal-setting and analysis, development of action plans and any follow-up activities.
5. Active (self-mobilization)	Participants take the initiative, and develop contacts with external institutions for resources and technical advice they need, but retain control over goals and resource-use.

Source: Adapted from Biggs (1989) and Pretty *et al.* (1995).

from consultation to joint decision-making and power-sharing (**Table 3**). Within the context of CFM participation refers to the active involvement of local people in goal-setting, planning, implementation, and monitoring of forest management activities on forest lands that are legally under public authority.

Although CFM is based on the principle of active participation of local people in managing state forest lands, the public forest services have the final authority over the forest lands. Through CFM, they delegate management authority to local people under the proviso that the management activities are in accordance with the general forest management policy. Thus, CFM is in essence based on an approach of decentralization and collaboration rather than an approach of devolution as is the case in the legal recognition of common property management regimes.

Schemes may be differentiated according to the type of forest lands involved (e.g., any forest lands of interest to local communities, only degraded lands but no commercial forest lands, or buffer zones around conservation areas). They can also be differentiated according to the level of involvement of the defined forest users in planning and implementing management. The management plan is always approved by the state forestry department or its equivalent, but in different contexts may be drawn up by the forest user group and submitted for approval, or drawn up by the foresters and approved by the forest users.

Table 4 Forest User Group (FUG) formation, Nepal

1. Forest Department (FD) officials identify forest area and users.
2. FD conducts meetings with community leaders and key informants.
3. Forest User Group (FUG) assemblies are called to discuss rules for the management of the community forest and of conflicts.
4. A committee is formed. This is generally between eight and 13 people, and has representatives from all groups (including women and low caste groups).
5. The FUG constitution is prepared.
6. The FUG is approved by the District Forest Office (DFO).
7. The FD and FUG survey the forest, and produce an operational plan (OP) (management plan). This usually focuses on timber value only.
8. The OP is approved by the DFO.
9. The FUG implements the OP with monitoring, support, and strengthening activities by the field staff of the FD.

Source: Hobley M and Ojha H, personal communication.

Global Overview

This section discusses CFM as it has developed around the world.

Nepal

Nepal has been heralded as a world leader of CFM. In the process termed 'community forestry,' the Forest Department (FD) retains some control over forest management (**Table 4**). Management plans, known as Operational Plans (OPs) in Nepal are developed with advice from the FD, in line with national legislation. Once the OP is approved, the forest is formally handed over to the Forest User Group (FUG), which then carries out the activities with advice from the FD only if sought. OPs generally span a 5-year period, and any alterations to them within this time require further approval from the FD.

CFM in Nepal has been strongly supported by donor organizations, and in the 1990s, the newly democratic government supported the devolution of management rights to FUGs. Transfer of rights has accelerated since then.

The relatively long history of CFM in Nepal has provided some important lessons regarding equity and benefit distribution. Wealthier members of communities are favored by a strong focus on timber species; women, scheduled castes, and poor people are marginalized when communities 'manage' forest solely by protecting it. Probably only 30% of FUGs are functioning according to democratic principles in decision-making. Claims that CFM is intended to support poverty alleviation are undermined by the slow expansion of CFM to the forest-rich Terai lowlands, where 50% of the country's population is underrepresented by only 2% of the country's FUGs.

Nevertheless Nepal continues to develop CFM by acting on lessons learnt, leading to continuing policy and implementation challenges such as the Forest Regulations (1995) requiring a detailed forest inventory by the FD before handover to the FUG. However, the FD is underequipped to meet the demand for inventory, and both new and established FUGs are suffering as a consequence.

India

CFM in India is known as Joint Forest Management (JFM) (**Table 5**), under a model whereby the forest is not handed over to the community, but is jointly managed by a Village Forest Committee (VFC) and the state Forest Department (**Table 6**). The earliest recorded case of JFM was in Arabari, West Bengal in 1972. Earlier attempts such as the 1948 and 1956 Industrial Policy Resolutions, which introduced the need for participatory management, were unsuccessful due to conflicting priorities and historical antagonism between local communities and the government. In 1988, the National Forest Policy explicitly emphasized the participation of local

Table 6 Village Forest (Management) Committee (VF(M)C) or Forest Protection Committee (FPC) formation, India

1. The FD hold a preliminary meeting in the village to explain the concept of JFM.
2. A VFC/FPC will be constituted if a minimum of 50% of adults pass the resolution for its formation.[a]
3. The VFC may be made up of all voting adults in the village, but more generally is made up of a certain percentage of them. Different resolutions have rules about the number of women and lower caste people that need to be in the VFC.
4. An executive committee of the VFC/FPC is elected (seven to 15 members), and generally must contain specified numbers of women, lower castes, and landless people.
5. A microplan is suggested by the FD after a survey conducted by them. This will set levels for harvesting firewood, etc.
6. The VFC/FPC can ask to be registered and boundaries to be demarcated.

[a] The different States of India have different JFM Resolutions; accordingly while some form VFCs, others form FPCs. The formation of VFC or FPC depends on the state, due to the differences in JFM Resolutions. Generally the formation follows the pattern above.

Source: Hobley M (1996) *Participatory Forestry: The Process of Change in India and Nepal*. London: Overseas Development Institute and Kinhal G, personal communication.

Table 5 Definition of Joint Forest Management

Definition	*Structure*	*Products*	*Purpose*
Joint Forest Management (JFM) is a forest management strategy under which the Forest Department and the village community enter into an agreement to jointly protect and manage forest land adjoining villages and to share responsibilities and benefits.	The village community is represented through an institution specifically formed for the purpose. This institution is known by different names in different states (e.g., Vana Samaraksha Samitis in Andhra Pradesh and Hill Resource Management Societies in Haryana) but most commonly referred to as Forest Protection Committee or FPC. In some states, panchayats can also enter into JFM agreement with the Forest Department.	Under JFM, the village community gets a greater access to a number of Non Timber Forest Products (NTFPs) and a share in timber revenue in return for increased responsibility for its protection from fire, grazing and illicit harvesting. The details vary from state to state as each state has issued its own JFM resolution/rules.	The essential difference between 'social forestry' and JFM is that while the former sought to keep people out of forests, the latter seeks to involve them in the management of forest lands. JFM also emphasises joint management by the Forest Department and the local community.

Reproduced from: Resource Unit for Participatory Forestry (http://www.rupfor.org/jfm_india.htm) people in the management and protection of forests, signifying the birth of JFM, later interpreted at state level where each state forest department has control over forest policy (**Table 5**).

JFM in India was, until recently, reserved for degraded forest lands. Guidelines passed in 2000 allow JFM to be implemented in forests with over 40% crown cover. The 1988 National Forest Policy is federal law, but is adapted by each state, so that the exact arrangements of JFM Resolutions differ between states. Twenty-two of India's 26 states have implemented JFM resolutions, and both the minutiae of the Resolution and the motivational levels of each state forest department influence its success.

JFM has been criticized for transferring too little power to community members. The language of many JFM resolutions is seen to reflect continuing control of VFC by FDs. Due to historical exclusion from forest reserves, and the state enforcement of their lack of rights to land, rural people have deep-founded mistrust of the state forest department and regional forest offices. In some cases, JFM is seen as a means for the FDs to organize local labor to improve public lands. Others note a tendency for JFM to be imposed on tribal people without consultation or consideration of their rights. Although results vary between states, JFM has achieved many of its goals, and has succeeded in increasing awareness about resource fragility, arresting depletion of forests, and the regeneration of degraded forests.

Elsewhere in Asia

Because of the wealth of many of the remaining forests in Southeast Asia, forest legislation still favors commercial logging. However, communal systems of forest management have existed for centuries, and an emerging peoples' movement forms the context for community-based resource management, whether of forests, national parks, or coasts. For example, Community Based Forest Management is a promising approach in the Philippines, but critics point to heavy dependence on donor support with little financial or political support from central government. Despite the enormous popularity of participatory methods among development organizations, by trying to build on incipient civil society initiative before any supportive national institutional change had been instated, at times the donor agenda has swamped the national reform process and, it is sometimes suggested, left indigenous people less empowered than before. The region is particularly supported in CFM by the presence of the Centre for International Forestry Research (CIFOR) (which has its international headquarters in Indonesia) and their innovative work on adaptive collaborative management, in developing the social learning processes essential for successful CFM.

Central Asia has recently undergone radical change with the collapse of Soviet rule in 1990. Kyrgyzstan is the only republic that has adopted democracy and decentralized administration, and with this new form of governance, has also embraced the system of CFM. The Swiss government has facilitated the introduction of CFM in Kyrgyzstan, and its influence has been high due to the decrease of state funding for forestry. One condition that may promote the success of CFM in this republic is the strong preference of the government for long-term leases of state forest land, with tenants managing the forests, and receiving the benefits of nontimber forest products (NTFPs) from their plots.

Africa

Despite its short history in Africa (less than 10 years), CFM policies exist in over 30 countries, with forestry administrations preferring collaborative arrangements to more devolutionary regimes such as community forestry. As in other parts of the world, the reluctance of governments to review forest tenure arrangements is one important reason for slow progress.

Different countries within Africa have adopted different strategies of CFM. Some, including Zambia, Cameroon, and Burkina Faso, have followed India and Nepal in only allowing CFM in 'poorer' forest areas. Other countries (e.g., Uganda, Guinea, and Ethiopia) support CFM within National Forest Reserves. Most other countries have no restrictions on the type of forest eligible for CFM activities.

As in the Philippines, critics warn against the dependency on community forest policy formulated by external organizations (donors or NGOs), with little knowledge of local social and environmental conditions. It has been argued that policies made in this way have a tendency to benefit Western donors and NGOs more than the rural communities who have to deal with the consequences. Most argue that sincere governmental support is essential for the success of CFM.

Latin America

Latin American nations are currently witnessing a high level of grassroots mobilization, and are calling for forest resources to be used for the benefit of local communities. However, policies remain centralized, and communities lack the capital and capacity to develop economically sustainable forest management models.

Land tenure is a key issue in Latin America. Failure of the state to uphold secure tenure management systems limits the potential for community management models, and many Latin American nations are in the midst of an ongoing debate over the nature of land ownership. Many indigenous common property management regimes are being eroded through central tenure legislation, the reality being that most state models do not recognize indigenous land use systems. Agrarian reforms have attempted to return land to campesinos (peasants, or rural farmers), but the late twentieth century has seen a state- and industry-led desire to privatize land in order to promote foreign investment. However, some innovative and exemplary policy changes in Bolivia and Colombia have created new opportunities for recognized indigenous groups to manage their land and forest collectively.

Latin America is characterized by the distinctiveness of indigenous people and their association with tropical forest communities, and the role of forest-dwelling communities in conservation is beginning to be valued. A number of countries in South America have CFM policies, but contradictory policy and legislation in other sectors is delaying implementation.

North America

Forest management in North America has been influenced strongly by the environmental movement of the 1980s. Most initiatives and developments arising from this influence emphasize the need for more collaborative and participatory approaches to forest ecosystem management. Both the USA and Canada are gradually developing policies that provide a framework for small forest-dependent communities and civil society at large to participate in public forest land management decision-making. Critics are concerned that if local communities are empowered with public forest decision-making responsibilities, they may not reflect the values of more distant stakeholders. Others point out that NGOs and policy-makers tend to be city-based, so the views of city-dwellers are more often represented, with rural communities marginalized in the decision-making processes.

In the USA, the CFM movement is still in its infancy, but it is growing in numbers and in its ability to influence forest policy and management. Forest policy-makers and public forest managers are increasingly drafting laws and management prescriptions that are sensitive to the needs of forest-based communities. Forest organization personnel show strong support for collaborative planning, but in some cases the public feel that their participation is inadequate in decision-making processes, and are unwilling to engage in the process, often choosing to meet their objectives through a reactive, conflict-based means.

In Canada, 96% of the forest area is state owned. The state leases its forest land-base to timber companies who manage the area under agreed provincial regulations. The federal government is limited to influencing forest policy indirectly, with the 13 provincial governments controlling their own legislation concerning forest management. Many jurisdictions have now passed regulations that require public and local community input to forest operations through structured committees that provide advice during the planning stages and/or comanagement during the implementation and operational stages. In general, current forest enterprise responses to the environmental movement and to indigenous peoples' issues have been proactive, and companies are aware of the need for a 'social licence to operate' (i.e., public acceptance of their management strategies). Both of these have contributed to the frequency with which public consultations are made before forest operations are carried out.

Europe

In Europe, as in the USA and Canada, governments are moving towards more pluralistic forms of planning and management, but in a context of forest decline and recovery, the changing values of a largely urbanized society, and declining rural social institutions. The governments of most countries in Western Europe support multiple-use forestry, and, as in North America, many new CFM initiatives have been motivated by environmental concerns. Two types of participation prevail: with the public, concerning state forest lands, and private forest owners in processes organized by themselves. The few European indigenous groups are also significant players in some European countries, although they too have had to prove their customary rights in judicial courts.

The high proportion of privately owned forests in Western Europe provides a special context for CFM. In most cases private ownership limits public access and influence over the land. However, it has provided opportunities for new patterns of collaboration such as the evolution of associations of small forest owners, e.g., in Austria or Finland. These have often been supported by governments through subsidies and tax reductions, and by providing technical support via the state forest agencies. Owners also benefit from overcoming the disadvantages of small size, and in addition, the Pan European Forest

Certification (PEFC) scheme is tailored towards all the private forest owners in an area working in collaboration.

The Impact of CFM

In general CFM is considered a promising forest management strategy, as it is believed to be able to contribute on the one hand to forest conservation and sustainable forest use, and on the other hand to livelihood improvement of local communities. Much aid, and aid-related research, is linked to the search for compatibility between conservation and sustainable livelihoods, or poverty alleviation, and CFM is one of its principle vehicles. In reality, different stakeholders often have their own distinctive aims for being involved in or stimulating such strategies (**Table 7**). These aims and aspirations may not be made explicit to all stakeholders, and may in fact be incompatible (see 'Social Aspects' below).

Potentially conflicting goals complicate the evaluation of 'successful' or 'sustainable' CFM, and leave supporters and skeptics alike with confusing evidence. Notably, the evaluations and impact assessments that are published tend to reflect the views of the institutional stakeholders and the voices of the local forest users are little heard. There is also very little documented evidence of the impact of CFM on biodiversity or livelihoods. Given the propensity for donor funding it is essential not to confuse inputs, or management outputs, with successful outcomes.

It is beginning to be recognized that more participatory approaches must be developed to make sure that local stakeholders have a say in how impact is achieved and measured.

Table 7 Summary of the different achievement goals that different stakeholders expect from CFM

Stakeholder	*Goal*
Donors	Poverty alleviation
Policy-makers	Reduced deforestation
	Poverty alleviation
Forest Departments/ governments	Reduced pressure on forest resource
	Reduced pressure on Forest Department
	Improved regeneration
	Improved quality of forest resource
	Devolution of decision-making
	Transition in roles and power
NGOs	Empowerment of rural poor/ forest-dwelling communities
	Equitable distribution of benefits
Local communities/rural poor	Securing livelihood resource
	Stabilization and improvement of livelihoods
	Development of income
	Control over culturally important resource
	Decreased vulnerability to shocks
	Increased control over life

Factors Contributing to Success

This lack of evidence of the success of CFM does not negate emerging patterns of factors contributing to successful CFM, as judged by the participating stakeholders themselves. The case study approach taken by the World Conservation Union (IUCN) series on CFM is particularly valuable in this regard. For example, the very different approaches in Bangladesh (lowest forest cover, high population density, distinction between tribal and lowland communities, and the rise of private nurseries) contrast with Sri Lanka (long tradition of agroforestry management in home gardens, recent history of conflict). These summaries are given credibility by drawing on interviews and on government, NGO, and academic sources to present a realistic view, pointing to ecological, social, economic, political, and institutional factors.

Ecological Factors

Ecological factors include the original forest type, as well as its condition when CFM is initiated. While it is widely accepted that CFM improves ecosystem functioning and the quality and quantity of forest area and products, this remains to be demonstrated on a general scale. Studies in India have shown that CFM can improve diversity of tree species, although general impacts on biodiversity conservation have yet to be proved. More CFM has worked in subhumid and semi-arid forests than in high tropical forest. The widespread tendency to hand over poorer-quality forest for local management is currently being addressed by advances in forest policy in Nepal and India (see above).

Social Aspects

Stakeholder analysis CFM often assumes the ideal of a 'community.' Contrary to idealized assumptions, communities are often culturally heterogeneous, governed by top–down approaches rather than historical customs and traditions, and have few or no regulations relating to resource use. Stakeholder analysis is essential for successful CFM, as rapid and participatory rural appraisals (RRAs and PRAs) often do not identify the most vulnerable and poorest members of the community, or understand local political dynamics. For example, women are often the most regular forest users, but, due to cultural barriers and traditions, are often not consulted on forest management decisions.

Indigenous or 'tribal' people are often culturally more closely linked to forests than their immigrant neighbors, and are (often correctly) perceived as more likely to conserve their ancestral lands. However, the breakdown of respect for traditional social structures and resource management techniques heralds the need for more CFM, social learning, and adaptive management.

Conflict management Inevitably, working with such an array of stakeholders, the goals, ideas, and values of forest management often vary considerably between (and within) groups. This plurality often requires high levels of conflict management, a technique that has developed in synchronization with CFM. In general, experiences with CFM have increased respect for indigenous forest management systems, knowledge systems, and modes of organization, although the often-traditional forestry sector is at times slow to accept and initiate change. Foresters may feel that CFM initiatives are a reallocation of their former powers and, despite training programs, may remain unconvinced by CFM.

Civil society The emergence of civil society can add support to CFM, as shown by the effect of campaigning by the educated middle classes in the Philippines and Indonesia, and the increasing popularity of CFM in Kyrgyzstan in post-Soviet rule. Nevertheless, while quality timber still exists in these forests, the power of logging companies and corrupt officials is enough to frustrate many attempts at CFM.

Economics

In order to become established, CFM needs short-term benefits for local participants as the rural poor are unable to invest labor or funds into long-term management. Interest and motivational levels decline markedly if financial rewards are not seen within the first few years of CFM. Benefits depend on local markets for products that can be harvested regularly and to an acceptable quality. Information about markets and good access to them are important factors of successful CFM, and many local groups say that these are the biggest constraint to success. However, financial aspirations can also undermine sustainability, although a management plan can help to prevent overharvesting for instant monetary gain.

Organizations and Institutions

Local organization and power structures Experience particularly highlights the importance of incorporating existing local organization and power structures, with or without NGO support, and of forming partnerships and coalitions. Success in individual cases can be linked to the attitude of individual professionals, and to local people with strong leadership qualities.

In both India and Nepal, success of CFM has often been attributed to the formation and functioning of the core management team (VFC/FUG). Guidelines suggest that for these groups to be effective, numbers should be limited to 30–40 participants, members should be as socially homogeneous as possible, and membership should include representatives of all user groups (including women, landless poor, and lower caste members).

Sometimes community structures that appear to be 'participatory' can in fact be very top–down, with decision-making rights unfairly distributed to the elites of the group. However, if existing rules in the user groups are strong and fair, and methods for dealing with common problems and rule-breaking are in place, the rate of success tends to be higher.

Government As mentioned above, government forest departments can be reticent in their acceptance of CFM approaches. Often successful CFM is dependent upon one key official with undivided support for the venture. Even if extensive training is provided, the remit of foresters changes considerably with the introduction of CFM.

In most cases the government is responsible for providing technical support for the CFM ventures. The amount of technical support for management activities varies depending on the needs of the user group, and respect for local knowledge of how to manage the resource; recognition of when scientific knowledge is needed and appropriate is a key determinant. For example in severely degraded forests, the government will most likely be needed to play a major role in forest regeneration activities before user groups can be given more power.

Developmental agencies and NGOs The influence of international development agencies and/or NGOs in pioneering CFM systems is evident particularly in countries such as Pakistan, that have no policy mechanisms to support CFM. However, strong interest and availability of funding from these agencies may reduce support of the CFM process by national government.

Networks A key to successful CFM development is the learning-by-doing approach, which engages user groups in forest management activities, creates a sense of ownership of the process, and can empower users through their new knowledge. Regular formal and informal meetings between forest officials and locals can help to create trust and understanding among stakeholders. Study tours enable horizontal exchange of experience (farmer to farmer, forester to forester). NGOs, networks, and collaborations between user groups provide useful routes for information exchange (**Table 8**). The more links between communities, NGOs, and governments that exist, the more likely it is that CFM will be successful. Links are particularly beneficial for mutual learning, encouraging synergistic relationships with respect to resource management, and enhancing efficiency and effectiveness of the CFM program.

Policy and Governance

Flexibility of policy processes are an important aspect of successful CFM; India and Nepal, having the longest experience in CFM, have demonstrated the value of adapting forest policy in response to experience. Policy factors affecting success can be seen as external and internal constraints. External aspects are under the control of national and local governments, and global markets: forest tenure, tax burdens, and market development for forest products. Factors internal to the community of forest users include organization, transparency of resource management, participation by the community (or

Table 8 CFM networks and organizations

International organizations	*Area-specific organizations*
The International Network of Forests and Communities. Works internationally to provide and enhance networking between stakeholders. network@forestsandcommunities.org	Asia RECOFTC (The Regional Community forestry training center for Asia and the Pacific) Supports work in Cambodia, China, India, Indonesia, Laos, Nepal, Philippines, Thailand, Vietnam. http://www.recoftc.org/index.htm Members of RECOFTC include: Nepal–UK Community Forestry Project (NUKCFP), Nepal–Swiss Community Forestry Project (NSCFP), and Nepal–Australia Community Resource Management Project (NACRMP).
The UN FAO Forestry Program. Addresses how to use forests to improve people's economic, environmental, social, and cultural conditions while ensuring that the resource is conserved to meet the needs of future generations. There is an exhaustive list of links on the programs website, including government agencies, nongovernmental organizations, and research projects. www.fao.org/waicent/faoinfo/forestry/forestry.htm	Resource Unit for Participatory Forestry (RUPFOR). A neutral stakeholders' forum promoting interaction among various stakeholders in participatory forestry in India. http://www.rupfor.org/jfm_india.htm
The UN FAO Community Forestry Program. Provides information including topics covering communal management, decentralization and devolution, gender, market analysis and development, participatory processes, rural learning networks. www.fao.org/waicent/faoinfo/forestry/FON/FONP/cfu/cfu-e.stm	Federation of Community Forest Users of Nepal (FECOFUN) Europe Confederation of European Forest Owners (CEPF) http://www.cepf-eu.org/
Forests, Trees and People Program. This is designed to share information about improving community forestry activities and about initiatives of interest to its members. Links CFM initiatives throughout the world.	South America Central American Community Agroforestry Network (Agroforesteria comunitaria en Centroamericana)
Rural Development Forestry Network (Overseas Development Institute's Forest Policy and Environment outreach group). Disseminates information to over 2000 members around the world. http://www.odifpeg.org.uk/network/index.html	Indigenous and Peasantry Coordinator for Community Agroforestry in Central America (CICAFOC) North America National Network of Forest Practitioners (NNFP). Aims to strengthen the efforts of individual groups to achieve a common vision of sustainable economies and healthy ecosystems. http://www.nationalcommunityforestrycenter.org/presearch.html
The Community-Based Natural Resource Management Network (CBNRM). Aims to enhance and provide networking opportunities worldwide. http://www.cbnrm.net/	Canada's Model Forest Programme. http://www.nrcan.gc.ca/cfs-scf/national/what-quoi/modelforest_e.html

user group) as a whole, and attention to equity issues.

CFM illustrates the importance of looking beyond explicit policy objectives to examine implicit policy, and requires the mixing of different policy disciplines. For example, rural development policy bears on the traditionally separate domain of forest administration.

Tenure Perhaps the most effective policy tool is change in tenure. Most CFM is initiated in state or community forests, and is most successful when the tenants or owners have long-term leases or secure land rights. In countries where communities have no access rights to forest land or products, encroachment and conflict is common; in contrast CFM in Nepal has created a legislative process whereby communities can acquire the right to manage their forests, and across Southeast Asia legislation to recognize ancestral lands of indigenous groups has encouraged those groups to formulate management plans. Little CFM has been recorded on private land, and the incidence of CFM on 'open access' land is low.

Devolution of rights and responsibilities In the devolution of rights and responsibilities to the user group, it is essential that customary rights as well as legal rights be recognized. There is often confusion as to whether the community is being involved as a forest user or a forest manager, and for success, rights and responsibilities need to be clearly defined. Case studies show that motivation of communities for management is highest when power-sharing is most complete and implemented within management regimes that define the community as a whole as the source of decision-making. For community interest and participation to be maintained, it is important to ensure they feel a sense of 'ownership' of the process.

Reduction of poverty Development advisers question whether CFM can be successfully implemented with the rural poor if their basic development needs are not met first. Interest and motivation levels decline if local people have to wait several years to see any returns, and success is related to markets and benefits linked to labor inputs. Donor-funded CFM ventures often include the double and difficult remit of improved livelihoods and conservation.

Governance A number of international, pan-European, and national policies and treaties are beginning to support sustainable forest management and to provide a more enabling context for CFM. The Convention on Biological Diversity addresses forests through its work program on forest biological diversity, implemented by the United Nations Food and Agricultural Organization, the UN Environment Programme, the Global Environment Facility, the UN Framework Convention on Climate Change, the UN Forum on Forests, and the Centre for International Forestry Research. The program emphasizes the ecosystem approach, socioeconomic considerations, conservation and sustainable use. Objective 3: Goal 4 in the Forest Work Programme approved at the 6th meeting of the parties to the Convention on Biological Diversity reads:

> Enable indigenous and local communities to develop and implement adaptive community-management systems to conserve and sustainably use forest biological diversity.

The Aarhus Convention on 'Access to Information, Public Participation in Decision Making and Access to Justice in Environmental Matters' also supports CFM initiatives.

Future Directions

For CFM to continue its success, supportive legislation and policy need to be developed and enacted at institutional, organizational, and ground levels. Foresters need to be trained in how to impart technical knowledge to forest users about forest management. With regular contact and trust-building exercises, there should be a reduction of the exploitation of communities. Forest departments should clarify the benefits for them of the devolution of forest management responsibilities, to make it easier for professional foresters to accept and advocate the new CFM approach.

Many practitioners and planners do not have access to information because of poor dissemination or because it is presented without lessons being sufficiently distilled to convey general principles across cultural boundaries. There is also a strong sense that 'knowledge cannot be transported directly' but that there is a need to create the conditions in which knowledge can be generated. Thus more and more detailed case studies, with particular attention applied to documentation of community experience, should be encouraged, along with greater dissemination and information exchange.

CFM has great potential in linking with participatory monitoring and evaluation (PM&E) and adaptive management. By personally assessing their impact on the forest, communities become more aware of the need for sustainable management, and motivation levels increase as a sense of ownership of the process develops.

See also: **Landscape and Planning**: Perceptions of Nature by Indigenous Communities. **Social and Collaborative Forestry**: Canadian Model Forest Experience; Common Property Forest Management; Forest and Tree Tenure and Ownership; Social and Community Forestry; Social Values of Forests.

Further Reading

Carter J, Steenhoff B, Haldimann E, and Akenshaev N (2003) Collaborative forest management in Kyrgyzstan: moving from top-down to bottom-up decision-making. http://www.iied.org/docs/gatekeep/GK108.pdf.

Dubois O and Lowore J (2000) *The 'journey towards' collaborative forest management in Africa: Lessons learned and some 'navigational aids' – An overview*. London, UK: International Institute for Environment and Development.

Fisher RJ (1995) *Collaborative management of forests for conservation and development*. Gland, Switzerland: IUCN, WWF International.

Hobley M (1996) *Participatory Forestry: The Process of Change in India and Nepal*. London: Overseas Development Institute.

Jeanrenaud S (2001) *Communities and Forest Management in Western Europe*. Gland, Switzerland: IUCN.

Kant S and Cooke R (1999) Jabalpur District, Madhya Pradesh, India: minimizing conflict in joint forest management. In: Buckles D (ed.) *Cultivating Peace: Conflict and Collaboration in Natural Resource Management*, pp. 81–97. Ottawa, Canada: International Development Research Centre and World Bank.

Khare A, Sarin M, Saxena NC, Palit S, Bathla S, Vania F, and Satyanarayana M (2000) *Joint Forest Management: Policy, Practice and Prospects*. India: IIED Forestry and Land Use, WWF.

Lawrence A (ed.) (2000) *Forestry, forest users and research: new ways of learning*. ETFRN, Netherlands. Individual chapters can be downloaded from: http://www.etfrn.org/etfrn/workshop/users/index.html.

Poffenberger M (1999) *Communities and Forest Management in Southeast Asia*. Gland, Switzerland: IUCN.

Poffenberger M (2000) *Communities and Forest Management in South Asia*. Gland, Switzerland: IUCN.

Poffenberger M and McGean B (eds) (1996) *Village voices, forest choices: joint forest management in India. 356.* Delhi, India: Oxford University Press.

Pretty JN, Guijt I, Thompson J, and Scoones I (1995) *Participatory Learning and Action: A Trainer's Guide*. London: IIED.

Richards M (1997) *Tragedy of the Commons for Community-Based Forest Management in Latin America*. London: Overseas Development Institute.

Richards M, Davies J, and Yaron G (2003) *Stakeholder incentives in participatory forest management: a manual for economic analysis*. London, UK: ITDG Publishing.

Forest and Tree Tenure and Ownership

C Danks, University of Vermont, Burlington, VT, USA
L Fortmann, University of California–Berkeley, Berkeley, CA, USA

What is Social and Community Forestry?

Community forestry is a set of institutional arrangements in which communities are involved wholly or in part in decision-making and benefits and contribute knowledge and labor to achieve healthy forests and social well-being. Social forestry encompasses both multiple forms of locally initiated and implemented forest management as well as externally initiated social forestry projects. It ranges from formal, legally recognized arrangements such as comanagement agreements between communities or individual citizens and government forest bureaucracies, to:

- community management of government forest land
- the cumulative effect of tree planting and management on individual parcels
- forest commons
- communities that without government sanction management government forest land as a *de facto* commons.

Social forestry is a development strategy to stimulate community forestry. Analysis of property and land and tree tenure arrangements enable us to understand the distribution of costs and benefits of social forestry as well as the pitfalls that may befall it.

Basic Concepts in Property and in Land and Tree Tenure

Although people often think of property as a thing or the possession of a thing by someone, it is better understood as social relations between people regarding the possession and use of things, that is, as a claim to some use or benefit of something that will be enforced by society or the government. Lawyers make a distinction between real property (that is, land in particular but also trees, water, and minerals) and personal property (clothing, copyrights, goodwill, and so forth). Lawyers are, as a general rule, interested only in property rights recognized by the government. They ask the question: what does the law say?

In contrast, social scientists are also interested in the interface between rights and reality often referred to as tenure. They ask the question: How do claimants to rights actually behave regardless of the law? Tenure is a term borrowed from archaic English property law and refers only to real property. The doctrine of tenures which dates to eleventh-century England established the terms on which rights to land were granted. The doctrine of estates determined how long a person had the right to hold land. The present-day study of land and tree tenure encompasses both the doctrine of tenures and the doctrine of estates.

Legal Pluralism

When land tenure differs from formal property rights in land, scholars use the analytical concept of legal pluralism. Legal pluralism encompasses situations in which at least two legal systems coexist. In addition to national statutory and case law, legal pluralism takes into account legal regimes such as customary or traditional law codified and recognized by colonial regimes, religious law, and law created and enforced by smaller social groups. An example of legal pluralism can be found in the differentiation of property recognized under government law (*de jure* property) from property not recognized under government law but recognized by other social groups (*de facto* property). Depending on the circumstances, *de facto* property may be more important than *de jure* property in determining who may be where, when, and doing what. Legal pluralism may be especially relevant to social forestry in a forest area where an indigenous system of customary law coexists with government statutory law. Social forestry may be used to legitimate, and thereby strengthen, indigenous tenure and management.

Property as a Bundle of Rights

Property rights to trees and tree products on a parcel of land may be held by someone other than the landowner. The complexity such property relations introduce to understanding the role of property in social forestry can be analyzed with the concept of property as a bundle of rights (e.g., rights to use, sell, loan, give away, lease, destroy, bequeath) which may be held separately by different people at different times. While useful in revealing what kind of rights a particular property relation may entail, the bundle of rights concept has been criticized for not recognizing the interconnections and interdependence among different rights. The bundle of rights is often portrayed as a bundle of sticks in which removing one stick from the bundle has no effect on other sticks. Other images such as interconnected strings of genes have been suggested but have not achieved much currency in the literature.

Usufructuary rights Usufructuary rights, the rights to use something, add complexity to the bundle of rights. Different and overlapping usufructuary rights may be asserted simultaneously against the same forest or same tree. This is discussed below in the example of palm trees in the Dominican Republic. The rights to the trees on a parcel of land may be held by different people or institutions. For example, the rights to the fruit of date palms in Sudan were divided among the man (and they were all men) who obtained the shoot and planted it, the man who owned the land where it was planted, and the man who watered the young palm. Since these rights were inheritable, the number of right-holders grew in subsequent generations. Multiple claimants of this sort can make social forestry extremely complicated.

Different types of rights Types of rights included in a bundle of rights could include any combination of a variety of rights. One general cluster includes the rights to sell, loan, lease out, mortgage, or bequeath the tree itself or any or all of its products. A farmer might mortgage her cocoa trees or sell an entire mango crop before it is ripe to get immediately needed cash. The right to plant perennials such as trees is often constrained. Consumptive uses such as chopping down a tree for timber or poles constitute another set of rights.

Usufructuary rights may differ depending on where the tree or the product is located. Anyone may pick up fruit from the ground but taking fruit from the tree may constitute theft. Harvesting from a tree growing inside a compound (particularly if it is fenced) usually requires permission of the owner. Using trees growing elsewhere may not require permission. There may be differences in the rights to use different parts of or attachments to a tree such as leaves, flowers, needles, bark, roots, twigs, branches, nests, fruit, seed pods, and cones. Similarly within a forest rights to (among others) grazing or browsing, thatching grass, medicinal plants, water for human use, water for livestock use, water for irrigation, mushrooms, berries, dead and downed wood, green wood, or wildlife may vary widely.

Security of Tenure

Security of tenure consists of three elements: breadth, duration, and assurance. Breadth refers to the composition of rights such as usufructuary rights, the right to sell, the right to bequeath, and the right to destroy. Larger numbers of rights are associated with more secure tenure. Duration is the length of time a right is legally valid. Longer duration is associated with more secure tenure. Assurance is the certainty with which a right is held. It reflects the predictability and enforcement ability of the tenure-granting regime. Security of tenure does not require private property rights. Rather secure tenure can be found in every form of property regime whether or not it is sanctioned by the government. It is often assumed that the greater the security of his/her/their tenure, the more likely a person or group will be to invest in the maintenance and enhancement of property. This relationship does not always hold. For example, forest owners with secure tenure might clear-cut and not replant because they have an urgent need for capital from the sale of timber.

Access

Access is the ability to benefit from things. A step beyond property-rights-based focus on 'who may' benefit, the ability-based focus of access is on 'who actually' benefits and how. The property question is who has rights to this resource. The access question is who actually uses and/or controls this resource. That is, it asks who does (or does not) get to use what, in what ways, when.

Mechanisms of access fall into three general categories.

Rights-based access Access may depend on rights defined by law or custom, encompassing both property and tenure.

Illegal access Illegal access involves the ability to benefit without the sanction of the government or society. It may involve stealth, violence, or establishing relations with people who control access. Illegal access differs from *de facto* rights in that *de facto* rights are sanctioned by a local community or group. In illegal access we see people who are not officially recognized beneficiaries helping themselves to the benefits of social forestry.

Structural and relational mechanisms of access Property rights in or access to forest land and trees are not the only kind of property or access that matters in community forestry. Access to technology, capital, labor, knowledge, and markets can affect the ability of people to benefit from social forestry. For example, the value of timber harvested from a community forest may depend on access to processing machinery such as a sawmill. If that machinery is owned by others, then the size of the benefits received by social foresters depends on the terms of access to the machinery.

Gendered Property and Tenure

There is no entry on women and forestry in this Encyclopedia. This is indicative of a general problem of which gendered property rights in forests and trees is only one manifestation. Women and their knowledge about and their uses of trees and forest resources are often invisible to forest agency staff, foresters, forest project planners, and implementers, and even to their own husbands.

Three aspects of gendered property and tenure are related to social forestry.

Gender and security of tenure When the household is assumed to be a homogeneous unit, women's property rights (or the lack of them) are made invisible, often with adverse consequences for women. Even in households with secure tenure, women's property rights are often insecure. In most of Africa, for example, the breadth of women's security of land tenure is narrower than men's since it significantly less frequently than men's includes the ability to rent, give away, loan, lease, sell, or bequeath. In many places women acquire access to land not in their own right but through their fathers, husbands, and brothers. Daughters may have no rights of inheritance from their parents or may be unable to exercise their inheritance rights. The corollary to this principle of access to land is that the fruits of a woman's labor on the land often belong to her husband or his relatives, not to her. Security of duration of tenure is a matter of particular concern for women living under a gendered property regime in which changes in marital status can be catastrophic for them. It is not uncommon in the case of divorce for property acquired by a woman during marriage to become her husband's property, leaving her destitute. Widows may have limited property rights. They may have no right to inherit their husband's property, including trees that they themselves have planted and tended. In central Zimbabwe such insecurity of land and tree tenure for women appears to have resulted in significantly less tree planting by women than by men.

Women's usufructuary rights may be even less secure. In the Dominican Republic, palm trees owned by the men were subject to two sets of usufructuary rights. Women had usufructuary rights to the fronds while men had usufructuary rights to the fruit which they fed to their pigs. After their pigs were destroyed in a national campaign to contain an outbreak of swine flu, the men simply cut down the now useless (to them) palms, leaving their wives without access to a source of fronds.

Gender and title Governments may undertake land titling programs in the hopes that it will increase security of tenure and, therefore, will increase productivity of agricultural or forest land. Generally the title is put in the name of the male head of household, although in some cases widows and/or divorcees may receive the title in their own name. Wives, however, may lose land that is theirs by right as well as long-standing usufructuary rights. For example, in the current land titling under way in Laos, the title to all household land (including land that came from the wife's family) is put in the name of the husband. If the title includes the right of the titleholder to sell the land, the wife is in a precarious position. Thus, if social forestry includes land titling, women may end up worse off in terms of their rights to land and trees.

Gender and access Women may have secure property rights in land or trees but lack access to or control of their own property due to gendered power relations. Intrahousehold power relations may lead to men controlling the use of and the distribution of benefits from forest land and trees that their wives, mothers, sisters, or daughters legally own. Women may acquiesce in such arrangements either because they have no choice or as a conscious investment in long-term social capital.

Property and Social Forestry

The outcome of social forestry can be affected by property and tenure relations in a number of ways. The relationship of tree planting and harvesting to the creation of property rights can be a key factor. Under some circumstances clearing forest creates rights to the land on which the trees grew, while in others planting trees creates rights to the land on which the trees are planted. People's willingness to plant trees or harvest trees or allow others to do so may depend on the property outcomes of these acts. Social forestry may include a wide variety of usufructuary rights such as collecting firewood, moss, leaves, or pine needles, cutting poles or timber, grazing domestic animals, hunting, gathering wild foods and medicines, as well as religious practices.

Social Forestry on Private Land

Private property (also called freehold property) is owned by an individual or group of individuals or legal persons such as partnerships or corporations. Within the limits set by the government (in such forms as taxation and zoning) or social practice, the owner has the right to use the land or trees as s/he sees fit. Social forestry programs may take the form of sponsoring the planting and maintaining of trees on private property. When tree planting creates property rights or when the closing canopy will make other uses impossible, tree planting for a social forestry project may also be used as a weapon in property struggles. This use of tree planting to seize control of land is sometimes called the 'green machete.' For example, in The Gambia, men used tree planting sponsored by an agroforestry project to drive women off the land they had been using for lucrative vegetable production.

Social forestry may involve privatizing public forest land on the grounds that this will lead to better management. This is not necessarily so. Both large and small holders of privatized parcels may be under financial pressure to harvest their parcel or sell it to speculators. In either case, privatization may lead to conflicts between the new private *de jure* right holders and pre-existing *de facto* right-holders.

Social Forestry on Forested Commons

Joint ownership, management, and use of forest and tree resources by a designated group of users, often all or part of a community, is known as the commons or a common pool resource. In contrast to private property, the resource can not be sold, mortgaged, leased, or bequeathed outside the group. Common pool resources are sometimes confused with open access resources that anyone may use. Garrett Hardin's 'tragedy of the commons' argument that common property is inevitably degraded actually describes an open access resource, not a commons. Contrary to the 'tragedy of the commons' argument, when it is difficult to exclude users from resources such as forests that are subject to degradation, a commons system often constitutes the most effective property regime. One reason for this is that common property regimes generally include specific responsibilities as well as rights.

Elinor Ostrom's 'design principles' regarding the sustainability of common property resources are discussed in detail elsewhere (*see* **Social and**

Collaborative Forestry: Common Property Forest Management). The importance of each principle differs under different circumstances; however, monitoring has been found in many systems to be the most crucial component.

A clearly defined user group is an important component of effective common property regimes. Since local communities are rarely socially or economically homogeneous, it would be erroneous to assume that local user groups represent all community inhabitants. Externally initiated projects on forest commons may attract the interest of village elites and hence have the potential to harm women, the poor, and migratory users unless careful attention is paid to access, property, and tenure.

Women In social forestry systems on common property, if the decision-makers are male, women's uses of forest and tree products may not be incorporated into the management plan. The loss of access to these resources may create serious hardship for women.

The poor An initially widely praised social forestry project of tree planting on a common turned out to have been a successful move by village elites to seize the common land by planting trees on it. In another case, poor villagers begged visiting agroforestry experts not to replace the crooked thorny trees on the commons which only they used with productive multipurpose trees which would attract the attention of the rich and reduce their access to the resource.

Migratory users Nomadic pastoralists who have seasonal usufructuary rights, for example to graze their animals on a forest commons, are frequently overlooked when a social forestry project introduces a new management system with the result that they lose their access to the common resource.

Social Forestry Undertaken by a Community on Government Land that is not Effectively Controlled by the Government

Not every government controls every inch of its territory. In places where central government control is weak, local systems of rules may have a far greater effect on behavior than the government legal system. For example, in Teri Garhwal, India local communities managed parts of oak forest that was *de jure* government forest. A community's *de facto* rights to clearly defined areas of the forest were recognized and respected by other communities. The government's *de jure* property claim was simply irrelevant to local practice.

Social Forestry Undertaken in Collaboration by the Government and Local Communities on Government Controlled Forest Land

One of the earliest and probably the best-known example of social forestry undertaken in collaboration by the government and local communities on government controlled forest land is Joint Forest Management (JFM) initiated by the Indian Forest Service. This kind of social forestry in which the government forest is protected and/or managed by local people in return for usufructuary rights to forest and tree products or the right to farm in the forest is common throughout South and Southeast Asia and parts of Africa. In a related model, the government may give local people rights to harvest subsistence goods from individual trees such as trees on roadsides.

In a different kind of social forestry in the USA, the government allows local people to participate in decision-making about and/or implementation of forest management of government forest land as a means of reducing legal challenges to its management decisions. It also benefits from local expertise and sometimes labor.

Although they may be interested in access to forest resources, local citizens may also participate in such social forestry out of personal commitments to forest health, hope of employment, or a desire to protect or enhance their private property adjacent to a forest. For example, residents of mountain forest communities in California participate in fire management planning and implementation on adjacent government forest land in order to ensure effective forest fire management to protect their privately owned homes. This is another example of the point that property rights in or access to forest land and trees are not the only kind of property or access that matters in social forestry.

The Butter Creek Watershed Analysis in California is another example of this sort of social forestry. The US Forest Service hoped to get buy-in from local citizens holding diverse, often opposing views about government forest management by involving them in identifying desired future outcomes, analyzing current conditions, and choosing suitable management activities to achieve their goal. A long and sometimes contentious process of consultation and analysis resulted in what was widely viewed as a higher-quality watershed analysis than usual, increased understanding of the new forest management policy, improved relations between the US Forest Service personnel and the community, support for later projects, and a total absence of legal appeals against the plan.

In both of these cases, property rights remained unchanged but citizens gained access to the decision-making process affecting adjacent forest resources and, in theory, to the benefits of a healthy forest.

See also: **Landscape and Planning**: Perceptions of Nature by Indigenous Communities. **Social and Collaborative Forestry**: Canadian Model Forest Experience; Common Property Forest Management; Joint and Collaborative Forest Management; Social and Community Forestry; Social Values of Forests.

Further Reading

Agarwal B (1994) *A Field of One's Own: Gender and Land Rights in South Asia*. Cambridge, UK: Cambridge University Press.
Baker M and Kusel J (2003) *Community Forestry in the United States: Learning from the Past, Crafting the Future*. Washington, DC: Island Press.
Bruce JW (1989) *Community Forestry: Rapid Appraisal of Tree and Land Tenure*. Rome: FAO.
Fortmann L and Bruce JW (1988) *Whose Trees? Proprietary Dimensions of Forestry*. Boulder, CO: Westview Press.
Fortmann L and Rocheleau D (1985) Women and agroforestry: four myths and three case studies. *Agroforestry Systems* 2: 253–272.
Hulme D and Murphree M (eds) (2001) *African Wildlife and Livelihoods: the Promise and Performance of Community Conservation*. Portsmouth, NH: D. Philip and Heinemann.
Leach M (1994) *Rainforest Relations: Gender and Resource Use among the Mende of Gola, Sierra Leone*. Washington, DC: Smithsonian Institution Press.
Macpherson CB (ed.) (1978) *Property: Mainstream and Critical Positions*. Oxford, UK: Basil Blackwell.
Merry SE (1988) Legal pluralism. *Law and Society Review* 22(5): 869–896.
Ostrom E (1990) *Governing the Commons: The Evolution of Institutions for Collective Action*. Cambridge, UK: Cambridge University Press.
Peluso NL (1992) *Rich Forests, Poor People: Resource Control and Resistance in Java*. Berkeley, CA: University of California Press.
Poffenberger M (ed.) (1990) *Keepers of the Forest: Land Management Alternatives in Southeast Asia*. West Hartford, CT: Kumarian Press.
Ribot JC and Peluso NL (eds) (2003) A theory of access. *Rural Sociology* 68(2): 153–181.
Rocheleau D, Thomas-Slayter B, and Wangari E (eds) (1996) *Feminist Political Ecology: Global Issues and Local Experiences*. London: Routledge.
Rose C (1994) *Property and Persuasion: Essays on the History, Theory and Rhetoric of Ownership*. Boulder, CO: Westview Press.
Schroeder R (1999) *Shady Practices: Agroforestry and Gender Politics in the Gambia*. Berkeley, CA: University of California Press.

Canadian Model Forest Experience

J E Hall and B Bonnell, Canadian Forest Service, Ottawa, Canada

Introduction

As a partnership-based strategy, Canada's Model Forest Program (CMFP) provides an excellent case study of collaborative forest management (CFM). In model forests, the partnerships and their goals are expanded beyond the relationships usually associated with CFM that are between industry or government professional forest managers and local communities. Model forest partnerships include a broad array of participants from all levels of government, industry, academia, Aboriginal communities, and other groups representing a wide diversity of timber and non-timber forest values. Canada, through the Canadian Forest Service (CFS) and the Canadian Council of Forest Ministers (CCFM) initiated this approach in 1991 as part of a long-term, nationwide experiment in developing approaches to sustainable development in forestry. The scale of CMFP is representative of Canada's forest sector, its diversity of socioeconomic circumstances, and its variety of forest types; it is the largest such undertaking in the world.

Origins of Canada's Model Forest Program

After the concept of sustainable development was introduced by the Brundtland Commission Report of 1987, it was clear that maximizing social, economic, or ecological goals independently through conventional management systems would not lead to sustainable development. To incorporate the concept of sustainable development, managers must integrate the goals of all three elements of development (social, economic, and ecological) and optimize these goals as a suite where balance is sought among all over time.

In developing an approach to sustainable development in forestry, Canada recognized the strengths demonstrated by CFM partnerships in integrating the goals of different partners, increasing awareness of forest values, improving knowledge to create potential solutions, and broadening the type of benefits derived from the forest and their distribution. By building on these strengths and increasing the constituency of participants in the partnerships beyond that of conventional CFM (which is generally characterized by industry – community or government – community partnerships), Canada designed model forests to provide Canadians with an opportunity to participate in developing and demonstrating approaches to sustainable development in forestry, otherwise termed sustainable forest management (SFM). To date, model forests continue to be very active in Canada and have since expanded to many countries around the world.

Purpose of Canada's Model Forest Program

Canada's Model Forest Program was developed to support Canadians interested in participating in partnerships that represent a broad array of interests for the development of approaches to sustainable development for the forest area of their choice.

In 1991, the Canadian Forest Service invited interested groups or individuals across Canada to form partnerships and to compete to become one of 11 model forests that would form a national network and receive federal government funding to support their work. Successful proposals would describe comprehensive and innovative approaches to SFM that would include the production of timber as well as other forest-based values as determined by the partnership. The partnership would focus its efforts on an area of forest of their choice that would reflect the scale of Canada's forest sector and be no less than 100 000 ha. **Figure 1** illustrates the forest type and location of Canada's model forests.

What Is a Model Forest?

A model forest is a partnership of individuals and groups representing diverse forest values working together to develop and demonstrate approaches to SFM that are locally acceptable and nationally relevant. Model forests are designed as large-scale, living laboratories where people with an interest in the forest participate in decisions about how to manage the forest sustainably. They provide a process that helps participants recognize the impact of their activities on the land base, develop a shared understanding of SFM, and demonstrate this in operational terms. A model forest is of a size that includes the full range of forest uses and needs that are considered in the surrounding geographic region and which is representative of a broad ecosystem. In Canada, model forests are of a scale that is representative of the country's vast forest and range from 100 000 ha up to 7.7 million ha. The basic elements that describe Canada's model forests are provided in **Table 1** including forest type, tenure, participants, governance, and objectives.

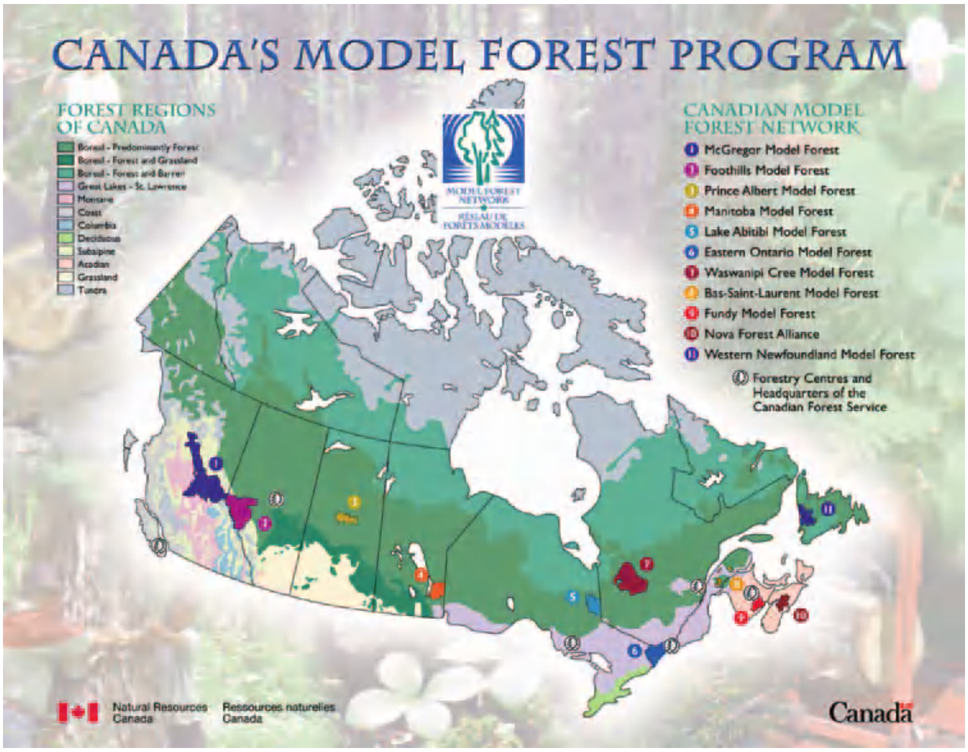


Figure 1 Major forest regions of Canada and the Canadian Model Forest Network.

Table 1 Summary of model forest characteristics including forest type, tenure, participants, governance, and objectives

Model forest	*Forest type*	*Size ($ha \times 10^3$)*	*Tenure*	*Number of partners*[a]	*Key partner types*	*Governance*	*Objectives*
Western Newfoundland	Boreal	923	Public, industry license, national park	17	Forest industry; federal and provincial government; communities; NGO; national park; trapper association; academia/research; education	Not-for-profit corporation; small Board of Directors; Management (Partnership) Committee; Scientific Advisory Committee; Executive Committee; two activity committees; issue-oriented working groups; consensus-based decision-making	1. Develop SFM systems and tools, and increase capacity for partners to implement approaches to SFM; 2. Communicate national, provincial, and local SFM priorities through the dissemination of acquired results and knowledge; 3. Increase public understanding of SFM and provide opportunities for effective participation.
Nova Forest Alliance	Acadian	458	Public, private (small land holdings), industry license	40	Large and small forest industry; federal and provincial government; First Nations; small landowner associations; NGOs; ENGOs; academia/research; education	Not-for-profit corporation; Partnership Committee; sector-based Executive Committee; standing committees; project working groups; consensus-based decision-making	1. Develop and test a landscape-level SFM system; 2. Generate and transfer new knowledge on key SFM issues; 3. Design and test model processes to assist in forest certification; 4. Increase capacity of landowners to implement best management practices; 5. Facilitate transfer of SFM practices; 6. Increasing understanding of SFM; 7. Nurture local involvement in model forest.
Fundy	Acadian	419	Public, industry license and private, national park, private (small land holdings)	34	Forest industry; federal and provincial government; communities; First Nation; small landowner associations; NGOs; ENGOs; national park; academia/research	Not-for-profit corporation; Partnership Committee; Executive Committee; Working Groups; consensus-based decision-making	1. Develop knowledge of ecosystem integrity and impacts; 2. Develop cooperative approach to research, monitoring, and planning; 3. Technology transfer of SFM tools and processes; 4. Provide education and training to forest professionals; 5. Collect and report on SFM and ecosystem information; 6. Provide a forum for discussion of SFM issues; 7. Increase public awareness.

Bas-Saint-Laurent	Boreal	113	Industry private, private (small land holdings)	40	Forest industry; federal and provincial government; small landowner associations; academia	Not-for-profit corporation; small Board of Directors; Partner Committee; Advisory Committees; consensus-based decision-making	1. Promote development and adoption of forest management models; 2. Help improve SFM systems; 3. Foster the development and application of new forest management techniques; 4. Communicate and disseminate results.
Waswanipi Cree	Boreal	3300	Public, industry license	18	First Nation; forest industry; federal and provincial government; academica/research; communities; NGOs	Administered under First Nation Band Council; Board of Directors (proponents); consensus	1. Develop and adopt SFM systems and tools based on Western science and Cree values and principles; 2. Disseminate results and knowledge at local, regional and national levels; 3. Increase local level (Cree) participation in SFM decision-making and implementation.
Eastern Ontario	Great Lakes-St Lawrence	1530	Public, industry license and private, national park, private (small land holdings)	>200 members	Forest industry; First Nation; federal and provincial government; small landowners and landowner associations; NGOs; ENGOs; academia; conservation organizations; communities	Not-for-profit corporation; open membership structure; 10-member Board with four permanent members; five standing committees; working groups; consensus-based decision-making	1. Increase quality and health of existing forests of eastern Ontario; 2. Increase forest cover to improve forest sustainability and biodiversity; 3. Increase awareness and understanding of SFM; 4. Increase transfer of SFM principles and practices; 5. Strengthen SFM efforts through equity generation, partnership building, and program evaluation.
Lake Abitibi	Boreal, claybelt	1100	Public, industry license	19	Forest industry; federal and provincial government; communities; NGOs; community groups; academia; First Nations	Not-for-profit corporation; Board of Directors; Executive Committee; Strategic Advisory Committee; standing committees; consensus-based decision-making	1. Effect positive change by building a legacy of SFM knowledge; 2. Effectively promote the adoption of model forest technical knowledge to forest practitioners; 3. Enhance local involvement in SFM; 4. Expand web of influence.

continued

Table 1 Continued

Model forest	*Forest type*	*Size (ha × 10^3)*	*Tenure*	*Number of partners*[a]	*Key partner types*	*Governance*	*Objectives*
Manitoba	Boreal	1050	Public, industry license	26	Forest industry; Aboriginals; federal and provincial government; communities; academia; ENGOs	Not-for-profit corporation; Board of Directors (full partnership representation); Executive Committee; Advisory Committee; consensus-based decision-making	1. Facilitate opportunities for local level participation in SFM with emphasis on Aboriginal involvement, planning, and diverse economic opportunities; 2. Ensure that the value of forests and the results and knowledge gained were communicated to practitioners, forest users, and general public; 3. Increase development and adoption of innovative forest stewardship practices, systems, and tools; 4. Share knowledge and participate in joint ventures with other model forests and organizations.
Prince Albert	Boreal, parkland	360	Public, industry license, national park	11	Forest industry; federal and provincial government; First Nations; Metis; academia; NGOs; research institutions; national park; communities	Not-for-profit corporation; Board of Directors (full partner representation); Executive Committee; standing committees; consensus-based decision-making	1. Increase the development and adoption of SFM systems and tools among the partners; 2. Extend the Prince Albert Model Forest program through mentoring and partnerships; 3. Increase public awareness of results and knowledge gained through the practice of SFM; 4. Ensure that results and knowledge are disseminated broadly; 5. Increase opportunities for local level participation in the development of SFM systems and tools; 6. Strengthen model forest network activities in support of Canada's SFM priorities.

Foothills	Boreal, montane, subalpine	2750	Public, industry license, national park	81	Forest industry; federal and provincial government; mining, and oil and gas sectors; NGOs; communities; First Nations; national park; academia	Not-for-profit corporation; Board of Directors; Executive Committee; Program Implementation Team; Activity Teams; Scientific/Technical Committee; partner categories (sponsoring, management, program, project, other) consensus-based decision-making	1. Demonstrate SFM; 2. Develop and implement mechanisms that result in wider understanding and application of SFM; 3. Deliver communications and outreach programs that improve understanding of and support for SFM; 4. Support and influence policy that improves the practice of SFM.
McGregor	Boreal, montane, subalpine	7700	Public, industry license	41	Forest industry; federal and provincial government; communities; First Nations; academia; NGOs; consultants	Not-for-profit corporation; Board of Directors (based on membership classes); Technical Steering Committee; consensus-based decision-making	1. Build a legacy of ecological knowledge and management expertise applicable to SFM; 2. Foster the implementation of knowledge and expertise to SFM planning and decision-making, improving forest practices, and maintaining environmental values; 3. Enhance local understanding of, participation in, and support for SFM; 4. Expand influence through local, provincial, national and international networks, organizations, associations, and institutions.

ENGOs, Environmental Non-Governmental Organizations; NGOs, nongovernmental organizations; SFM, sustainable forest management.

[a] Some partnerships have increased since the time of writing of the Action Plans.

Source: Information derived from the 2002–2007 5-Year Action Plans developed by each model forest.

Introduction to Stages of the Collaborative Partnership Process: Form, Storm, Norm, Perform, Reform

Collaborative forest management is both a process and a learning environment. Experience shows that the process of CFM consists of recognizable stages through which participating groups continually journey. To effectively participate and support the collaborative process, all stakeholders must be aware of the purpose and the role of the partners in each stage. The group begins with the 'Form' stage where it agrees on who will be involved, how they will be selected, and the purpose for which they will work. After the group is formed it then faces the 'Storm' stage where the participants explore their limits and boundaries and agree in how they will operate the partnership and work together. Storm is followed by the 'Norm' stage where the group comes to agreement on what it can and will do. Next is the 'Perform' stage where the group's ideas are actually put into action. After performing, the partnership goes through a 'Reform' stage that has two aspects. One is where their performance is evaluated, the circumstances are revisited, and based on the new information and experience gained in the preceding round(s), the partners undertake to return to the appropriate stage and continue the process at the point deemed necessary. The other aspect is where a partner changes its practices based on the lessons learned from the 'model' developed by the partnership. **Figure 2** provides an outline of the various stages.

The stages of CFM will be used as a framework to present the model forest approach. Where applicable, specific examples from model forests will be included to illustrate the change in practice brought about as a result of collaborative forest management.

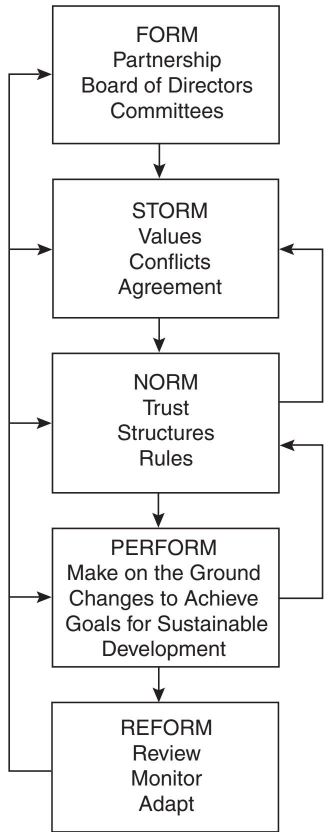


Figure 2 Overview of the stages of the collaborative partnership process.

Stage 1: Form

In this stage, usually catalyzed by an individual or small group, the potential partners are brought together to determine who should and who is able to participate, what forest tenure(s) will be involved, and the ground rules governing involvement.

Initiators of model forests seek to establish a voluntary, broadly based group open to views of interested parties who can identify an area of forest land of mutual interest and who ensure that their group includes, on a voluntary basis, those having land management authority and others with an interest in the SFM of that forest area. Typically model forest partnerships include stakeholders such as land users, land managers, industry, community groups, government agencies, nongovernmental environmental and forestry groups, academic and educational institutions, national parks, Aboriginal groups, private landowners, and others as appropriate. The character of each model forest partnership is a function of the local conditions including who is present, who is interested in participating and is available, and local issues. The number of partners can change over time but has generally increased.

Model forests are managed in an integrated manner for all forest values identified as important by the partnership. Model forest management is a transparent, democratic, and usually consensus-based process where the ground rules for the group are defined by all the participants. The governance structure is designed to reflect the cultural, social, political, and economic realities of the region, allow for greater empowerment of people who often have little or no say in the decision-making processes, and ensure consideration of each identified value in the management planning process. Typically, model forests have an 'open seat' policy to provide for and encourage new perspectives at the table. It is not uncommon for new members to be invited to participate and contribute their expertise as the model forest explores additional and more complex SFM issues. The fundamental challenge of the partnership is to discover how they can continue to move forward together which often requires extensive discussion.

Because each model forest organization is founded on collaboration and establishes a self-governance structure, according to the standards and norms that apply in the model forest's region their management structures create unique relational frameworks that promote vertical, horizontal, and cross-sectoral linkages over time. In general, a model forest partnership will constitute itself as a legal, not-for-profit public association where overall accountability rests with the Board of Directors who seek input from the broader partnership, management committee, staff, technical committees and advisory boards.

The partnership group At the center of each model forest is the partnership group. It is composed of key land users and other stakeholders of the region who volunteer to work together towards the common goal of SFM. Generally there is a core group of partners who manage model forest activities; typically these include the tenure holders (forest industries), government, environmental specialists, Aboriginal and other local communities, nongovernmental organizations, and academia.

The board of directors Each model forest has a body to which model forest staff report and receive direction and authorization on substantive issues. The partnership generally elects a president or chair, and board of management (directors) from among its members, who are charged with ongoing program oversight and ensuring implementation of annual plans as endorsed by the partnership group. The size of the body is highly varied and ranges from as few as four members to nine or more. In the case of the Manitoba Model Forest in Canada, the Board of Directors comprises over 30 members – one representative for each partner. In that instance, the Board and the Partnership Group are the same.

Technical committees Model forests attract a wealth of professional expertise and benefit greatly from the input and guidance of these specialists. Expert input is often structured around formal or informal technical or advisory committees. Generally, there is at least one permanent technical committee that operates in an advisory capacity to both the board and management.

Demonstrating Diversity in Governance Model forest structures depend on local circumstances and choices. For example, the Eastern Ontario Model Forest (EOMF) has a population base of over 1 million people and 88% of its 1.5 million ha land base is made up of small, privately owned land holdings. To provide access to the EOMF organization, the EOMF established a membership program whereby individuals can join the model forest for a small annual fee. Membership provides regular newsletters, access to special events, and the right to stand for election and to cast a vote for members of the Board of Directors over and above the four 'seats' on the board that are reserved for the founding organizations (Canadian Forest Service, Ontario Ministry of Natural Resources, Domtar Communication Papers, and the Mohawk Council of Akwesasne).

Stage 2: Storm to Norm

During the 'storm' stage, model forest participants generate ideas, express values, bring knowledge and science into play to support decision-making, and enhance their understanding of each other and local SFM issues. Agreement is reached on how the partnership will operate and the activities to be undertaken – the 'norm' stage.

The common goal of the new partnership is also decided at this stage. For model forests, while this is sustainable forest management, the partnership must define their vision for SFM for the area selected within which they will operate. This can take time as the participants must begin to understand each other and each other's perspectives before a common vision can be articulated and agreed upon.

Inherent within model forest partnerships is the ability for the participants to have access to a wide range of expertise, technology, and information. Scientists have participated on various committees and brought their scientific perspectives, knowledge, and other capacities to activities within the model forest governance. Model forests and their partners develop computerized decision-support systems which greatly strengthened the ability of planners and managers to analyze information accurately and quickly along both spatial and temporal scales. They also engage in research activities that lead to a greater understanding of ecological processes, the impacts of various anthropogenic and natural disturbances on forest ecosystems, wildlife habitat and population dynamics, sivicultural applications, biological control mechanisms, and the socioeconomic dimensions of SFM.

Activities that will assist in achieving the vision are also discussed and decided upon during the 'storm' stage. A model forest's objectives include a range of sociocultural, economic, and environmental needs that are considered in an integrated manner by all partners with respect to the overall goal of SFM. Therefore, as the partners identify, develop, and test activities that reflect the values and needs at the community, regional, and national levels, they are supported by a combination of pure and applied research, and undertake to report formally on outcomes, assess impacts, and modify new approaches to SFM. Activities are wide ranging and have included: research on riparian buffers, natural disturbance regimes, and wildlife habitat; development of best management practices; production of guidelines on minimizing soil disturbance; development and implementation of local level indicators of SFM; examining certification schemes and their applicability to small landholders; and thousands of others.

Creating new norms of local involvement in integrated resource planning at the provincial level Starting in 1998, the Prince Albert Model Forest (PAMF) initiated development of an ecosystem-based integrated resource management plan for the PAMF region. The entire PAMF partnership, including three levels of Aboriginal government and three levels of non-Aboriginal government, participated in the process. The interests and diverse values of First Nations, industry, government, area residents, and others were weighed over a 2-year period. The development of the initial plan has resulted in a planning process that is currently being implemented in six additional areas in the province by the Saskatchewan government.

Stage 3: Perform

In this stage, the partnership takes the ideas it has generated, conducts any research needed to confirm the ideas, and tests the ideas on the ground to create its 'models' of practice. It undertakes technology transfer and outreach to inform its partners and others of the results of the partnership's work.

An important characteristic of model forests is that the model forest organization itself does not and can not exercise decision-making authority over the land base. Instead, the model forest includes in their partnership those with legal tenure and management responsibilities over the land. Without jurisdictional responsibility, a model forest becomes a forum within which the partners can feel free to discuss a wide range of issues and approaches to solutions without feeling either powerless to do something (those without responsibilities) or under intense pressure to make immediate changes on the ground (those with jurisdictional responsibilities). Changes occur because those with management authority see the benefit to initiate such changes. The model forest provides the information on alternatives that is created through the joint effort of the partners working within their shared commitment to SFM.

Sustaining rural infrastructures through forest employment The forest tenant farmer system of the Bas-Saint-Laurent Model Forest exemplifies an innovative approach to collaborative forest management. Forest tenant farming is a land leasing system defined as: 'Allocation of a unit of land to an individual, called a forest tenant farmer, who agrees to manage it in a sustainable manner and to share the ensuing revenues with the landowner.' Abitibi Consolidated Inc., a major forest industry, is providing the land and the model forest has hired staff to assist the landowners with both direct technical assistance and in building linkages with others. Planning of forest management activities is based on a multi-resource management plan developed by consensus among the diverse model forest partners. In addition, forest tenant farmers cooperate on a landscape level with respect to joint management of hunting, fishing, and recreational and tourism activities. An evaluation concluded that tenant farms are viable enterprises and that the socioeconomic impacts are tangible and concentrated at the local and regional levels.

Stage 4: Reform

This stage refers to the decisions that are made based on the wisdom gained by the partners and the group as a whole as a result of going through the previous stages in the process. There are two aspects to this stage. One is a change in practice by a given partner as a result of the model forest's demonstrations. In addition, the partnership decides to re-examine their outputs and, based on new knowledge and experiences, return to any one of the previous stages and redo the process.

Successfully managing endangered species within an industrial forest landscape The pine marten is an endangered mammal in Canada's eastern province of Newfoundland and Labrador. The majority of the estimated 300 animals left on the island of Newfoundland are mainly found on the west coast in an area that has important timber resources for the island's pulp and paper industry. The area was the site of the longest environmentally based conflict in the province and was a key factor in selecting the area as a model forest. The Western Newfoundland Model Forest (WNMF) was instrumental in bringing together 22 organizations, including government departments, forest industry, mining interests, environmental groups, national parks, trappers, and others, to discuss the issue and develop a unified strategy for the protection of the marten. The WNMF supported research and facilitated an exchange of views which finally led to the establishment of a reserve area to protect the marten's critical habitat by provincial authorities.

Networking: A Defining Activity of Canada's Model Forests

Local model forest participation in a broader, national network was part of the original design of Canada's Model Forest Program. The premise for the need for a network came from the realization that each participant and model forest group would be breaking new ground and, being in such a unique situation, would benefit from having a 'peer group.' The network is a structure within which the individual model forests collaborate and share information and experiences and, by learning from each other, reduce duplication of efforts, and create synergies that can be applied to larger challenges. The network facilitates communication of ideas and cooperative efforts among the model forests, development of linkages with other organizations at the national level, and engagement in projects to further accelerate the advancement of SFM at each site and throughout Canada. The network and its activities are supported by a national Secretariat within the Canadian Forest Service.

Where the network identifies issues or needs of major importance to SFM in Canada and to model forests, a network strategic initiative is developed. To date strategic initiatives have been created to enhance Aboriginal involvement in SFM, to develop local level indicators of SFM (or measures of progress towards SFM), carbon accounting, and managing private woodlots for SFM.

The International Model Forest Network

The International Model Forest Network (IMFN) was announced by Canada at the UNCED Summit in Rio in 1992 to pilot the model forest concept outside of Canada. The IMFN has since grown from three sites in two countries (outside of Canada) in 1994 to 19 sites in 11 countries, in addition to numerous additional sites proposed and at early stages of development. The IMFN is supported by a Secretariat established in 1995 and housed with the International Development Research Center located in Ottawa, Canada. In 2002, a Regional Model Forest Center for Latin America and the Caribbean was established to provide additional support for the establishment of model forests throughout that region. A similar regional center is under development for Asia.

Lessons Learned

Based on Experiences with the Model Forest Concept to Date in Canada, the Following Key Lessons can be Suggested

1. Collaborative forest management as manifested through the model forest concept has proven to be well suited to address a wide range of SFM and development issues in a broad range of circumstances that are important to participants as well as observers interested in emulating the approach. These issues include governance, environment, biodiversity, natural resource management and conservation, and economic development.
2. The collaborative approach adopted by model forests has been beneficial in successfully providing an open forum through which all interested parties, in particular marginalized and indigenous peoples, are able to become involved in the forest management decision-making process and generate tangible benefits to improve and sustain the forests upon which their livelihoods depend.
3. Inherent in the model forest concept is the recognition that there was no one solution to SFM. By facilitating the development of bottom-up approaches, the model forest concept, by design, allows for the development of local solutions within broader contexts that are innovative in the design of sites and in approaches undertaken to advance SFM.
4. A model forest is not a project, rather it is a process. Both individual model forests and national and international model forest networks and programs are continually in a learning phase within which participants learn to adapt as conditions and issues change and evolve and as challenges emerge or fade.
5. If forests are to be managed in a sustainable fashion then real benefits must be apparent for the full range of values that forests offer (e.g., water, biodiversity as well as forest products both timber and non-timber in nature). Model forests and the networks that have developed have demonstrated that real benefits are accrued that far exceed individual partner inputs and that duplication is reduced by collaborating in the

exchange of information and focusing efforts and resources on common goals.

6. Through local partnerships and national and international networking, model forests facilitate both global to local and local to global linkages that are important to creating effective SFM strategies.
7. The combination of broad-based partnerships working together in a respectful forum towards common goals, the use of science and technology to aid in decision-making within increasingly complex issues, and enhancement of participant capacities allows model forests to be highly adaptable to situations and issues beyond just forests.
8. By collaboratively addressing the identified issues and sharing information, the education and expertise of both individual partners and the partnership as a whole is substantially increased contributing to the long-term sustainability of the partnership. Over time, an integrated process of decision-making develops within which participants cannot only envision how their interest or value fits into the framework but also where others fit in. The mutual learning and understanding which take place within this process (and partnership) builds a synergy between the participants allowing the development of a much broader vision than the individual visions of the participants. SFM requires this broader vision that cannot be achieved through an isolated, individualistic sectoral approach.
9. Partnerships may create new challenges and increase the complexity of current ones, but they also offer the chance to create a learning environment rather than conflict to share information, to make trade-offs between conflicting objectives, and to develop better and more effective solutions to resource management issues. Model forests illustrate that the partnership (collaborative forest management) approach, although demanding of time and patience, leads to better and more sustainable decisions.
10. Successful collaborative relationships for SFM developed within the model forest partnerships creates the springboard for continued collaborative approaches in other sectors and spheres of activity.
11. Not having the capacity to ensure that each element of collaboration (i.e., full participation; the consideration of multiple values and a scientific basis for decision-making) are at play within the model forest has been shown to compromise their long-term success. Despite having done much valuable work, one model forest in Canada did not continue beyond the second 5-year phase as it was unable to demonstrate its capacity to fulfill each of these elements.
12. One very important role in collaborative forest management is that of the interventionist or champion. The interventionist is defined as any individual or group that undertakes to initiate change. In getting CFM started, the interventionist must fill two roles: first as the facilitator of the collaborative process, and second as a stakeholder in that resource management system. To do this the interventionist must establish a role of 'honest broker' with interests that accord with the provision of SFM. The interventionist must also be able to both understand and solve problems and be able to negotiate effectively with the full spectrum of stakeholders. Once the initial interventionist has established the collaborative group it is crucial for the success of the process that all participants take on interventionist characteristics.
13. Perhaps the most important lesson to be learned from the model forest experience is that collaborative forest management as a process must become the 'norm' to achieve SFM rather than just a series of individual projects.
14. Model forests are tackling the complex issue of SFM through a partnership process that is based on an expanded approach to CFM. The successful establishment of model forests around the globe further demonstrates the flexibility, versatility and utility of the model forest concept in helping interested individuals and organizations participate in the challenge of SFM. However, there are a number of factors that frustrate success in working towards SFM. These include and are not restricted to circumstances where there is insufficient political support, there is a history of unresolved conflict, there is a lack of clear purpose, goals or deadlines are unrealistic, the distribution of benefits is unsatisfactory, and partnerships are not managed in an equitable, respectful, and transparent manner.

Concluding Remarks

Resource managers are dealing with increasingly complex issues in sustainable forest management such as endangered species, landscape-level forest values, and an increasing demand for forest products. These complex issues require both diverse information and cooperation among a wide range of interests, organizations, and agencies. Collaborative forest management aptly provides for these needs.

Since its inception in 1992, the model forest concept has grown from an original 10 sites in Canada to over 30 sites in 11 countries (in 2003) with more sites in the planning stages. Clearly this demonstrates that collaborative forest management can be applied and can often flourish in a wide range of geographic, institutional, and cultural settings where the model forest approach is taken. This growth also attests to the relevance and still unrealized potential of collaborative forest management to make lasting and significant contributions to critical internationally shared challenges to achieving SFM in practice.

From the experience of the model forests, resource managers should, with confidence, apply CFM elsewhere in order that CFM increasingly becomes a normal operating procedure rather than the exception.

See also: **Social and Collaborative Forestry**: Forest and Tree Tenure and Ownership; Joint and Collaborative Forest Management; Social and Community Forestry; Social Values of Forests.

Further Reading

Besseau P, Dansou K, and Johnson F (2002) The International Model Forest Network (IMFN): elements of success. *Forestry Chronicle* 78(5): 648–654.

Canadian Model Forest Network (2003) http://www.modelforest.net

Carter J (2002) *Recent Experience in Collaborative Forest Management Approaches: A Review of Key Issues*. Geneva, Switzerland: SDC, Intercooperation.

Hall JE (1996) Canada's Model Forest Program: an experiment in the application of sustainable development in forest management. A paper presented at the *Integrated Application of Sustainable Forest Management Practices International Workshop*, 22–25 November 1996, Kochi, Japan.

Hall JE (1997) Canada's Model Forest Program: a participatory approach to sustainable forest management in Canada. *Commonwealth Forestry Review* 76(4): 261–263.

Ingles AW, Musch A, and Qwist-Hoffmann H (1999) *The Participatory Process for Supporting Collaborative Management of Natural Resources: An Overview*. Rome: Food and Agriculture Organization.

International Model Forest Network (2003) http://www.imfn.net

LaPierre L (2002) Canada's Model Forest Program. *Forestry Chronicle* 78(5): 613–617.

Mayers J and Vermeulen S (2002) *Company–Community Partnerships: From Raw Deal to Mutual Gains*. London: International Institute for Environment and Development (IIED).

Public Participation in Forest Decision Making

S R J Sheppard and C M Achiam, University of British Columbia, Vancouver, BC, Canada

Introduction

Over the last few decades, the formal practice and supporting science of public participation have emerged as key components of forest management and decision-making in many countries. The Montreal Process and virtually all certification systems call for appropriate public participation in decisions on forest management. Some cultures and traditional practices have incorporated what we would now term participatory decision-making for centuries. The formal methods and structures used more recently to make decisions in forestry, particularly in western nations, have evolved considerably, with a trend towards more public involvement in decision-making. This can be seen at both the local level (increasing control over use of local resources) and the global level (in terms of public opinion affecting policies and practices at the level of the global marketplace).

This article briefly describes potential benefits of applying public participation in forestry, and identifies some key theoretical concepts and broad empirical reviews of practice which inform the field. General findings and emerging principles for public participation are summarized, and criteria for assessing the performance of public participatory techniques and processes are identified. Selected techniques in use in forest decision-making are described briefly, together with indications of their performance where information is available. The article concludes with general guidance from current knowledge on the design of good processes for public involvement in forestry.

This article focuses on the scientifically documented aspects of public participation in forest planning, rather than in the broader arenas of public education and governance. Much of the literature reviewed comes from the democratized and more industrially developed nations, especially applying to the public forests of temperate countries. Many of the principles apply more broadly, however, including to private lands in western nations and forest management in developing countries or nations in transition. Readers should also consult the related articles on community forestry and collaborative management (*see* **Social and Collaborative Forestry:** Canadian

Model Forest Experience; Joint and Collaborative Forest Management; Social and Community Forestry) for more on participatory mechanisms in tropical regions worldwide. It should not be assumed that methods of community involvement in less industrialized nations are necessarily less effective or equitable than those in Europe or North America.

Public participation has been defined by the FAO/ECE/ILO Joint Committee Team of Specialists on Participation in Forestry as:

> various forms of direct public involvement where people, individually or through organized groups, can exchange information, express opinions and articulate interests, and have the potential to influence decisions or the outcome of specific forestry issues.

Public participation is an inherently two-way process, and should not be confused with public relations which attempts to convey information in one direction in a manner favorable to the disseminator of the information.

Stakeholders have been defined as all individuals or organized groups interested in the issue or opportunity driving the participatory process. This includes both recognized 'interest groups' and other, sometimes less visible, sectors of society affected by or concerned with some aspect of forest management.

Potential Benefits of Public Participation

Why is public participation important, and what good does it do? The potential benefits often described include:

- increasing public awareness of forests and forestry among the public through interaction and collaborative learning
- increasing the overall flow of benefits to society by contributing to better decisions and outcomes for multiple forest uses and products, and more equitable sharing of costs and benefits
- improving social acceptance of sustainable forestry through better information and involvement in the decision-making process
- building trust in institutions.

Other practical benefits include gaining information from stakeholders that would otherwise be ignored (e.g., traditional ecological knowledge), and streamlining the process of plan and project implementation by avoiding delays, resolving conflicts among competing interests, and reducing risks of legal action. However, increasingly, there is seen to be an overarching moral purpose in incorporating public values into forestry decisions.

Theoretical Concepts and Broad Empirical Reviews

The scientific background to public participation stems from various sources, many of them outside the field of forestry. Most notably, the science of sociology and the discipline of community and regional planning have contributed to our understanding of participatory mechanisms, though influenced by various social sciences and professions. In less industrialized countries, much knowledge on effective processes has been gained from the broad application of participatory rural appraisal methods for assessing local resources and development options with local community involvement. Public participation in forestry is now conducted by public participation specialists, foresters, planners, and land managers, in addition to social scientists.

The concept of public involvement in forestry has changed considerably since Gifford Pinchot's 'scientific forestry' ethos in the early 1900s, where the public interest was to be served by having experts apply conservation policies that produced the greatest good for the greatest number for the longest time. More recently the public has become increasingly adamant about accountability in government and has begun to demand more direct involvement in the decision-making process. The role of government has evolved from decision-maker based on expert knowledge to that of arbiter among different interests within a pluralist public.

Sociologists have identified two normative models of participation in a democratic political framework where public participation is encouraged: participatory democracy and representative democracy. In a participatory model, the broadest cross-sections possible would be involved in decision-making to be representative of the widest majority in the society. Several challenges face this model, including the reality that individual citizens may not have the time, knowledge, or interest to participate in resource decision-making. The alternative normative model is representative democracy, which suggests that to compensate for the lack of capacity to participate in multiple decision-making activities, individuals join together in forming or supporting various interest groups which, in combination, can fairly represent the balance of individual interests in society.

Specific theoretical frameworks have been developed which attempt to explain or structure the range of participatory processes, in various settings. Sherry Arnstein in 1969 developed a ladder of public participation (**Figure 1**) which described the role of citizens in decision-making, ranging from nonparticipation, through token participation, to degrees of

8.	Citizen control	Degrees of citizen power
7.	Delegated power	
6.	Partnership	
5.	Placation	Degrees of tokenism
4.	Consultation	
3.	Informing	
2.	Therapy	Nonparticipation
1.	Manipulation	

Figure 1 Arnstein's ladder of public participation. (Reproduced with permission from Arnstein SR (1969) A ladder of citizen participation. *American Institute of Planning Journal* 35(4): 216–234.)

citizen power. While this typology has been criticized for creating unrealistic expectations that citizens could or should make public policy decisions, it has also been praised for its simplicity, and continues to be one of the most widely cited references in public participation literature.

Another model, developed in the 1970s, was the widely tested Vroom–Yetton Model, originally designed to assist business managers to determine what level of participation by subordinates (on a scale similar to Arnstein's ladder) would improve the effectiveness of decision-making in the corporate business setting. Attempts have been made to adapt the Vroom–Yetton Model to the needs of natural resource management; in one such application, R Lawrence and D Deagen developed a scheme for managers to determine whether and how public consultation should be used, using a hierarchy of questions addressing the likelihood of public acceptance of management actions, the manager's knowledge of salient public preferences, the likely benefits of public learning on the issue, and other aspects relating to efficiency of the process.

Beierle and colleagues have developed a framework for evaluating public participation in environmental decision-making which can be directly applied to forestry. This framework recognizes three major components: context, process, and results. Context refers to all the conditions or features of a given situation that a public participation process should address, such as the institutional setting and history of prior participation or conflict. Process encompasses what actually happens in a participatory program of exercise, including the kind of participation mechanisms used and various associated factors which influence their effectiveness, such as responsiveness of the lead agency. Results refer to the outcomes of the context and process, in terms of the decisions or actions enabled, the relationships built among the participants, and capacity-building achieved through the process.

Empirical reviews have also sought to develop classification systems for participatory mechanisms. Thomas Beierle and Jerry Cayford recognized four categories of participatory mechanisms to address environmental issues: public meetings and hearings; advisory committees not seeking consensus; advisory committees seeking consensus; and negotiations and mediations (seeking consensus). They described these mechanisms by relating the number of participants to be involved with the level or intensity of involvement desired. The FAO/ECE/ILO Joint Committee Team considered public participation that was specific to forestry in 13 countries, and identified several types of participation at various levels from national to local; types of public involvement processes included (1) those addressing forest policies, programs, and plans, (2) those promoting specific forest projects, (3) those used in audits of forestry projects or practices, and (4) those involving advisory boards or permanent councils. Max Hislop and Mark Twery, working at the UK Forestry Commission, produced a menu of participatory techniques, with matrices that arrayed appropriate techniques against the various stages of the decision-making process and the number of stakeholders to be involved.

A simple classification that has been suggested by various authors and researchers to describe participatory methods recognizes three typical levels of involvement: information exchange or directive participation (where information is communicated primarily in one direction); consultation, where public opinions are sought and considered in expert or managerial decision-making; and collaboration, where representatives of the public are involved actively in developing solutions and directly influencing decisions. **Figure 2** presents a simple scheme using this classification, and listing various techniques (some of which are described below) under each level of involvement. In addition, mechanisms providing fuller control of decisions to public groups (such as Community Forests) are described in articles (**Social and Collaborative Forestry**: Joint and Collaborative Forest Management) and (**Social and Collaborative Forestry**: Social and Community Forestry).

Many examples of particular participatory techniques have been documented in various ways in the scientific and professional literature. Apart from occasional illustrative examples, this article draws primarily on the broad reviews mentioned above, as well as a recent review of public processes conducted by the author and other researchers in British Columbia. These sources include empirical studies, normative papers, and professional practice.

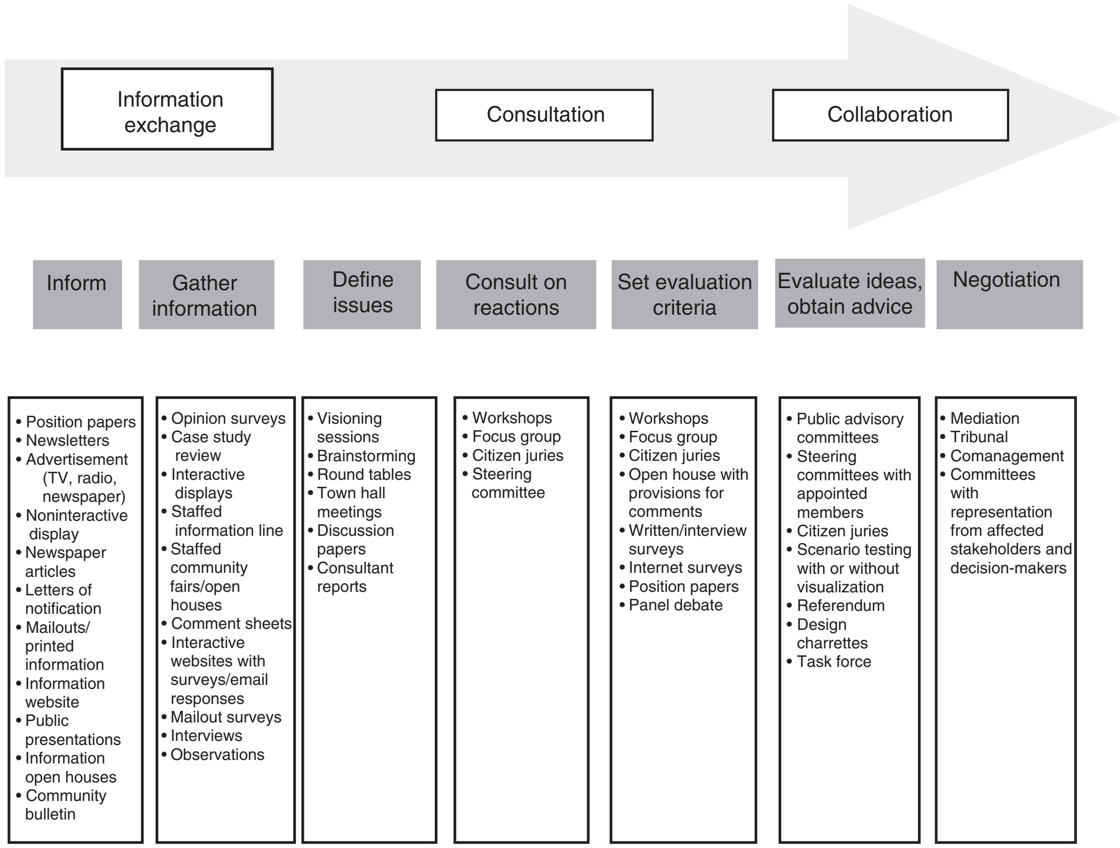


Figure 2 The public participation continuum. Courtesy of Forest Investment Account and Slocan Forest Products. Derived in part from Hislop M and Twery M (2001) *A Decision Framework for Public Involvement in Forest Design Planning*. Final Report Prepared for Policy and Practice Division. Roslin, UK: Forestry Commission.

The concepts and methods applied to public participation in forestry also relate strongly to other allied regulatory processes in certain jurisdictions, e.g., environmental and social impact assessment, land use and resource planning, and sustainability assessment, certification, and monitoring.

General Findings and Principles

This section describes some of the patterns of use of participatory approaches in forestry, general findings on the performance and quality of participation, and principles for successful participation which emerge from the current state of our knowledge.

The FAO/ECE/ILO review of studies from various nations suggested that participatory processes in forestry occur at all levels from national to local, but most commonly at the regional and local levels. These processes appear to be affecting decisions in most cases. Public participation applies both to public and private forestry, though often with different purposes and constraints: not surprisingly, more effort is expended in public involvement on public forest land than on private land. Public processes range from the formal to the informal. They may be part of the statutory process, e.g., more formal/procedural and institutionalized processes, such as the public process under the National Environmental Protection Act governing the US Forest Service Forest Resource Management Plans; they may be scientifically procedural but discretionary, as in the use of social science/research tools such as surveys to inform the process; and they may be procedurally informal but built into ongoing management or governance structures such as community forest initiatives (*see* **Social and Collaborative Forestry**: Common Property Forest Management; Joint and Collaborative Forest Management; Social and Community Forestry) or voluntary comanagement agreements with First Nation aboriginal groups.

In terms of the range of participatory mechanisms on the scale of Arnstein's ladder or the simpler three-category classification described above (see **Figure 2**), the more collaborative mechanisms are least common. They tend to be more difficult to introduce and implement and require considerable flexibility on the part of participants and enlightened attitudes on the part of the agencies or vested interests; they can consume more time than other methods, although it is argued that they may save time in the long run by improving understanding and reducing conflict.

Empirical research shows that many public participation processes in practice to-date have not lived up to their potential or public and agency expectations. The FAO/ECE/ILO study found that project-oriented processes tended to address certain sectors of the public and not others. Many researchers have commented on the failure of processes to engage the silent majority. Some have suggested that environmental groups, for example, have successfully used the process to shift the focus on to environmental interests at the expense of other values, thereby distorting the real public interest, although there are also many instances of apparent domination of the public agenda by industry, landowners, or government. As an example, the US Department of Agriculture Forest Service conducted a public participation process in the Nantahala National Forest and researchers evaluated the representativeness of the public involvement. The research indicated that the socioeconomic characteristics of participants in the public process did not reflect the make-up of the local public: participants tended to have more general education, more formal education about forests, greater incomes, and a higher proportion with occupations related to natural resources, as compared with the general public. State government, environmental, and timber interests were overrepresented. Nonetheless, the research concluded in this case that the preferences of the participants, on balance, broadly reflected the general public's values.

Various barriers commonly prevent or discourage voluntary participation by some groups. These can include:

- lack of information, either explaining the process itself or why the issue is important
- lack of access to the participatory process due to cultural or psychological factors, such as inexperience or perceived repercussions; women, young people, and aboriginal groups are often under-represented in conventional processes, as well as other groups who lack organizational capacity, such as small-scale forest owners or less affluent social classes
- belief that participants have little or no ability to influence the process/decision
- tactical behavior, whereby some interest groups perceive they can be more influential by staying outside the process
- lack of interest, often compounded by the cost or time commitment required to sustain a participatory effort; people choose to participate only as long as they perceive the benefits outweigh the costs of their participation.

Public participation in forestry land use planning has met with mixed success, often leading to low public satisfaction with the processes concerned. Many processes are institutionalized, and not agreed to or influenced by the participants. Recent Canadian research indicates that some conventional techniques for eliciting public input such as noninteractive public displays and open houses with highly technical material have generated less than useful results. Recurring problems in some political climates include long and acrimonious processes that appear to favor certain lobby groups while marginalizing other values. The links between the public process and final decisions or implementation of forest plans are often not transparent. Evaluation of the success of processes, to gauge effectiveness and satisfaction of participants, is seldom conducted routinely in practice. In this article, some more specific evaluations of the performance of particular public involvement mechanisms are provided with the descriptions of key techniques below.

According to some researchers, successful public involvement may be more affected by the specific context of the geographic area and issues such as the available time, budget, and pre-existing relationships between the stakeholders, than by the specific public involvement techniques employed. Even the most sophisticated public involvement processes can sometimes be unsuccessful due to internal and external contextual factors; however, there is some evidence in recent research that innovative processes facilitated by neutral third parties can influence the pre-existing stakeholder or institutional dynamics and revitalize productive participation (**Figure 3**).

The growing body of research evaluating public participation in forestry leads to some emerging general principles. The UK Forestry Commission has concluded that the process of community participation is as important as the product (management decisions), if public support for decision-making is to be maintained. This process is iterative, cyclical, and woven into other aspects of management and decision-making; it should not be thought of as a single event or the application of a single technique; it continues after the planning process is 'complete.'

The process needs to recognize multiple publics, not just the extreme interests. Consensus among stakeholders is not necessarily a realistic outcome for an effective process, even though many processes are designed to achieve this; sometimes, providing inclusive and balanced information to the decision-makers for use in a structured and controlled

Figure 3 Workshops facilitated by researchers with separate stakeholder groups to assess forest management alternatives, using model-based time-lapse maps and visualizations, were deemed more effective than conventional public processes in the politically charged atmosphere of British Columbia's Slocan Valley.

decision process may be enough, and better than the alternative of a simplistic majority vote process. Not all participatory processes need to involve all stakeholder groups in the same venue at the same time; more constructive results may be obtained by granting equal access to each stakeholder group separately. Researchers have found that using a small group of stakeholder representatives can be more efficient in reaching solutions than processes that directly involve large numbers of people, but risks divorcing the participants from the groups they are intended to represent.

The context of political and cultural norms and traditions is important, as is building trust. This can take a long time, especially if cultural and communication barriers between scientists or managers and indigenous groups (for example) need to be overcome. The skill and capacity of participants to engage with a public process may need to be enhanced for an equitable process to occur.

Belief in the fairness of the decision-making process is key. However, merely increasing participation in the decision-making process does not always enhance satisfaction with the perceived fairness of either the process or the decision. Besides conducting procedurally fair public involvement processes, it is necessary to demonstrate that the decision-makers acted in good faith by impartially considering the views of participants in the decision-making process.

Evaluating the Effectiveness of Participatory Processes

How is a good public involvement process determined? This section goes beyond the general principles outlined above, to describe criteria for evaluating the effectiveness of participatory processes. The following criteria have been proposed by or derived from various authors and researchers.

1. Logistical effectiveness. The process should be appropriate to the scope, financial resources available, and the time limitations of the project requirement.
2. Clearly structured and integrative decision-making framework. The nature and scope of the participatory process should be articulated at the outset and used throughout the process as a guide to keep the tasks on track; mechanisms for structuring and

working through the decision-making process should be clear and well coordinated.

3. Representation. The process should provide inclusive representation of all interests concerned by the issue driving the participatory process, including administrators, actual and potential users, and people whose livelihoods or other interests are affected by the decisions. Participants should have an equal right to express their opinion and a fair chance to assert their interests and rights.
4. Open communication and access. Steps should be taken to ensure that participants have multiple opportunities or choices for involvement e.g., different event times, length of time and format involved, and intensity of involvement in a culturally appropriate manner. In addition, all participants should have access to needed resources and should be involved in the process as early as possible and as need arises.
5. Participants' agreement. The process should be based on participants acting in good faith, and agreeing not to use shared information to abuse or sabotage the process. Participants should be included in the design of the process, agreeing to ground rules for the process; participants in collaborative processes should ensure good communication with their respective interest group.
6. Transparency. The process should be transparent to participants and the broader public, and the information understandable and readily available.
7. Independence and neutrality. The process should be conducted in an independent, unbiased manner. Participants should be free to conduct themselves in a voluntary and self-directed manner without coercion, and process management should be neutral. The process should seek the common good, not just accommodating specific interests.
8. Influence and accountability. It should be clear that the process and recommendations are capable of genuine impact on decisions. The process should not guarantee or predetermine the outcome, and should be open to consideration of reasonable alternatives and choices, including at a minimum a 'do nothing' alternative to the proposed action. Action should follow decisions and designated parties should ensure their follow-through. Participant satisfaction with the process should be documented.

Individual Participatory Techniques

This section reviews selected participatory techniques applicable to forest planning, as examples of the methods and tools in use or available. Methods range from the highly scientific to the pragmatic: some can be submitted to rigorous statistical analysis consistent with the high standards of social science research methods (utilizing techniques such as random sampling and adequate sample size calculation to ensure validity, reliability, and generalizability of results); others apply simple descriptive statistics to characterize findings from available participants, or yield only qualitative discussion of general preferences and decisions, as with many public advisory groups.

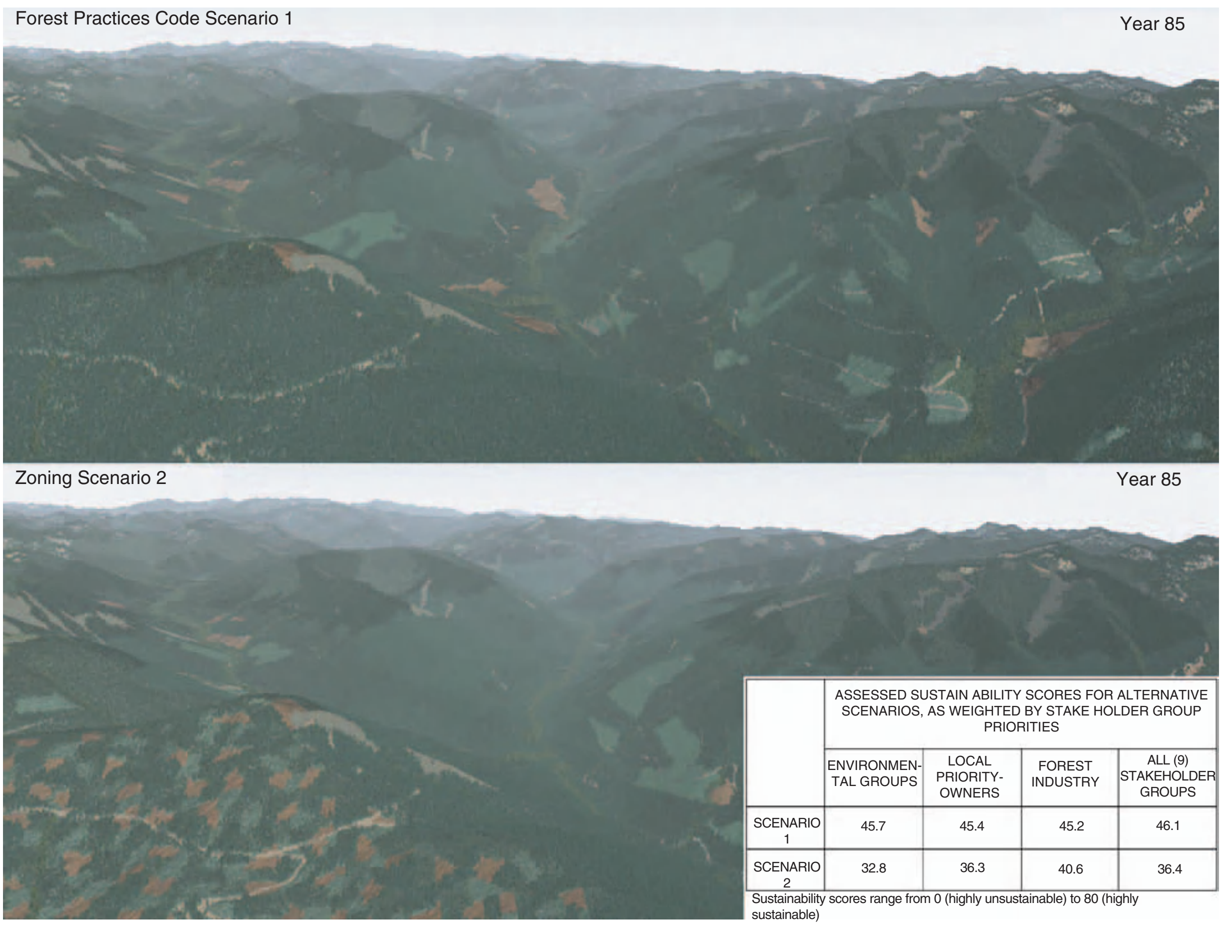
A menu of some key techniques follows, loosely arranged on a scale from informational through consultative to collaborative; results of empirical studies on these techniques are summarized where these are available and pertinent.

1. Information open house. The public is invited to visit a specific venue during a specified time period where information on a project or issue is displayed and a presentation may be made. There are usually opportunities for comments to be received. This can represent an easy form of public participation to manage, and is useful early in the process, but may not secure input from various affected stakeholder groups; it is often inadequate as the primary mechanism to support decisions.
2. Surveys (e.g., mail-out questionnaires and person-to-person or telephone interviews). These are a means to gather information using a representative sample that reflects the opinions of the larger population. Return rates are sometimes quite low, and participants may be skewed demographically, but surveys usually expand significantly the range of opinion gathered, as compared with meeting-based techniques. They do not enable dialogue.
3. Interactive websites with surveys/email responses. Use of the World Wide Web can provide information to the public as well as gather responses. This promises broad and open participation to local and global interests alike, is cost effective in relation to the breadth of outreach, and allows updating of information and some dialogue; however, its weaknesses include only being open to people connected to the Web, and experience has demonstrated the risk of overuse/distortion of the system by certain motivated interest groups.
4. Citizen advisory committee or public advisory group (PAG). This is a public involvement forum which advises forest managers on issues and initiatives as an ongoing mechanism for public consultation. The level of responsibility and influence of the group can vary. The PAG is intended to provide an avenue for local constituencies to represent their interests and views regarding forest management; however, the

Canadian Forest Service has found that PAG members can differ systemically from the general public in sociodemographic characteristics and values and attitudes to forest management, suggesting that the process for selecting community representatives is critical.

5. Focus groups. These are small groups of people, formally or informally organized, and randomly selected or carefully chosen to represent various interests, for the purpose of interactive and spontaneous discussions of one particular topic or plan. Focus groups can be used at any stage of the public involvement process to accomplish tasks ranging from gathering information, or defining issues or criteria, to providing perceptual data (*see* **Landscape and Planning**: Perceptions of Forest Landscapes). As with other methods, representation of the wider public interests is key. A variant of the focus group technique is to hold structured workshops with various stakeholder groups to assess alternative forest plan scenarios, against multiple agreed criteria. The scenarios can then be compared and the results tabulated to quantify commonalities or differences in preference between each stakeholder group (**Figure 4**). Workshops can also be used to generate new or preferred solutions collaboratively.

Various new participatory techniques are emerging to expand the tools available to researchers and forest managers; examples include self-directed photosurveys of community values by local participants; cable TV channels providing opportunities for community dialogue and instant opinion polling; and decision support tools using real-time integrated resource-forecasting models linked to forest visualizations (*see* **Landscape and Planning**: The Role of Visualization in Forest Planning).



	ASSESSED SUSTAIN ABILITY SCORES FOR ALTERNATIVE SCENARIOS, AS WEIGHTED BY STAKE HOLDER GROUP PRIORITIES			
	ENVIRONMEN-TAL GROUPS	LOCAL PRIORITY-OWNERS	FOREST INDUSTRY	ALL (9) STAKEHOLDER GROUPS
SCENARIO 1	45.7	45.4	45.2	46.1
SCENARIO 2	32.8	36.3	40.6	36.4

Sustainability scores range from 0 (highly unsustainable) to 80 (highly sustainable)

Figure 4 In a participatory multi-criteria analysis process conducted under the Arrow Forest District IFPA pilot study in British Columbia, different stakeholder groups weighted sustainability criteria and generally agreed on preferred forest management scenarios, as shown here in landscape visualizations. Visualizations by J Salter and D Cavens, Collaborative for Advanced Landscape Planning; reproduced with permission from Sheppard SRJ and Meitner MJ (2003) Using multi-criteria analysis and visualization for sustainable forest management planning with stakeholder groups. In: *IUFRO Decision Support for Multiple Purpose Forestry Conference Proceedings*, Vienna, Austria.

Towards Best Practices in Participatory Forest Decision-Making

Public participation is more than just a set of tools or a mechanical process: it has been called 'a way of thinking and acting.' Nonetheless, research and practical experience suggests some ways to design and structure an appropriate public participatory process. Beierle and colleagues have suggested five steps in designing public participation processes: (1) determine the need for public participation; (2) identify goals in the process; (3) determine key design decisions on appropriate participants, level of engagement, degree of public influence desired, and governmental role; (4) select and modify appropriate process; and (5) carry out a post-process evaluation. The FAO/ECE/ILO outline three stages and nine steps to consider when planning a participation process (**Table 1**). The overall decision-making process into which the public involvement fits, generally involves the selection of stakeholders, identification of issues, establishment of goals and objectives, agreement on evaluation criteria, generation of options, assessment of alternatives, and, finally, the selection of a course of action to achieve the plan.

In any public process, an analysis of stakeholders early on is essential: omissions or misrepresentation at this stage can hamper success throughout the remaining process. Stakeholder analysis requires a thorough search of stakeholder groups and contact details, including affected individuals, nonorganized stakeholder types (whether involved in or excluded from the usual processes), and a sample of the wider public. A typical range of stakeholders in western countries might include:

- indigenous communities if present
- other neighbors, local residents, and the community at large
- industry, labor, and local economy interests
- special-interest groups representing other forest users, such as tourism providers, recreation user groups (including visitors), environmental groups, and nontimber forest products users
- government agencies
- experts (to provide technical knowledge).

Stakeholders can be characterized in terms of the degree to which they are affected, their level of organization and influence over planning processes, and their capacity to participate meaningfully. Some attempts have been made to identify primary, secondary, and tertiary stakeholders, based on issues such as proximity to the area and how salient a forest resource is to them, but there is disagreement on how this classification should be used, for example, to influence levels of access to the participatory process. The stage of the decision-making process along with the level of involvement and the purpose of the public consultation will influence the selection of the type of stakeholders to be engaged. Within stakeholder interests, some researchers recommend leaving the choice of representatives to the stakeholders themselves wherever possible. Different levels of planning may require different skills and knowledge from the participants. The public involvement process may have to include capacity-building in order to achieve meaningful responses.

In terms of selecting appropriate participatory techniques (such as those described above) as part of the larger designed process, some researchers such as Hislop and Twery at the UK Forestry Commission have provided menus and selection guidance. However, it is generally accepted that multiple approaches are generally required: one technique is usually not enough to address the different publics, cultures and contexts identified through stakeholder analysis and

Table 1 Stages in planning a public participation process (adapted from FAO/ECE/ILO Joint Committee, 2000)

Stage		*Steps*
Define the context	1	Identify issue (e.g., proposed forest management activities), geographic scope, and potential stakeholders (stakeholder analysis)
	2	Define objectives, needs and budget for public participation, and possible approaches/mechanisms
	3	Commit to conducting a participatory process (or opt for another type of decision-making)
	4	Disseminate information about the issues and public process, and collect initial reactions/concerns
Plan the process	5	Develop a participation plan with participants, including goals, timetable, scope, rules and responsibilities, information management, techniques to be used, needs for training/capacity building, internal and external communications, and evaluation.
Implement the process	6	Implement the participation plan, and adapt if necessary
	7	Evaluate the participation plan and outcomes with stakeholders
	8	Communicate the outcomes of the public process to all stakeholders and wider interests
	9	Implement the outcomes (e.g., forest management activities) and provide feedback on progress

Source: FAO/ECE/ILO Joint Committee (2000) *Public Participation in Forestry in Europe and North America*. Geneva, Switzerland: International Labour Office.

scoping. The selection of the appropriate processes to match the given time, budgetary, and staffing constraints, and other external influences, is key. Clarification of the intent and intensity of the public involvement required will help differentiate between ongoing techniques, such as PAGs, versus more occasional major efforts at regular intervals, such as participatory forest management plan development.

Transparent documentation and monitoring of the process over time is important in helping to demonstrate social sustainability. Feedback to participants is critical to building trust over the longer term, together with evaluation of the effectiveness of processes and the level of public satisfaction achieved, as part of adaptive management of the public process itself. Beyond decision-making processes, constructive public involvement can be extended to include participation in implementing management actions, forest protection, and monitoring of sustainability criteria and indicators.

See also: **Landscape and Planning**: Forest Amenity Planning Approaches; The Role of Visualization in Forest Planning. **Social and Collaborative Forestry**: Canadian Model Forest Experience; Common Property Forest Management; Joint and Collaborative Forest Management; Social and Community Forestry; Social Values of Forests.

Further Reading

Arnstein SR (1969) A ladder of citizen participation. *American Institute of Planning Journal* 35(4): 216–234.

Beckley TM, Boxall PC, Just LK, and Wellstead AM (1999) *Forest Stakeholder Attitudes and Values: An Annotated Bibliography*. Northern Forestry Centre Information Report no. NOR-X-365. Edmonton, Canada: Natural Resources. Canada, Canadian Forest Service.

Beierle TC and Cayford J (2002) *Democracy in Practice: Public Participation in Environmental Decisions*. Washington, DC: RFF Press.

Brown K, Adger WN, Tompkin E, *et al.* (2001) Trade-off analysis for marine protected area management. *Ecological Economics* 37: 417–434.

FAO/ECE/ILO Committee on Forest Technology, Management, and Training (2000) *Public Participation in Forestry in Europe and North America*. Report of the Team of Specialists on Participation in Forestry. Geneva, Switzerland: International Labour Office.

Hamersley Chambers F and Beckley T (2003) Public involvement in sustainable boreal forest management. In: Burton PJ, Messier C, Smith DW, and Adamowicz WL (eds) *Towards Sustainable Management of the Boreal Forest*, Chapter 4, pp. 113–154. Ottawa, Canada: NRC Research Press.

Hislop M and Twery M (2001) *A Decision Framework for Public Involvement in Forest Design Planning*. Final Report Prepared for Policy and Practice Division. Roslin, UK: Forestry Commission.

Lawrence RL and Deagen DA (2001) Choosing public participation methods for natural resources: a context-specific guide. *Society and Natural Resources* 14: 857–872.

Overdevest C (2000) Participatory democracy, representative democracy, and the nature of diffuse and concentrated interests: a case study of public involvement on a National Forest District. *Society and Natural Resources* 13: 685–696.

Parkins J (2002) Forest management and advisory groups in Alberta: an empirical critique of an emergent public sphere. *Canadian Journal of Sociology* 27(2): 163–184.

Sheppard SRJ and Lewis JL (2002) Democratising the SFM planning process: the potential of landscape visualization as a community involvement tool for First Nations. In: Veeman TS, Duinker P, MacNab B, *et al.* (eds) *Advances in Forest Management: From Knowledge to Practice*, Proceedings 2002 Sustainable Forest Management Network Conference, pp. 304–309. Edmonton, Canada: Sustainable Forest Management Network.

Shindler B and Neburka J (1997) Public participation in forest planning: eight attributes of success. *Journal of Forestry* 95(1): 17–19.

Susskind L and Cruickshank J (1987) *Breaking the Impasse: Consensual Approaches to Resolving Public Disputes*. New York: Basic Books.

SOIL BIOLOGY AND TREE GROWTH

Contents

Soil Biology

C J Weston and K L Whittaker, University of Melbourne, Creswick, Victoria, Australia

Introduction

Forest soils harbor an enormous variety of life forms that principally derive their energy from organic matter produced by photosynthesis and shed from plant structures and from animals. The major biological components of forest soils are plant roots, microbes, and soil animals. As other articles deal with tree roots (*see* **Soils and Site**: Tree Roots and their Interaction with Soil) and the mycorrhizal and rhizosphere organisms associated with them (*see* **Soils and Site**: Soil Organic Matter), this article will concentrate on the freeliving microbial and faunal components of the soil biota. Together these organisms play a critical part in the function of forest ecosystems through their role in organic matter breakdown, decomposition, and release of materials to the soil environment and atmosphere. Through these processes they have a positive influence on the availability of nutrients for plant growth and on soil structure.

Forest Soil Biota

The structure of cells and the way they obtain energy gives rise to the fundamental classification of all life forms. Two domains, prokaryotes and eukaryotes, and six kingdoms are recognized. There are two kingdoms within the prokaryotes, bacteria and archaea; within the eukaryotes are the four kingdoms – protoctista (under revision), plantae, fungi, and animalia (**Table 1**). Viruses are less than 0.3 μm in size and make a negligible contribution to microbial biomass and ecology in forest soils; they are not discussed further here. All these life forms have representatives in forest soils; indeed it is thought that soils provide habitat for the majority of earth's biodiversity. The extent of microbial diversity in soil remains largely unknown (**Table 2**), mainly due to the difficulties of studying such small organisms that have simple morphology. Furthermore, only a small percentage of the soil microbial community responds to cultivation in laboratory media, so that only a small fraction of them has been isolated and cultured. The best evidence for the vast biodiversity among soil biota is derived from molecular techniques, some of which are listed in **Table 3**. Overall, there is an extremely high diversity of decomposer species in forest soils that is undoubtedly related to the heterogeneity of the forest soil environment. This diversity ensures the maintenance of matter and energy fluxes and it confers resistance against disturbances to decomposition. For example, both fungi and heterotrophic bacteria play a role in nitrification, particularly in acid forest soils.

Despite recent advances in our knowledge of the range of bacteria occurring in soils, we have little knowledge of the ecology and biogeography of most microorganisms in forest soils. The relatively recent application of rRNA sequence analyses in determining the phylogenetic relationships between organisms has led to some reclassification within and among microbial groups.

Prokaryotes

From an evolutionary point of view the prokaryotes were the first life form to appear, evolving about 3.5 billion years ago. Prokaryotes are molecules surrounded by a membrane and cell wall; they lack subcellular membrane-enclosed organelles.

Bacteria

The bacteria are single-celled prokaryotic organisms that lack a true nucleus, and at between 0.2 and 1 μm in length they are among the smallest forms of life in forest soils. They have rigid cell walls and, where motile, move by means of a flagellum. There are three basic cell shapes among the bacteria: cocci, rods, and spirals. Among the 12 or so phyla of bacteria, three are generally associated with forest soils: the purple bacteria, the Gram-positive bacteria,

Table 1 Overview of the major biota found in forest soils. The dashed line shows the division of biota according to size

Size group	*Cell type*	*Kingdom or domain*	*Important groups found in forest soils*	*Example subgroup* or *genus*
Microflora (0.1 μm–10 μm)	Prokaryotes	Archaea	Methanogenic archaea	*Methanobacterium, Methanococcus*
		Bacteria	Purple bacteria	Nitrifying bacteria
			Sporogenic bacilli	Bacillales
			Cyanobacteria	Nostocales
			Actinomycetes	Thermomonosporas
	Eukaryotes	Mycota or fungi	Zygomycota	Zygomycetes, *Mucor*
			Ascomycota	Ascomycetes, *Aspergillus*
			Basidiomycota	Mushrooms, *Agaricus, Gloeophyllum*
			Deuteromycota	Deuteromycetes, *Arthrobotrys*
		Protoctista	Algae	Chlorophyta, *Chlorella*
			Oomycetes	Saprolegionales, *Phythium*
Microfauna (body width< 100 μm)			Ciliophora	Ciliates, *Paramecium*
			Sarcomastigophora	Naked and testate amoebae
			Mycetozoa	*Dictyostellium*, *Acrasis*
		Animalia	Nematodes	Nematodes
Mesofauna (body width 100 μm to 2 μm)			Rotifers	Rotifers
			Microarthropods	Acari (mites)
				Collembola (springtails)
			Annelids	Enchytraeidae (enchytraeids)
Macrofauna (body size generally ranges from 2 mm to 20 mm, but may be greater)				Lumbricidae (earthworms)
				Megascolecidae (earthworms)
			Macroarthropods	Hymenoptera (ants)
				Isoptera (termites)
				Chilopoda (centipedes)
				Diplopoda (millipedes)
				Pauropoda (pauropods)
				Isopoda (crustaceans)
				Coleoptera (beetles/weevils)
				Mollusca (mollusks)
Macroflora		Plantae		Plant roots

Adapted from Coleman DC and Crossley DA (1996) *Fundamentals of Soil Ecology*. London: Academic Press and Lavelle P and Spain AV (2001) *Soil Ecology*. London: Kluwer.

Table 2 Known and estimated total species numbers

Group	*Known species*	*Estimated total species*	*Percentage known*
Vascular plants	220 000	270 000	81
Bryophytes	17 000	25 000	68
Algae	40 000	60 000	67
Fungi	69 000	1 500 000	5
Bacteria	3 000	30 000	10
Viruses	5 000	130 000	4

Adapted from Coleman DC and Crossley DA (1996) *Fundamentals of Soil Ecology*. London: Academic Press.

and the cyanobacteria. These bacterial groups are capable of exploiting a wide range of energy sources – a trait that is important in the functional processes of forest ecosystems. Overall, because bacteria are not able to penetrate organic material their progress as cellulose decomposers is limited to the surface erosion of substrates; their rate of substrate breakdown is proportional to the rate at which exoenzymes are produced and diffuse out from the bacterial colonies. The purple bacteria cover a diverse range of metabolism including aerobes, anaerobes, chemoautotrophs, chemoheterotrophs, and chemophototrophs. The Gram-positive bacteria include the actinomycetes and the sporogenic bacilli. Members of both these groups (including the free-living *Clostridium*) are able to fix atmospheric nitrogen. The cyanobacterial group comprises obligate photoautotrophs that occur in unicellular, colonial, and filamentous forms with cell diameters usually within 1.0 to 10 μm. The relatively recent development of 16S ribosomal RNA (rRNA) gene sequence studies has revealed evidence in soil of bacterial divisions not usually associated with soil, including green nonsulfur bacteria, planctomycetes, spirochaetes, and novel methane-producing archaea.

Table 3 Examples of current methods for analyzing microbial diversity in soils and their application

Method	*Comments*
Culturing of microbes	Generally not representative of biota present
16S rRNA gene sequence analysis with polymerase chain reaction amplification	Provides identification of members of a community
In situ hybridization	Can be used to identify metabolically active microorganisms
Substrate utilization	Measures metabolic diversity
Flow cytometry	Enumeration of microorganisms
Terminal restriction fragment length polymorphisms	Comparative analysis
Polymerase chain reaction amplification or expression cloning	Functional diversity targeted
RNA dot or slot block	Representation of metabolically active members of a community

Reproduced with permission from Rondon MR, Goodman RM, and Handelsman J (1999) The Earth's bounty: assessing and accessing soil microbial diversity. *Trends in Biotechnology* 17(10): 403–409.

Archaea

This group has generally been known as the archaeabacteria, with recent studies preferring to call them archaea because of significant differences in their cell structure compared with bacteria. Members of this classification are subdivided into a range of groups on the basis of photosynthetic ability, means of locomotion, and nature of the cell wall where one is present. The archaea lack a muramic acid component in their cell walls, which contain branch-chained, ether-linked lipids that differ greatly from cell walls in eukaryotes. This radically different cell wall structure has led some taxonomists to claim that, in evolutionary terms, archaeans are more distant from the bacteria than are animals. Although the group includes organisms capable of flourishing in extreme conditions not usually associated with forests (e.g., the extreme halophytes and extreme thermophiles), there are a few reports of archaea occurring in nonextreme environments in forest soils. In addition, a number of groups may be important under certain conditions in forest soils; among these are the methane-producing archaea (methanogens; e.g., *Methanobacterium, Methanococcus*) and the thermoacidophiles (*Sulpholobus, Acidothermus*). The latter group are chemoautotrophic sulfur archaea capable of transforming sulfur forms in soil. In boreal forest soils the first reports of the genetic diversity among archaea have begun appearing in the literature over the last 5 years.

Eukaryotes

The eukaryotes appeared about 1.5 billion years ago. The basic eukaryote cell consists of a plasma membrane, glycocalyx, cytoplasm, cytoskeleton, and membrane-enclosed subcellular organelles. All of the soil animals and fungi are eukaryotes.

Fungi

The fungi (Mycota) are eukaryotic organisms that have a mycelial structure formed from slender filaments or hyphae (2–10 μm in diameter) that may be unbranched or branched, septate or nonseptate and which are commonly multinucleate. The fungi are subdivided on differences in mycelium structure and method of reproduction. Some of the main classes common in forest soils include the chytridiomycetes, the zygomycetes, the ascomycetes, and the basidiomycetes. Despite the wide range of fungi they are all chemoheterotrophic and in forest soils most are aerobic. None of the fungi is capable of fixing nitrogen from the atmosphere. Fungi are particularly prevalent in forest soils because of their ability to decompose lignin, which is a major component of wood, and to tolerate a wide range of soil pH. Fungi use exoenzymes to decompose substrates and their filamentous habit allows them to invade and ramify through substrates, applying mechanical pressure with their elongating hyphae. In this way fungi are able to import nutrients to enable them to break down substrates. These life-form advantages of fungi in decomposition mean that only in anaerobic habitats, such as waterlogged soils, do the bacteria predominate over the fungi. Fungi are the most abundant decomposing organisms in aerated forest soils, with typical biomass ranges of $500–5000\,kg\,ha^{-1}$. In the forest floor the fungi can represent between 10% and 60% of the total biomass; only plant roots exceed them in terms of biomass in soil.

Soil Fauna

Based on body size, habitat preference, and food consumed, soil fauna are generally assigned to one of three functional groups – microfauna, mesofauna or macrofauna (**Table 1**). In forests, approximately 90% of the soil faunal biomass is usually found in the top 10 cm of humus and soil. The relative abundance of soil fauna changes among forests at different latitudes; macrofauna tend to be more abundant in the tropics than they are in temperate regions, while microfauna are often more common in temperate regions than in the tropics. The microfauna, of which nematodes and protozoa are the major taxa, are single-celled fauna with a body width of $<100\,\mu m$; they lack mitochondria and live in water-filled pores and water films around soil particles. Some are motile. Most are heterotrophic and feed by engulfing their prey, usually other soil microbes. They are predominantly restricted to the topsoil for this reason. Among the protozoa are a number of groups that are common in forest soils – the ciliates, the amoebae, and the slime molds. Ciliates (Phylum Ciliaphora) are mostly freeliving in water films in soil; they feed by grazing on bacteria and particulate organic matter. Amoebas (Subphylum Sarcodina) are either naked or shelled, with the encased or testate amoebae largely inhabiting freshwater and moist soils. Slime molds (Phylum Mycetozoa) are divided into cellular and true slime molds, both of which are found in moist soils where they feed on live bacteria. The mesofauna, including the microarthropods, such as mites, collembolans (wingless insects), and enchytraeid worms, have a body width of 100 μm to 2 mm. The mesofauna are litter-transformers that produce organic structures in the form of faecal pellets that act as incubators for microbial digestion; their effect on soil structure is minimal.

The macrofauna, often termed ecosystem engineers, include earthworms, ants, termites, myriapods (centipedes and millipedes), snails, and slugs. Their body size generally ranges from 2 to 20 mm but may be much greater, particularly in the case of earthworms. The macrofauna directly or indirectly modulate the availability of resources and microhabitats for other soil biota by causing physical changes to the soil environment and biotic materials. While the role of the larger soil animals such as earthworms in litter mixing with other soil components is accepted, their role in decomposition is largely unknown. We know that earthworms ingest and move organic material but the extent of direct decomposition by soil animals is relatively unknown.

Energy Sources and Modes of Nutrition of Soil Biota

Soil microorganisms in forest ecosystems function through control of decomposition and the release of materials from organic substrates. In particular, they mediate carbon (C), phosphorus (P), nitrogen (N) and sulfur (S) biogeochemical cycling. The way in which soil microorganisms satisfy their demands for energy and nutrients is a guide to their particular role in the flow of energy and nutrients in forests and, more broadly, to their role in ecosystem function. A useful functional classification of these organisms is based on the nature of their principal carbon sources and energy. On the basis of principal carbon source organisms are classified as either autotrophic (inorganic C source; mostly CO_2; also referred to as lithotrophic) or heterotrophic (organic C source; diverse range of compounds; also referred to as organotrophic). In a similar way, organisms are classified based on their energy source; those using radiant energy (phototrophs) and those dependent on energy released during chemical oxidation (chemotrophs) (**Table 4**). Microorganisms regulate a wide range of processes critical to forest ecosystem function including denitrification, sulfate reduction, methanogenesis, and manganese reduction (see **Table 5** for a comprehensive listing of chemoautotrophic transformations).

Heterotrophs and Autotrophs

The vast majority ($>90\%$ biomass) of bacteria and fungi in forest soils are chemoheterotrophic (derive

Table 4 Energy and carbon sources for classes of soil organisms

Class of soil organism	*Energy source for generating ATP*	*Source of carbon for the cell*	*Example of organisms*
Photoautotroph	Light	CO_2	Cyanobacteria, plants
Chemoautotroph	Inorganic compounds	CO_2	Non-purple sulfur bacteria
Photoheterotroph	Light	CO_2, organic matter	Bacteria
Chemoheterotroph	Organic matter	Organic matter	Most bacteria, fungi

Table 5 Physiological groups of soil chemoautotrophs

Physiological group	*Life form*	*Energy source*	*Oxidized end product*	*Organism*
Hydrogen bacteria	Bacteria	H_2	H_2O	*Alcaligenes, Pseudomonas*
Methanogens	Archaea	H_2	H_2O	*Methanococcus*
Carboxydobacteria	Bacteria	CO	CO_2	*Rhodospirillum, Azotobacter*
Ammonium oxidizing bacteria	Bacteria	NH_3	NO_2^-	*Nitrosomonas*
Nitrite oxidizing bacteria	Bacteria	NO_2^-	NO_3^-	*Nitrobacter*
Sulfur oxidizers	Bacteria	H_2S or S	SO_4^{2-}	*Thiobacillus*
	Archaea	H_2S or S		*Sulfolobus*
Iron bacteria	Bacteria	Fe^{2+}	Fe^{3+}	*Gallionella, Thiobacillus*

both energy and materials for cell growth from an organic substrate). Because of the dominance of this group in most soil conditions they are often simply referred to as the heterotrophs. In well-aerated forest soils, aerobic heterotrophic respiration dominates, but fermentation and anaerobic respiration take over as soils become waterlogged. Among the bacteria two groups of heterotrophic nitrifiers exist, one oxidizing ammonium and the other the various organic forms of N including hydroxylamine, amino acids, peptones, oximes, and some aromatic compounds. Autotrophic microflora carry out a wide range of transformations and also play a critical role in ecosystem functioning. **Table 5** summarizes the major groups and end products of these organisms. Foremost in forest soils are the chemoautotrophic nitrifying bacteria that are responsible for the transformation of ammonium (NH_4^+) into nitrite (NO_2^-) and nitrate (NO_3^-). Autotrophs grow more slowly and are less abundant in soil than heterotrophs, due to their lower energy yield. Despite this there is good evidence to show that chemoautotrophic bacteria are the main nitrifying agents in most acid forest soils.

Activities and Impacts of Soil Biota in Forest Ecosystems

Forest floor litter type provides evidence of differences in composition and activity of forest soil biota. The activity of soil biota is directly related to the three humus forms generally recognized in forests (see **Table 6**). A mull humus results from the rapid disappearance of leaf litter under the influence of a wide range of faunal groups (macro-, meso-, and microfauna). Mull is typical of grasslands and deciduous forests and is associated with rapid litter decomposition and relatively nutrient-rich soils. A mor humus is characterized by the accumulation of undecomposed plant remains that form a distinct organic horizon overlying the mineral soil. Compared with mull humus, biological activity is low in a mor with minimal animal and lignin-decomposing fungal activity. This humus type is associated with acidic surface soils, cool to cold climates and relatively nutrient-poor soils. Typically, mor humus is associated with coniferous forests where decomposition of the acidic litter is dominated by saprophytic fungi; and the 'ecosystem engineer' functional group is dominated by ants rather than deep-burrowing earthworms, which tend to be acid-sensitive. Moder humus is intermediate between mull and mor, with reduced macrofaunal activity compared with a mull and a microflora dominated by fungi due to the predominantly acid conditions. Moder humus forms are mainly found in deciduous and coniferous forests.

Functional Groups Among Forest Soil Biota

Each group of soil organisms contributes either directly or indirectly to the breakdown of organic matter, decomposition and the release of nutrients back into the soil environment for plant growth (**Table 7**). The following section outlines the roles of microbial and faunal organisms in the process of decomposition. In forest ecosystems only about 1.5–5% of primary production is consumed by herbivores. A very large portion of primary production is consumed by the soil organisms. The microbial component of the soil biota is the main consumer of this organic matter in forest soils, being responsible for over 90% of decomposition and mineralization. The soil fauna play an important role in the physical breakdown or comminution of litter that a exposes a surface area for subsequent microbial attack.

The Decomposers

Bacteria and fungi drive the decomposition and release of nutrient ions from organic substrates; they are central to the functioning of forest ecosystems and more broadly to the functioning of the biosphere. Soil microorganisms are unable directly to ingest the often large and complex range of

Table 6 Summary of biological features associated with the three main humus forms found in forests

Characteristic	*Mull*	*Moder*	*Mor*
Biodiversity and productivity	High	Medium	Low
Phenolic content of litter	Low	Medium	High
Humification rate	Rapid	Slow	Very slow
Mycorrhizal partners	Zygomycetes	Basidiomycetes	Ascomycetes
Faunal group dominant in biomass	Earthworms	Enchytraeids	None
Microbial group dominant in biomass	Bacteria	Fungi	None

Reproduced with permission from Ponge J-F (2003) Humus forms in terrestrial ecosystems: a framework to biodiversity. *Soil Biology and Biochemistry* 35: 935–945.

Table 7 Influences of soil biota on soil processes in forest ecosystems

Group	*Nutrient cycling*	*Soil structure*
Microflora (fungi, bacteria, actinomycetes)	Catabolize organic matter; mineralize and immobilize nutrients	Produce organic compounds that bind aggregates; hyphae entangle particles into aggregates
Microfauna (e.g., protozoa, nematodes)	Regulate bacterial and fungal populations; alter nutrient turnover	May affect aggregate structure through interactions with microflora
Mesofauna (e.g., Acarina, Collembola, enchytraeids)	Regulate fungal and microfaunal populations; alter nutrient turnover; fragment plant residues	Produce fecal pellets; create biopores; promote humification
Macrofauna (e.g., isopods, centipedes, millipedes, earthworms)	Fragment plant residues; stimulate microbial activity	Mix organic and mineral particles; redistribute organic matter and microorganisms; create biopores; promote humification; produce fecal pellets

Adapted from Hendrix PF, Crossley DA Jr, Blair JM, and Coleman DC (1990) Soil biota as components of sustainable ecosystems. In: Edwards CA *et al.* (eds) *Sustainable Agricultural Systems*, pp. 637–654. IA: Soil and Water Conservation Society.

molecules that comprise soil organic matter; instead they secrete enzymes that digest organic matter outside the cell and they accumulate nutrients – either from the decomposing substrate or the surrounding soil solution – against a concentration gradient; most are aerobic. Overall, fungi are a crucial link in terrestrial nutrient cycling as they are involved in decomposition, in mycorrhizal associations, and in predatory and pathogenic activities. The activity and abundance of fungi in forest soils can be assessed by a number of means including analysis for ergosterol (a major sterol found in most fungi but not in higher plants) that can be used to measure fungal penetration of plant material. Another relatively recent and promising line of investigation is analysis for C and N stable isotope abundance in fungal sporocarps, a technique that can differentiate between ectomycorrhizal and saprotrophic forest fungi. For example, forest basidiomycetes become enriched in ^{13}C relative to their bulk C source, and either enriched or depleted in ^{15}N relative to atmospheric N. The coupling of molecular marker methods with stable isotope abundance in biomarkers offers considerable promise in linking bacterial identity with function in the environment. These molecular and isotope techniques are likely to become important diagnostic tools and will help elucidate ecological roles of various fungi and bacteria in the field.

The Ecosystem Engineers

Soil fauna play an indirect role in decomposition and mineralization through regulation and stimulation of microbial populations, fragmentation of plant residue and alteration of the physical soil environment. From a functional perspective, organisms that regulate the availability of resources to other species by physically rearranging biotic materials – to modify, maintain and/or create habitats – have become known as ecosystem engineers. Foremost among ecosystem engineers in forest soils are earthworms and termites. The natural tilling effect of earthworms in soils has been long known; they may pass up to 30 tonnes ha^{-1} of soil through their bodies, some of which is excreted as casts which may be enriched in nutrients relative to bulk soil.

Climate Change, Forest Management, and Soil Biota

Impact on Soil Processes

There is considerable interest in fluxes of CO_2, N_2O, and CH_4 from forest soils because of the potential for climate change to alter emission rates of these greenhouse gases. Soil organic matter (SOM) is a major pool of carbon and its magnitude and dynamics are largely controlled by soil microbial activity. For this reason, there is interest in improving our understanding of humus formation and degradation as controlled by soil microorganisms; however, research into the direct effects of increased atmospheric CO_2 on the soil microbial community is not sufficient to predict outcomes. Where nitrogen deposition or inputs to forests are high there is concern for increased N_2O emissions through either heterotrophic denitrification or, possibly, through leakage from autotrophic nitrification. For example, N_2O emissions of the order of 1–4 kg N ha^{-1} $year^{-1}$ occur from spruce forests in southern Germany, where N deposition is around 30 kg N ha^{-1} $year^{-1}$. These N_2O emissions are thought to result mainly from the activities of facultative anaerobic heterotrophs, such as *Pseudomonas*, that switch to NO_3^- as

Table 8 Denitrifying bacteria in soil, and their metabolism and energy source – an example of the diverse range of organisms potentially involved in converting nitrate to gaseous N in forest soils

Denitrifying organism	*Metabolism*	*Energy source*
Pseudomonas	Chemoheterotroph	Soil organic matter
Paracoccus denitrificans	Chemoautotroph	H_2
Thiobacillus denitrificans	Chemoautotroph	Reduced S
Rhodopseudomonas	Photoautotroph	Light

a terminal electron acceptor when O_2 diffusion is limited by high soil moisture. There is also some evidence of N_2O production in woodland soils by heterotrophic fungi, where NO_3^- is used as an alternative for O_2 in respiration, and denitrification occurs simultaneously. Because of the broad range of processes with potential to produce N_2O in forest soils (summarized in **Table 8**), further studies are required to determine the impacts of forest management and climate change on N_2O emissions. There has been considerable interest in the impacts of forest management on methane (CH_4)-oxidizing bacteria because temperate forests are major sinks for atmospheric CH_4. For example, forest clear-cutting can reduce the activity of methane-oxidizing bacteria and therefore the net CH_4 consumption in forest soils; changes that apparently result from the inhibition of CH_4 oxidation by elevated soil inorganic N. Less invasive forms of management such as thinning have been associated with increased CH_4 consumption.

Impact on Species Composition and Abundance

Determining the impact of climate change and forest management on soil biota and the critical processes they mediate in forest soils remains a significant challenge for the future. For example, the current literature indicates that there is not enough information to predict the impact of increased atmospheric CO_2 on the soil microbial community. Progress towards this task will rely on linking, through empirical testing, functional groups and key species among the soil biota with key processes maintaining ecosystem stability, such as decomposition and nitrogen fixation. In this way the contributions of the huge diversity of soil biota may be simplified to allow a better understanding of changes in the soil environment on ecosystem processes and stability.

Further Reading

Blondel J (2003) Guilds or functional groups: does it matter? *Oikos* 100: 223–231.

Coleman DC and Crossley DA (1996) *Fundamentals of Soil Ecology*. London: Academic Press.

Hendrix PF, Crossley DA Jr, Blair JM, and Coleman DC (1990) Soil biota as components of sustainable ecosystems. In: Edwards CA *et al*. (eds) *Sustainable Agricultural Systems*, pp. 637–654. IA: Soil and Water Conservation Society.

Jones CG, Lawton JH, and Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69: 373–386.

Killham K (1994) *Soil Ecology*. Cambridge, UK: Cambridge University Press.

Lavelle P (2002) Functional domains in soils. *Ecological Research* 17: 441–450.

Lavelle P and Spain AV (2001) *Soil Ecology*. London: Kluwer.

Paul EA and Clark FE (1996) *Soil Microbiology and Biochemistry*, 2nd edn. London: Academic Press.

Ponge J-F (2003) Humus forms in terrestrial ecosystems: a framework to biodiversity. *Soil Biology and Biochemistry* 35: 935–945.

Richards BN (1987) *The Microbiology of Terrestrial Ecosystems*. New York: John Wiley.

Rondon MR, Goodman RM, and Handelsman J (1999) The Earth's bounty: assessing and accessing soil microbial diversity. *Trends in Biotechnology* 17(10): 403–409.

Swift MJ, Heal OW, and Anderson GM (1979) *Decomposition in Terrestrial Ecosystems*. Oxford, UK: Blackwell Scientific Publications.

Woese CR (1987) Bacterial evolution. *Microbiology Reviews* 51: 221–271.

Soil and its Relationship to Forest Productivity and Health

J A Burger, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

Forest Soil and its Functions

Soil is a mixture of mineral materials, organic matter, water, air, and plant and animal life. It varies in depth from a few centimeters to several meters across most of the earth's terrestrial surface. Its rock, sand, silt, clay, and organic matter physical composition varies in texture and structure, which controls the infiltration, percolation, and storage of water and the balance between water and air in its pore space. The amount and nature of clay and organic matter and the influence of parent material and vegetation largely control its chemistry and level of fertility. Soil also contains and is made up of myriad macro-, meso-, and microorganisms, both plant and animal, essential for organic matter decomposition, nutrient cycling, energy conversion, and soil formation processes. Soils vary greatly across the landscape due to soil forming factors, including the nature of parent rocks and minerals from which they are derived, the amount of relief in the local topography, the types of plants and animals in and on the soil, the nature of the local climate, and the amount of time a soil has been in place. Soils can vary in age from a few years to millions of years.

Soils serve a variety of functions in forest ecosystems. They serve as a medium for tree growth; they anchor the tree physically and supply water and nutrients for uptake by tree roots; and they serve as water-transmitting layers on the earth's surface. During rain events or snowmelt, water moves into soil, percolates to a saturated zone or water table, and remerges downslope in streams and rivers. Absorption of water into soil regulates the flow and controls the quality of water in watersheds. Finally, soil serves as an ecosystem component. It controls the flow of energy, the cycling of chemical elements, the rate of organic matter decomposition, carbon sequestration, and biodiversity. The interaction of soil properties and processes determines forest health and productivity.

Forest Health and Productivity

Forest Health

Forest health is a qualitative term that refers to the general condition of a forest. A healthy forest is one that is relatively free of insect infestations, diseases, exotic weeds, and air pollution. All species making up the forest are able to grow at rates commensurate with the local climate, geographic position, and soil resource to complete their life cycles. A healthy forest can resist damage from catastrophic events like acute insect and disease attacks, fire, wind, and flooding, and fully recover from these perturbations to continue its life history functions over decades, centuries, or millennia. Soil influences forest health by securely anchoring trees' roots, by regulating energy flow among ecosystem components, and by controlling water and nutrient availability for the benefit of the entire forest system. The habitat of soil organisms that play a role in decomposition and nutrient cycling processes is also controlled by the presence and nature of the soil. During dry periods, droughty soils may predispose forests to insect and disease attack, but if the forest can recover normally, natural, periodic stress caused by soil-induced limits on water or nutrients is not considered unhealthy over the long term.

Forest Productivity Definition and Concepts

Forests that grow quickly and produce large amounts of biomass in a short period of time are said to be highly productive. For example, a mixed tropical forest in the Amazon basin of Brazil is more productive than a black spruce forest in Canada. Forest productivity is the rate of accumulation of forest dry matter per unit area per unit time. It is commonly expressed as net primary productivity (NPP). NPP includes the biomass accumulation of all plants' stems, leaves, roots, and reproductive structures, and it includes litterfall, root sloughing, and the plant biomass consumed by herbivores and plant and animal decomposers. NPP is expressed in units of dry mass accumulation per square meter per year ($g\,m^{-2}\,year^{-1}$), or dry mass per hectare per year ($Mg\,ha^{-1}\,year^{-1}$). The belowground component of NPP is difficult to measure. Most measures of NPP are for the more easily determined aboveground component only (ANPP).

Forest productivity can be depicted and defined as a logistic curve of production as a function of time (solid line in **Figure 1**). Just after forest establishment, when light, water, and nutrient resources are in ample supply, biomass increases exponentially until a point in time (inflection point) when resources are fully exploited by the forest. This usually coincides with stand closure and maximum leaf area development. After this point of inflection on the curve, production decreases exponentially due to light, water or nutrient limitations. Biomass accumulation reaches a maximum when light, water, or nutrient

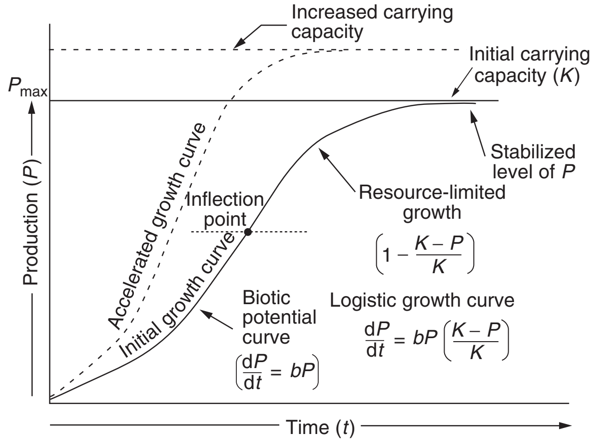


Figure 1 The forest biomass production curve is a logistic function based on the relative availability of light, water, and nutrient resources through time. Dashed lines show the potential for increasing productivity with site treatment over that of a nontreated condition (solid lines). Increasing soil quality (carrying capacity) increases productive potential (P_{max}), and alleviating water and nutrient limitations shortens the time required to reach carrying capacity. Reproduced with permission from Burger JA (2002) Soil and long-term site productivity values. In: Richardson J, Bjorheden R, Hakkila P, Lowe AT, and Smith CT (eds) *Bioenergy from Sustainable Forestry: Guiding Principles and Practice*, pp. 165–189. Dordrecht, The Netherlands: Kluwer.

resources limit the rate of photosynthetic carbon fixation to the level of carbon depletion via respiration; this is called the compensation point. This level of maximum production is the site's carrying capacity or potential.

Measuring Forest and Site Productivity

Historical production records from multiple harvests of fully stocked stands growing on the same site would provide the best and most direct measure of forest and site productivity; however, records for multiple growth cycles are not available for most forest sites. Foresters estimate forest productivity by measuring the rate of growth, or the volume accumulation of live, standing, aboveground woody biomass ($m^3\,ha^{-1}\,year^{-1}$) contained in the stems of desired crop trees. The mean, or average annual growth, is determined by dividing the total stand volume of live, standing tree stems by the total age of the tree stand; this is also called mean annual increment (MAI).

Forest sites that have the potential to produce biomass at a rapid rate are said to have high site quality. Site quality is the sum of the effect of all site factors on the capacity of a forest to produce biomass. MAI can be used for a relative measure of site quality. To estimate site quality, MAI is determined at the culmination of the increase in mean annual increment, the age at which mean annual increment peaks.

A faster, easier, but indirect measure of site quality is a tree's height relative to its age. Trees grow faster on good sites and slower on poor sites, while height remains well correlated to tree volume. As the quantity and quality of soil improves, trees grow at faster rates and will be taller at a given age (**Figure 2**). Their height growth is sensitive to site factors, but relatively independent of stand density. This height/age relationship is called the site index and is usually defined as the height of dominant and codominant trees in well-stocked, even-aged stands at a preselected or index age. Index ages of 25, 50, and 100 years are commonly used for fast-growing pines and eucalypts, hardwoods, and slow-growing northern conifers, respectively.

For the purpose of spatially mapping forest land and prescribing silvicultural treatments to areas based on site potential, site quality is commonly ranked by class, depicted by Roman numerals I through V, with site quality class I being the most productive and class V the least. **Table 1** shows the relationship between site quality, volume, product class, and value. As trees grow, diameter increases exponentially; therefore, volume and value increase exponentially. Wood in large tree stems is disproportionately more valuable than wood in small tree stems due to the products associated with each. For example, sawtimber is more valuable than firewood and results in a much greater return on investment from forest stands managed as a business enterprise.

Site and Soil and their Relationship to Forest Productivity

Overall, tropical rainforests have the greatest ANPP, followed by temperate and boreal forests. This gradient in productivity with latitude is mostly due to length of growing season, temperature, and amount of available water. ANPP increases as

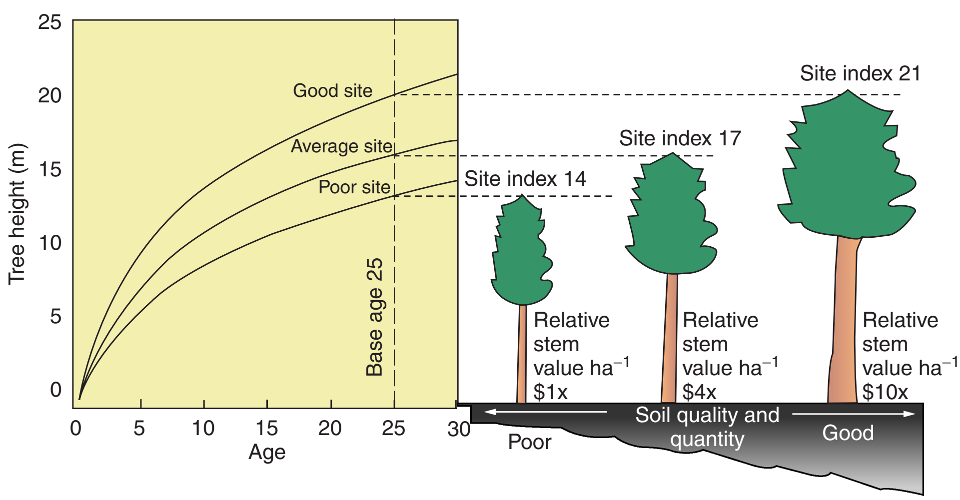


Figure 2 The depth and quality of soil influences the rate at which trees grow and accumulate biomass. Site index, the height of dominant and codominant trees in stands at an index age (e.g., age 50), is the most common method used by foresters to estimate site quality.

Table 1 The influence of site quality on wood production, product class, and return on investment; Appalachian oak is used for this example

Site quality class	*I*	*II*	*III*	*IV*	*V*
Oak site index (m)	26	23	20	17	14
Stem volume MAI ($m^3 ha^{-1} year^{-1}$)	8.0	6.2	4.6	3.0	1.8
Commercial use and value	Furniture, veneer	Sawtimber	Railroad ties	Firewood	None
Return on investment (%)[a]	10	7	3	0	−5

[a] Return on investment estimates were based on average stumpage values and management costs for the Appalachian region during 2001. Emphasis is on the relative difference in values among site quality classes; absolute values vary with regional economic conditions.

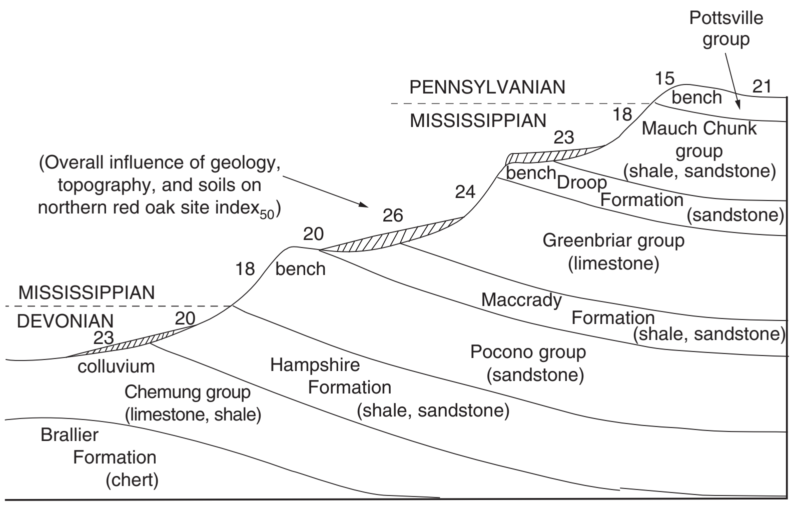


Figure 3 Hillslope in the Appalachian Mountains region of West Virginia. Site quality varies greatly on this hillslope gradient due to geologic, topographic, and soil features.

growing season, temperature, and available water increase. Across this gradient, ANPP varies by more than an order of magnitude, from more than $20\,Mg\,ha^{-1}\,year^{-1}$ for tropical rainforests to less than $2\,Mg\,ha^{-1}\,year^{-1}$ for boreal forests. Within a region of relatively uniform temperature and rainfall, ANPP can vary tenfold due to topographic position, geology, and soil quality. These site and soil factors influence tree growth primarily through water and nutrient availability.

Geologic and Topographic Site Factors

Soils are formed from residual material or from material transported and deposited by water, wind, ice, or gravity. The productivity of residual soils is influenced by rock and mineral type and the rate at which they weather. Limestones and shales weather faster than most sandstones creating deeper, more fertile soils. Common igneous and metamorphic soil-forming rocks are generally more resistant to weathering, although most are rich in minerals required by plants. Soils derived from transported materials are generally very productive, as they are found in low landscape positions and consist of existing soil materials transported from higher elevations. The position, orientation, and layering of geologic materials also influences soil weathering rates, soil water movement and storage, and depth of rooting. In the northern hemisphere, steep, mid-slope positions with southwest aspects have the shallowest soils and highest evaporative demand. The deepest, most productive soils are found on northeast-facing slopes at slope bottoms. Topographic features influence productivity predominantly by controlling plant available water and controlling the harmful effects of fire, wind, snow, and ice. On flatter terrain, slight changes of only a few centimeters in elevation can influence the depth to a water table and the effective soil depth that trees can exploit. In the case of soils with high water table, productivity is more often nutrient limited due to insufficient aerated soil volume.

Figure 3, a not-to-scale drawing of an actual hillslope in the Appalachian Mountains of the USA, illustrates the interaction of geologic, topographic, and soil factors influencing site productivity. The site index of northern red oak (*Quercus rubra*), a native species that occurs naturally across the entire hillslope gradient, ranges from 15 to 26 meters as a function of these interacting factors. It is most productive at mid-slope, growing in colluvium and residuum of a limestone-derived soil. It is least productive growing on bench positions above weathering-resistant, quartzitic meta-sandstone layers (Pocono and Pottsville formations). Its productivity is intermediate on soils derived from shale formations. Productivity is intermediate (higher than expected due to site factors alone) at the top of the mountain due to higher rainfall caused by orographic precipitation.

Soil Factors

Soils have basic physical, chemical, and biologic properties that influence soil climate and fertility, the two general conditions that influence forest productivity and health. The complex structural and functional components of soil climate and fertility are conceptualized in the drawing in **Figure 4**. Soil depth, horizonation, texture, structure, and porosity determine the rate of flow and storage of heat, water, and air that in turn influence rates of metabolic activity in roots and their growth. Soil fertility and nutrient availability is determined, in part, by organic matter decomposition and mineralization, and the weathering of soil parent materials. The extent to which soil climate and fertility processes are optimized determines the availability of water, oxygen, and nutrients for uptake by forest plants.

Measurable soil factors influencing tree growth include total depth or depth of certain layers, organic matter content, nutrient content, air/water balance, and depth to a water table or restricting layer. There are dozens of studies in the literature that correlate ANPP with soil properties. Different soil properties are more influential than others in different regions. For example, numerous correlation studies have shown that, in the Atlantic coastal plain region of the USA, southern pine growth is most influenced, in order of listing, by thickness of the subsoil, depth of the surface soil, drainage, depth to mottling, nutrient content, and organic matter content. In the northwest region of the USA, mixed conifers are most influenced by soil depth, surface soil texture, water-holding capacity, nutrient content, subsoil texture, and coarse fragment content.

Increasing Forest Productivity by Increasing Soil Quality

Forest productivity is determined by tree genetic potential, soil and site factors, and silvicultural inputs. Therefore, forest productivity can be increased (dashed line in **Figure 1**) by improving the genetic make-up of the trees, and by temporarily alleviating deficiencies in water and nitrogen by irrigating or fertilizing. These silvicultural inputs usually shorten the length of time required for biomass to reach the site's carrying capacity, which is one way to increase forest productivity (shorter rotations). A second way of increasing productivity is to increase site carrying capacity for additional

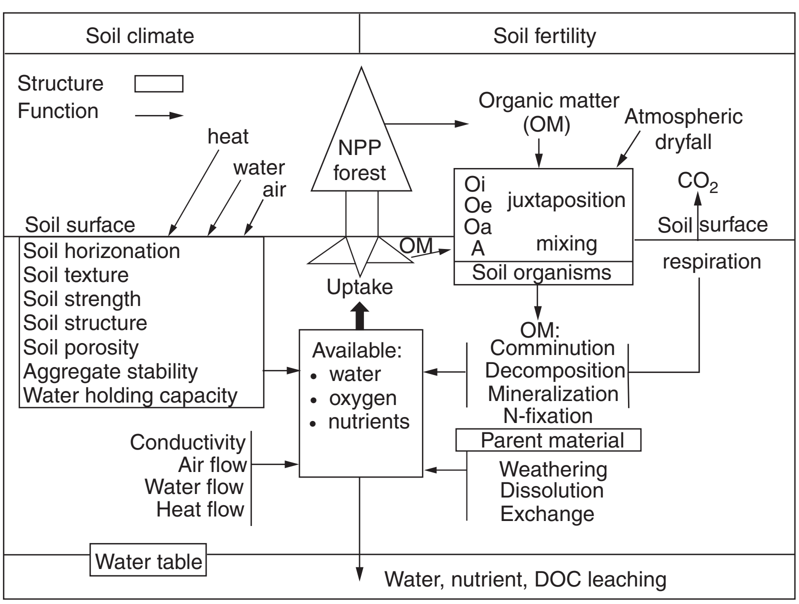


Figure 4 Conceptual model of soil properties and processes influencing forest productivity. DOC, dissolved organic carbon; NPP, net primary productivity. Reproduced with permission from Burger JA (2002) Soil and long-term site productivity values. In: Richardson J, Bjorheden R, Hakkila P, Lowe AT, and Smith CT (eds) *Bioenergy from Sustainable Forestry: Guiding Principles and Practice*, pp. 165–189. Dordrecht, The Netherlands: Kluwer.

production potential. Carrying capacity can be increased with site treatments that cause a more or less permanent change in site carrying capacity, such as increasing effective rooting depth by eliminating barriers to root growth, by draining wet soils, by adjusting soil acidity or alkalinity, or by adding phosphorus to deficient soils. These modifications of the soil resource raise the P_{max} on the y axis in **Figure 1**. The dashed production curve depicts an increase in forest productivity due to an increase in site quality or carrying capacity, and a further increase due to a shorter growth cycle.

In most cases it is not practical to irrigate forest stands. Instead, foresters shift limiting water resources to crop trees by eliminating competing vegetation and by thinning crop trees at appropriate times during the growth cycle. ANPP is not increased, but the amount of merchantable wood is increased by shifting resources to fewer, merchantable trees at the expense of nonmerchantable vegetation. Nitrogen is often growth limiting in both managed and nonmanaged forests throughout the world. In managed forests, deficiencies can be aggravated by removing harvest slash and soil organic matter in the process of preparing the site for planting, and by accelerating nitrogen mineralization through soil tillage. Deficiencies usually occur in managed, even-aged forests during or just after canopy closure. Adding nitrogen at mid-rotation temporarily fertilizes the trees, but usually has little long-term effect on soil fertility. Multiple additions of nitrogen through time are usually needed to completely alleviate deficiencies. Because nitrogen additions fertilize the trees with little permanent effect on the soil, forest productivity increases, but site quality remains unchanged.

Phosphorus limits forest productivity in some forested regions of the world where total soil phosphorus levels are inherently low, or where phosphorus is chemically or physically bound and unavailable to plants. Deficiencies are alleviated by applying phosphorus at time of planting or site preparation. Because of the unique chemistry of soil phosphorus, it remains for long periods of time, increasing fertility for the length of the growth cycle and beyond. This long-lasting effect improves soil quality and increases site carrying capacity.

High soil strength and soil air and water imbalances are physical problems that can be addressed with site treatments. In all cases, forest practices that improve soil physical properties increase the amount and quality of the rooting environment. The amount of soil available for rooting is usually a function of depth, but can be a function of physical impedance or the inability of roots to physically penetrate soil, especially when dry. The physical quality of soil is mostly a function of soil structure and consistence that allows water and air to flow and be stored at optimum amounts. Naturally compacted soils, or soils compacted by machine trafficking, can be subsoiled, bedded, or harrowed to create better rooting environments. Poorly drained soils can be ditched to lower the water table, and sites can be bedded to elevate planted seedlings above water-saturated soil.

Forest productivity can also decrease if soil quality is damaged by forestry practice. Soil damage is usually an unintended side effect of forest harvesting, with the exception of chronic air pollution causing soil acidification and base leaching in forest soils of some industrialized regions of the world. Forest harvesting on wet soils compacts and puddles soils, which can restrict root growth and impede normal soil drainage. Site clearing after harvest, either mechanically or with intense fire, can remove significant amounts of organic matter and nitrogen, causing nutrient deficiencies at some point in the growth cycle. Forest practices and site treatments invariably change a variety of soil properties and processes, with both positive and negative effects. Sustainable forestry practices will ensure that the net effect is positive for sustainable forest productivity and health.

Human communities throughout the world desire forests that sustain plant and animal productivity, maintain balanced hydrologic, carbon, and mineral nutrient cycles, and maintain protective and environmental forest functions. Forest soils play an important role in each of these functions. Research for a better understanding of soil and its relationship to forest productivity and health is ongoing. Given that soils have complex properties and processes and are highly variable across the landscape, carefully prescribed soil- and site-specific forest management practices and treatments should ensure the maintenance of soil quality in both extensive and intensively managed forests.

Summary

Forest health is the condition of a forest relative to being free of insect, disease, water, and nutrient stresses, and to its ability to survive and recover from catastrophic events like fire, tornadic winds, and floods. Forest productivity is the rate of forest biomass accumulation per unit area per unit time. Forest productivity is controlled by the genetics of the species and individuals that make up the forest, and site and soil factors that include local climate, geology, topography, and soil properties that control water and nutrient availability and a tree's ability to root and anchor itself. Forest productivity can be increased by silvicultural site treatments that mitigate naturally compacted soils and those compacted by trafficking of heavy equipment. Improving drainage of wet soils, and reducing evaporative demand of dry soils by conserving organic matter and harvest debris, increase forest productivity by optimizing the balance of air and water in soils. Conservation of soil organic matter and harvest slash during forest operations conserves essential nutrients and helps regulate their availability, especially nitrogen, phosphorus, and calcium that are found limiting in some forest soils. Careful management of all site and soil resources will ensure sustainable forest productivity and health for the production of products and ecosystem services such as water control, carbon sequestration, wildlife habitat, and biodiversity.

See also: **Health and Protection**: Biochemical and Physiological Aspects. **Soil Biology and Tree Growth**: Soil Biology; Soil Organic Matter Forms and Functions; Tree Roots and their Interaction with Soil. **Soil Development and Properties**: Forests and Soil Development; Landscape and Soil Classification for Forest Management; Nutrient Cycling; Nutrient Limitations and Fertilization; Soil Contamination and Amelioration; The Forest Floor; Waste Treatment and Recycling; Water Storage and Movement. **Tree Physiology**: A Whole Tree Perspective. **Wood Formation and Properties**: Wood Quality.

Further Reading

Adams MB, Ramakrishna K, and Davidson EA (eds) (1998) *The Contribution of Soil Science to the Development of and Implementation of Criteria and Indicators of Sustainable Forest Management*. Madison, WI: Soil Science Society of America.

Boyle JR and Powers RF (eds) (2001) *Forest Soils and Ecosystem Sustainability*. Amsterdam, The Netherlands: Elsevier.

Burger JA (2002) Soil and long-term site productivity values. In: Richardson J, Bjorheden R, Hakkila P, Lowe AT, and Smith CT (eds) *Bioenergy from Sustainable Forestry: Guiding Principles and Practice*, pp. 165–189. Dordrecht, The Netherlands: Kluwer.

Doran JW, Coleman DC, Bezdicek DF, and Stewart BA (eds) (1994) *Defining Soil Quality for a Sustainable Environment*. Madison, WI: Soil Science Society of America.

Dyck WJ, Cole DW, and Comerford NB (eds) (1994) *Impacts of Forest Harvesting on Long-Term Site Productivity*. London: Chapman & Hall.

Gessel SP, Lacate DS, Weetman GF, and Powers RF (eds) (1990) *Sustained Productivity of Forest Soils*. Vancouver, Canada: University of British Columbia, Faculty of Forestry.

Greenland DJ and Szabolcs I (eds) (1994) *Soil Resilience and Sustainable Land Use*. Wallingford, UK: CAB International.

Proe M, Smith CT, and Lowe AT (eds) (1999) *Indicators of Sustainable Forest Management*. Amsterdam, The Netherlands: Elsevier.

Raison RJ, Brown AG, and Flinn DW (eds) (2001) *Criteria and Indicators for sustainable Forest Management*. Wallingford, UK: CAB International.

Stone EL (ed.) (1984) *Forest Soils and Treatment Impacts*. Knoxville, TN: University of Tennessee.

Tree Roots and their Interaction with Soil

K H Ludovici, US Department of Agriculture Forest Service, Research Triangle Park, USA

Introduction

Root systems provide three key elements for the establishment and productivity of a tree: stability, uptake, and storage. Site characteristics such as slope, aspect, drainage, and land use history will directly and indirectly impact the success of these elements. Many species use the plasticity of their root system to adapt to site conditions, but others simply do not occur on sites incompatible with their normal root system. Edaphic factors such as temperature, soil water potential, oxygen concentration, mechanical resistance, and the content of nutrient ions will influence the growth and function of the roots themselves. At the same time, root systems have a profound effect on the physical and chemical characteristics of the multiple soil horizons. As roots grow, they stabilize, penetrate, enlarge cracks and crevices, and lower water and nutrient contents. Finally, root decay allows infiltration of water and surface materials downward through old root channels and organic material is concentrated within the soil profile.

Root System Characteristics

Root Mass and Configuration

Root systems provide stability or anchoring to trees and are most often characterized as one of three principle forms: taproot, heart root, or sinker root (**Figure 1**). Although site conditions will influence root growth and the array of diameter size classes, root form tends to be under a degree of genetic control. The taproot form is characterized by one

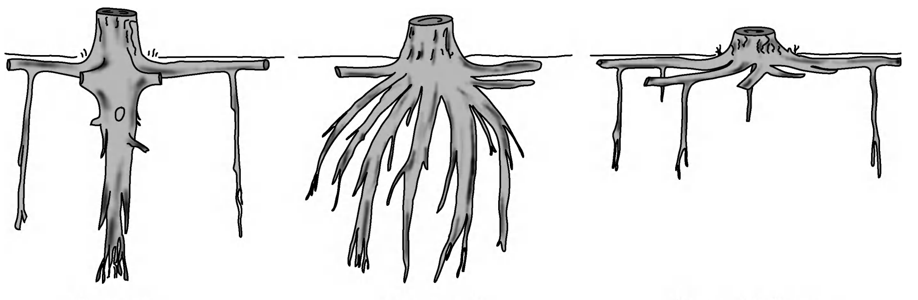


Figure 1 Principal tree root forms. Reproduced with permission from Fisher RF and Binkly D (2000) *Ecology and Management of Forest Soils*, Third Edition, Wiley.

primary, deeply penetrating taproot. Such root systems occur in species of *Carya*, *Juglans*, *Quercus*, *Pinus*, and *Abies*. Many taprooted species have extensive laterals and sinkers that allow them to survive on shallow soils or soils with seasonally high water tables. Species of *Larix*, *Betula*, *Carpinus*, and *Tilia* develop the heart root form which is characterized by numerous lateral and oblique roots radiating from the tree base. This form grows best on deep permeable soils and is more capable of exploiting fractures in bedrock than other root forms. The sinker or flat root form has an advantage on shallow soils and is characterized by shallow laterals from which vertical sinkers grow downward. This form is seen in species of *Populus*, *Fraxinus*, and *Picea* and can be found on a wide range of soil conditions.

Root structure Root diameter is commonly used to differentiate function and often correlates with degree of suberization and longevity. Taproots primarily function as physical support, but also provide valuable storage. They comprise 10–30% of mature tree biomass and as much as 90% of total root biomass. Even though taproots have been documented to extend >20 m, the bulk of most root systems is 1.5 m from the surface and within the canopy drip line. Larger primary lateral roots emanate from the taproot in patterns influenced by genetics and site. Secondary laterals extend from primary laterals and combine to represent the bulk of the coarse root fraction. Coarse roots are >15 mm, generally have a well-developed bark, which is marked by lenticels and cracks which facilitate their contribution to water and nutrient uptake. These roots are perennial and contribute 5–20% of mature tree biomass and as much as 40% of the total root biomass. Fine roots are commonly referred to as the absorbing roots and in many species include any roots <15 mm. Roots 5–15 mm provide continuity of nutrient and water flow. Roots 2–5 mm are generally suberized roots that provide extension, uptake, and transport, but are not observably infected with mycorrhizae. Roots <2 mm are often termed feeder roots, as they principally function to absorb water and nutrients. Feeder roots are not suberized, can exhibit root hairs and may be noticeably infected by mycorrhizae. In some species, roots <1 mm diameter provide much greater surface area to dry weight correlation than do roots 1–2 mm, and are more accurately termed very fine feeder roots.

Root hairs and mycorrhizae are the smallest root features but are responsible for measurable increases in water and nutrient uptake. Root hairs are microscopic extensions of root epidermal cells which greatly increase the surface area of the root. They are delicate and easily ruptured when the soil is disturbed, suggesting why newly transplanted seedlings and plants need to be protected from water loss for the first few days after transplantation. Mycorrhizal fungi infect roots and can develop extensive hyphal networks which increase the uptake capacity of the system. The amount of ectomycorrhizal fungal mycelium can be so extensive that its total mass is comparable to the mass of fine roots themselves; however, the endomycorrhizae make up only a small mass of fungal material and are unlikely to exceed 10% of the fine root weight.

Root function Plant roots grow continuously, but their proliferation depends on the availability of water and minerals in their microenvironment. At the same time, the ability of plants to absorb both water and mineral nutrients from the soil is related to their capacity to develop an extensive root system.

Solute absorption occurs in a zone behind the root tip, where the processes of cell elongation and root hair formation occur (**Figure 2**). Within this zone of elongation, the pathway of least resistance occurs in the apoplast of the cortex up to the endodermis. Older root surfaces can absorb soil solution through cracks and breaks in cortical tissues, creating discontinuous zones of absorption along the root length. In roots of woody angiosperms and gymnosperms, a periderm arises and the epidermal and

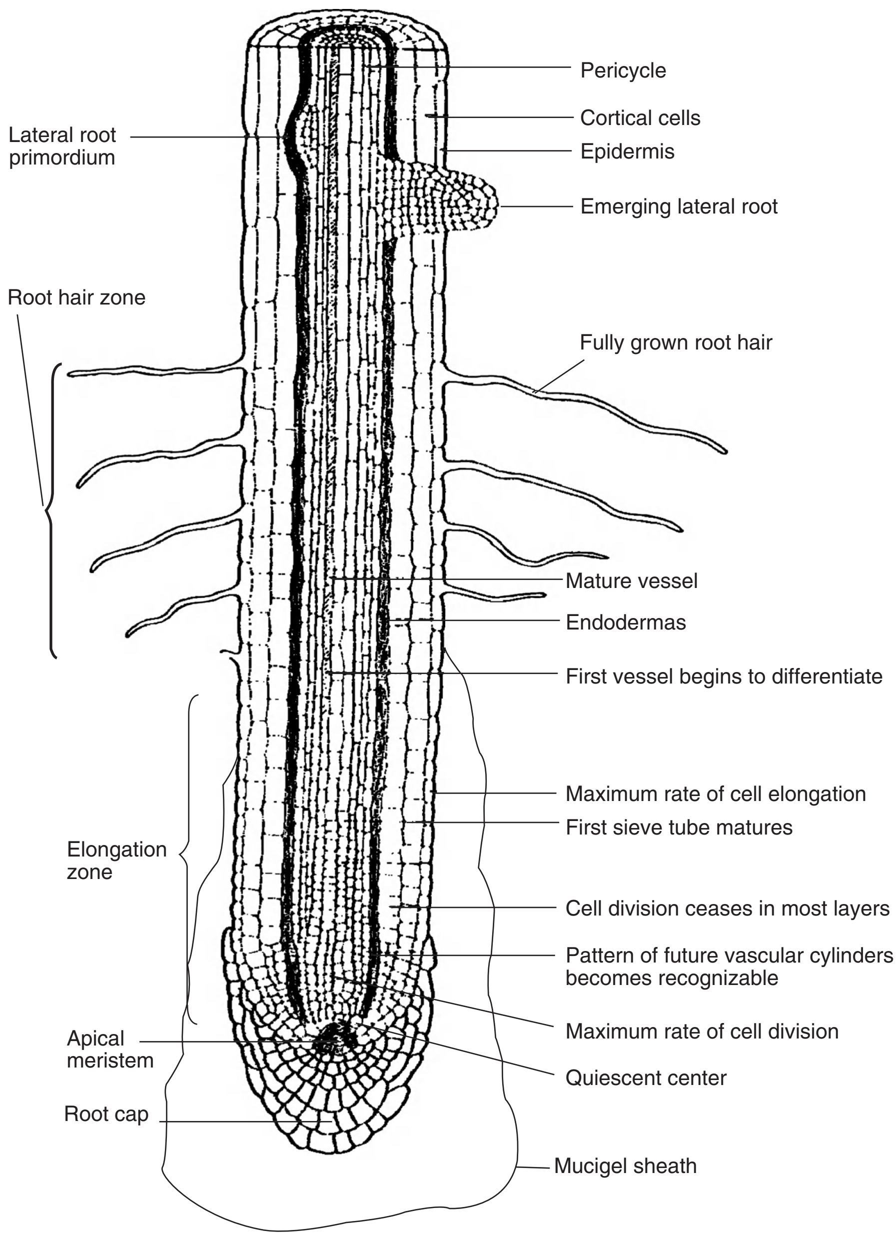


Figure 2 Schematic of root thin section. Reproduced with permission from Lake JV, Gregory PJ and Rose DA (1987) *SEBS 30 Root Development Function*. Cambridge University Press.

cortical tissues exterior to it are shed leaving a highly variable, but appreciably permeable layer of cork cells. Because these roots dominate the root system in mature plants, this contribution to the water supply of the plant must outweigh that of the younger unsuberized tissues.

Water contacts roots in two ways: (1) mass flow of water (Darcy's law) to the root, or (2) interception of water as roots grow through moist soil. The rate of water flow through soils depends on the size of the pressure gradient and on the hydraulic conductivity of the soil which will vary with soil texture. As water is absorbed from the soil near the rhizosphere, the water potential of the soil decreases and a gradient toward the root is created. As more of the soil spaces become filled with air, there are fewer contiguous channels through which water can easily flow. Root hairs may traverse air gaps between the root and moist soil particles. When a soil dries out enough, the water potential can fall below what is called the permanent wilting point. This is the point at which the water potential of the soil is so low that plants could not regain turgor even if all transpiration were stopped. The permanent wilting point is not a unique property of the soil, but depends on the plant species.

Roots absorb mineral nutrients at low concentrations from the soil solution and translocate them to various parts of the plant for utilization. Uptake can be active (as is the case of phosphorus) or passive (as is the cases for calcium, magnesium, and other cations). Experimental evidence supports nutrient absorption at the apical region of the root axes, and along the entire root surface, depending on the nutrient being investigated. Soil chemistry and parent material will greatly influence the bonding and binding of anions and cations to clay lattices and soil colloids, thereby determining the degree of availability. Rainfall and soil texture will also impact uptake capacity, as tortuosity and pore size distribution impact mass flow and desorbtion characteristics.

Tree root systems are vital in their capacity to store water, nutrients, and carbohydrates. It is well documented that tree boles shrink and swell within a day in response to water use patterns, and studies have observed a similar pattern in large lateral roots. However, the degree of elasticity and propensity for deep water recharge remain important study points. The tremendous reservoir of nutrients in root systems is not retranslocated from roots before they die, thus they are returned to the soil where they can be utilized by other plants. At the same time, tree roots are an immediate source of labile and stored carbohydrates. Starch storage in mid-rotation loblolly pine (*Pinus taeda*) has been documented to contribute $>14\%$ of the total carbon needed for annual tree growth.

Root systems also produce hormones that function to regulate whole tree growth. Roots are known to produce and export cytokinins and abscicic acid (ABA) to the xylem sap. When dehydration of the root medium occurs, the cytokinin content in the xylem decreases and a large increase in ABA concentrations can be measured in the roots. The ABA content of the leaf epidermis is closely related to the degree of stomatal closure even without a change in leaf water potential, and stomatal closure can occur even if only part of the root system is dehydrated. In addition, while the absolute magnitude of osmotic adjustment is less in roots than in leaves, as a percentage of the original tissue potential it can be greater in roots than in leaves. These adjustments may only slightly increase water extraction from previously explored soil, but they also enhance turgor and maintain root growth.

Root longevity There is little disagreement that taproots and coarse roots can be as old as the bole itself, and generally root diameters increase with age. The common misconception is that fine roots live only a very short time. In fact, research has shown that fine roots of pine can live 8 years or more. Evidence suggests that fine roots of other species also have a substantially longer lifespan than previously believed.

The anatomy and morphology in parts of the root system vary greatly according to the age of the tissue and the soil environment. In the apical zone of the root, cells are thin-walled, rich in cytoplasm, and have a high rate of respiration. However, relatively old tissues with thick-walled suberized endodermis and few passage cells can be effective in transport of phosphorus and potassium. The movement of calcium and magnesium into the xylem is, by contrast, greatly restricted by the development of suberized lamellae in the endodermis, suggesting normal transport across the plasma membrane of young endodermal cells.

Mycorrhizal Infection

Mycorrhizae are widespread in natural conditions and extensively infect tree species, creating mutualistic relationships through which the fungi receive sugars from the host plant, in exchange for increasing mineral uptake efficiency. Mycorrhizae occur in two major classes: ectotrophic and endotrophic. The ectotrophic mycorrhizal fungi typically form a thick sheath or mantle of fungal mycelium around the roots, with some of the mycelium penetrating between cortical cells. This network of internal hyphae is called the Hartig net. Endotrophic or vesicular–arbuscular (VA) mycorrhizal fungi do not produce a fungal mantle around the root, but form ovoid structures called vesicles and branched structures call arbuscules within plant root cells.

Fungal mycelia extend into the soil, forming hyphal rhizomorphs and hyphal strands supporting fruiting bodies. This extension of fungal hyphae beyond the nutrient-depleted soil zones near roots increases the capacity of the root system to absorb nutrients. Ectotrophic mycorrhizae may also proliferate in the organic layer of the soil and hydrolyze organic phosphorus for the root. Studies have shown that mycorrhizal fungi can transport phosphate at a rate more than four times higher than that of an uninfected root.

A key factor in the extent of mycelial development is the nutrient status of the host plant and site. Deficiency of a nutrient such as phosphorus tends to promote mycorrhizal infection, whereas, infection tends to be suppressed in well-fertilized soil. A correlation also exists between volume of root surface fungi and bacteria (closely related to biomass), and shoot nitrogen. Although such a correlation could be caused by the microorganisms increasing the plant's nitrogen uptake, it is more likely that increased nitrogen in the plant causes increased microbial growth through increased exudation. This interaction has significant application in forest systems where species competition, spacing, and site preparation continue to impact site productivity.

Tree Allometry

Allometry is an empirical expression of the distribution of biomass between aboveground and belowground tissues. In general this relationship will be species specific and it will shift as a stand develops. Trees generally shift from a predominance of belowground tissue to aboveground tissues with age and stand development; however, it may be difficult to separate this pattern from seasonal effects. Site conditions including temperature, planting density, and competition do not usually change the root to shoot ratio (R/S), but may impact the rate of growth and the absolute root density.

It is frequently reported that the relative allocation of carbon for root growth decreases drastically with fertilization, and that trees respond to improved site fertility by shifting the allocation of tree mass belowground on infertile sites and aboveground on fertile sites. Research also shows shifts in root size distribution toward fewer fine roots in response to increased site fertility. However, roots proliferate in microsites with high nutrient contents and it is most likely that total tree growth changes rather than the allometry of that growth changing. Similar arguments can be made for impacts of competition. In any event, even insignificant shifts in allometry may be biologically important to stand productivity and longer-term carbon storage.

Soil Conditions and Root Growth

Soil Texture

Root form is closely associated with tree species, but the mixture of sand, silt, and clay in a soil will impact water availability and resistance to root penetration, thereby influencing the expression of that form. Higher clay contents increase resistance to penetration, may restrict vertical and horizontal root growth, and can result in thinner roots and slower growth. Sandy soils provide lower resistance to penetration, allow extension through large pore spaces, and can contain roots that are on average of greater diameter.

Bulk density is the representation of mass of soil per unit volume. The lower a bulk density reading, the lower the resistance to root penetration, while the higher the bulk density, the greater the resistance to root penetration. Within a range of values, root growth is possible regardless of soil texture or water availability, but beyond a value of approximately $2.65\,g\,cm^3$, root penetration is restricted.

Impeded roots are known to develop a layer of suberized lamellae close to the root tip which greatly increase resistance to the radial flow of water, and delay re-establishment of continuous films of water when roots are moistened after a period of desiccation. Uptake of potassium would not be affected in impeded roots, but transfer of calcium and magnesium across the root would be hindered.

Historically it has been accepted that roots will grow unrestricted only in pores of diameter greater than their own, and only enter those of at least a similar size to the root tip. While this growth strategy may be predominantly true, advancement of root and mycorrhizal research has shown that a root tip needs only a single cell to pass through a pore space before it continues to extend through unrestricted media. Extension of root tips and hyphae through restricted pore sizes in many soil structures leads to the physical breakdown of organic and inorganic impediments.

Soil Moisture

Clearly there are tree species better adapted at living on wetter sites than drier sites, and vice versa. A large portion of this adaptation is in how plant roots adjust to and thrive in conditions of low oxygen. The supply of oxygen to the roots is essential for cellular respiration, the source of metabolic energy that drives mineral uptake processes. In general, roots require a minimum oxygen level and will cease to elongate when water levels are high. Unsuberized roots may become thicker in response to high water levels, but whether the cause for this is expansion of individual cells, or growth of additional cells is not known.

Soils at field capacity have 10–30% of the volume composed of air-filled spaces, and this percentage decreases as water content increases. Under most conditions, the oxygen supply in air-filled pore spaces is in the range of 15–20% but plant roots cannot obtain oxygen when soils are flooded, and anaerobic environments are created. In wetlands and along the shores of oceans, lakes, rivers, and ponds, pore spaces become saturated with water, the rates of water and nutrient absorption are suppressed, and death of roots can occur. While some woody species are tolerant to flooding during dormancy, formation of adventitious roots and aerenchyma after flooding (linked to increased ethylene production) has been shown to alleviate the effects of root injury to some species.

In contrast to flood-sensitive species, wetland vegetation is well adapted to growth for extended periods in saturated soil. Even when shoots are partially submerged, they grow vigorously and show no signs of stress. In these plants, the stem and roots develop longitudinally interconnected, gas-filled channels, known as aerenchyma, which provide a low-resistant pathway for diffusion of oxygen and other gases. Hypoxia stimulates greater production of ACC and ethylene, and the latter promotes the breakdown (lysis) of cells in the root cortex. As roots extend into oxygen deficient soil, continuous formation of aerenchymas just behind the tip allows oxygen movement within the root to supply the apical zone. This retained oxygen aerates the apical meristem and allows growth to continue 50 cm or more into anaerobic soil.

Under adverse soil conditions the extension of roots is retarded and differentiation is slowed less than extension. In this way, cell maturation occurs much closer to the apex than in rapidly extending roots. Suberization of roots in response to dry soil conditions corresponds to a cessation of root extension and formation of a continuous suberized layer just beneath the root cap. Thus the hypodermis and endodermis are found to develop closer to the apex when soil conditions are unfavorable. As long as desiccation does not cause cortex cells to collapse, the root apices are able to rupture the suberized layer and extension resumes within a few days of soil rehydration.

Temperature

Soil temperature influences both adsorption of water and nutrients by existing roots and affects future root growth. As soil temperature increases, root carbohydrate demands increase due to increased respiration and as the carbon sink strength of the roots increases. In the long term, shoot biomass production is decreased at the expense of root maintenance and growth. Conversely, changes in phospholipids in the roots, as a response to gradual shifts in temperature, may influence transport processes across cell membranes by maintaining them in a fluid condition at lower temperatures. This cell membrane level mechanism may serve as a root adaptation to seasonal changes in soil temperature.

The optimum root temperature for shoot growth is a function of the R/S ratio. Optimum root growth occurs at approximately 35°C for subtropical plants, 27.7°C for warm temperate plants, and 20°C for cool temperate plants. There are ranges of temperature within which plants and microorganism can grow and function, but it is important to remember that temperature impacts are not independent for roots and shoots. Increasing root temperature decreases the R/S ratio, just as increasing shoot temperature increases the R/S ratio.

Nutrient Availability

Tree roots usually favor a slightly acidic pH, one in which fungi predominate the rhizosphere. A low pH favors the weathering of rocks, the release of ions such as potassium, magnesium, calcium, and manganese, and the increased solubility of carbonate, sulfate and phosphate salts present in the soil solution. Increasing solubility facilitates absorption by the root.

The inorganic particles of the soil solid phase act as a reservoir of nutrients such as potassium, calcium, magnesium, and iron. Also associated with this solid phase are organic particles containing nitrogen, phosphorus, and sulfur. Nutrient movement to the root surface can occur by mass flow and by diffusion. Mass flow describes movement of nutrients along with the convective flow of water moving through the soil toward the root. The amount of nutrient provided to the root by mass flow will be dependent on the rate of water flow to the plant and the concentration of nutrients in solution. Where water flow is high and nutrient concentrations are high, mass flow can play an important role in nutrient supply.

Diffusion occurs when mineral nutrients move from a region of higher concentration to a region of lower concentration. Because active nutrient uptake by the root will lower nutrient concentrations at the root surface, concentration gradients are created surrounding the root. Diffusion of nutrients can supply nutrients to the root surface from areas of high concentration to areas of lower concentration. When diffusion is too slow, a nutrient depletion zone is formed adjacent to the root surface.

Carbon Dynamics of Tree Roots

Growth

Production and growth of roots require more plant resources and energy than production or growth of aboveground tissues. This idea is largely driven by attempts to complete and balance models with only a black-box understanding of root production and turnover. Research has shown that the carbon compounds used by roots, in order of preference, are carbohydrates > amino acids > soluble proteins > insoluble proteins. Because carbon is fixed during photosynthesis, site properties that are linked to photosynthetic capabilities and sink strength will impact root growth.

Root growth varies seasonally in response to carbon fixation by leaves and demand by various parts of the tree. Deciduous species have wide range in photosynthetic capacity, while evergreen species maintain some photosynthetic capacity all year. Under these two scenarios we understand that an excess of carbohydrates would be available to deciduous species roots only after leaf-out in the spring, whereas evergreen root production would be bimodal, with excess carbohydrates produced in the early spring and autumn.

Root development is critical during seedling establishment. Establishment may be limited by site-specific properties (such as nitrogen or phosphorus availability, or aeration) or by process-limiting situations (such as establishment of a mycorrhizal hyphal network, production of absorbing root surface area, or allocation of resources between sources and sinks).

Exudates

Interest in the rhizosphere effect on microbial activity and plant health did not gain momentum until about 1955. Since that time, researchers have calculated that carbon released from roots growing in soil can amount to approximately 20% of the total plant dry matter. Exudates are produced from carbohydrates which are primarily synthesized in the shoot during photosynthesis and then translocated to the root system. A majority of total root exudates, approximately 60%, are cations and to a lesser extent anions. The carbon components of root exudates are typically composed of 66% organic acids, 29% carbohydrates, and 5% amino acids.

The presence of microorganisms in the rhizosphere increases root exudation, either through physical damage to the root tissues, or through release of metabolites from the microorganisms which affect root physiology. In this way, measuring microbial population in the rhizosphere in response to various factors indirectly assays exudation. Research has generally shown that change in any biological or physical factor that affects plant growth also affects the quantity of exudates released by roots. The principal factors affecting the type and quantity of substances released by roots into the rhizosphere include species and developmental stage of plant, soil physical stress factors, plant nutrition, mechanical or disease injury, microbial activities, and foliar-applied chemicals.

Decomposition

Decomposition of root systems provides a network of continuous root channels, and improves soil porosity. Roots are the principal source of organic matter in the deeper soil layers, and their decomposition directly and indirectly influences nutrient release. Studies of several tree species indicate that decomposition rate decreases as a function of increasing root diameter. Decomposition of large lateral roots and taproots can potentially impact nutrient release over several decades while decomposition of fine roots affects nutrient release on a seasonal basis.

Typically, a 'wet' forest has more living than dead roots, while a 'dry' forest has more dead than living roots. The major influence of increasing soil moisture is to improve decomposition and mineralization of dead roots and their nutrients. Because carbon dioxide, produced as a by-product of decomposition of organic material, equilibrates with the soil water, we can measure changes in respiration and link this to biological activity. Conversely, site disturbances including fire and clear-cuts will affect biological respiration presumably with little change in belowground biomass.

See also: **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Tree Physiology**: Mycorrhizae; Nutritional Physiology of Trees; Root System Physiology.

Further Reading

Harley JL and Russel RS (1979) *The Soil–Root Interface*. London: Academic Press.
Lambers XY (1987) Root development and function. In: Gregory X, Lake Y, and Rose Z (eds) *Root Development and Function*. Society for the Study of Experimental Biology Seminar Series vol. 30. Cambridge, UK: Cambridge University Press.
Taiz L and Zeiger E (1991) *Plant Physiology*. New York: Benjamin/Cummings.

Soil Organic Matter Forms and Functions

L A Morris, University of Georgia, Athens, GA, USA

Introduction

Soil organic matter is important in determining both relatively stable soil properties as well as dynamics of soil systems. This article focuses on the contribution of organic matter to mineral soil horizons dominated by inorganic sand, silt, and clay-sized particles. The role of the organic forest floor is described elsewhere (*see* **Soil Development and Properties**: The Forest

Floor). Within mineral soil horizons, organic matter contributes to soil development through its role as food and nutrient sources for soil fauna and heterotrophic flora that give life to the soil, through production of organic acids and stabilization of structure, through its contribution to relatively stable characteristics such as color, water holding capacity and nutrient retention and release, and as the primary soil reservoir and sources of several plant nutrients. Soil organic matter consists both of relatively simple organic compounds as well as large complex and ill-defined molecules of high molecular weight classified based on chemical solubility or other characteristics. Elemental composition varies, but generally the least soluble and most complex organics have increased concentrations of nitrogen (N) and carbon (C) and decreased concentrations of oxygen (O). Functional groups of alcohol, carboxyl, enol, and phenol impart high capacity to adsorb and exchange nutrients and retain inorganic and organic contaminants. Human activities and forest management can alter the quantity and distribution of organic matter. This has ramifications both for forest productivity and ecosystem functions as well as for global carbon cycles.

Functions

Contributions to Soil Development (Pedogenesis)

Food source Organic matter created by binding of atmospheric C with water during photosynthesis and incorporated into leaves, roots, and wood is the base of a complex and still partly unknown universe of soil organisms. Beginning with large wood-boring beetles and other organisms that feed on freshly fallen logs or leaves, and ending with microbes that are involved in decomposition of the most recalcitrant organic compounds, organic matter sustains life within the soil. Between 10% and 20% of the CO_2 released from the soil during organic matter decomposition is associated with soil fauna. Fauna play an essential role in breaking down coarse debris with low surface area to weight ratio deposited on the surface soil as litter, or within the soil as roots, into finer particles and mixing these particles with mineral soil fractions where they can be further decomposed by the microbial community. It is through the activity of this microbial community that most of the C fixed through photosynthesis is returned to the atmosphere; however, the portion that remains in the soil is converted to complex, relatively stable compounds through a combination of biological and physiochemical processes.

Acid leaching Decomposition of organic matter in forests results in formation of soluble organic acids that, over time, have a major impact on soil formation. Acids produced during decomposition of litter on the surface move down through the soil with percolating water removing base cations such as calcium (Ca^{2+}), magnesium (Mg^{2+}), and potassium (K^{+}) weathered from minerals. Charge balance is maintained through accumulation of H^{+} and concentration of acid forming aluminum (Al) in the process. This acid leaching creates soils that tend to be slightly (pH_w 6.5) to very acidic (pH_w 3.8) in the surface and contributes to development of distinct profile features associated with some forests. For instance, organic subsoil horizons resulting from leaching of organic acids from the surface and subsequent precipitation as organic–metal complexes deeper in the profile are characteristic of conifer stands grown on coarse textured soils throughout the world.

Stabilization of soil structure Organic matter is important to development of soil structure in two important ways. First, it serves as a food source for soil fauna. Through their movement, soil fauna create large pores that serve as major pathways for water and gas movement thereby increasing the depth of biological activity. Also, soil fauna that ingest organic and mineral material bring surfaces in close proximity where they can react with one another. Second, organic matter can directly bind soil particles together or combine with metals to create bridges that link individual soil particles. The size, shape, and stability of these aggregates are considered an important characteristic affecting water and gas flow, soil strength and suitability for root growth, ease with which the soil can be tilled, and the soil's resistance to erosion.

Contributions to Soil Properties

Color The dark surface colors of forest soils, particularly soils beneath productive hardwoods, are largely due to particulate organic matter and organic matter coatings of mineral surfaces. Even low concentrations of organic matter can create dark-colored soils, especially where dark colors are associated with organic coatings on mineral surfaces. For example, dark organic subsoil horizons resulting from accumulation of organic matter leached from surface organic layers can contain only 3–5% organic matter (2–3% organic carbon) on a mass basis. Color is important as characteristic for recognizing and describing soil profiles in all soil classification approaches. Additionally, color can affect thermal properties of soils. Dark surface soil colors promote soil warming and biological activity in cool climates.

Available water holding capacity Soils with high organic matter content generally have improved available water holding capacity. Water holding capacity is affected both directly and indirectly. Increases in organic matter content are associated with improved aggregation of soil particles into structural units. As a consequence of improved aggregation, the volume of large pores that drain under gravitational forces and provide air passages from the soil surface to deeper in the profile is increased. This is particularly important in fine textured (clay and clay–loam) soils. In coarser textured soils, organic matter can increase the volume of fine pores that retain water against gravitational drainage contributing to increased water holding capacity. General relationships between an increase in soil organic matter expressed as organic C and available water holding capacity have been developed and tested by several authors. Increases in available water holding capacity between 1% and 2% for each 1% increase in organic matter content (about 2–4% for each 1% increase in organic C content) are average for mineral soils.

Provision of reactive surfaces for nutrient and element retention In many soils, soil organic matter is responsible for the majority of charged sites that interact and hold nutrients and metals to soil surfaces. For each 1% increase in soil organic matter, there is between a 1–3 cmol kg^{-1} increase in cation exchange capacity (CEC). The charge of organic surfaces results from the presence of various functional groups such as carboxylic, phenolic, alcoholic, and amides (**Figure 1**) from which hydrogen can disassociate creating negative charges that serve as sorption sites. The degree to which disassociation occurs varies as a function of pH of the soil. When pH is low, the abundance of H^+ limits disassociation and positive charge can exceed negative charge. When pH is increased, and OH^- concentrations in solution are high relative to H^+, then H^+ disassociates from the surface creating negative charge than can hold cationic nutrients and metals. Under soil reaction (soil pH) typical of natural field conditions, the CEC of soil organic matter ranges from 60 to 3000 cmol kg^{-1}.

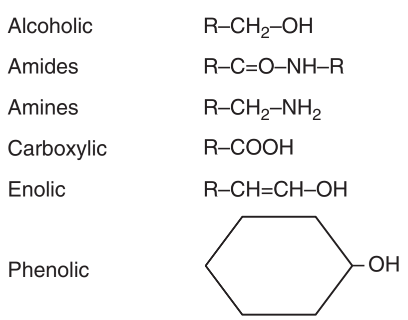


Figure 1 Important functional groups associated with soil organic matter.

Formation of complexes The variable physical structure and multiple functional groups in organic matter enables it to form complexes with inorganic compounds. These complexes have a number of important effects. Organic matter competes with P for sorption sites on minerals and can displace it from these sites rendering it available for plant uptake. Organic matter can increase availability of trace metals through formation of soluble organic–metal complexes. For example, organic matter forms soluble complexes with Fe that protect it from formation of insoluble inorganic precipitation products and increase its plant availability in near neutral pH soils. Conversely, formation of insoluble products that reduce plant availability can also occur. Formation of insoluble complexes limits copper (Cu) availability in many organic soils. Finally, organic matter plays a critical role in the contaminant retention (*see* **Soil Development and Properties**: Soil Contamination and Amelioration).

Nutrient source Organic matter is the chief reservoir and source of several key plant nutrients. Nitrogen, in particular, does not occur in appreciable quantities in primary minerals or on soil exchange sites. For instance, the surface soil beneath an upland forest may contain from 1500 to over 5000 kg ha^{-1} of total N. Less than 1% of this normally exists in inorganic forms retained on surfaces or in soil solution, a quantity much too small to support forest growth for extended periods. Sufficient supplies of N to support forest growth depend upon release of nutrients from bound organic forms into inorganic forms that are readily available for plant uptake during decomposition, a process termed mineralization. Organic sources of P and sulfur (S) are also important, particularly on sandy forested sites where both primary minerals and soil exchange is low.

Forest Productivity

Many of the soil properties affected by soil organic matter have direct bearing on rooting conditions, water retention and release, and nutrient availability. Thus, a relation between forest productivity and measures of total soil organic matter content or concentration should exist. Attempts to establish such relations have met with various degrees of success. On upland sites with good drainage, a positive relation often exists between soil organic matter in the surface soil or entire soil profile and measures of productivity such as site index (**Figure 2**).

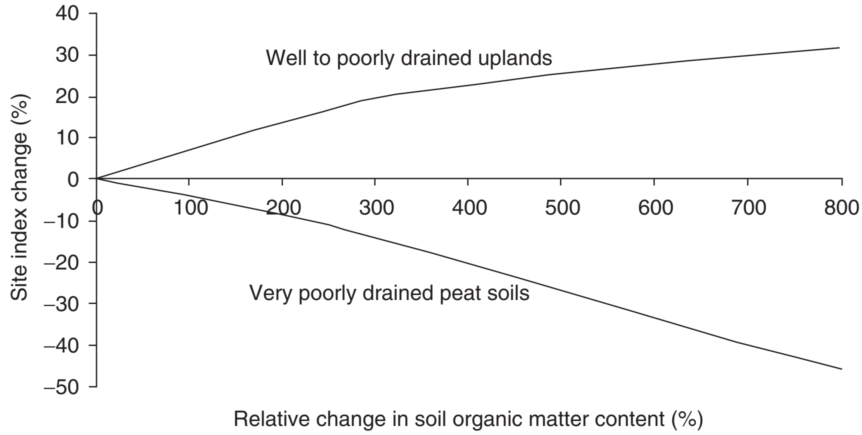


Figure 2 General relation between total soil organic matter content and forest productivity as measured by site index.

On these sites, increases in soil organic matter are associated with reductions in soil density and more favorable rooting conditions, improved moisture holding characteristics, and greater nutrient availability. Productivity increases associated with increased organic matter tend to be greater at low organic matter contents and are particularly important in sandy soils which have low water holding capacity and CEC in the mineral fraction. On very poorly drained bog or peat sites, a negative relation occurs between organic matter content and productivity. Under these very poorly drained conditions, increases in soil organic matter reflect increasingly unfavorable conditions for organic matter decomposition, nutrient mineralization, and root growth (**Figure 2**). For agricultural crops, specific fractions of organic matter (see following section) have been shown to be more closely related to productivity than total soil organic matter. Such relationships are being investigated for forests, but have not yet been established.

Characterization of Organic Matter

Soil organic matter consists of: (1) light fraction and particulate components that are largely recognizable as to chemical composition and consist of primary plant remains and (2) organic compounds called humus that have passed through one or more stages of decomposition and have been recombined into more complex molecules. Separation of the light fraction and particulate components can be accomplished by particle size sieving and density separation. These organics have a density less than 1.0 g cm^3. This fraction of organic matter is largely composed of identifiable organic polysaccharides such as cellulose and hemicelluloses, amino acids, chitin, waxes, and lignin. This organic fraction is extremely important in forest systems, particularly within the forest floor, because of its high energy content. It is an important source of mineralizable nutrients and is relatively sensitive to changes in the soil environment. In contrast, the humus fraction is less reactive and more important in development of stable characteristics of the mineral soil horizons. Traditional methods of classifying the humus fraction into constituent parts depend upon differences in solubility under alkaline and acidic conditions as illustrated in **Figure 3**. Three major components of soil humus are recognized in this classification approach: humin, which is the portion that is not soluble under alkaline (OH-rich) conditions, humic acid, which is the portion that is soluble under alkaline conditions but insoluble under acidic (H^+) conditions, and fulvic acid, which is soluble in both alkali and acid. Molecular weights, N and C concentrations decrease with humin > humic acid > fulvic acid. CEC, acidity and O concentrations decrease in the sequence: fulvic acid > humic acid > humin.

The chemical composition and structure of soil organic matter are not precisely known. Average element composition are about $C_{10}H_{12}O_5N$ and $C_{12}H_{12}O_9N$ for humic and fulvic acids, respectively. Structurally, they are largely comprised of aromatic rings heavily substituted with functional groups (carboxyl, hydroxyl, and carbonyl) and alkyl chains up to 20 C long that include bound proteins and carbohydrates. The molecules are randomly coiled and cross-linked. An example structure for a unit of fulvic acid is illustrated in **Figure 4**. There is a range in structure and the abundance of specific functional groups among humin, humic, and fulvic acids as well as within materials classified within any of these fractions from different locations.

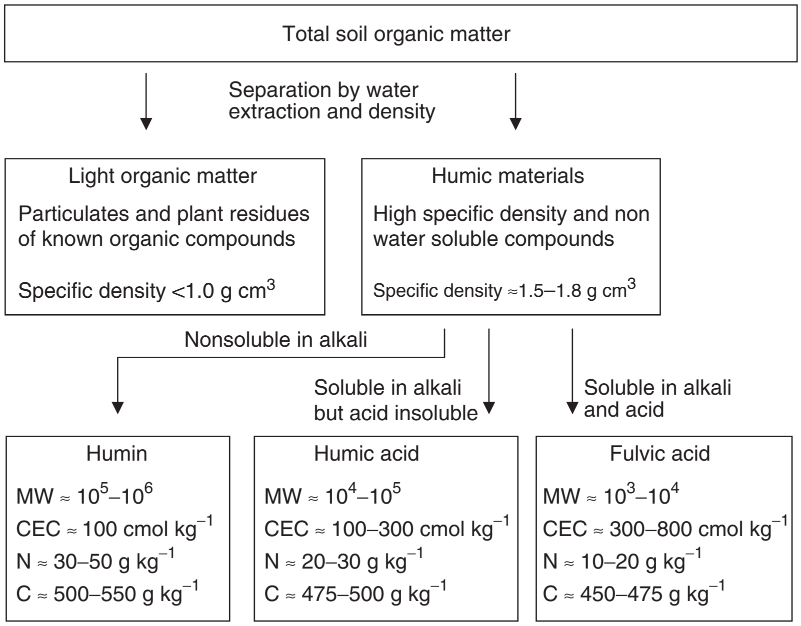


Figure 3 Major fractions of soil organic matter and approximate characteristics. CEC, cation exchange capacity; MW, molecular weight.

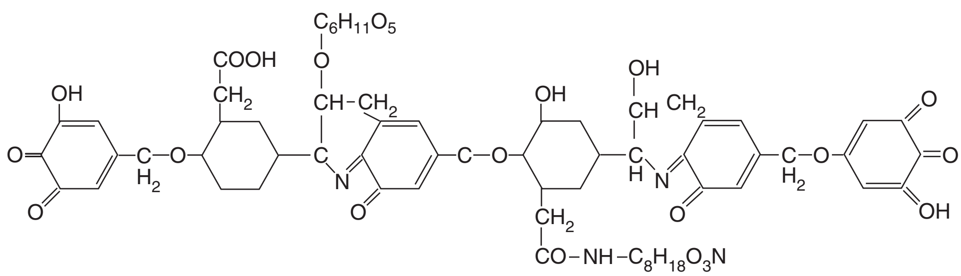


Figure 4 Possible structure of humic acid illustrating aromatic rings, peripheral chains, and functional units. Redrawn after Dragunov SS (1948) A comparative study of humic acids from soils and peats: Pochvovedenie 7. In: Kononova MM (1961) *Soil Organic Matter: Its Nature and Role in Soil Formation and in Soil Fertility*, p. 65. New York: Pergamon Press.

Quantity and Distribution

Comparisons among Forest Ecosystems

The quantity of soil organic matter within a given forest ecosystem reflects a balance between annual C inputs and loss through decomposition. In mature undisturbed forests, inputs and losses tend to approach an equilibrium condition determined by site factors such as overall forest productivity, species, soil and rooting depth, and soil physical and chemical properties. Increased precipitation is generally associated with increased soil organic matter, apparently because of its association with increased productivity. Under conditions of similar precipitation, organic matter tends to decline as temperatures are increased. Despite these general relationships, a clear pattern of differences in soil organic matter content does not exist among ecosystems from different climatic biomes (**Table 1**). Highly productive tropical soils may contain the same quantity of soil organic matter as some low productivity boreal forests. Production and incorporation of organic matter into boreal forest soils is slow, but so is decomposition. Additionally, several factors other than temperature and moisture affect soil organic matter content. Organic matter can adsorb to the surface of clay particles and this adsorption protects organic matter from decomposition; consequently, clay soils tend to have higher concentrations of organic matter than nearby coarser-textured sandy or loamy soils. Chemical composition plays an equally important role. High concentrations of multivalent cations (e.g., Ca^{2+}, Mg^{2+}, Fe^{3+}, or Al^{3+}) can potentially protect organic matter from decomposition in two ways. First, clays tend to

Table 1 Soil organic matter content as a proportion of total organic content (aboveground biomass, forest floor organic matter and soil organic matter to specified depth for several mature forest ecosystems)

Forest Ecosystem	*Aboveground biomass ($Mg\,ha^{-1}$)*	*Forest floor biomass ($Mg\,ha^{-1}$)*	*Soil organic matter[1] ($Mg\,ha^{-1}$)*
Boreal–*Picea mariana*, Alaska[2]	120	119	47
Boreal–*Picea abies*, Sweden[3]	289	19	207
Subalpine–*Picea nobili*[4]	606	53.5	244
Temperate–*Pseudotusuga menziesii* plantation[5]	158	10.9	56
Temperate–*P. taeda*[6]	247	70	192 (6 m)
Temperate–Mixed Hardwoods[7]	207	62	260
Temperate–*Liriodendron tulipifera*, USA[8]	134	6	159
Temperate–Mixed *Quercus*, Belgium[9]	322	5	300
Tropical–*Celtis-Triplochiton*[10]	334	27	106

[1] For rooting zone and exclusive of root mass.
[2] From Cole and Rapp, Stand No 3.
[3] From Cole and Rapp, Stand No 9.
[4] From Turner and Singer 1976, standing dead included with aboveground biomass.
[5] From Harmon *et al*. 1990.
[6] Estimated assuming carbon content of OM is $0.5\,Mg\,Mg^{-1}$ from Richter *et al*. 1995.
[7] Estimated assuming carbon content of OM is $0.5\,Mg\,Mg^{-1}$ from Johnson *et al*. 1995.
[8] From Cole and Rapp, Stand No 22.
[9] From Cole and Rapp, Stand No 28.
[10] Estimated from Greenland and Kowal (1960) and Sanchez (1976).

remain flocculated in soils with high concentrations of multivalent cations. The flocculation protects organic matter adsorbed to surfaces and within aggregates from microbial decomposition. Second, these multivalent cations form complexes with organic matter that, again, protect it from microbial attack.

Forestation and Afforestation

Changes in soil organic matter content resulting from forest removal and conversion to agricultural use are well documented, especially where old-growth forests are replaced by farming that includes regular tillage. Although the amount of reduction varies, the pattern is consistent from cool to tropical climates. Prior to forest removal, organic matter content is high and considered to be in near equilibrium with inputs and outputs. Following forest removal, organic matter content decreases rapidly reaching a new equilibrium determined by the inputs and outputs and the new management regime. On average, soil organic matter declines average from 25–30% of the predisturbance levels; however, on individual sites, declines can be much greater. This is particularly true on sites with coarse-textured (sandy) soils that afford little physical protection of organic matter from decomposition. Increases in soil organic matter similarly occur when areas formerly in agriculture or reclaimed mines are returned to forest; however, the processes of soil organic matter accumulation are much slower than loss and the period for a new equilibrium to be reached is decades or longer.

Harvesting and Management

Forest management affects the amount and composition of soil organic matter in two ways: by changing the quantity and composition of organic inputs and by altering decomposition rates. In the absence of other forest management activities, harvesting trees has only a small impact on soil organic matter content. Most data indicate that changes in soil carbon resulting from harvesting alone are less than 10% with almost an equal change of an increase as a decrease. It is likely that increases in soil organic matter content observed following harvest occur when large amounts of slash are left on site and allowed to decompose and become incorporated with the surface mineral soil. On sites that had initially low amounts of soil organic matter, such as reclaimed mines or degraded agricultural sites, long-term increases in soil organic matter can be expected when forests are managed with normal growth and removal cycles. In contrast, when forest harvest is followed by soil preparation treatments that displace or remove the forest floor and organic rich surface soil, then organic matter may be reduced from 20% to 50%.

Management activities other than harvest can affect soil organic matter. Fertilization can have either a positive or negative affect on organic matter contents depending upon the type of site. Where fertilization increases production without concomitant increases in decomposition rate, soil organic matter can be increased. In contrast, on sandy sites fertilization can decrease soil organic matter content even though forest production is increased. In this case, organic matter is poorly protected against decomposition by structural aggregates or clay–organic complexes and fertilization stimulates decomposition rates of organic matter by lowering the carbon-to-nitrogen ratios and/or carbon-to-phosphorus ratios. Although productivity is stimulated and overall site C content may be increased, the increase is in aboveground forest components and not in soil organic matter. Another management operation that can affect soil organic matter is understory vegetation control. In theory, removal of understory vegetation with a large proportion of production belowground can decrease inputs of soil organic matter. However, the limited research on this management activity tends to suggest it has a relatively small influence on soil C content.

Global Carbon Cycles

Conversion of forests into other land uses results in a release of CO_2 into the atmosphere both as a result of biomass burning or use and eventual decomposition and as a result of mineralization of soil organic matter and CO_2 evolution from the soil. In boreal and temperate regions of the world, little net deforestation is occurring. Most deforestation is occurring in tropical regions where about 17 million - ha of tropical forest are deforested annually and converted to other uses. As a result of this conversion, about 1.6 Pg C are contributed to the atmosphere annually. This represents about 20% of the annual input of CO_2 to the atmosphere from all sources. From 15% to 25% of this contribution can be directly attributed to loss of soil C.

Reforestation of former agricultural lands will increase soil C storage, the increase depending on how badly degraded the soil was prior to reforestation and the productivity of the forest. Projections of C storage potential in the worlds forests based on land availability suggest that between 1 and 2 Pg C could be stored in forests over the next 50 years with 20% of this storage attributable to increases in soil C.

See also: **Soil Development and Properties**: Nutrient Cycling; Soil Contamination and Amelioration; The Forest Floor.

Further Reading

Baldock JA and Nelson PN (2000) Soil organic matter. In: Sumner ME (ed.) *Handbook of Soil Science*, pp. B25–B84. Boca Raton, FL: CRC Press.

Cole DW and Rapp M (1980) Elemental cycling in forest ecosystems. In: Reichle DE (ed.) *Dynamic Processes in Forest Ecosystems*, pp. 341–409. London: Cambridge University Press.

Dragunov SS (1948) A comparative study of humic acids from soils and peats: Pochvovedenie 7. In: Kononova MM (1961) *Soil Organic Matter: Its Nature and Role in Soil Formation and in Soil Fertility*, p. 65. New York: Pergamon Press.

Greenland DJ and Kowal JML (1960) Nutrient content of the moist tropical forests of Ghana. *Plant Soil* 12: 154–173.

Grigal DF and Vance ED (2000) Influence of soil organic matter on forest productivity. *New Zealand Journal of Forest Science* 30: 169–205.

Johnson CE, Dricoll CT, Fahey TJ, Siccama TG, and Hughes JW (1995) Carbon dynamics following clear-cutting of a northern hardwood forest. In: McFee WW and Kelly JM (eds) *Carbon Forms and Functions in Forest Soils*, pp. 463–488. Madison, WI: Soil Science Society of America.

Johnson DW (1992) The effects of forest management on soil carbon change. *Water, Air and Soil Pollution* 64: 83–120.

Orlov DS (1985) *Humic Substances of Soils and General Theory of Humification*. Washington, DC: US Department of Agriculture.

Richter DD, Markewitz DD, Wells CG, *et al.* (1995) Carbon cycling in a loblolly pine forest: implications for the missing carbon sink and for the concept of soil. In: McFee WW and Kelly JM (eds) *Carbon Forms and Functions in Forest Soils*, pp. 233–251. Madison, WI: Soil Science Society of America.

Turner J and Singer MJ (1976) Nutrient distribution and cycling in a sub-alpine forest ecosystem. *Journal of Applied Ecology* 13: 295–301.

SOIL DEVELOPMENT AND PROPERTIES

Contents

Forests and Soil Development

S Torreano, The University of the South, Sewanee, TN, USA

Introduction

Soils are formed by the interaction of five factors: geology (parent material), landscape and topography, climate, animals and vegetation (biotic factors), and time. The interaction of biotic and abiotic factors in the development of soil beneath forest vegetation is highly complex and unique as compared to soils derived under other vegetation types. Because trees dominate forests, their multilayered canopies have a unique and complex effect on environmental conditions at the forest floor. The level of solar radiation, humidity, and effective precipitation under forest canopies vary markedly from nonforest communities. Also, trees are deeply rooted and long-lived, they can access water and nutrients from greater depths compared with other vegetation. Trees extract and cycle nutrients at different rates compared with other vegetation.

Soil genesis and its interaction with forests are complex and do not conform well to generalizations. However, three concepts are crucial to understanding the interaction between forests and soils:

1. Soils and vegetation develop together.
2. Soil includes both the largely mineral material as well as the layers of organic matter (forest floor) that form in undisturbed forests. The presence of this forest floor is a major difference between agricultural and forest soils and is a major reason for differences in characteristics.
3. Many agricultural soils are derived from soils originally developed under forest vegetation; however, removal of the forest canopy and forest floor during conversion to agriculture has such important impacts that they no longer resemble forest soils.

Soil Forming Factors and Forest Vegetation Development

Parent Material

Parent material influences weathering (the breakdown of parent bedrock) rates and, consequently, the stage of soil development and the prevailing vegetation. Although the initial mineralogical composition of the parent material matters, similarities in other soil forming factors, together with time, can result in mature soils of very similar physical and chemical properties from differing parent material. Under forest vegetation, the result is usually a clay-rich, acidic, and relatively infertile soil. These conditions result from specific pedogenic (soil forming) processes as follows:

1. Additions of organic and mineral substances as solids, liquids, or gases.
2. Losses from a portion of the soil, including movement within the profile from one horizon to another.
3. Changes in molecular form among organic and mineral compounds.

Soil physical and chemical properties that result from differences in these processes determine the development of forests. The four primary soil physical factors are texture (the relative proportions of sand, silt, and clay particles), structure (the three-dimensional arrangement of individual soil particles into aggregates such as single-grained, blocky, columnar, prismatic, or massive), size distribution of fines (particles <2 mm) versus stones (mineral solids

>2 mm), and depth available for rooting. Other soil characteristics such as soil bulk density, aeration, and hydraulic conductivity also determine the extent to which root systems and soil organisms will utilize a given soil. Together with climate, time, and parent material, knowledge of the soil physical factors helps predict the successional patterns of vegetation on a landscape. However, these soil physical factors are, in turn, influenced by vegetation dynamics.

Two classifications of soils based on the origin of parent material are generally used:

1. Residual soils result from *in situ* weathering of parent material (the underlying bedrock) on relatively stable landscapes. With time, intense weathering results in fine-textured surface soils, and coarser fragments with depth. Soil development is linked to the zone of biological and chemical weathering.
2. Transported soils tend to be more uniform in textural composition with depth than residual soils but they can vary drastically in texture. They often contain material from soils formed in place at other locations. These soils are further classified by their mode of transport. Alluvial soils are derived from materials transported by water and deposited in the floodplain associated with the watercourse. Waterborne sorting of grain sizes can lead to soils of distinctly textured layers, the finest of which are deposited near the surface. Speed of the transport waters is the greatest influence on sorting. Lacustrine deposits result from suspended sediments in lake water, and tend to be fine-textured. Colluvium is material transported downslope at varying speeds. Textural differences can be large or small with little sorting by size class. Aeolian materials are windborne deposits, usually of particles silt-sized (called loess), or smaller.

There are some general relationships between parent material and vegetation type. Under a given set of climatic conditions, limestone, shale, and similar fine-textured rocks weather into clay-rich, high base nutrient status soils. Acid crystalline rocks (those with high quartz content) such as granites generally form acidic, coarse-textured (sandy) soils of relatively low base nutrient status compared to siltstones and shales. Less moisture- and nutrient-demanding tree species, such as pines, tolerate these conditions better than most angiosperms (hardwoods).

Topography and Landscape Position

Energy from topographic relief, aspect (position of the slope relative to the radiant energy of the sun), and position in the landscape (top, mid-slope, or bottom) drive the formation of soil. Steeper slopes usually experience greater erosion from soil and water movement. These high-energy environments may be so dynamic as to preclude the development of a mature soil no matter how much time passes (see discussion of zonal model of soils, below).

Local topography influences the development of soils and forests through its influence on erosion and drainage. For example, microsite differences in elevation can result in dramatically different dissolved oxygen contents in the soil, which affects soil chemistry. Under anaerobic conditions, metals such as iron, manganese, and aluminum are reduced to more soluble and mobile forms that may leach or be reoxidized to precipitates. The color of a soil, especially in the subsoil, can be used to predict drainage class. Reds and oranges signify oxidized conditions, whilst darker grays and bluish colors indicate reduced conditions typical of impeded drainage.

Climate

Climate and, in particular, the amount and seasonality of available moisture, is important in soil formation and key to the development of vegetation. Moisture and temperature drive chemical reactions. Chemical and physical weathering of parent material leads to the development of soil horizons. Climate also dictates the development of vegetation and can override the influence of parent material by precluding or enabling the establishment of specific types of vegetation, which in turn contributes to the type of soil formed.

Forest growth (biomass production) is usually proportional to available moisture. As litter falls to the forest floor, it decays and is transformed by a series of chemical reactions and biologically mediated decomposition into organic acids and humus (*see* **Soil Biology and Tree Growth**: Soil Organic Matter Forms and Functions. **Soil Development and Properties**: The Forest Floor). Soils high in organic matter are typically dark-colored by humus. Organic acids assist in the weathering of minerals in the uppermost layer of soil (A horizon), the products of which leach (a process called eluviation) into the underlying zone (B horizon). The soil directly above this zone of accumulation is sometimes so highly leached of metals (especially oxides of Al and Fe) and soluble organic matter that a distinctly light-colored horizon develops (E horizon) at the bottom of the A horizon. The products of leaching which have moved out of the E horizon give a darker color to the B horizon. Horizon development beneath a New Zealand forest is illustrated in **Figure 1**.

Organic matter dynamics is largely a function of moisture availability, temperature, and biotic

Figure 1 A soil profile beneath a kauri (*Agathis australis*) forest on old coastal sands (North Island, New Zealand). Note the dark surface horizon (A horizon) beneath the forest floor. Beneath this horizon is a 30-cm thick lighter zone (E horizon) leached by organic acids. Translocated humic and aluminum compounds have accumulated into the reddish-colored B horizon (Bhs horizon). Reproduced with permission of the New Zealand Soil Science Society.

activity. As with any chemical reaction, decomposition is fastest when rate limiting factors are at optimum levels. Low concentrations of oxygen, low temperatures, and extremes of moisture content slow decomposition of organic matter.

Biological Factors of Soil Formation

Biological interactions are essential to pedogenesis. The diversity of life in soil, as measured by species, variety, and number, far exceeds that of aboveground communities. Forest soils are especially diverse compared with agricultural environments. Flora and fauna populate and modify the soil, especially in the rooting zone, an area known as the rhizosphere. Three major impacts of organisms are:

1. The movement of soil particles and organic matter between the surface and subsurface of the soil.
2. The mediation of some chemical reactions and resultant nutrient availability.
3. Forming a significant source of organic matter and nutrient additions to the soil.

The soil food web is a complex community ranging from predatory vertebrates like shrews and moles to tens of thousands of invertebrate species such as worms, arthropods (bugs), and decomposing fungi and bacteria, all which mediate the decomposition of soil organic matter (**Table 1**). Soil organic matter is the source of energy and nutrients used by plants and other organisms. Because they move within the soil, vertebrates, earthworms, and arthropods aerate and mix the soil as they feed. Shredders, such as millipedes, termites, sowbugs, and roaches process tens of tonnes of organic matter yearly derived from the forest floor and plant roots. Soil structure is improved through burrowing and the creation of fecal pellets, rich in readily available nutrients. In terms of biomass and overall activity in the soil, earthworms dominate the invertebrates. Earthworms dramatically enhance the porosity of soil as they burrow, thereby creating conduits for water. Moreover, they move large amounts of mineral soil and organic matter throughout the soil by providing deep cultivation. Compared with other terrestrial ecosystems, forest soil food webs are by far the most complex in the number of separate functional organismal groups.

As organisms consume food, they add to their biomass and they release wastes. Bacteria play a crucial role in mediating the chemical transformation of nutrient elements, like N and P, which are bound in the organic form (unavailable to plants), to elemental (inorganic) forms readily used by plants. This process is known as mineralization. In addition to their crucial role in decomposing organic matter, fungi also enter into a mutually beneficial relationship with tree roots. These fungal–root relationships are known as mycorrhizae (*see* **Tree Physiology**: Mycorrhizae). Roots, and their fungal and bacterial symbionts, have been found to release carbohydrates, vitamins, and amino acids into the rhizosphere, resulting in greatly increased populations of bacteria and fungi. In turn, the increased activity accelerates mineral and organic matter weathering.

Table 1 Characteristics of organisms in the forest soil food web

Class of soil organism	*Important functions*	*Biomass*[a] ($g\,m^{-2}$)
Protozoa	Bacterial feeders	2–20
Bacteria	Decomposition, conversion/release of nutrients to plant available forms	40–500
Fungi	Decomposition, binding soil, enhance root function in uptake of nutrients	100–1500
Nematodes	Feed on fungi, roots, bacteria	1–15
Arthropods	Shred litter; mix soil; feed on bacteria and fungi	2–5
Earthworms	Same as arthropods; enhance soil structure and fertility; most important macrofaunal species	10–150

[a] To a depth of 15 cm.

Perhaps the greatest impact of bacteria in forest soils is their mediation of the chemical transformations of N. Nitrogen availability limits forest productivity globally more than does any other single nutrient. Because the supply of N is so important, nature has developed means to provide that supply, yet to also preserve stocks so that they are not lost from the ecosystem. The ultimate source of N in the soil comes from the abundance of N_2 in the atmosphere. Plants cannot use N_2. In a microbially mediated process, rhizosphere bacteria (and a few other microbes) convert N_2 to ammonium. This is called biological N-fixation. However, most plants require N in the form of NO^{-3} (nitrate), so bacteria must convert ammonium to nitrate. Unused ammonium and nitrate are lost easily from the soil, so conversion back to forms (insoluble) not easily lost is essential to preserving ecosystem productivity.

Tree roots grow where soil conditions are favorable. Thus, the proliferation of fine roots (the growing root tips) is usually greatest in the surface soil, as a result of greatest resource availability. Although roots of some forest species may extend to depths of 10 m or more, 90% of the root length and surface area occurs within the first 1 m of the surface. Together with the biotic activity of other soil flora and fauna, roots occupy and modify the top zone of soil, with activity decreasing exponentially with soil depth. The most important factors are availability of oxygen and moisture, soil temperatures, amounts of available (inorganic) nutrients, and organic matter quality. Turnover (herbivory, and root death and decomposition) of roots accounts for a significant portion of the soil organic matter pool. Studies of root mortality and decomposition have found that as much as 50% of annual biomass production may be invested in root production, with 20–45% of that as annual root turnover.

Observations of changes in a soil following deforestation and afforestation, and the resulting morphological soil traits, indicate that the relationship between forest vegetation and soil is interactive. Students are often introduced to this relationship by considering the influence of forest vegetation on the genesis of podzols (spodosols). The litter from certain tree and shrub species decomposes to an especially acidic form of humus, which results in a lowering of soil pH, especially if the soil is not well buffered (*see* **Soil Biology and Tree Growth**: Soil Organic Matter Forms and Functions). The acidic, nutrient-poor status of these soils results in an edaphic climax. For example, certain conifers, such as the Pinaceae, *Picea*, and *Tsuga* (northern hemisphere), and the broadleaved evergreen *Agathis* (southern hemisphere), commonly form on Spodosols, and under certain conditions, result in a site-specific soil climax. Experts question whether the formation of these morphological features is merely accelerated by certain vegetation or if they are most likely examples of forest vegetation adapting to pre-existing edaphic constraints. Podzolization can occur on pure, relatively sterile sands after a few hundred years under conifer forest, although well over 1000 years is considered usual. It has been noted that successional change to hardwoods can result in changes in nutrient cycling and soil chemistry, leading to a reversal of the podzolization process.

An especially illustrative example of the relationship between forests and soil development are the 'egg-cup' podzols formed under some New Zealand podocarps (in particular old-growth forests of kauri (*Agathis australis*). In this case, moisture, parent material, and vegetation combine to form a unique soil morphology consisting of well-developed E and B horizons. Years of litter fall, and the concomitant leaching from the products of litter decomposition result in a distinct, bleached, egg-cup shaped E horizon beneath the roots of giant, old-growth kauri, underlain by a zone (spodic horizon or Bhs horizon) of accumulated sesquioxides, soluble bases, clays, and colloidal organic compounds, largely from the E horizon beneath the stems of individual trees (**Figure 2**). This process is aided by soil textures dominated by sands of acid crystalline minerals, such as quartz.

Figure 2 An 'egg-cup' podzol formed under the stems of long-lived trees in New Zealand, where extra leaching of water down the stems of Kauri trees results in distinct zones of leaching and accumulation. Reproduced with permission of the New Zealand Soil Science Society.

Another important forest-mediated soil process is known as desilication, wherein high uniform temperatures and rainfall along with the acidic products of litter decomposition favor loss of silica from the upper soil profile. Simultaneously, iron- and aluminum-rich oxides concentrate and form an oxic horizon. Typically, this is a clay-rich, but lacking in any mineralizable primary minerals (those containing calcium, magnesium, and potassium). This process is characteristic of the intensely red tropical soils known as Oxisols.

Figure 3 Example of a fallen tree and the development of pit and mound topography in a hardwood forest in the USA.

The ecology of soil change as forests are cleared and grow back has been studied around the world. The magnitude of change depends on management practices and the differences among sites. It is important to remember that farmed soils are a result of constant human inputs and harvests as opposed to forested soils which, depending on harvest intensity, are largely a product of natural soil-forming factors. Our knowledge of these changes have been aided by research which quantifies the change in soil properties as forests are cleared to make way for farming, followed by reversion to forest.

Another example of the interaction between forest and soil development can be observed in the 'pit and mound' microtopography created by tree falls. Windthrow and uprooting results in a pit at the former root collar and a mound nearby where the displaced surface soil clings to the remaining roots and tree stem (**Figure 3**). Tree falls increase in mature and old-growth forests, and where predisposing environmental conditions such as restricted rooting depth and meteorological conditions exist. The resulting effects on soil formation include: litter accumulation and decomposition, respiration, soil climate (humidity, moisture content, temperature, solar radiation), sequence and thickness of soil horizons, and biotic diversity/activity. Forest floor tends to accumulate in pits due to increased trapping of litter, and reduced decomposition rates resulting from higher moisture contents. Greater moisture in surface soil may facilitate the weathering process unless oxygen is limiting. Horizon differentiation is slowed on mounds due to attenuation of weathering from a decrease in moisture levels and organic matter inputs from litter fall. Pits have the highest amounts of organic matter, nitrogen, and carbon, while mounds have the least, and the surrounding undisturbed (flat) areas are intermediate. Calcium and other soluble bases are often higher in pits, resulting in higher soil pH. The occurrence of pit and mound microtopography varies from as little as 1–2% to as much as 30–40% of the forest floor in especially prone areas.

Pits, when associated with high water tables, can lead to the formation of vernal (ephemeral) pools. These pools remain as long as the water table remains high, or longer when sediments coat and seal the edges of the depression. Microtopography, and the resulting creation of soil microsites, has been found to influence the distribution of understory plants. Animal activity is also tied to the availability of favorable microsites. Variation in earthworm and other invertebrate activity contributes to the fine-scale heterogeneity in forest soils characteristic of pit and mound landscapes.

Time

Changes occur constantly in soils as a result of parent material weathering and vegetation dynamics. Given enough time and a particular set of climatic and vegetative factors, most soils will stratify, developing the characteristic horizons and other features we use to distinguish among them. The concept of soil maturity, or that a predictable type of soil will develop over time, is referred to as the zonal model of soils. Although this concept is manifest under certain conditions, it does not adequately explain the variation in soils under all conditions and the concept does not have universal acceptance. Similarly, the idea of climax vegetation communities in equilibrium with the soil is a largely misleading one based on studies of limited time scales, within relatively few old-growth forests. Thus, it is difficult to predict how long it will take for soil to develop. It may take 100 years to add 1–2 cm of topsoil in residuum under harsh climatic conditions. In contrast, well over 10–20 cm of soil may form on volcanically derived parent material under tropically moist conditions in that same 100 years. Because soil is constantly being lost by erosion on some landscapes, it is probably best to discuss time and forest soil formation in terms of soil profiles and horizons.

Under temperate climatic conditions, such as those found in the continental USA and Western Europe, a well developed A horizon can form in as little as 150–400 years, with full profiles averaging 1500–12 000 years. Extremes in environment such as high moisture content, arid conditions, or dynamic landscapes due to slope or depositional intensity, can slow development dramatically. Ultisols (red–yellow podzolic soils) and Oxisols (Latosols, Ferralsols) are commonly the most ancient of soils ranging in age from 50 000 to well over 500 000 years. Some clayey soils, especially those rich in aluminum or iron, are particularly resistant to change.

Soil Classification Systems

The most widely used classification systems are the US Department of Agriculture (USDA) *Soil Taxonomy* and the United Nations Food and Agriculture Organization (FAO) *Legend*. *Soil Taxonomy* is an hierarchical system based on morphological variables that are quantitative, and thus easily interpreted. The system groups all soils into 12 soil orders based on their current properties (color, clay content, etc.), similarities in pedogenic factors (climate, presence or absence of diagnostic horizons) and overall profile development (**Figure 4**).

Table 2 provides a comparison of the world distribution of soil, by percentage of land area, for the FAO Legend, and Soil Taxonomy. Entisols and shifting sand or rock constitute the largest categories.

Distribution of Soil among and within Forest Biomes

Past and present differences in climate and landscapes have created the forests we view today. Discounting the role of humans, the species composition of the worlds forests correspond to areas of distinctive landscapes, climates, and biota referred to as biomes. Because the extent of biomes can extend across continents, large differences can occur in the types of soils encountered. Describing this variation is really a matter of the scale chosen. However, three major points are:

1. soils commonly differ as much within regions as around the globe
2. soil types are distributed unevenly around the globe
3. a particular forest biome can occur on a variety of soils.

Patterns of soil properties vary in relation to the five soil-forming factors. However, variation in a given parameter can be as great within a forest stand as among biomes. Variation across a landscape can be as great as among soil types on a continent. Therefore, a given forest type can occur across a range of soils, and a particular soil type can occur in multiple forest regions.

Within the temperate regions, Entisols, Alfisols, Inceptisols, and Ultisols support the majority of forest (**Figure 5**). Other orders, excepting Aridisols and

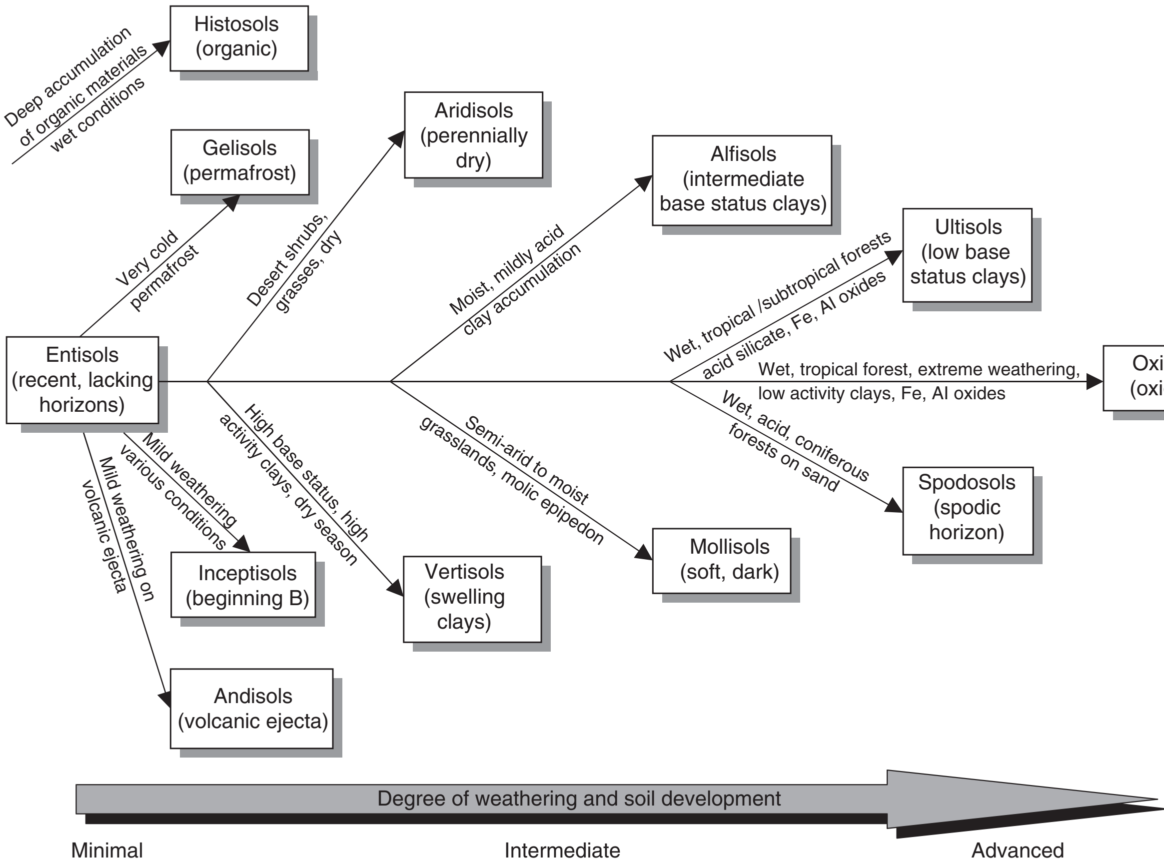


Figure 4 Diagram showing general degree of weathering and soil development in the soil orders within the US Department of Agriculture *Soil Taxonomy*, including the general climatic and vegetative conditions under which the orders are formed. Modified from Brady NC and Weil RR (2002) *The Nature and Properties of Soil*, 13th edn. Upper Saddle River, NJ: Prentice-Hall.

Table 2 World distribution of soil orders by percentage of land area

US Taxonomy Soil Order	*Analogous categories in FAO and other widely used classification systems*	*Percentage of ice-free land*
Entisol	Regosols, lithosols, arenosols	16.2
Inceptisol	Acid brown soils, gleysols, cambisols	9.8
Mollisol	Prairie soils, chernozems, rendzinas,	6.9
Histosol	Bog soils, histosols	1.2
Gelisol	Gelic members of gleysols, cambiosols, and others	8.6
Spodosol	Podzols	2.6
Alfisol	Grey wooded soils, luvisols, planosols	9.7
Vertisol	Grumusols, vertisols	2.4
Ultisol	Red–yellow podzols	8.5
Oxisol	Latosols, ferralsols	7.5
Aridisol	Xerosols, solonetz, solochaks, yermosols	12.0
Andisol	Andosols	0.7
Shifting sand or rock		14.0

Source: Modified from US Department of Agriculture Natural Resources Conservation Service.

Gelisols, are also capable of supporting forests, but large portions have been reserved for nonforest uses, particularly agriculture. Aridisols are too dry to support forests, and Gelisols are too cold. Boreal forests occur mostly on Spodosols, Entisols, Inceptisols, and Histosols. In most of the world, Alfisols indicate the potential for broadleaved forests. Because of their volcanic origins, Andisols are limited in occurrence, usually near the edges of continental plates, but can support some of the world's most

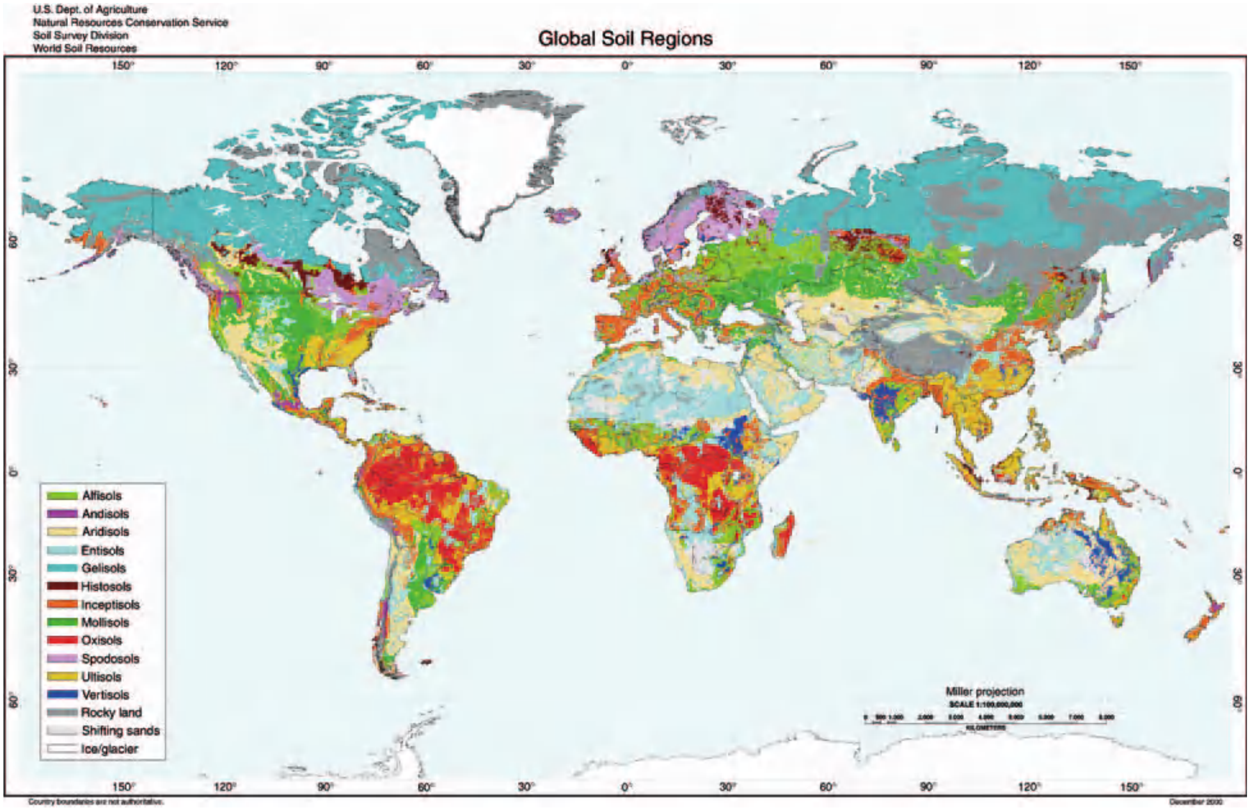


Figure 5 Map of global soil regions using the US Department of Agriculture *Soil Taxonomy's* Soil Orders. From US Department of Agriculture Natural Resources Conservation Service.

productive forests. Ultisols are most common in tropical and near tropical latitudes, and the warmest, moistest regions where soils have been permitted to weather in place for long periods of time. Both broadleaved and conifer species are common, with the broadleaves dominating on the moister and more fertile Ultisols. Oxisols are the worlds most weathered and mature soils, occurring in the tropics. A synopsis of the world's forested communities follows.

Tropical Forests

Tropical forests begin at the equator, and span north to the Tropic of Cancer, south to the Tropic of Capricorn. Approximately 33% of the world's forests occur here amidst considerable variation in climate, elevation, and geology. The major soil orders are Inceptisols, Andisols, Ultisols, and Oxisols.

Tropical rainforest These moist tropical forests comprise about 30% of the tropics. The nutrient cycle between the vegetation and the soil is essentially closed. Rainfall is generally between 2000 and 4000 mm year^{-1}. Constant litter fall and decomposition throughout the year (udic environments) and the virtual absence of leaching permit the development of luxuriant forest with no nutrient deficiency symptoms in soils of low native fertility. The only marked vegetation differences outside of swamps that can be correlated with soils are the reduced stature of rainforests growing on very sandy Spodosols.

Seasonally dry deciduous and semideciduous tropical forest Deciduous and semideciduous forests occur where the dry season is sufficiently strong to exclude rainforests but grasses are not dominant. Rainfall is between 1200 to 2000 mm year^{-1}. About 15% of the tropics are covered by semideciduous, deciduous, and thorn forests. The nutrient cycle, however, is markedly different from that of the rainforest. With substantial litter fall during the dry season, the solar radiation reaching the soil surface increases drastically, and the litter layer does not decompose during the dry season.

Savanna These are transitional areas between the tropical forests and deserts. Rainfall is in the range of 900 to 1500 mm year^{-1}. Also known as tropical grasslands, savannas have widely scattered trees that are generally deciduous. Fire frequency is important in maintaining these communities as trees are normally excluded when burn frequency and intensity increases.

Temperate Deciduous Forests

These forests reach maximum abundance between the tropics and 45° N latitude. The climate is characterized by relatively cold winters and warm summers with reasonably evenly distributed rainfall (averaging 750 to 2500 mm year^{-1}) throughout the year. Leaf fall corresponds to a period of cold and unavailability of water. Conifers become more prevalent at the drier and colder, and mountainous margins of this biome. Entisols, Inceptisols, Alfisols, Spodosols, and Ultisols are the most common soil orders.

Boreal Forest

The boreal regions of the world are characterized by long, cold, snowy winters. These biomes are the result of a climate found only in the interior of large continental landmasses in the northern hemisphere. Conifers are the most abundant tree species with some cold-tolerant, deciduous broadleaved vegetation occurring at the southern and milder margins. Entisols, Inceptisols, Spodosols, and Histosols are the most common soil orders.

Further detail on the extent and development of the world's forest biomes can be found in the section on Further Reading.

Summary

Forests provide a unique set of environmental factors influencing soil formation. The most important of these is the microclimate at the earth's surface engendered by the canopy of trees and understory vegetation, the role of tree roots in cycling nutrients from great depths, and the large additions to soil organic matter made by tree roots and foliage. Fully one-third of the earth's soils developed under a original cover of forest. Although forests can occupy very fertile soils, much of the world's remaining forest exists on landscapes marginally suited for other human uses.

The two dominant soil-forming processes in forests are podzolization and desilication. These two processes occur in the two forest biomes least influenced by humans, the boreal and tropical forests, respectively.

Some tree genera and species assemblages will thrive on most of the soil orders making it difficult to predict forest composition based solely on soil. Forest composition and productivity depend more on local-scale factors such as topography, soil physical properties, and inherent differences in local climate, than to soil categories.

See also: **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health; Soil Biology; Soil Organic Matter Forms and Functions; Tree Roots and their Interaction with Soil. **Soil Development and Properties**: Landscape and Soil Classification for Forest Management; Nutrient Cycling; Nutrient Limitations and Fertilization; The Forest Floor. **Tree Physiology**: Nutritional Physiology of Trees; Root System Physiology.

Further Reading

Brady NC and Weil RR (2002) *The Nature and Properties of Soils*, 13th edn. Upper Saddle River, NJ: Prentice Hall.

Fisher RF and Binkley D (2000) *Ecology and Management of Forest Soils*, 3rd edn. New York: John Wiley.

Hendricks RL (2001) Forest types and classification. In: Evans J (ed.) *The Forests Handbook*, vol. 1, pp. 23–60. Oxford, UK: Blackwell Science.

Soil Survey Staff, US Department of Agriculture (1976) *Soil Taxonomy*, 2nd edn. Pittsburgh, PA: US Government Printing Office. Available online at http://www.nhq.nrcs.usda.gov/WSR

Soil and Water Conservation Society (2000) *Soil Biology Primer*. Ankeny, IA: Soil and Water Conservation Society.

Landscape and Soil Classification for Forest Management

L T West, University of Georgia, Athens, GA, USA

Soil Classification

Soils vary across the earth's surface, and understanding and managing this variation is key to understanding, managing, and sustaining both natural and anthropogenic ecosystems. Properties of the soil at any point in the landscape are the product of an array of complex processes, tempered by the environmental factors climate, biota, and topography, acting on a parent material over time. Because of the vast numbers of combinations and intensities of these five state factors, the number of different soils is seemingly endless. It is generally agreed, however, that it is possible to group soils into classes having many properties that are similar which is the basis for soil classification.

Properties chosen to form classes vary among soil classification systems, and the choice of properties used as the basis for developing classes and the property limits used to separate classes are often debated. The goal of all systems, however, is to provide classes that have similar properties and/or similar responses to external inputs. In addition, soil classification provides a means for organizing knowledge about soils and for enhanced communication among soil scientists since a few terms can be used to convey a great deal of information. Grouping soils into classes with similar properties also provides a mechanism for identifying appropriate uses of the soil, for estimating production, for extrapolating knowledge gained at one location to other locations, and for determining research needs.

Most national and international soil classification systems, such as *Soil Taxonomy*, are general-purpose natural classification systems. The systems were developed to group soils based on their properties without consideration of any particular use. Thus, these systems use many properties to form classes, and interpretations of soil behavior under any of a broad range of uses can be made from an understanding of how properties that define the class affect the intended use.

This is in contrast to soil classification systems developed and used for more narrow purposes such as forest management. Forest managers are mostly interested in soil properties that influence the occurrence and productive potential of a forest stand such as texture, rooting depth, native fertility, and water supplying capacity. Because only a subset of all possible soil properties are of interest, classes are defined based on combinations of properties thought to affect the narrow purpose of the classification system. Thus, the system will be more precise than natural classification systems in predicting expected behavior for the intended use. If land use or management system changes, however, the use-specific classification system may not include the properties needed to effectively implement the change without major changes to the system.

Soil Taxonomy

This section presents a general overview of the structure, basis for class differentiation, and nomenclature of *Soil Taxonomy* which was developed in the USA. Presentation of *Soil Taxonomy* is not meant to imply that it is the only or the best system of soil classification. The structure and nomenclature used in *Soil Taxonomy* are similar to those used in other classification systems. *Soil Taxonomy* is presented as an example that is intended to provide a basis for understanding the basis behind and structure of natural soil classification systems. Its use as an example reflects the author's base of knowledge and experience as do other examples presented in this article.

Soil Taxonomy comprises six categorical levels. These are: order, suborder, great group, subgroup, family, and series. The structure of the system is somewhat analogous to the plant and animal taxonomies in that the highest category (order) is the most general and has the fewest classes (12), and the lowest category (series) is the most specific and has the most classes (16 000 +).

Details of criteria used to separate taxa in *Soil Taxonomy* at all categorical levels are beyond the scope of this text. The general criteria used for each category, however, are given below:

- Order: properties resulting from major soil-forming processes that aid in understanding and interpreting soils at a grand scale.
- Suborder: properties that have a major influence or that reflect these influences on current soil formation processes. Many are also important for plant growth and interpreting soil behavior.
- Great group: properties that impose or reflect subordinate or additional controls on current soil-forming processes and soil behavior such as horizons that retard water movement and root extension.
- Subgroup: properties that reflect either (1) a transition from one taxon to another at a higher category, (2) a transition to properties not recognized at higher categories but are common among many classes (shallow rock, water, etc.), or (3) the central concept of the great group (Typic).
- Family: properties that reflect important conditions affecting soil behavior or potential for further change.
- Series: lowest level of *Soil Taxonomy*. Differentiating criteria are the same as those for higher categories, but ranges in properties are defined more narrowly to aid interpretations of soil behavior and response to management at a local level.

A robust classification system must be based on properties of the population of individuals being classified and not abstract concepts of the processes that have led to the different individuals. Thus, differentia used to separate classes in *Soil Taxonomy* are based on soil properties. However, because understanding a soil's genesis is important for understanding its properties and expected behavior, properties that reflect or influence processes of soil formation have great importance in this system. For this reason, *Soil Taxonomy* is considered a morphogenetic system, i.e., the system is based on observable and measurable soil properties, but many of these properties represent pathways and processes important to soil genesis.

A soil's placement in a particular taxon in *Soil Taxonomy* depends on the presence or absence of diagnostic horizons and features that are considered to be marks of the soil's genesis but that are rigidly defined by morphological, physical, chemical, and mineralogical properties of the soil. Thus, a soil's classification offers information on processes that have been important in its development, but more importantly, because taxa are defined by soil properties, they can be interpreted in terms of expected behavior and response to management. The interpretive detail that can be ascertained from a soil's classification depends on the categorical level at which the interpretations are made. At the order level, few specifics can be said about interpretation for a particular use. The number of specific interpretative statements increases at lower levels of classification to a maximum at the series level.

Most users of soil information that includes a classification are unlikely to have the depth of understanding of diagnostic horizons and features needed to properly classify a soil. However, with an understanding of the nomenclature is used to indicate specific horizons and features, a great deal of information about the properties of a soil can be determined from its classification. In *Soil Taxonomy*, most of the formative elements used to name classes are terms derived from Latin or Greek, and many have similar meaning to terms used in everyday speech. Thus, the nomenclature of a class can reveal many general properties of soil even if the exact definition of the diagnostic horizon or other differentiating characteristic is unknown. The formative elements and concept of the 12 orders is given in **Table 1**. A list and brief definition of formative elements for properties most important to forest management are given in **Table 2**.

Orders

Names of orders end in 'sol.' The formative element for orders begins with the vowel preceding the 'o' or 'i' before 'sol' and ends with the last consonant before the 'o' or 'i.'

Suborders

Names of suborders have two syllables. The first connotes something about the diagnostic properties of the soil, and the second is the formative element from the order. For example: Udalfs – Alfisols with udic moisture regimes, Psamments – sandy Entisols, Aquults – Ultisols with an aquic moisture regime.

Great groups

Names of great groups consist of the suborder and a prefix that is formed by one or two formative elements suggesting something of the diagnostic properties of the soil. For example: Paleudalfs – old (deeply weathered) Udalfs, Udipsamments – Psamments with a udic moisture regime, Epiaquults – Aquults with seasonal saturation from water perched above a water restrictive horizon.

Table 1 Formative elements and the central concept of the 12 orders in *Soil Taxonomy*

Order	*Formative element*	*Central concept*
Alfisols	alf	Soils with an argillic or kandic horizon and greater than 35% base saturation in the lower subsoil. Generally considered to have developed under forest vegetation.
Andisols	and	Soils developed from volcanic ejecta.
Aridisols	id	Soils occurring in a dry climate that have undergone sufficient soil development to have a diagnostic horizon.
Entisols	ent	Soils with no diagnostic horizon because of young age, resistant parent materials, or other factors that prevented soil development.
Gelisols	el	Soils in cold climates that have permafrost within 100 cm.
Histosols	ist	Soils composed of organic soil materials.
Inceptisols	ept	Weakly to moderately developed soils that do not have horizons or features that are diagnostic for other orders.
Mollisols	oll	Soils with mollic epipedons generally considered to have developed under grassland vegetation.
Oxisols	ox	Soils that have an oxic horizon or clayey surface horizon with a kandic horizon; commonly found on old stable tropical landscapes.
Spodosols	od	Soils with a spodic horizon; commonly sandy and developed under coniferous or other vegetation that produces acid leachates.
Ultisols	ult	Soils with an argillic or kandic horizon and less than 35% base saturation in the lower subsoil. Generally considered to have developed under forest vegetation.
Vertisols	ert	Soils with the amount and type of clay to generate high shrink – swell.

Table 2 Formative elements used in names of suborders, great groups, and subgroups that relate to forest composition and productivity

Formative element	*Derivation*[a]	*Connotation*
Abruptic	L. *abruptum,* torn off	Abrupt textural change
Aeric	Gr. *aerios*, air	Aeration (not as wet)
Al	Modified from Aluminum	High aluminum, low iron
Alb, Albic	L. *albus*, white	An albic horizon
Aqu	L. *aqua*, water	Aquic moisture regime
Ar	L. *arare*, to plow	Mixed horizons
Arenic	L. *arena*, sand	Sandy epipedon between 50 and 100 cm thick
Arg	L. *argilla*, white clay	Presence of argillic horizon
Cry	Gr. *kryos*, icy cold	Cold
Cumulic	L. *cumulus*, heap	Thickened epipedon
Dystr, Dys, Dystic	Gr. *dys*, ill	Low base saturation
Endo	Gr. *endo*, within	Saturated by a groundwater table
Epi	Gr. *epi*, on, above	Saturated by a perched water table
Eutro, Eu Eutric	Gr. *eu*, good	High base saturation
Fluv	L. *fluvius*, river	Floodplain
Frag	L. *fragilis*, brittle	Presence of a fragipan
Fragloss		Combination of frag and gloss
Grossarenic	L. *grossus*, thick + L. *arena*, sand	Sandy epipedon > 1 m thick
Hist	Gr. *histos*, tissue	Presence of organic materials
Hydr, Hydric	Gr. *hydor*, water	Presence of water
Lithic	Gr. *lithos*, stone	Presence of shallow lithic contact
Molli	L. *mollis*, soft	Presence of a mollic epipedon
Natr, Natric	L. *natrium*, sodium	Presence of natric horizon
Oxyaquic	Combination of oxy (oxygen) and aquic	Aerated
Pachic	Gr. *pachys*, thick	A thick epipedon
Pale	Gr. *palaeos*, old	Excessive development
Petroferric	Gr. *petra*, rock + L. *ferrum*, iron	Presence of a petroferric contact (continuous ironstone)
Psamm	Gr. *psammos*, sand	Sand texture
Quartz	Ger. *quarz*, quartz	High quartz content
Terric	L. *terra*, earth	A mineral layer under organic soil
Torr	L. *torridus*, hot and dry	Torric moisture regime
Ud	L. *udus*, humid	Udic moisture regime
Ultic	L. *ultimus*, last	Low base saturation
Umbr, Umbric	L. *umbra*, shade	Presence of umbric epipedon
Ust	L. *ustus*, burnt	Ustic moisture regime
Xer	Gr. *xeros*, dry	Xeric moisture regime

[a] Gr., Greek; L., Latin.

Subgroups

Names of subgroups consist of the great group modified by one or more adjectives. The adjective 'Typic' is used for the subgroup thought to typify the central concept of the great group. Other types of subgroups are (1) intergrades toward other great groups, e.g., Aquic Paleudalfs are intergrades to the Paleaqualfs, and (2) extragrades – subgroups not intergrading toward any known kind of soil, e.g., Lithic Udipsamments are intergrading to rock.

Families

Names of families are polynomial and consist of the subgroup and three or more descriptive terms that indicate the particle-size class, mineralogy, cation exchange activity, soil temperature, and other properties of the soils. For example, fine, smectitic, active, thermic Aquic Paludalfs are the Aquic Paleudalfs that have a fine particle size class (35–60% clay), dominantly smectitic clays, an active cation exchange capacity class (0.4–0.6 $cmol\,kg^{-1}$ clay), and a thermic temperature regime (18–22°C mean annual temperature at 50 cm). The particle-size, mineralogy, and cation exchange activity classes are based on the weighted average of upper part of the subsoil. More or fewer terms may be part of the family depending on the subgroup.

Series

Names of series are abstract place names. The name of a series has no meaning to people who have no other source of information about properties that define the series. Common use of classification systems specific to forest management raises the question of the utility of Soil Taxonomy or other natural classification systems to management of the forest resource. By definition, forest management classification systems only consider a subset of soil properties and are often developed for use in a specific region. Thus, properties considered and terminology used to describe these properties may vary among systems. Because of these variations, communication, soil-based technology transfer, and understanding of the soil system across wide regions can be enhanced through use of classification based on Soil Taxonomy or other natural classification systems.

Soils and Landscapes

Because topography is one of the five state factors (climate, topography, biotic influences, parent material, and time) that control soil formation, soils and landscapes are intimately linked. Likewise, the slope, aspect, and shape of the landscape have a strong influence on forest ecology and productivity. Major landscape influences on both soil and ecosystem properties are related to redistribution of water from precipitation, landscape redistribution of solutes, parent material, and, in steep landscapes, slope and slope aspect.

Slope shape is the three-dimensional geometry of a slope which is derived by combining the shape of the vertical slope profile with the shape of the profile along the slope contour. In each direction, the slope can be linear, concave, or convex, and any point in the landscape can be designated as concave – concave, concave – linear, etc. to better communicate the conformation of the landscape. The shape of hillslopes strongly influences lateral movement of water across the landscape as both overland flow and in the shallow subsurface as throughflow. Flow tends to be parallel on linear slopes, convergent in landscape segments with concave slope, and divergent in landscape segments with convex slope. The influence of slope shape on redistribution of water from precipitation creates microenvironments on the landscape in which areas of divergent flow are drier than the landscape as a whole and areas of convergent flow are wetter than the general landscape. These microclimates influence both soil development and vegetation composition and productivity.

Hillslopes can be divided into segments along a two-dimensional profile that is based on slope shape and inflections in the slope gradient. In humid climates, the most commonly used terms for these segments are summit, shoulder, backslope, footslope, and toeslope (**Figure 1**). The summit is the level or slightly convex uppermost part of a hillslope profile. Water movement on summits is mostly vertical although there may by an appreciable lateral component on narrow convex summit positions. Soils on summits are often well drained, but the interior of broad level summits may have poorly drained soils if soil horizons or geologic strata slow the rate of vertical water movement. The shoulder is the convex portion of the hillslope below the summit. The shoulder position commonly has greater lateral flow of water and soils may be drier than the summit. Below the shoulder is the more linear backslope where surface runoff is greatest. Relative proportion of lateral and vertical water movement on backslopes depends on slope gradient and the stratigraphy of soil horizons and geologic strata. The backslope descends to the concave footslope which is an area of convergent flow and accumulation of sediments and solutes transported from upslope by overland flow and throughflow. Downslope from the footslope is the toeslope which has linear or slightly concave slope shapes and low slope gradient. Toeslopes tend to have alluvial parent materials from adjacent or upslope streams.

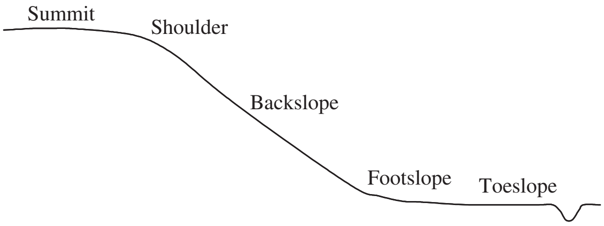


Figure 1 Terms used to describe various hillslope positions.

General types of soil parent material are commonly related to certain landscape positions and/or geomorphic surfaces. Although exceptions are common, especially in areas with extensive windblown materials, soils on summit, shoulder, and upper backslope positions tend to be developed from residual parent materials, and soil properties will be related to properties of the underlying rock or sediment. Gravity and water transported colluvial parent materials are usually found on lower backslope and footslope positions, and soil properties will be influenced by the properties of the colluvium which may or may not be similar to that of the subjacent residuum. Alluvial parent materials are found on floodplains and terraces, and properties of the soils in these settings will be influenced by the textural, chemical, and mineralogical characteristics of the sediment and by the position of the soil within the floodplain or terrace as it relates to stream transport capacity during deposition, i.e., coarse-textured sediments on levees and fine-textured sediments in backswamp positions.

Slope gradient and aspect can have implications for forest productivity and ecology. Slope gradient impacts are mostly related to its effects on rate and amount of overland flow, especially in managed forests. Both tree harvest and forest roads can lead to high amounts of soil erosion in strongly sloping areas if management and construction practices are not carefully planned and implemented. Slope aspect, especially on steep mountainous slopes, has impact on species composition, forest productivity, and soil development. These impacts arise from differences in the amount of solar radiation and corresponding temperature differences that are related to direction to which the slope faces. Because of the sun angle, aspects that face the equator and the afternoon sun (south and west in the northern hemisphere) receive more solar radiation and are warmer than those that face away from the equator. Higher temperature results in greater amounts of evapotranspiration and thus, these slopes have drier soils and less water available for plant growth than those facing away from the equator. This difference in water availability affects species composition and productivity and soil properties, especially thickness and organic carbon content of the surface horizon. In addition, reduced evapotranspiration on slopes facing away from the equator results in more water leaching through the soil, and soils on these slopes often are more developed than soils on similar warmer and drier slopes facing the equator.

In most cases, landscape differences will be reflected in soil map units and/or the classification of the named soil. There may be landscapes, however, in which differences are not reflected in the soil map units because of scale of mapping or intensity of the soil survey. In these cases, it may be useful to employ differences in landscape properties in conjunction with the classification and properties of the soil in evaluating forest ecology and productivity of a site.

Soil Survey

Although classification and mapping are closely related, they are not the same thing. Classification is best applied to individual pedons, and the classification of the pedon is a product of the classification system, which have arbitrary definitions. As a means to inventory the soil resource and/or provide a basis for land management, soil classification has limited applicability. Only when the classification is applied to land areas through a soil survey is the full utility of the classification systems realized for management.

A soil map unit is a natural segment of the landscape that is composed of one or more dominant soils. Environmental factors that influence soil formation (parent material, topography, and vegetation) are generally observable on the landscape, and when one or more of these factors changes, it reflects a change in the soil. Thus, landscape properties are used to infer occurrence of a particular soil on that landscape segment. This is the science that is the basis for soil survey. After relationships between type of soil and landscape properties have been identified through careful study, the landscape characteristics can be used to identify and map soils with only limited observations of the soil with depth.

Because soil map units are geographical bodies that are delineated on the ground, they almost always contain soils different from the named taxonomic unit. The soils other than the named taxa are referred to as inclusions. Inclusions are commonly categorized as similar to the named soil, i.e., different taxonomically but having similar interpretations of behavior, or dissimilar from the named soil, i.e., different both taxonomically and interpretively. Similar inclusions may be present by design in order to reduce map clutter and the number of potential management units. However, soil properties that result in similar interpretations for one land use may result in different interpretations for a different use. Thus, expected land use over the foreseeable future must be a consideration in map unit design.

Dissimilar inclusions occur because of (1) an incomplete understanding of the relationship between observable landscape characteristics and the type of soil or, more commonly, (2) because of map scale. If the smallest feature that can be drawn on the map is 2 ha in size, soils that occur as smaller bodies cannot be shown on the map even if the soil surveyor is aware they are present. Thus, the goal of soil mapping is to design and delineate map units that have a minimum amount of dissimilar inclusions.

Soil–Site Productivity Relationships

Soils and vegetation are intimately linked. A forest soil has been defined as one developed under and currently supporting forest vegetation. This implies that given sufficient time, properties of soils developed under a forest will have different properties from those developed under types of vegetation. These differences in genesis are reflected in soil classification systems. Differences in root distribution and relative amounts of above and below ground biomass between trees and grasses result in different surface soil properties which are reflected in differentia for Mollisols from other orders. Acid leachate from coniferous forest litter combined with sandy parent material results in podzolization being a dominate soil forming process leading to

Table 3 Recognition of soil properties that affect forest composition and productivity by taxa in *Soil Taxonomy*

Soil property	*Relation to site quality*	*Indicative classes in* Soil Taxonomy
pH (base saturation as covariable)	Affects nutrient availability	Soil orders (Mollisols, Alfisols, Ultisols), dystric and eutric great groups and subgroups, acid and nonacid families
Base saturation	Affects K, Mg, and Ca supply	Soil orders (Mollisols, Alfisols, Ultisols), dystric and eutric great groups and subgroups
Organic matter content	Source of N and P, promotes structure	Mollisols, umbric great groups and subgroups
Particle size distribution	Affects water and nutrient storage	Family particle-size class
Cation exchange capacity	Affects nutrient storage	Family cation exchange capacity classes, family particle-size and mineralogy classes, kandi and kanhapl great groups
A horizon structure	Promotes aeration and root proliferation	Mollisols and umbric great groups and subgroups
Depth of A horizon	Affects biological activity	Mollisols and umbric great groups and subgroups
Root restrictive horizons and strata	Limits rooting depth	Fragi great groups and subgroups, lithic subgroups, shallow families
Soil moisture regime	Soil moisture availability and aeration	Aquic, udic, ustic, xeric, and aridic suborders, great groups, and subgroups
Soil temperature regime	Affects root growth and microbial activity	Soil temperature regimes as family classes
Depth to redoximorphic features	Depth to seasonal saturation and related aeration	Aquic suborders, aquic and oxyaquic subgroups

development of spodic horizons and Spodosols (Podzols). Ancient conversion of forests to cropland has been shown to appreciably alter subsoil properties and resulting classification (Spodosols converted to Inceptisols). Numerous other examples of vegetation affects on soil development are available in the literature. Because vegetation affects soil genesis and properties, it is reasonable to expect the converse to be true. Soil conditions will have a major effect on forest composition and productivity.

The composition and productivity of a site depends on the inherit quality of the site and management inputs. Site quality is strongly influenced by soil, topography, and climate. Soil properties that affect site quality include soil temperature, nutrient supply and availability, soil organic matter content, texture, structure, consistence, depth to redoximorphic features (drainage), thickness of the A horizon, stone content, depth to horizons that restrict water movement and root elongation, and the thickness of the B horizon. Many of these properties are used to differentiate among taxa in *Soil Taxonomy* and other natural classification systems (**Table 3**).

Thus, classification and soil map units have often been interpreted as to their potential forest composition and productivity. These interpretations are based on observations, often unsystematic, of forest conditions over the area in which the soil occurs. Attempts to develop firm relationships between soil map units and forest productivity, however, have met with mixed success. Many studies have used soil map units to predict site productivity with considerable success while others have reported little or no relationship between map units and productivity. A part of this discrepancy is related to the landforms and species being considered, but the major factor may lie in the fact that map units in most soil surveys, at least in the USA, were designed for agricultural purposes with forest management as a secondary consideration if considered at all. Better communication and cooperation between forest managers and soil scientists during the initial stages of a soil survey so that soil and landscape differences that are important for forest management can be considered in map unit design may well improve the utility of soil surveys for forest management.

See also: **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Soil Development and Properties**: Forests and Soil Development; Nutrient Cycling.

Further Reading

Ahrens RJ and Arnold RW (2000) Soil taxonomy. In: Sumner ME (ed.) *Handbook of Soil Science*, pp. E117–E135. Boca Raton, FL: CRC Press.

Arp PA and Krause HH (2002) Forest soil properties and site productivity. In: Lal R (ed.) *Encyclopedia of Soil Science*, pp. 590–593. New York: Marcel Dekker.

Buol SW, Hole FD, McCracken RJ, and Southard RJ (1997) *Soil Genesis and Classification*, 4th edn. Ames, IA: Iowa State University Press.

Carmean WH (1975) Forest site quality evaluation in the United States. *Advances in Agronomy* 27: 209–269.

FAO/ISRIC/ISSS (1998) *World Reference Base for Soil Resources*. World Soil Resources Report no. 84. Rome: Food and Agriculture Organization.
Fisher RF and Binkley D (2000) *Ecology and Management of Forest Soils*, 3rd edn. New York: John Wiley.
Krogh L (2002) Classification systems, major. In: Lal R (ed.) *Encyclopedia of Soil Science*, pp. 176–182. New York: Marcel Dekker.
Nortcliff S (2002) Classification, Need for. In: Lal R (ed.) *Encyclopedia of Soil Science*, pp. 166–168. New York: Marcel Dekker.
Spaargaren OC (2000) Other systems of soil classification. In: Sumner ME (ed.) *Handbook of Soil Science*, pp. E137–E174. Boca Raton, FL: CRC Press.
Soil Survey Staff (1999) *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys, 2nd edn*. Agricultural Handbook no. 436. Washington, DC: US Department of Agriculture Natural Resources Conservation Service.
Wysocki DA and Schoeneberger PA (2000) Geomorphology of soil landscapes. In: Sumner ME (ed.) *Handbook of Soil Science*, pp. E5–E39. Boca Raton, FL: CRC Press.

The Forest Floor

R D Briggs, State University of New York, Syracuse, NY, USA

Introduction

One of the most striking features of forests is the canopy, which consists of leaves and branches forming a noticeable layer that shades the ground and provides habitat for numerous birds, mammals, and insects. In addition to providing habitat, the canopy provides a substantial input of organic litter to the soil surface as the trees cyclically shed foliage, flowers, fruit, twigs, and bark. Over time as forests grow and develop, organic remains of plants and animals accumulate on the soil surface. The accumulation of foliage and branches is collectively referred to as the forest floor. The forest floor, along with tree roots, is an integral component of the forest soil system that distinguishes forest soils from agricultural soils.

The forest floor has a tremendous impact on the soil environment. One of the most important factors affecting tree growth is the capacity of the soil to transfer energy, water, and gases from the soil surface to organisms and roots living deeper in the soil. One of the fundamental soil physical properties influencing this transfer is soil structure, which refers to the aggregation of primary soil particles (sand, silt, clay) into secondary units. Well-developed granular structure occurs in the surface mineral soil horizons creating pores that are large enough for water to flow freely through. Soil structure is described by shape (i.e., granular refers to small spheres, and blocky refers to larger aggregates). There is no quantitative expression currently available to describe soil structure.

Bulk density is a commonly used soil physical property that is influenced by soil structure. Bulk density is a measure of dry mass per unit volume of undisturbed soil. The undisturbed volume includes both the solid particles as well as pore space. For a given type of soil particle (organic vs. mineral), increased pore space results in lower values of bulk density. The particle density of organic matter is approximately half that of mineral soil, which averages $2.65\,\mathrm{Mg\,m^{-3}}$. The combination of low particle density and a relatively high volume of pores impart a low bulk density to the forest floor, which ranges from less than 0.1 to $0.30\,\mathrm{Mg\,m^{-3}}$. Contrast that figure with the range for typical surface mineral soil horizons of $1.0\text{–}1.3\,\mathrm{Mg\,m^{-3}}$. For purposes of comparison, the density of water is $1.0\,\mathrm{Mg\,m^{-3}}$.

The large pore space volume associated with the forest floor has several important consequences. Air filled pores of forest floors act as an insulator, buffering soil temperature by reducing daily high and increasing daily low temperatures. Water infiltration, the movement of water into the soil, and water storage capacity are high because of the large volume of pore space. Consequently, overland water flow in forest soils is rare. The forest floor provides a physically favorable environment for plant roots and soil fauna. Low bulk density does not restrict root growth or organism movement, while high pore space and water holding capacity ensure adequate moisture and aeration required by aerobic organisms. These favorable physical properties promote a high level of biological activity which decreases with depth below the soil surface.

Characterization of Organic Horizons

The forest floor is differentiated from mineral soil on the basis of organic matter expressed as carbon (C) concentration. The organic material comprising the forest floor exists in a decay continuum, ranging from relatively undecayed plant material on the surface to black, highly decomposed organic material referred to as humus. The US soil classification system divides the decay continuum into three discrete layers or horizons (**Figure 1**): (1) Oi, fibric material, relatively undecomposed; (2) Oe, hemic material, moderately decomposed; and (3) Oa, sapric

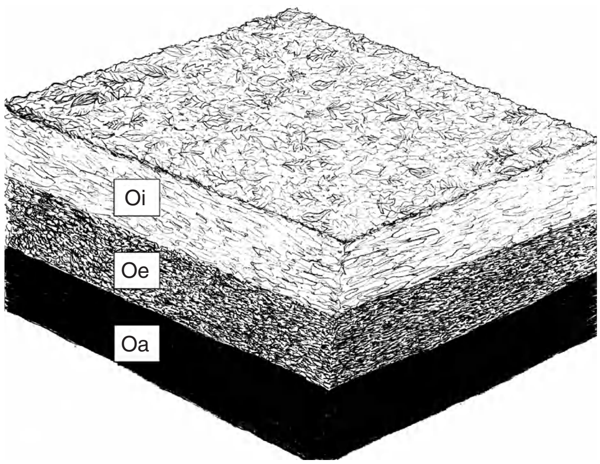


Figure 1 Idealized schematic of forest floor organic horizons. Proceeding downward from the fibrous Oi to the highly decomposed Oa horizon, litter identity is lost and the C : N ratio becomes smaller. *In situ* boundaries among organic horizons often are indistinct along the decay continuum and are not easily differentiated. Illustration by Rachael Briggs.

Table 1 Comparison of organic horizon designations for three soil classification systems

US	*Canada*	*FAO*[a]
Oi (L)	Of	O
Oe (F)	Om	O
Oa (H)	Oh	O

[a] The Food and Agriculture Organization (FAO) system does not differentiate on the basis of degree of decomposition among organic horizons. Organic horizons that are saturated are designated as H.

material, highly decomposed amorphous humus. Comparison with other classification systems is provided in **Table 1**. The letter O signifies the organic master horizon. The accompanying lowercase letters indicate the relative degree of decomposition. All three horizons may not always be present in the forest floor. The presence or absence and degree of development of each horizon depends on a variety of factors including amount and type of organic inputs, decomposition rate, and the activity of soil fauna.

Degree of decomposition is quantitatively defined on the basis of rubbed fiber content. Rubbed fiber content is the proportion of sample volume comprised of fibers that remain after rubbing between the fingers under a stream of water. Highly decomposed material is removed by this simple process, leaving only fibers. The Oi horizon, which consists of relatively undecomposed material that can be identified as to original plant component, has a rubbed fiber content exceeding 75%. At the other extreme, the highly decomposed Oa horizon has a rubbed fiber content less than 17%. The Oe horizon has a rubbed fiber content between 17% and 75%.

The use of quantitative criteria has improved field identification of the boundaries among organic horizons as well as the boundary between the Oa and the mineral soil. Mineral soil horizons contain less than 18% organic carbon on a weight basis. Laboratory analysis is often used to confirm field determinations. Prior to the use of rubbed fiber content to classify organic horizons, they were designated qualitatively as L (litter), F (fermentation), and H (humus) layers. Those classes approximately correspond to the current Oi, Oe, and Oa horizons, respectively. Differentiation among L, F, and H horizons in the absence of quantitative criteria often proved difficult; there was considerable inconsistency among forest soil scientists. Inconsistency was also noted for individual scientists over time.

Forest Humus Types

The concept of humus type, which is the classification of forest floors on the basis of morphology and arrangement of organic horizons, originated in Denmark in the late nineteenth century. The concept has evolved to generate detailed hierarchical classification systems with numerous subcategories. One of the most comprehensive was published in 1993 as a monograph. Three general categories associated with productivity and the rate of nutrient cycling described in this early work continue as the foundation for all of these systems: mor, duff mull (also referred to as moder), and mull.

The mor forest humus type is sometimes referred to as acid humus. It is associated with coniferous species that produce recalcitrant, nutrient poor litter. In this humus type, there is an abrupt boundary between the Oe or Oa and the mineral soil horizon. This abrupt boundary indicates that there is very little if any incorporation of organic matter with the underlying mineral soil, reflecting a relatively low level of biological activity. In addition, incomplete decomposition of the nutrient poor organic material generates large quantities of organic acids. As the organic acids are washed down the profile by percolating water, they strip organic matter and sesquioxides from mineral soil particle surfaces, carrying them downward and depositing them in an underlying horizon.

The mull forest humus type, associated with fertile systems and high rates of nutrient cycling, represents the other extreme of the spectrum. The mull is characterized by highly decomposed, amorphous organic matter intimately incorporated into the mineral soil (A horizon). Thick organic horizons do not accumulate; Oe and Oa horizons are absent due to the high rate of biological activity. Decomposition is relatively rapid, releasing nutrients and preventing immobilization in organic residues. The mull forest humus type is associated with fertile sites supporting nutrient demanding species such as sugar maple (*Acer saccharum*), basswood (*Tilia americana*), and white ash (*Fraxinus americana*).

The duff mull forest humus type is intermediate between the mor and mull types described above. There is greater incorporation of organic matter in the mineral soil than for the mor forest humus type but less than the complete incorporation associated with mulls. The rate of nutrient cycling and decomposition is intermediate.

Decomposition and Nutrient Cycling

The forest floor serves an important role in cycling of nutrients and organic matter. Organic matter chemical composition reflects that of the material from which it originated; approximately 90% of plant dry weight consists of carbon, hydrogen, and oxygen. Nitrogen comprises 1–2% and the remainder is comprised of plant nutrients such as phosphorus, potassium, calcium, magnesium, etc. The organic horizons provide habitat for a diverse biota. In addition, organic matter is a substrate, serving as a source of energy and nutrition for a multitude of organisms. Ultimately, aerobic organisms convert organic matter to carbon dioxide and water. In the process, essential plant nutrients are converted from organically bound to soluble plant available forms, a process known as mineralization. Biological activity is greatest for mull and least for mor forest humus types.

A host of organisms ranging in size from moles and gophers down to microscopic bacteria and fungi participate in mineralization. Macrofauna that tunnel and burrow generate large pores that facilitate removal of excess moisture and transfer of oxygen from the atmosphere to the soil atmosphere. These macrofauna indirectly affect decomposition by improving soil aeration. The role of earthworms in improving soil physical properties, as well as soil chemical properties, is well documented. A variety of organisms physically reduce particle size, a process known as comminution. Reduced surface area: volume ratio facilitates microbial attack, biochemical decomposition and synthesis of new compounds.

Organic matter decomposition rates can be estimated by successively measuring mass loss of confined organic residues (i.e., foliage, fine roots) in nylon mesh bags over time. The mesh is small enough to contain decaying material and large enough to permit mesofauna entry. Numerous such studies have found that the negative exponential function can be used to model the loss of mass over time:

$$y = e^{kt}$$

where y is the proportion of mass remaining at time t, k is the decomposition constant, and t is time (years). This model is convenient because the proportion of mass remaining over time can be described by a single variable, k. The model is a monotonically decreasing function bounded by 1 and 0 (**Figure 2**).

Environmental Variables Constraining Decomposition

Numerous studies in forest systems have demonstrated the degree to which organic matter decomposition rates are constrained by aeration, temperature, precipitation, and litter quality. Decomposition is promoted by a plentiful supply of oxygen for aerobic organisms. In the absence of oxygen, organic matter decomposition is very slow and organic matter builds up. Organic soils, which form in saturated conditions, illustrate what happens in the absence of oxygen. Saturated conditions prevent aerobic organism activity, effectively stopping the decomposition process. When organic soils are drained, they are very productive for both agriculture and forestry because of their desirable physical and chemical properties. One of the problems associated with drainage of organic soils is subsidence. Organic matter exposed to atmospheric oxygen decomposes and the organic soil depth decreases rapidly.

Given adequate oxygen, temperature and moisture constrain decomposition. In the absence of adequate

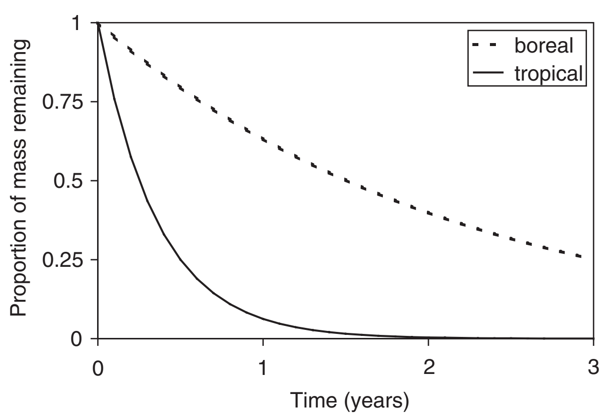


Figure 2 Mass of deciduous leaves over time modeled for deciduous leaves using the model $y = e^{kt}$, with $k = -0.46$ for *Betula papyrifera* in the boreal forest and $k = -2.77$ for *Pentaclethra macrolobal* in the tropical forest. Values of k were obtained from published literature.

moisture, biologic activity is limited and decomposition proceeds slowly even at warm temperatures. Decomposition rates are notably reduced in arid environments. When moisture is not limiting, decomposition rates increase with increasing temperature and litter disappears more rapidly. The minimum temperature for appreciable biological activity (5°C) is often referred to as biological zero. Comparison of the rate of mass loss for deciduous leaves in boreal and tropical rainforests illustrates the influence of temperature on decomposition (**Figure 2**). Organic matter builds up in cold, wet conditions characteristic of the boreal forest and the tundra.

Within a given climatic regime, decomposition rate increases with increasing litter quality. Generally, high quality litters have narrow C : N ratios and relatively low proportions of recalcitrant constituents such as complex fats and waxes. Nitrogen is required by the bacteria and fungi that decompose plant tissue. When adequate quantities of nitrogen are available to those organisms, decomposition proceeds more rapidly. As decomposition proceeds, the C : N ratio decreases. Consequently, the C : N ratio is higher for the Oi than the Oa horizon.

Decomposition Influences Productivity

Rates of organic matter decomposition, which are reflected in the forest humus type classification, are related to forest productivity. During the process of decomposition, carbon bound in the forest floor is converted to carbon dioxide. Plant essential nutrients undergo mineralization, which is the conversion from organic to a readily soluble plant available form. Higher rates of decomposition result in a more rapid cycling of essential plant nutrients and higher productivity.

The thick forest floors of boreal forests accumulate and immobilize large quantities of nutrients. In some boreal forests, the average time litter resides in the forest floor before it is completely decomposed, or its mean residence time, is 350 years. Thus, in spite of the large amount of nitrogen contained in the forest floors, trees in the boreal forest may exhibit nitrogen deficiency because the nitrogen is bound in an organic form that is unavailable to plants. This situation also may occur in upland conifer forests where litter quality is low. Rates of nutrient cycling in the humid tropical forests, in contrast, are much more rapid. Mean residence time for organic matter in tropical rainforests is on the order of 4 years. Consequently, forest floors generally do not build up except where saturated conditions prevent aerobic organism activity.

Forest Floor Mass: Accumulation – Decomposition

Forest floor mass is the difference between litter accumulation and decomposition. Global patterns for litterfall reflect the effects of climate on production. Although there are wide ranges within latitudinal zones, annual litterfall generally increases with decreasing latitude from boreal (2–4 $\mathrm{Mg\,ha^{-1}}$) to tropical (5–13 $\mathrm{Mg\,ha^{-1}}$) forests. Rates of organic matter decomposition also vary with latitude, increase with increasing temperature from the boreal forests to the tropics when moisture is not limiting.

Published values for forest floor mass range from a few to more than 100 $\mathrm{Mg\,ha^{-1}}$. Although accumulation and decomposition vary with latitude, it is not possible to make generalizations regarding forest floor mass because of additional factors that operate at a more local scale. Disturbances such as fire, tornadoes, hurricanes, and timber harvesting are common features of all forest ecosystems. The cyclical nature of disturbance in a variety of ecosystems has a profound effect on density and species composition. Large-scale disturbances that remove portions of the canopy reduce litter inputs for a given time period. In addition, the exposure of the forest floor to increased light and moisture levels due to reduction of the canopy and in plant transpiration, increases the rate of decomposition. At some point in stand development, accumulation rate may equal decomposition rate and the forest floor mass remains relatively constant. Steady state is the term used to describe this condition.

Forest Management and the Forest Floor

An important goal of forest management is to minimize disturbance to the forest floor, in order to preserve the integrity and function of this vital component of the forest ecosystem. The intact forest floor has a high infiltration capacity and absorbs the kinetic energy of falling raindrops. The combined effects of the highly absorbent forest floor and the presence of numerous large pores from roots and organism activity eliminates overland flow of water and prevents soil erosion. Soil loss from forested systems, the result of streams cutting through their banks, is the benchmark rate of natural erosion, against which rates of accelerated erosion are compared.

It is clear that the forest floor is a dynamic entity having a profound impact on the functioning of forest ecosystems. The forest floor modifies the forest soil environment, increasing the capacity for exchange of water, energy, and gases between the atmosphere and the soil system. Decomposition of the forest floor over time provides a continual source of nutrients for vegetation preventing excessive losses through leaching and insuring high levels of forest productivity. In addition, the forest floor provides favorable habitat and substrate for a diversity of organisms that contribute to cycling of nutrients through the forest ecosystem.

See also: **Ecology**: Forest Canopies; Natural Disturbance in Forest Environments. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health; Soil Biology. **Soil Development and Properties**: Forests and Soil Development; Water Storage and Movement. **Tree Physiology**: Physiology and Silviculture; Root System Physiology.

Further Reading

Federer CA (1982) Subjectivity in the separation of organic horizons of the forest floor. *Soil Science Society of America Journal* 46: 1090–1093.

Fisher RF and Binkley D (2000) Soil organic matter. In: *Ecology and Management of Forest Soils*, pp. 139–160. New York: John Wiley.

Green RN, Trowbridge RL, and Klinka K (1993) *Towards a Taxonomic Classification of Humus Forms*. Forest Science Monograph no. 29. Bethesda, MD: Society of American Foresters.

Hole FD (1981) Effects of animals on soil. *Geoderma* 25: 75–112.

Post WM, Emanuel WR, Zinke PJ, and Stangenberger AG (1982) Soil carbon pools and world life zones. *Nature* 298(8): 156–159.

Waring RH and Schlesinger WH (1985) Decomposition and soil development. In: *Forest Ecosystems: Concepts and Management*, pp. 181–210. New York: Academic Press.

Nutrient Cycling

L A Morris, University of Georgia, Athens, GA, USA

Introduction

Worldwide, healthy, productive forests grow on a variety of sites that are of low fertility such as mountains, coastal plain deposits, old highly weathered tropical soils, abandoned agricultural lands, and lands reclaimed after mining. The ability of forests to grow and prosper on such sites is due to the ability of forests to accumulate essential plant nutrients, to utilize these nutrients in production of foliage, and to return these nutrients to the soil or recapture them internally for reuse in subsequent year's growth. This is the process of nutrient cycling.

Geochemical, Biogeochemical, and Biochemical Nutrient Cycles

Nutrient cycling in forests can be divided into three individual but interconnected cycles (**Figure 1**).

The Geochemical Cycle

The geochemical cycle is associated with transfers of elements into or out of the ecosystem. Inputs to the forest from the geochemical cycle include nutrients added to the forest as solutes in precipitation, associated with fine particulates or as aerosols. Additionally, nitrogen (N) can be removed from the atmosphere and added to the forest ecosystem through symbiotic associations of nitrogen-fixing rhizobium or actinorrhiza or through free-living nitrogen fixing organisms. Weathering and release of nutrient elements from parent rock is also considered an addition in the geochemical cycle because of long time factors involved in this process and the conversion of nutrient elements from non plant available to plant available forms. Losses of nutrients from the forest occur as ions dissolved in runoff water and associated with soil particles eroded from the site and moved as suspended sediment or bed load in streams. Nutrients can also be leached below the rooting zone. Fires can play an important role in the geochemical cycle of forests. Large quantities of N and sulfur (S) can be volatilized by fire and returned to the atmosphere. Ash produced during forest fire can be transported long distances and be a significant loss of nutrients from the forest.

The Biogeochemical Cycle

The biogeochemical cycle involves external transfers of elements among different components of a forest system. Uptake of nutrients from the soil and return of these nutrients in leaf fall, branch shedding, root growth and death, or through tree mortality is a major component of the biogeochemical nutrient cycle. Nutrients returned to the soil in this way are not available for plant reuse until decomposition occurs and nutrients are converted from organic to mineral forms, a process termed mineralization. Mineralization of nutrients from organic matter of the forest floor plays an important role in the supply of nutrients available for forest growth. Also included with the biogeochemical cycle is the washing of nutrients from leaves and stem tissue and its return to the soil in precipitation falling through the canopy or flowing down the stem as stemflow.

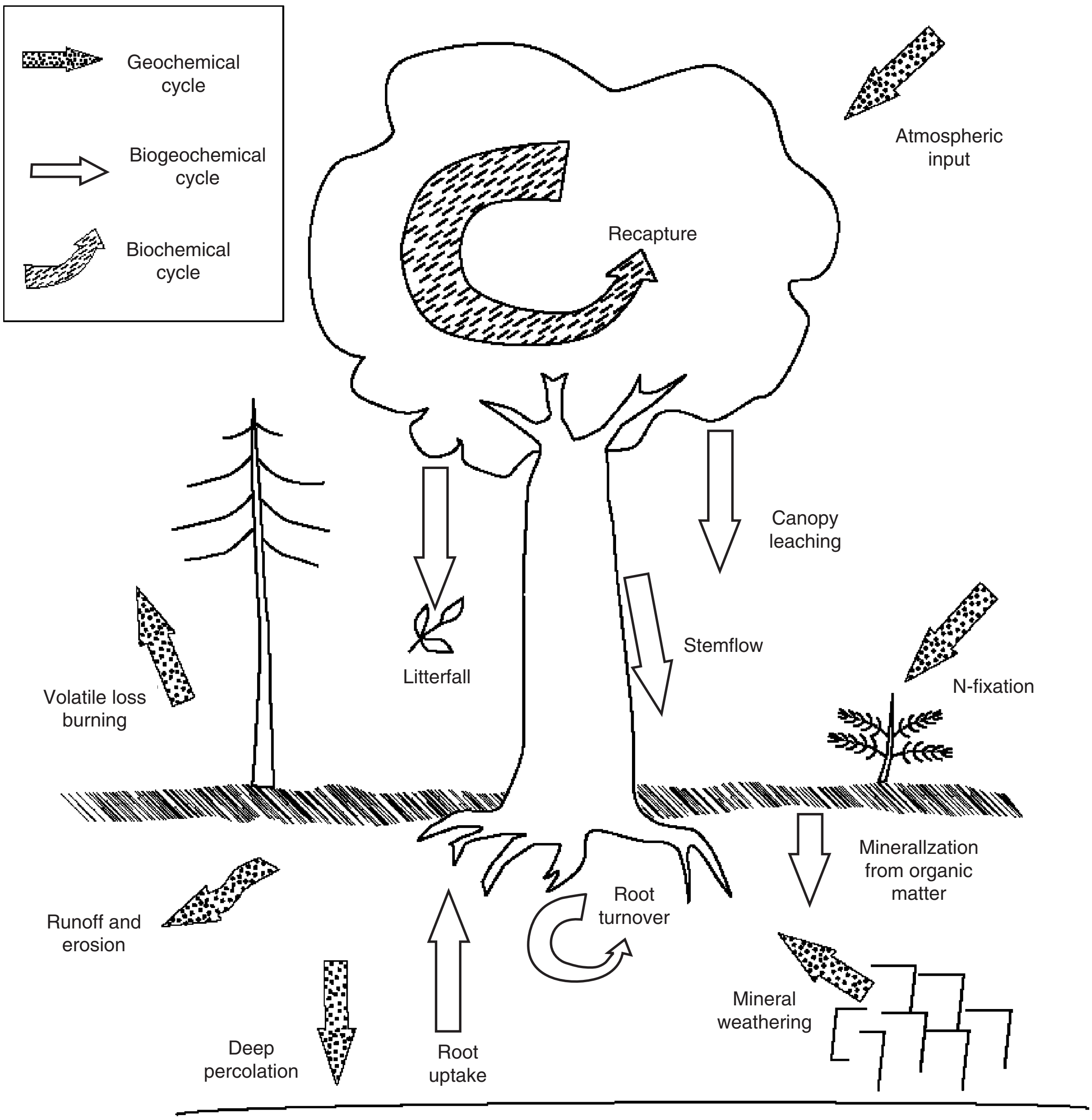


Figure 1 Potential pathways of nutrient flux within the geochemical, biogeochemical, and biochemical nutrient cycles.

The Biochemical Cycle

The biochemical cycle involves the process of transfer and retention of nutrients within an individual plant. In particular, trees can withdraw some nutrients from leaves prior to abscission and store these nutrients within woody tissue where they can be mobilized to supply a portion of the nutrient requirements for subsequent growing seasons.

Contribution of Nutrient Cycles to Nutrient Requirements for Growth

A major portion of the annual nutrient requirements of a forest for growth is supplied by recycling and reuse of nutrients. An example annual nutrient cycle is presented for a hypothetical *Pinus elliottii* forest in the southeastern USA in **Table 1**. On an annual basis, fluxes of nutrients through the geochemical cycle are small in comparison to fluxes through the biogeochemical and biochemical cycles. While the balance of nutrients in the geochemical cycle is important from a long-term forest productivity standpoint, the biogeochemical and biochemical cycles play a much more important role in supplying the annual nutrient requirements for foliage production and annual growth increment.

Major differences exist among individual nutrients in the predominant pathways of transfer within

Table 1 Annual fluxes (in kg ha^{-1} $year^{-1}$) of nutrients through three components of the nutrient cycle for a mature *Pinus elliottii* forest in the Coastal Plain of the southeastern USA

Cycle and pathway	*Nitrogen*	*Phosphorus*	*Potassium*	*Calcium*
Geochemical				
Inputs to ecosystem (+)				
Atmospheric	7.8	0.2	6.0	15.0
N-fixation	2.0			
Weathering	0	0	0	0
Export from ecosystem (−)				
Watershed runoff	6.0	0.13	2.3	5.8
Leaching	0.1	0.03	0.1	1.1
Forest ecosystem balance	+3.7	+0.04	+3.6	+8.1
Biogeochemical				
Mineralization of forest floor (0)	10.2	0.3	3.2	22.8
Inputs to trees (+)				
Root uptake	56.0	3.4	21.0	50.0
Losses from trees (−)				
Litterfall return to forest floor	23.2	0.8	2.7	19.1
Root mortality (turnover)	23.5	1.7	8.5	9.6
Canopy leaching	4.4	0.35	7.3	14.5
Stemflow	0.1	0.01	0.1	0.4
Net tree balance	+4.8	+0.5	+2.4	+6.4
Biochemical				
Retention by trees (+)	28.3	1.5	8.1	0

Based on data of Riekerk H, Jones SA, Morris LA, and Pratt DA (1979) Hydrology and water quality of three small Lower Coastal Plain forested Watersheds. *Soil Crop Science Society of Florida Proceedings* 38: 105–111. Burger JA (1979) *The Effects of Harvest and Site Preparation on the Nutrient Budgets of an Intensively Managed Southern Pine Forest*. PhD thesis, University of Florida, Gainesville. Shan J (2000) *Accumulation, Allocation and Dynamics of Carbon in Slash Pine along a Management Intensity Gradient*. PhD thesis, University of Georgia, Athens and others.

biogeochemical and biochemical pathways. Nitrogen is the nutrient most often limiting growth of forests. It is recycled through the pathway of leaf fall, root mortality, and biochemical retention in almost equal amounts. Canopy leaching and stemflow play a relatively small role in the cycling of nitrogen. This pattern can be contrasted with the patterns of cycling for calcium (Ca) and potassium (K). Calcium is structurally bound with the cell wall of foliage and woody tissue and there is little retention of Ca through the biochemical cycle or return of Ca to the soil in canopy leaching and stemflow. In contrast, K is not structurally bound within the cell and can be leached from plant tissue. The result is that stemflow, in particular, plays an important role in return of K to the soil where it can be recycled through root uptake. Biochemical cycling plays a particularly important role in phosphorus (P) nutrition. Soils of the southeastern USA where the *Pinus elliottii* forest is found contain low amounts of P and are also acidic. Because of high acidity in these soils, and fixation of P by oxides of aluminum and iron, concentrations of P in soil solution where it is available for plant uptake are low. Pine forests growing on these sites have adapted to ensure adequate quantities of P for future growth by translocating a major portion of the P contained in foliage (up to 60%) into permanent woody tissue prior to leaf abscission at the end of the growing season. This P is then available to be recycled back to the foliage at the start of the subsequent growing season.

Species differences, age and differences in inherent site fertility all influence nutrient cycling patterns. For example, differences in geochemical cycling occur for forests located within industrialized areas of the world such as in the northeastern USA and central Europe. These forests receive greater atmospheric inputs of nutrients, particularly N. In some places, high N inputs threaten long-term productivity of the forests. Forests containing N-fixing species as a significant component of the stand have much greater geochemical inputs and outputs of N. For instance, N inputs in red alder stands of the northwestern USA can exceed 100 kg ha^{-1} $year^{-1}$. Biogeochemical and biochemical fluxes also vary as a function of species and site characteristics. Forests located on young soils with high concentrations of easily weathered primary minerals often export quantities of K, Ca, and other nutrients in runoff that greatly exceed the amounts entering the forest in atmospheric inputs. Hardwood species generally have higher Ca demands and uptake than do pine species. Consequently, uptake and return of Ca is much greater in hardwood stands than in conifer stands grown on similar sites. Species differences in the capacity for biochemical withdrawal of P from senescing foliage occur and these differences produce differences in nutrient cycling for different species grown on the same site. Thus, while nutrient cycling plays a role in the growth of all forests, the role varies depending on specific conditions of the forest and nutrient of interest.

Nutrient Accumulation in Forests

The accumulation of specific nutrient elements varies widely among forest ecosystems. Large differences occur among climatic regions due to factors that control overall biologic activity such as temperature and moisture, but other differences are associated with species, age, and overall site fertility. **Table 2** provides examples of accumulation of macronutrients in some forest ecosystems. Observe that each nutrient element has a unique distribution pattern within the forest ecosystem and that this distribution pattern varies among forests. For example, forest ecosystems on young soils in fertile regions contain large amounts of nutrients such as P, K, and Ca found in minerals of parent rocks (e.g., mixed *Quercus*). In contrast, forests growing on quartz sands of marine origin contain low amounts of these nutrients in soil and relatively greater amounts of storage is associated with biomass of the vegetation and the forest floor (organic soil horizon) (e.g., *Pinus elliottii*–*P. palustris*). Accumulations of these nutrients in mineral soils also appear to be particularly low in tropical regions (*Celtis*–*Triplochiton*). It is important to note that the soil accumulations presented in **Table 2** represent different analytical techniques and different soil depths. Depth of rooting is great in many tropical soils and, thus, the content of nutrients available to trees is greater than is represented by the shallow depth of soil included in the contents presented in this table.

A number of other general differences in nutrient accumulation exist among forest ecosystems. Relatively greater accumulations of nutrients occur in the forest floor of boreal forest ecosystems than in either temperate ecosystems or in the tropics. This is due both to the low temperature and reduced biological activity in boreal ecosystems and the relatively low decomposability of foliage of coniferous tree species characteristic of boreal forests. These accumulations can be contrasted with the low accumulations of nutrients in forest floors of tropical systems. Although nutrient inputs in litter of tropical systems are much greater, rates of decomposition and

T0010 **Table 2** Nutrient content (in kg ha^{-1}) and distribution in aboveground biomass, forest floor, and mineral soils of several forest ecosystems

Forest type, location	*Vegetation*				*Forest floor and organic debris*				*Mineral soil*[a]				*Reference*
	N	*P*	*K*	*Ca*	*N*	*P*	*K*	*Ca*	*N*	*P*	*K*	*Ca*	
Abies procera, subalpine, USA	347	54	843	1 025	675	57	312	568	15 855	3 212	85 780	180 960	Turner and Singer (1976)
Picea – *Abies*, boreal, Canada	387	52	159	413	1465	100	1 052	253	559	114	9 383	766	Weetman and Webber (1972)
Pinus banksiana, boreal, USA	346	29	146	294	544	40	37	254	5 554	495	500	1 727	Green and Grigal (1980)
Pseudotsuga menziesii – Tsuga temperate, USA	566	86	189	687	445	62	80	619	4 560	660	2 040	34	Cole and Rapp (1981)
Mixed *Quercus*, temperate, USA	415	29	185	1 250	150	12	20	160	3 725	1 041	23 205	6 270	Johnson and Todd (1987)
Fagus sylvatica, temperate, Europe	285	39	187	152	180	11	20	51	6 640	42	254	365	Ovington (1962)
Pinus taeda, temperate, USA	320	48	225	ND	306	30	28	ND	1 752	270	403	ND	Wells and Jorgensen (1975)
Pinus elliottii – *P. palustris*, subtropical, USA	140	12	43	150	271	10	9	96	2 959	24	82	396	Morris and Pritchett (1982)
Celtis – *Triplochiton*, tropical, Nigeria	1 530	103	702	2 140	514	34	204	530	4 592	13	650	2 576	Greenland and Kowal (1960)

ND, not determined.
[a]To approximate rooting depth using a variety of extraction procedures. Refer to original citation for information on soil depth and method utilized.

mineralization of nutrients are also much greater; consequently, storage is low. Except in the tropics, accumulations of nutrients in the forest floor are relatively large and, in many systems, exceed accumulation in tree biomass.

Forest age also has a major influence on nutrient accumulation in biomass. A typical pattern of nutrient accumulation for a developing forest is illustrated in **Figure 2**. Accumulations of nutrients over time reflect both tree demands and the physiological use of the nutrient. Nitrogen and Ca are both used in large quantities and for the example illustrated are accumulated more than other nutrients. Nitrogen accumulation is much more rapid early in stand development as it is concentrated in foliage, which develops rapidly. In contrast, Ca is accumulated more slowly, but because it is an integral part of the cell wall of woody tissue, it tends to continue to accumulate as long as the forest is continuing to increase biomass.

Mineralization of Nutrients Accumulated in Biomass

Nutrients contained in organic matter returned to the forest floor or soil are not available for plant use until they are released from the structures in which they are

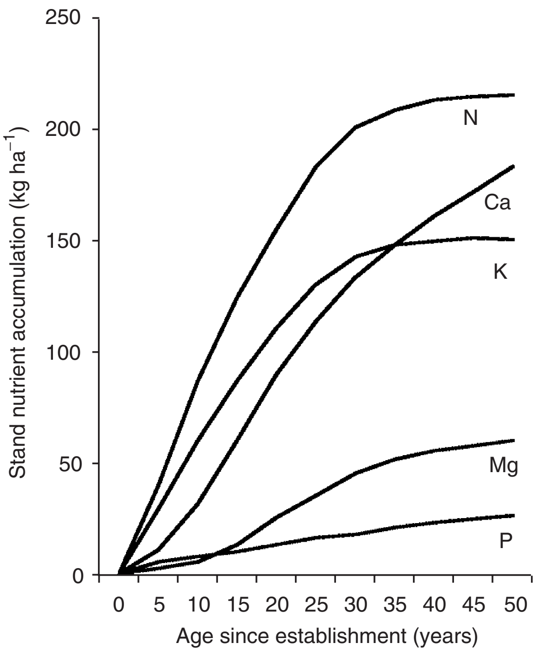


Figure 2 Accumulation of nutrients in biomass of a pine forest in the southern USA. Note the differences in total accumulation among nutrients as well as the difference in pattern. Based on Switzer GL and Nelson LE (1972) Nutrient accumulation and cycling in loblolly pine (*Pinus taeda* L.) plantation ecosystems: the first twenty years. *Proceedings of the Soil Science Society of America* 36: 143–147.

chemically bound. The processes of release of nutrients into inorganic plant available forms is termed mineralization. As organic matter is decomposed, CO_2 is released through respiration and bonds between elements and organic molecules are broken. Mineralization rates are, thus, closely associated with overall decomposition rates. Both characteristics of the substrate being decomposed and environmental conditions affect the rate of decomposition and mineralization. Organic materials that contain a relatively high concentration of compounds easily used by microorganisms involved in decomposition, such as sugar and cellulose, are more rapidly decomposed than compounds that have complex bonds that are not easily broken and used by this decomposer community. Examples of such compounds are polyphenols and lignin. Differences in the decomposition rate among substrates under the same environmental conditions are expressed in terms of a substrates decomposition rate constant. Decomposition rate constants are based on the observation that decomposition of most organic materials tends to follow the pattern of a negative exponential curve:

$$C_t = C_i e^{-kt}$$

where C_i is initial carbon (or organic matter) mass, C_t is carbon (or organic matter) remaining at time t, k is the decay rate constant, and t is time (usually expressed in days or years).

For comparison among species, decay rate constants are usually developed for leaves or ground materials and, thus, are not limited by physical characteristics of the material. Foliage of coniferous species tends to have lower decay rates than species of deciduous angiosperms. Wood and branches have lower decay rates than leaves due to chemical differences. In addition, few surfaces available for microbial colonization exist in branch and stemwood falling to the forest floor. Decomposition of these materials is greatly accelerated by the activity of soil fauna that bore into, create galleries in, or otherwise expose internal surfaces to microbial colonization.

Nutrient mineralization can also be modeled using an exponential decay model, but the actual process is more complicated. Before nutrients will be released into the soil where they are available for plant uptake, the nutrient requirements of decomposing organisms must be satisfied. When a large amount of C, the energy source of heterotrophic decomposers, is available, nutrients released from broken chemical bounds of organic molecules are immediately re-incorporated into the bodies of the decomposing community, a process termed immobilization. This occurs because under this condition, nutrients are in low supply relative to C. Only after a balance is achieved between C availability and nutrient availability does net mineralization of nutrients occur.

The chief environmental variables affecting mineralization of nutrients are temperature, moisture, and oxygen availability. The rate of decomposition, expressed as the decay rate, approximately doubles for each 10°C increase in temperature between 5°C (biological zero) and 35°C. Decomposition and mineralization rates in subpolar regions are so slow that despite large storage of nutrients in the forest floor, forest growth is constrained by low nutrient availability. In contrast, many tropical forests with relatively low nutrient storage have high growth due to rapid decomposition and mineralization of nutrients in organic debris falling to the forest floor. Moisture limits decomposition under either extremely wet or extremely dry conditions. Oxygen does not diffuse rapidly through water. When soils are saturated and all pores filled with water, oxygen will be, essentially, unavailable below the water surface and decomposition and mineralization will not proceed. Bog forests of subpolar regions and swamp forests throughout the world contain large amounts of nutrients but growth is slow because of nutrient limitations. Decomposition also ceases under very dry conditions because water remaining in soil is held so tightly by particle surfaces that microbes cannot incorporate it into their bodies to support their growth. Decomposition is most rapid under moist soil conditions when water is available and soils contain air-filled pores to facilitate oxygen transport.

Forest Management Impacts on Nutrient Cycles

Forest management affects nutrient cycling in a variety of ways. Selection of species for rapid growth increases the demand for, and accumulation of, nutrients in the forest. Harvesting of wood, branches, and/or foliage removes nutrients from the system. Losses of nutrients may be accelerated due to more rapid mineralization and leaching loss or through increased erosion following harvest. Slash reduction and preparation of the site for planting also accelerate leaching and erosion losses. Finally, efforts to reduce competing vegetation regrowth through herbicide application or mechanical removal can contribute to this accelerated leaching and erosion. On the other hand, fertilization or use of N-fixing species has the opposite effect and can greatly increase both the storage and rate of nutrient cycling within forest ecosystems. A summary of the effects that forest management can have on nutrient cycling is presented in **Table 3**.

In undisturbed forests, atmospheric inputs of most nutrients, or inputs from weathering, exceed losses and these systems accumulate nutrients. Over time, forests tend to become more productive as their storage of nutrients increases and the potential for nutrient cycling increases. Removal of wood, branches, and leaves for fuel, timber, or pulp can remove nutrients more rapidly than they are naturally replaced. Over the long term, this can lead to declines in forest growth.

The greatest concentrations of plant nutrients are found in needles and leaves. Wood and branches contain relatively low concentrations of nutrients. Since foliage contains a disproportionate amount of nutrients, harvesting foliage will increase nutrient removal and, in the absence of fertilization or other inputs, can lead to a reduction in nutrient storage and, eventually, loss of productivity. The significance of this tends to be greatest with genera that retain many years of needles (e.g., *Picea*, *Abies*) than in genera that retain only a few years' worth of leaves or needles. Also, because forests tend to accumulate nutrients most rapidly when they are young, shortening the period between harvests can also increase nutrient removal (**Table 4**). Generally, periodic removal of just the wood does not remove an unsustainable amount of nutrients from a forest site. However, frequent harvests especially when coupled with foliage removal will likely lead to unsustainable reductions of nutrient storage in forest ecosystems.

In intensively managed industrial forests, it is common practice to reduce slash from harvest prior to soil preparation and planting. Burning is one common method of slash reduction that can result in volatile losses of nitrogen. Volatile loss of N during burning tends to be very site-specific. Losses during site preparation can be large because large amounts of logging slash are often on the ground and fires are hot. Nitrogen volatilization during site preparation burns following harvest of forests in the northwestern USA may exceed 800 $kg\,ha^{-1}$. In contrast, cooler fires associated with understory control beneath an established forest canopy may volatilize only 20–50 $kg\,ha^{-1}$ N. A second method of slash reduction involves pushing slash and soil into long rows or piles. Such operations have been shown to displace large quantities of nutrients from the majority of the soil surface, concentrating them in a small area where they cannot be efficiently used. In some cases, two or three times more nutrients can be displaced from the soil surface during these operations than are removed from the site in harvest.

Table 3 Potential effects of selected forest management activities on nutrient cycling

Activity	*Geochemical cycling*	*Biogeochemical and Biochemical cycles*
Conversion of natural mixed forests to conifer plantation	Differences are small except where N-fixing species are used	Reduced uptake of base cations, decreased forest floor mineralization, lower overall biogeochemical cycling rates
Shortening length of time between harvests	Increase nutrient removal and slight increase in runoff and leaching losses due to accelerated erosion and increased mineralization	Young forests are building crown and biomass so uptake from soil and accumulation of nutrients predominates; biochemical transfer is less important than in mature forests
Increased utilization of branches and foliage	Foliage and small branches contain a disproportionate quantity of nutrients; utilization of foliage and branches can double the average annual nutrient removal by harvest	Short-term effects will be minor; long-term effects may be to reduce mineralization of nutrients from forest floor
Burning for slash reduction	Increase N losses from forest; amount varies from a low of 25 kg ha^{-1} to more than 800 kg ha^{-1}	More rapid mineralization due to warmer soil temperatures and the absence of carbon-rich woody debris
Piling of slash for improved access	Displaces nutrients from planting surface; N displacement from 200 to 600 kg ha^{-1} observed; small increase in actual loss from system due to accelerated leaching and erosion	More rapid mineralization due to mixing of mineral soil, forest floor and organic debris during operation
Soil tillage (disking or mounding)	Can be associated with small increase in nutrient loss in runoff and erosion	More rapid mineralization due to mixing of mineral soil, forest floor, and organic debris
Herbicide use to control competition	Operational herbicide application has little impact on geochemical cycle; repeated control of regrowth will increase nutrient losses and erosion	Reduced uptake and accumulation in vegetation early in the rotation
Use of N-fixing species	Potential to increase N inputs to forest by 50–150 kg ha^{-1} year^{-1}	Annual uptake and cycling of N will be increased
Fertilization	Can increase ecosystem storage of applied nutrients and compensate for harvest removals; small increases in runoff losses of applied nutrients can occur	Uptake of applied nutrients is increased; quantities of nutrients transferred in the biogeochemical cycle are often increased; absolute quantities of nutrients retained by biochemical cycling may be increased

Accelerated erosion losses are another impact on nutrient cycles. Losses associated with erosion can be considered either displaced productivity or as site loss. Generally, a strong relationship exists between bare mineral soil and erosion loss. Losses are often greatest during first year following harvest and planting and decrease as vegetation regrowth occurs on the site. Increased soluble losses of nutrients can also occur following forest operations due to improved conditions for decomposition. These losses are generally ephemeral and low in comparison to geochemical inputs over a rotation for many forests.

Fertilization is an important silvicultural technique for adding nutrients to forest ecosystems and balancing losses of nutrients in the industrialized world where the value of wood production provides economic justification. Nitrogen-fixing species also provide a way to add nitrogen to managed forests. Planting or seeding of N-fixing species at the time of forest establishment can add from 50 to 150 kg ha^{-1} N to the forest in the years prior to crown closure, sufficient N to more than balance losses associated with harvest and site preparation.

Summary

Nutrient cycling plays an important role in the nutrition of forest stands. The balance between inputs and exports of nutrients from the forest ecosystem included within the geochemical cycle has implications for long-term sustainability. Fluxes of nutrients through the biogeochemical and biochemical cycles are larger than through the geochemical cycle and supply a major portion of the annual nutrient requirements of the forest. These cycles provide a framework within which forest management activities can be evaluated. Activities that result in nutrient exports in excess of nutrient

Table 4 Comparison of nutrient removals and annualized removal rate with different levels of biomass utilization and rotation length for two commercial forest species

Forest type	*Harvest utilization*	*Rotation length (age)*	*Nitrogen*		*Phosphorus*		*Potassium*		*Calcium*	
			kg ha^{-1}	*kg ha^{-1} year^{-1}*	*kg ha^{-1}*	*kg ha^{-1} year^{-1}*	*kg ha^{-1}*	*kg ha^{-1} year^{-1}*	*kg ha^{-1}*	*kg ha^{-1} year^{-1}*
Pinus taeda	Stem only	20	293	14.6	17	0.8	169	8.4	178	8.9
		40	464	11.6	28	0.7	293	7.3	304	7.6
	Whole tree	20	385	19.2	27	1.4	212	10.6	205	10.2
		40	570	14.2	40	1.0	346	8.6	348	8.7
Picea	Stem only	50	217	4.3	20	0.4	248	5.0	278	5.6
		85	328	3.1	23	0.3	161	1.9	390	4.6
	Whole tree	50	842	16.8	80	1.6	442	8.8	463	9.2
		85	722	8.5	78	0.9	330	3.9	521	6.2

After Switzer GL and Nelson LE (1973) Maintenance of productivity under short rotations. *Proceedings of the International Symposium on Forest Fertilization*, pp. 365–389. Paris: International Union of Forestry Research Organizations and Tamm CO (1969) Site damage by thinning due to removal of organic matter and plant nutrients. *Proceedings of the International Union of Forestry Research Organizations Meeting on Thinning and Mechanization*, pp. 175–184. Stockholm: IUFRO.

inputs are unlikely to be sustainable without nutrient amelioration through fertilization or use of N-fixing species.

See also: **Environment**: Carbon Cycle; Environmental Impacts. **Hydrology**: Impacts of Forest Management on Water Quality; Soil Erosion Control. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health; Soil Organic Matter Forms and Functions. **Soil Development and Properties**: Nutrient Limitations and Fertilization; The Forest Floor.

Further Reading

Burger JA (1979) *The Effects of Harvest and Site Preparation on the Nutrient Budgets of an Intensively Managed Southern Pine Forest*. PhD thesis, University of Florida, Gainesville.

Cole DW and Rapp M (1981) Elemental cycling in forest ecosystems. In: Reichle DE (ed.) *Dynamic Properties of Forest Ecosystem*, pp. 341–409. Cambridge UK: Cambridge University Press.

Green DC and Grigal DF (1980) Nutrient accumulation in jack pine on deep and shallow soils over bedrock. *Forest Science* 26: 325–333.

Greenland DJ and Kowal JML (1960) Nutrient content of the moist tropical forests of Ghana. *Plant Soil* 12: 154–173.

Johnson DW and Todd DE (1987) Nutrient export by leaching and whole tree harvesting in a loblolly pine and mixed oak forest. *Plant Soil* 102: 99–109.

Manhendrapa MK, Foster NW, Weetman GF, and Krause H (1986) Nutrient cycling and availability in forest soils. *Canadian Journal of Soil Science* 66: 547–572.

Morris LA and Pritchett WL (1982) Nutrient storage and availability in two managed pine flatwoods forests. In: Coleman C, Mace AC, and Swindel BF (eds) *Proceedings of the Intensive Forest Management Practices Symposium*, pp. 17–26. Gainesville, FL: University of Florida.

Ovington JD (1962) Quantitative ecology and the woodland ecosystem concept. *Advances in Ecology Research* 1: 103–192.

Riekerk H, Jones SA, Morris LA, and Pratt DA (1979) Hydrology and water quality of three small Lower Coastal Plain forested Watersheds. *Soil Crop Science Society of Florida Proceedings* 38: 105–111.

Shan J (2000) *Accumulation, Allocation and Dynamics of Carbon in Slash Pine along a Management Intensity Gradient*. PhD thesis, University of Georgia, Athens.

Switzer GL and Nelson LE (1972) Nutrient accumulation and cycling in loblolly pine (*Pinus taeda* L.) plantation ecosystems: the first twenty years. *Proceedings of the Soil Science Society of America* 36: 143–147.

Switzer GL and Nelson LE (1973) Maintenance of productivity under short rotations. *Proceedings of the International Symposium on Forest Fertilization*, pp. 365–389. Paris: International Union of Forestry Research Organizations.

Tamm CO (1969) Site damage by thinning due to removal of organic matter and plant nutrients. *Proceedings of the*

International Union of Forestry Research Organizations Meeting on Thinning and Mechanization, pp. 175–184. Stockholm: IUFRO.
Turner J and Singer MJ (1976) Nutrient distribution and cycling in a subalpine coniferous forest ecosystem. *Journal of Applied Ecology* 13: 295–301.
Weetman GF and Webber B (1972) The influence of wood harvesting on the nutrient status of two spruce stands. *Canadian Journal of Forest Research* 3: 351–369.
Wells CG and Jorgensen JR (1975) Nutrient cycling in loblolly pine plantations. In: Bernier B and Winget CH (eds) *Forest Soils and Forest Land Mangement*, pp. 137–158. Quebec: Laval University Press.

Nutrient Limitations and Fertilization

H G Miller, University of Aberdeen, Aberdeen, UK

Historical Background

While the benefits of applying manure to land has long been appreciated the idea of a plant nutrients probably only dates from 1727 when Stephen Hale noted that 'we find by chemical analysis of vegetables, that their substance is composed of sulphur, volatile salt, water and earth.' Despite observed growth responses of plants to compounds such as saltpetre (a nitrate salt), Epsom salts (magnesium sulfate), and phosphates, further advance in the understanding of plant nutrition was stymied by the widespread acceptance of the idea of Wallerins that humus itself was the fundamental source not only of nutrients but also of carbon. Progressively this came to be questioned and in 1845 Liebig, on the basis of calculations of the yield of carbon as wood and agricultural produce from nonmanured land, concluded that 'it is not denied that manure exercises an influence upon the development of plants; but it may be affirmed with positive certainty, that it neither serves for the production of carbon, nor has any influence on it.'

Building upon the work of Liebig, chemists such as Bossingault in France and Lawes and Gilbert in Britain weighed and analyzed manure and plants to construct early nutrient input–output balance sheets for a range of agricultural crops. Bossingault's data were used by Ebermayer in 1882 to compare nutrient accumulation in forest stands with that in agricultural crops. Earlier Ebermayer had been the first to diagnose nitrogen (N) deficiency in trees in Bavaria on sites that had been degraded by long histories of litter removal for animal bedding and other agricultural purposes. Despite this new understanding, foresters of a century ago seldom showed much interest in tree nutrition, being able to turn to the work of Dengler who had demonstrated that the nutrient requirements of a closed-canopy forest stand were on average only about one-twelfth of that of agricultural crops. Indeed, in his silvicultural textbook of 1904 Schlich enunciated the orthodoxy of his time when he stated that 'almost any soil can furnish a sufficient quantity of mineral substances for the production of a crop of trees, provided the leaf mould is not removed.' This sentiment was echoed by Baker in his book of 1934, for long one of the standard silvicultural texts.

Despite this complacency, at the start of the twentieth century foresters in Belgium, and later in Ireland and Scotland, were finding that trees newly planted on poor soils could show dramatic growth responses by application of the phosphate-containing basic slag (thomasphosphat) and some responses to wood ash application were reported from the Nordic countries (probably a response to potassium (K)). Similarly, in both Australia and New Zealand growth of the new forest plantation were found to be dependent on the application of phosphorus (P). In South Australia trees sometimes failed even where P had been applied until it was noted that those grown adjacent to galvanized wire fences were better than those distant from them, and so zinc deficiency was identified. In the decades that followed, forest scientists from many of the countries with large afforestation programs have identified deficiencies of one or more of nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), iron (Fe), zinc (Zn), copper (Cu), molybdenum (Mo), and boron (B) in young plantation trees. Calcium (Ca) deficiency has been confirmed in the nursery but the few reports of deficiencies of this element in the forest remain rather unconvincing. Additionally, by the middle of the twentieth century reports were also coming in of nitrogen deficiency in older coniferous forests in the boreal regions of Europe and North America.

Nutrient Cycles and Fertilizer Need

The study of nutrient cycling in forests of various ages has provided the explanations to a number of the conundrums posed by early work on fertilizer responses. The cycles within a well-established forest are characteristically very tight, that is there is efficient reuse of nutrients, largely through recovery (retranslocation) of nutrients from dying organs, notably leaves before they are shed, and through the efficient capture by roots and mycorrhizae of nutrients released through decomposition of litter. **Table 1** shows that retranslocation from foliage can contribute a quarter to half of the N, P, and K needed for new growth, and various studies suggest that the contribution from the decomposition of litter fallen from the same trees is not dissimilar (although with a lag phase for the time decomposition takes). The net consequence of this efficient recovery is that in a closed canopy forest, in which the amount of leaves produced annually is more or less equal to the amount dropped, the demand on fresh supplies of nutrients from the soil can be quite low. The position prior to canopy closure, however, when the both the green crown and the fine root biomass (both of which contain high concentrations of nutrients) are expanding the contribution internal cycling or litter decomposition can make to nutrient demands is limited and so a greater contribution has to come from the soil reserves (**Table 2**). Even though the total nutrient demands by the young trees are less than those of the older trees, the latter are asking much less of the soil reserves. Thus, the picture is one of high demands on soil reserves when a young crop is establishing its canopy, a demand that relaxes thereafter as the contribution from nutrient cycling increases. It is therefore, not surprising that nutrient deficiencies were seldom encountered until the twentieth century expansion of plantations onto poor ground.

As a forest ages further, if it is not harvested it starts to break up and growth declines while mortality increases. Uptake of nutrients may then become less than the release on decomposition and nutrients start to be lost from the site. However, prior to this stage in the coniferous forests of the boreal region the slow decomposition of litter can lead to such an accumulation of humus that an unacceptable proportion of the nitrogen capital of the site becomes locked up, the supply of available nitrogen progressively declines, and the trees start to show nitrogen deficiency. This seems to be the explanation for N fertilizer responses in areas such as Sweden, Finland, Canada, northwestern USA, and mountain forests in central Europe. The industrial importance of such forests has meant that considerable research effort has been devoted to them, contributing to the belief that N is the nutrient most commonly limiting in the forests of the world. However, this accolade should probably be given to P.

Because of the importance of nutrient retranslocation in nutrient cycles, anything that causes major loss of green foliage (i.e., before nutrients can be retranslocated back into the tree) can cause a short-term reappearance of any nutrient deficiency previously seen in youth. Such events include hail damage, insect damage, or even removal of trees in thinning. When a forest is thinned a significant proportion of the green foliage is deposited on the forest floor and the nutrients within it can no longer be accessed in the short-term through retranslocation. They will only become available in the medium term through mineralization on decomposition. Meanwhile, the remaining main crop trees have to fill the gaps that have been created in the canopy without recourse to the nutrients in the leaves that previously occupied these spaces. Their own internal supplies, coupled with whatever is available to the roots, may now be inadequate and deficiencies occur. Indeed, a positive interaction between thinnings and fertilizer application has often been recorded in situations where unthinned stands show no fertilizer response.

Table 1 Estimates of the contribution to nutrient demands by new growth that are met by retranslocation from old foliage prior to abscission

Species	*Age (years)*	*Percentage of nutrient requirement*		
		N	*P*	*K*
Pinus taeda	20	39	60	22
Pinus sylvestris	15	30	23	19
Pinus sylvestris	46	55	64	57
Pinus sylvestris	100	41	34	27
Pinus nigra	40	50	57	58
Abies amabilis	175	54	59	38
Mixed deciduous	Mature	54	25	15
Mixed deciduous	Mature	79	74	41
Eucalyptus obliqua	Overmature	34	46	28

Table 2 Sinks and sources (kg ha^{-1} year^{-1}) of nitrogen (N) and potassium (K) in young (2-m tall) and old (11-m tall) stands of *Pinus nigra*

	Nitrogen		*Potassium*	
	Young	*Old*	*Young*	*Old*
(1) Total required for new growth	66	138	29	66
(2) Supplied by retranslocation	11	69	7	38
(3) Taken by roots (i.e., 1 – 2)	55	69	22	28
(4) Available from litter decomposition[a]	7	39	1	16
(5) Uptake from soil reserves (i.e., 3 – 4)	48	30	21	12
(6) Net annual accumulation in trees	45	18	18	11

[a] Decomposition of litter fallen from current crop of trees only, release from pre-existing organic matter considered as being from soil reserves.

Predicting and Diagnosing Nutrient Deficiencies

The occurrence of nutrient deficiencies varies with the age of stand, soil type, and to some extent with species. Clearly, the forest manager needs to be able to diagnose a deficiency should this occur and, preferably, be able to predict what ameliorative treatment may be required. Four options are available; diagnosis on the basis of visual crop symptoms, diagnosis on the basis of soil analysis, diagnosis on the basis of tissue analysis, and prediction on the basis of some characteristic feature of the site.

Visual Symptoms

The various nutrients play specific physiological roles and if present in insufficient quantity disorders result which can lead to diagnostic visual symptoms. There is some variation between species, particularly between conifers and broadleaves, but general symptoms are as shown in **Table 3**. Because, these visual symptoms can be misleading, they are usually confirmed by foliar analysis.

Soil Analysis

Soil analysis has proved to be very useful in both agriculture and horticulture. In the forest, however, soil analysis has seldom proved to be of consistent value. In part this is because the perennial roots of trees, together with their mycorrhizae, seem able to access forms of nutrient elements not accessible to short-lived arable plants so the chemical soil extractants developed for agriculture may not be appropriate. Perhaps more significant, however, is that over time tree roots can exploit all the rooting volume available to them. This volume can be very variable between sites, often more variable than the quantities of available nutrients per unit volume (in agriculture and horticulture rooting is essentially consigned to the uniform depth of the plow layer). At all events, soil analysis in forestry has only proved most useful over limited areas where rooting volume is not a variable, such as glacial outwash plains, volcanic ash, or extensive areas of loess.

Table 3 Visual symptoms of nutrient deficiencies

Nutrient	*Symptoms*
Nitrogen (N)	Needles or leaves are small and pale green turning yellow throughout the crown but most severe on young foliage
Phosphorus (P)	Reduced needle or leaf size and an exaggerated if rather dull green color; in extreme cases a brownish tinge may develop and buds towards the top of the tree may die
Potassium (K)	A pale straw-yellow color that appears first on needles at the tips of current shoots or leaf margins; color may develop to a pinkish brown and is often more severe in winter
Magnesium (Mg)	Golden yellow discoloration of needle tips or of irregular blotches on broadleaves; this is more pronounced on upper parts of the tree and in autumn
Copper (Cu)	Little change in leaf size or color although there may be dark blotches on broadleaves; branches droop and leading shoot is very sinuous or even pendulous
Boron (B)	Death of buds and shoots, particularly after growth has commenced in summer; problem most pronounced on leading shoot and as tree dies back it becomes very misshapen; pith in shoots may show brown necrosis

Foliar Analysis

Analysis of almost any living tissue will give an indication of the nutrient status of a plant; however, foliage has consistently proved to be the most useful for this purpose. Nutrient concentrations in foliage vary both with position in the tree and with age of the leaf. Generally, the physiologically active nutrients increase in concentration up the tree, as illumination increases, although Ca usually shows the reverse trend. Some authorities have advocated using lower crown foliage on the grounds that it is from these that any nutrient under stress would be removed first. However, the position of the lower crown varies with stocking density so it is difficult to standardize and ensure comparability. The effect of age on nutrient concentrations is shown in **Figure 1**, emphasizing the need to standardize the time of sampling. These considerations have led most forestry organizations to standardize sampling such that for conifers current fully formed needles (usually sampled around October in northern regions and April in southern regions) are taken from the top whorl in high latitudes or the top three whorls in lower latitudes, whereas samples from broadleaved trees are taken from the upper third of the crown (ensuring full illumination) in August in northern latitudes or February in Southern latitudes.

The theoretical dependence of growth on nutrient concentration is shown in **Figure 2**. The optimum on this curve can be a well-developed turning point, which is usually the case for N, P, and K, or it can take the form of a long plateau, which is typically the case for Cu and particularly Mn. Along this plateau the plant is taking up increasing amounts of a nutrient without showing any change in growth. Uptake over this range is often referred to as 'luxury

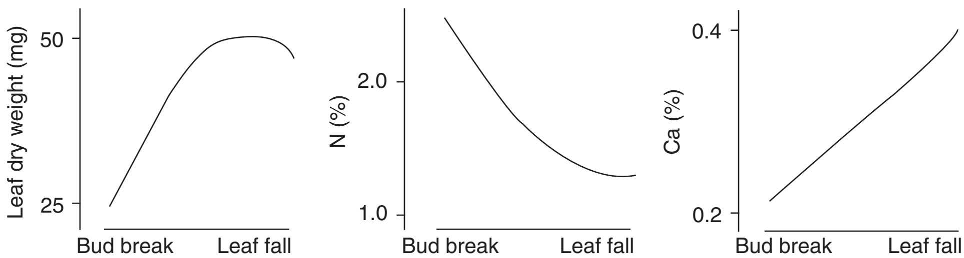


Figure 1 Changes in leaf dry weight and concentrations on nitrogen and calcium through the growing season from bud break to maximum leaf fall for a conifer such as pine.

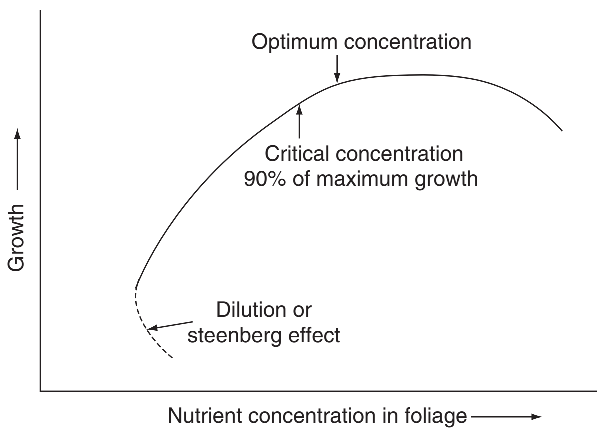


Figure 2 Generalized relationship between growth and foliar nutrient concentration.

Table 4 The foliage concentrations of nutrients below which tree growth starts to decline. These are values for young trees in the forest (*c.* 0.5–4.0 m tall) at the time when nutrient problems are most likely; for younger and perhaps older trees somewhat higher concentrations are necessary

Nutrient	*Evergreen conifers*	*Broadleaves and deciduous conifers*
Nitrogen (N)	1.50%	2.20%
Phosphorus (P)	0.14%	0.20%
Potassium (K)	0.50%	0.90%
Magnesium (Mg)	0.10%	0.10%
Boron (B)	8 ppm	ND
Copper (Cu)	2 ppm	ND

ND, no adequate data.

uptake,' although (as will be discussed later) this is a rather misleading concept in the case of perennial plants such as trees.

One factor that has to be kept in mind when using foliar analysis is that at least for N, and probably for the other major nutrients, the optimum concentration does shift with age of the tree. It is usually high in young seedlings but the declines as the tree becomes established, thus optimum N for seedling pine is about 3% but by the time the tree has reached a height of 2 m may be only 1.5%, rising to around 2% in a closed canopy crop. Suggested optimum concentrations are shown in **Table 4**.

Because the growth response to a fertilizer applied nutrient at the upper part of the curve, just below the optimum point, is small the concept of a critical nutrient level, usually 90% of the optimum, has been introduced. Below this critical level fertilizer responses may be worthwhile but above it not so.

When diagnosing on the basis of foliar analysis, results are presented as a concentration, that is the ratio of the weight of an element present to the weight of the leaf. Changes above or below the line will result in a change of concentration. For example, if a pollutant gas is reducing carbohydrate production this will be accompanied by an increase in concentration of nutrient elements without there having been any increase in nutrient uptake. Similarly, if growth is being reduced by a severe deficiency of one element, say P, other elements may appear to be present in adequate amounts. If the deficiency is alleviated by the application of the appropriate fertilizer a secondary deficiency of another element may be revealed the supply of which was sufficient when growth was restricted but not so after the restriction is removed.

Caution has to be exercised when interpreting foliar analysis and if time is available a small trial to confirm the diagnosis is often advisable. In Canada, a short cut has been devised, 'trajectory analysis,' whereby fertilizers are first applied and then the response measured in terms of needle weight and nutrient concentrations to determine which element, if any is deficient. This has some advantages in reducing the time to gain a diagnosis but is unlikely to be as accurate as more conventional approaches. If carefully used the straightforward use of concentrations of individual nutrient, coupled with sensible assessment of the site and, if need be, a confirmatory trial, remains the best approach.

Site Characteristics

Site as classified by one or more of soil type, geology, and ground vegetation can give a very good indication of whether any particular nutrient deficiencies might be anticipated. This is particularly valuable when creating a plantation on bare land. Of course such classifications will differ between bioclimatic regions but many forest services have developed classifications, or lists of indicator plants, based largely on experience, to predict future fertilizer needs if any. Such an approach has the great advantage of enabling advance assessment of the costs that might be incurred in plantation creation.

Effect of Species

As previously discussed, once a forest crop has closed canopy nutrient demands decline. The only continuing net accumulation is in the biomass of wood. Concentrations of nutrients in wood are low and usually do not differ much between species. Differences in nutrient demands reflect differences in growth rate of wood such that a linear relation can be demonstrated for this stage between uptake of N and P and mean annual increment. Prior to canopy closure, however, the situation is different for different species will develop very differing amounts of foliage in these early years. Generally, deciduous tree carry 3–6 tonnes ha^{-1} of foliage, pines some 6–12 tonnes ha^{-1}, and the white wooded conifers (spruces, firs, Douglas-fir, hemlock, etc.) 10–20 tonnes ha^{-1} of foliage. Differing amounts of nutrients, therefore, will need to be found in the early years of the rotation to develop the canopies of these trees to the stage when nutrient cycling will cover much the nutritional needs of the new leaves produced each year. This early difference is illustrated in **Table 5**.

Such a model produces the intuitively sensible prediction that spruces are more nutrient-demanding than pines. It also predicts that oak is less nutrient-demanding than either of them which does not concur with their known site requirements, oak usually requiring much more fertile soils. This introduces an important distinction between 'nutrient demands' and 'site demands.' Nutrient demands differ among species because of the amount of foliage they initially need to accumulate and, thereafter, because of differences in volume growth. Site demands, by contrast, reflect not only differences in nutrient demand but also the ability of the roots and associated mycorrhizae to obtain nutrients from intractable soil sources. Pine is good at this, oak is poor.

Table 5 Rate of change in weight of foliage carried with age for even-aged stands of pine and spruce at comparable locations

Age period (years)	*Increase in weight of foliage (tonnes $ha^{-1}year^{-1}$)*	
	Pine	*Spruce*
0–10	+0.2	+0.5
10–15	+0.4	+1.0
15–20	+0.8	+1.4
20–25	+0.2	+0.2
25–30	−0.1	−0.3

Use of Fertilizers

As a result of a desire to minimize the use of chemicals in forests, application of fertilizers is considered a remedy of last resort. Whereever possible, other approaches should be considered, notably selecting a species better suited to the site. Sometimes, however, this option may not be possible, either because the trees are already established or the soil is extremely nutrient deficient, as may be the case in nonnatural soils such as mine waste. In such cases fertilization is necessary.

Forms of Fertilizers

A wide choice in chemical forms of fertilizers is available. The decision of what to use is in part a function of ease of application and application cost, so urea which is 46% N has attractions over ammonium sulfate at 21% or ammonium nitrate at 35% because the cost of application is lower per unit weight of N. Availability is also important and so choice is often dictated by what is being used in agriculture.

In Finland and Scandinavia concern that rainwater acidity might accelerate soil leaching, or that N inputs in polluted rain might lead to 'unbalanced' nutritional conditions, has led to the development of complex mixed fertilizers ('reconditioning fertilizers') containing up to eight nutrient elements. In the medium to long term these may serve such a purpose but in the shorter term they appear to have no advantage over the application of the one or two elements known to be deficient. Acid rain has also led to a renewed interest in the application of lime to forests. Many thousands of hectares have been so treated but the advantages remain unproven. A vast number of liming trials have been carried out since the nineteenth century and these usually show no growth response, or even a short-lived depression. In a few cases, an eventual improvement in humus form has lead to better tree health but the response is long delayed and hard to predict.

Response to Fertilizers

If a nutrient deficiency is correctly diagnosed, application of an appropriate fertilizer will lead first to both a reduction in number of leaves shed and to an increase in photosynthetic efficiency of the leaves retained, and then to an increase in the number of leaves formed (this being the most important factor). Thus, by the second growing season the photosynthetic area will have been considerably increased leading to an increase in net primary production and so greater stem wood growth. Thereafter, the duration of the response is a function of the amount of the fertilizer nutrient the trees have been able to accumulate in their tissues. As shown in **Figure 3**, increasing the rate of fertilizer application may not lead to continuing growth rates in the years immediately after application but because more nutrient element might have been stored the response period will continue longer.

Only a portion of the added fertilizer nutrient is used by trees. A major portion goes into the ground vegetation, the soil microbial population, and, particularly in the case of P, becomes chemically fixed within the soil. The rate at which the nutrient will be then released from such pools is so slow as to be of negligible importance for subsequent tree growth. The only fraction that is important for tree growth, therefore, is that taken up by the trees soon after application and as this is used up growth declines until no further response is detected. This leads to the simple concept that fertilizers are applied to the trees, not the site. However, where the amount of nutrient applied is high relative to the active reserves within the soil, as can be the case with P or some trace elements, a long-term response may be recorded. Indeed in many areas around the world it is observed that although P had to be applied to the first rotation no further application may be needed in the second rotation.

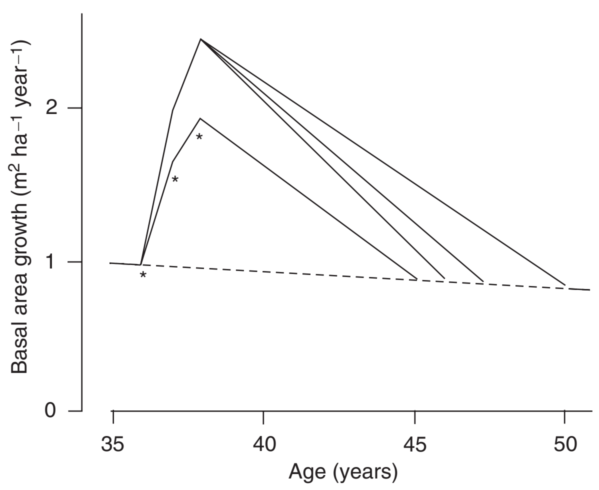


Figure 3 Basal area growth response shown by pine to nitrogen fertilizer applied at four rates in the 3 years marked with asterisks. Fertilizer treatments shown by solid lines and the untreated control by the dashed line.

When and How Much Fertilizer to Apply

In old coniferous forests of northern regions the immobilization of large amounts of N in the humus can lead to N deficiency and growth will respond to the application of fertilizer. For reasons of discounted cash flow such an application is usually made only 5–10 years before felling. More generally, however, fertilizer use is only necessary prior to canopy closure so a schedule such as that in **Table 6** might be appropriate.

The recommended rates of application vary remarkably little around the world and are generally, in terms of fertilizer element, are 150–200 kg N ha^{-1}, 60–80 kg P ha^{-1}, around 100 kg K ha^{-1}, and 7–10 kg ha^{-1} for both B and Cu.

Methods of Application

Often the most reliable method of application is still by hand to individual trees. An alternative while trees are still small is use of ground-based broadcast spreading equipment. However, as canopy starts to close both of these become impossible. Following crown closure aerial application, usually by helicopter, is the only option.

Environmental Considerations

Forest fertilization must be conducted so as to minimize negative environmental effects. The main concern is loss of nutrient into waterways where this might lead eutrophication, algal blooms and consequent damage to aquatic life, fisheries, and quality of drinking water. Applied fertilizer, therefore, must not fall into drains, streams, rivers, lakes, or reservoirs. This can seriously constrain the method of application chosen. The method often preferred is to apply by hand to individual trees. If other approaches are used, particularly involving aircraft,

Table 6 Suggested schedule for fertilizer application to spruce on different soil types (brackets indicate possible benefit)

Soil type	*At planting*	*Years after planting*			
		6	9	12	15
Brown earth	(P)	—	—	—	—
Iron podzol	P	—	P	—	—
Peaty podzol	P	—	P K	—	—
Heathland podzol	P	(N) P	N	N P	N

there has to be very careful planning and precise guidance (ideally using geographical positioning system (GPS)), accompanied by suitable supervision and monitoring, even although this may necessitate leaving significant areas untreated. Care must also be taken to ensure that that no leakage occurs from any storage stack in the woods and that all fertilizer bags are properly disposed of.

See also: **Health and Protection**: Biochemical and Physiological Aspects. **Soil Biology and Tree Growth**: Soil and its Relationship to Forest Productivity and Health. **Soil Development and Properties**: Nutrient Cycling. **Tree Physiology**: A Whole Tree Perspective; Mycorrhizae; Nutritional Physiology of Trees.

Further Reading

Attiwill PM (1987) *Forest Soils and Nutrient Cycles*. Melbourne, Victoria: Melbourne University Press.

Baule H and Fricker C (1970) *The Fertilizer Treatment of Forest Trees*, transl. CL Whittles. Munich, Germany: BLV.

Binns WO, Mayhead GJ, and MacKenzie JM (1980) *Nutrient Deficiencies of Conifers in British Forests*: An Illustrated Guide, Forestry Commission Leaflet no. 76. London: HMSO.

Bowen GD and Nambiar EKS (1984) *Nutrition of Plantation Forests*. London: Academic Press.

Cole DW and Gessel SP (eds) (1988) *Forest Site Evaluation and Long-term Productivity*. Seattle, WA: University of Washington Press.

Luxmore RJ, Landsberg JJ, and Kaufmann MR (eds) (1986) *Coupling of Carbon, Water and Nutrient Interactions in Woody Plant Soil Systems*. Victoria, Canada: Heron.

Mälkönen E (ed.) (2000) *Forest Condition in a Changing Environment*: *The Finnish Case*, Forest Sciences no. 65. Dordrecht, The Netherlands: Kluwer Academic Press.

Miller HG (1981) Forest fertilization: some guiding concepts. *Forestry* 54: 157–167.

Miller HG (1995) The influence of stand development on nutrient demand, growth and allocation. *Plant and Soil* 168/169: 225–232.

Nambiar EKS and Fife DN (1991) Nutrient retranslocation in temperate conifers. *Tree Physiology* 9: 185–207.

Nambiar EKS, Squire R, Cromer R, Turner J, and Boardman R (eds) (1990) *Management of Water and Nutrient Relations to Increase Growth*. Special issue *of Forest Ecology and Management* 30 (1–4).

Taylor CMA (1991) *Forest Fertilization in Britain*, Forestry Commission Bulletin no. 95. London: HMSO.

Will G (1985) *Nutrient Deficiencies and Fertilizer Use in New Zealand Exotic Forests*, FRI Bulletin no. 97. Rotorua, New Zealand: Forest Research Institute, New Zealand Forest Service.

Soil Contamination and Amelioration

H Goldemund, GeoSyntec Consultants, Atlanta, GA, USA

Introduction

Human activities have shaped and altered essentially all ecosystems on earth. Forest ecosystems are no exception to this and the effects of these activities can be observed throughout the forests of the world. While many of the activities leading to soil contamination have been necessary and positive (e.g., development of a sustainable agricultural system capable of feeding a growing world population), negative side effects are also widespread. Impacts range from clearly visible effects like unsustainable and large-scale logging and surface mining with all their associated problems of erosion, loss in soil fertility and productivity, and acid mine drainage, to less obvious effects including diffuse deposition of atmospheric pollutants or acid rain due to burning of fossil fuels. Many of these negative effects are reversible, and in particular, forested areas have the ability to buffer environmental impacts. Many physiological processes in forest systems such as evapotranspiration, photosynthesis, solute uptake, and effects of plant root exudates on contaminant degradation can be used to mitigate negative impacts and/or remediate existing contamination. This article focuses on forest soil contamination with regard to inorganic and organic contaminants and potential remedial strategies.

Soil Contamination

Contamination is generally grouped by origin as resulting from point (direct) or nonpoint (diffuse) sources. Point sources of soil contamination include spills and leaks, local emissions, and land applications, while atmospheric deposition and agricultural runoff are the main nonpoint sources of contamination. Point sources such as industrial outfall pipes or chemical spills are discrete, localized, and can be readily assessed and delineated, while nonpoint sources are more difficult to assess due to the large areas that can be affected and multiple sources that may contribute to the problem. Inorganic contaminants like trace metals and in some cases radionuclides (e.g., Chernobyl accident in 1986) can originate as both point sources and nonpoint sources. Organic contamination generally results from point sources, although elevated levels of some recalcitrant semivolatile organic compounds (SVOCs) including polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs) are becoming more ubiquitous and are the result of atmospheric pollution and subsequent deposition.

Once contaminants enter the soil environment, they undergo a multitude of processes that affect their fate and subsurface mobility, which in turn alters their bioavailability and risk to potential human and ecological receptors. These processes include sorption and desorption (organic and inorganic contaminants), precipitation (inorganic contaminants) and dissolution (organic and inorganic contaminants), complexation (organic and inorganic contaminants), leaching (organic and inorganic contaminants), volatilization (mainly organic, but some inorganic contaminants), and degradation (organic contaminants). Biogeochemical and physical soil properties affecting the fate and transport of contaminants include pH, oxidation–reduction potential (redox conditions), organic matter (OM) content, and the amount of clay and sesquioxides present in soils. The amounts of OM and clays affect the cation-exchange capacity (CEC) of a soil, a variable that indicates the soil's ability to retain positively charged ions, some of which are contaminants such as many trace metals. Trace metals also form strong complexes with organic matter, which may lead to both immobilization due to complexation with insoluble organic matter in surface soils, as well as mobilization due to complexation with dissolved organic carbon (DOC). Furthermore, nonionic organic contaminants have a strong affinity for soil organic matter, which in general renders them fairly immobile. Redox conditions affect the speciation, and therefore the mobility, of inorganic contaminants, as well as the geochemical environment for the potential degradation of organic contaminants. For example, many chlorinated organic compounds are completely degraded under reducing conditions, while most volatile organic compounds and explosives degrade more readily under aerobic conditions. For trace metals, pH is the master variable. With the exceptions of arsenic (As), molybdenum (Mo), selenium (Se), vanadium (V), and chromium (Cr), metals are more mobile under acidic soil conditions.

While this article focuses on soil contamination, it should be noted that soil contamination frequently leads to groundwater contamination. About 75% of all contaminated sites regulated under Federal programs in the USA involve groundwater contamination. Once in groundwater, contaminants that may have originated from a small localized area, such as a spill, may spread over a much larger area due to plume migration along a groundwater flow path or as separate-phase migration of a dense nonaqueous phase liquid (DNAPL) such as trichloroethylene (TCE). **Figure 1** conceptualizes soil contamination and remediation.

Table 1 summarizes the main classes of contaminants commonly found in soils and some of their important characteristics.

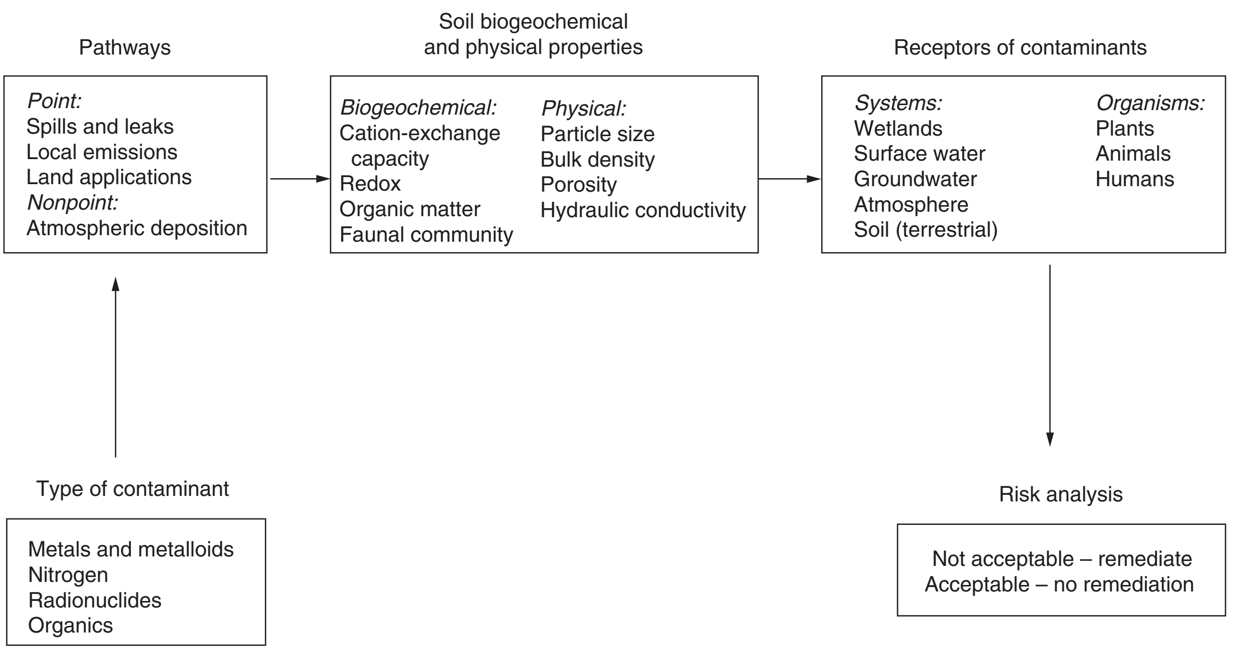


Figure 1 Conceptual model of soil contamination and remediation. Reproduced with permission from Adriano DC, Bollag JM, Frankenberger WT Jr., and Sims RC (1999) *Bioremediation of Contaminated Soils*. Madison, WI: American Society of Agronomy.

Table 1 Contaminant classes and compounds commonly found in soils

Contaminant class	*Compound class*	*Example compounds*	*Environmental characteristics*	*Potential sources*	*Remedial options*
Inorganic contaminants	Salts	NaCl, $MgCl_2$	High solubility/mobility; some plant toxicity; minimal human health risks	Ocean spray, roadside salts	Leaching; application of $CaSO_4 \cdot 2H_2O$
	Trace metal(loid)s	Hg, As, Pb, Cr, Cd	Mobility depending on pH and redox conditions; plant toxicity; significant human health risks	Metallurgy, paints, parent rock	Excavation; soil washing; liming; stabilization; phytoremediation
	Radionuclides	^{137}Cs, ^{238}U, ^{90}Sr	Geochemical behavior similar to certain plant nutrients (K, Ca); human exposure to radioactivity	Nuclear reactors and weapons	Similar to trace metals; mainly stabilization and excavation
Organic contaminants	Polycyclic aromatic hydrocarbons (PAH)	Naphthalene, phenanthrene, benzo(a)pyrene	Varying solubilities and mobility; significant human health risks	Coal tars, asphalt, fossil fuels	Solidification; composting; chemical extraction
	Nitroaromatics	TNT, RDX, HMX; pesticides	Human health risks; risk of initiation	Military explosives; pesticides	Biodegradation; soil washing; composting; phytoremediation
	Phenols	Pentachlorophenol, phenol, nitrophenol	Bioavailability depending on soil pH and OM content; human health risk	Wood preservatives, solvents; refineries	Biodegradation; solidification; soil flushing; land farming
	Halogenated aromatics	PCBs, pesticides, dioxins	Low solubility; limited mobility; toxic to humans	Pesticides, waste incineration	Solidification; excavation; dehalogenation
	Halogenated aliphatics	TCE, PCE, CCl_4	Present as NAPL and dissolved phase; high toxicity	Solvents, plastics	Bioremediation; chemical oxidation
	Petroleum hydrocarbons	Petroleum products (crude and refined oil)	Complex mixture of compounds; significant solubility/ toxicity	Cars, refineries, industry	Land farming; thermal desorption, biodegradation

HMX, cyclotetramethylenetetranitramine; NAPL, nonaqueous phase liquid; PCBs, polychlorinated biphenyls; PCE, tetrachloro ethylene; RDX, cyclotetramethylenetetranitramine; TCE, trichloroethylene; TNT, trinitrotoluene.

Salt-Affected Soils

In general, two types of salt-affected soils are distinguished: saline soils that have high electrical conductivity ($>4\,dS\,m^{-1}$) but low sodium content, and sodic soils that have high electrical conductivity ($>4\,dS\,m^{-1}$) and high sodium content. Salinity affects soils in three ways:

1. Excess sodium (Na) can lead to the destruction of soil structure through its ability to disperse clays. This leads to decreased aeration and consequently, restricts root growth.
2. Excess salts in soil solution affect the osmotic potential of soil water. The increase in soil water potential (i.e., more negative) makes water harder to extract and less available to plant roots, which can lead to water stress in plants.
3. The uptake of excess chloride can lead to direct damage to plant leaves. Roots of non salt tolerant plants have no mechanism to exclude the very mobile and soluble chloride ion. Once absorbed, chloride is quickly transported with the transpirational stream through the stem to the leaves, where it accumulates at the outer fringes of the leaves. This excess chloride leads to chlorosis of the leaves decreasing their capacity to conduct photosynthesis.

Four main sources of salinity exist. Three of these are anthropogenic sources with the fourth one being a natural source. A natural source of salts that may affect the species composition of forests originates from ocean sprays. Due to strong winds in the vicinity of large bodies of water, small droplets of salt water can be carried inland from oceans and seas and deposited onto forests along coastlines. While this may not be considered 'contamination,' it can clearly affect soils and tree species composition within these forests.

The three main anthropogenic sources of salinity to forests originate from the use of roadside deicing salts in cold climates, the land application of wastewater and biosolids and accidental spills of brines from the production of oil. Deicing salts can be carried into forests along roadsides through splashes and runoff of melted snow. In general, these transport processes are limited to within a few meters of a road, although salt effects have been measured as far away as 200 m into a forest stand. While small areas of forested lands can be affected by deicing salts, the soil chemical and plant physiological effects are more visible in urban areas where other factors contribute to tree stress and mortality such as air pollution, confined rooting space, and physical tree damage from parked cars.

During the last two decades the practice of land application of wastewater and biosolids has become more common as a means to manage the large quantities of treated wastewater and sludges generated in the industrialized world. While this practice has great potential for the beneficial reuse of 'waste' by providing a cost-effective source of nutrients, organic matter, and irrigation water, it may also lead to increased soil salinity.

The production of oil produces large quantities of brine (mainly connate brines) that pose a serious problem for treatment and disposal. Occasionally, brine spills and slow seepage through unlined impoundments can contaminate forests. Unlike damage from deicing salts, concentrated brines can kill entire forest stands.

Amelioration of saline and sodic soils is generally accomplished by leaching soils with low-electrolyte water and by applying gypsum ($CaSO_4 \cdot 2H_2O$) or $CaCl_2$ to the soil. In humid climates where infiltration exceeds evapotranspiration, it may be sufficient to stop the salt addition and allow for natural leaching of excess salts.

Trace Metals and Metalloids

Contamination of agricultural and forest soils with trace metals and metalloids has been a major concern for many decades. While metals in contaminated agricultural soils can enter the food chain and increase human exposure and risk (both carcinogenic and noncarcinogenic risks), metals in forests are mainly a potential problem for groundwater resources, ecological risk, and forest health.

There are both natural and anthropogenic sources contributing to elevated soil concentrations of trace metals. Natural sources are generally limited to weathering of parent rocks that contain appreciable concentrations of metals, and volcanic inputs. Anthropogenic sources are widespread and include fertilizers, pesticides, wastewater and biosolids, coal combustion residues, and atmospheric deposition. The main source of trace metals in natural forest ecosystems is atmospheric deposition. In intensively managed forest plantations, application of biosolids and the use of pesticides and fertilizers can also contribute trace metals to the system. Wood treatment facilities that used chromated copper arsenate (CCA) as a wood treatment product resulted in sites contaminated with arsenic and chromium as well as a variety of other (organic) constituents. Between 50% and 70% of contaminated sites regulated under Federal cleanup programs in the USA contain metals as major contaminants. Many of these sites, especially sites managed by the US Department of Defense and the US Department of Energy, contain large tracts of forested lands.

In general, forest soils are more acidic than agricultural soils, which are regularly limed and therefore, forest soils tend to have greater availability of trace metals. Among forest types, coniferous forests exhibit a lower soil pH than deciduous hardwood forests due to slower forest floor decomposition, greater concentrations of organic acids from decomposing litter, and lower contents of base cations. Furthermore, forest soils contain numerous old root channels that provide pathways for preferential water flow. Preferential flow bypasses the soil matrix, which may lead to increased mobility of contaminants to deeper depths. In addition, decomposing organic matter may yield appreciable concentrations of DOC to the soil solution, which can increase metal mobility due to metal–DOC complexes that move readily with percolation water. Therefore, potential subsurface metal mobility is higher in forested settings in comparison to agricultural systems. However, phytostabilization of metals in the root zone through root sorption (absorption and adsorption) may provide a mechanism for immobilization of otherwise mobile metal contaminants. **Figure 2** illustrates a generalized biogeochemical cycle for trace elements in forest ecosystems.

The most commonly found trace metals at contaminated sites include lead (Pb), cadmium (Cd), zinc (Zn), nickel (Ni), mercury (Hg), chromium (Cr), and arsenic (As). Forests (especially at higher elevations) sometimes act as 'filters' for airborne

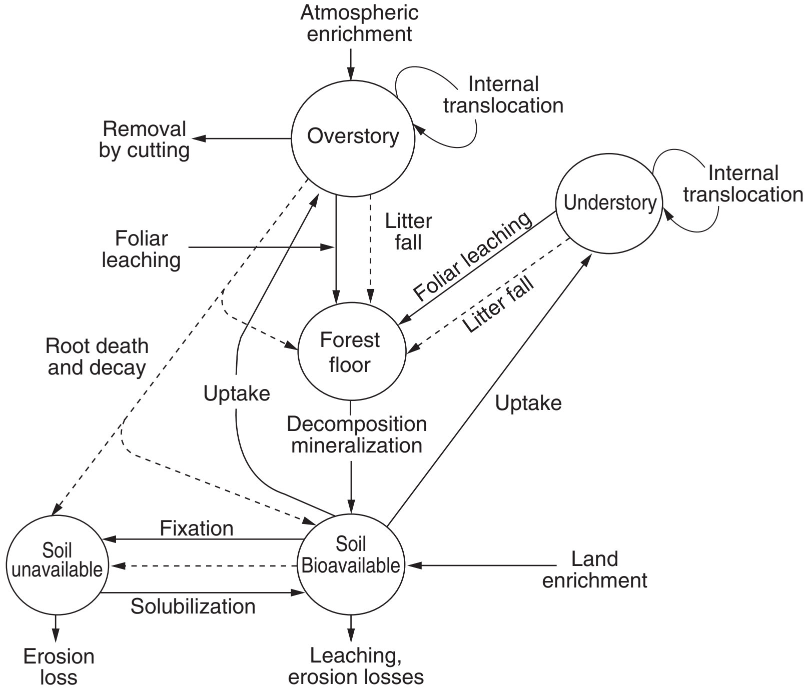


Figure 2 Generalized biogeochemical cycle for trace elements in forest ecosystems. Reproduced with permission from Adriano DC (2001) *Trace Elements in Terrestrial Environments*, 2nd edn. New York: Springer-Verlag.

metal contamination, rendering even remote forest stands into metal sinks. Lead is a widespread metal contaminant in forests due to airborne deposition and the use of forested areas as shooting ranges. In some alpine areas, for example, Pb concentrations of up to 700 mg kg^{-1} have been measured in forest soils far away from potential industrial point sources. Excess metal deposition in conjunction with acidic atmospheric deposition (i.e., 'acid rain') may lead to a decrease in forest health due to phytotoxic effects of metals, as well as create a potential groundwater problem. In Europe, the concept of calculating critical loads for deposition of metals to forest systems is commonly applied. Metal depositions below a critical load are considered harmless to the environment.

Unlike organic contaminants, metals do not degrade and have to be either immobilized or extracted. Potential technologies for remediating metals-contaminated soils are fairly limited and include *ex situ* technologies (e.g., excavation and disposal, incineration, soil washing, and thermal desorption) and *in situ* technologies (e.g., liming, solidification/stabilization, capping in place, electrokinetics, natural attenuation, and phytoremediation). Due to limited access in established forest stands, relatively low concentrations of metal contaminants, and the desire to apply less invasive approaches over larger areas, *in situ* approaches such as liming and phytoremediation are the preferred options for metal-contaminated forest soils.

Acid Deposition

Acid deposition, commonly referred to as 'acid rain,' has long been suspected as a contributing factor to the decline in forest vigor and the observed dieback of forests in central Europe, Scandinavia, and North America (USA and Canada). While agricultural soils and most soils under deciduous forests have sufficient capacity to buffer acidic atmospheric inputs, some coniferous forests, especially on shallow, nutrient-poor soils derived from 'acidic' parent rocks like granite, are susceptible to acid rain. Acid rain is a consequence of the combustion of fossil fuels, which leads to the emission of sulfur and nitrogen compounds (i.e., SO_x and NO_x) that form strong acids in contact with water (i.e., H_2SO_4 and HNO_3). While the emission of sulfur compounds has decreased dramatically over the past 30 years, the emission of nitrogen compounds has continued at a very high level. These acids accelerate the natural process of soil acidification under forest stands and may contribute as much as 40% to soil acidification. This process leads to excessive leaching of base cations (especially Ca and Mg), decreases a soil's acid neutralizing capacity, increases the mobility of potentially toxic trace metals, and releases excess aluminum into soil solution. Elevated concentrations of aluminum are toxic to tree roots and cause an antagonistic effect on ion uptake (especially with Mg). In combination with an increasing ratio of aboveground to belowground biomass, such as observed in nitrogen-saturated forest systems of central Europe, this increases drought stress and the susceptibility to windfall and disease. The combined effects of these and other stresses such as shallow, naturally poor or acidic soils, drought conditions, management practices like removal of forest litter that lead to decreased fertility, other air pollutants, and animal damage are believed to be responsible for forest diebacks and the decline in tree vigor.

Strategies for mitigating these effects include continued efforts to limit the emissions of N- and S-containing compounds, improvements in forest management practices, and liming and fertilization of susceptible sites.

Organic Contaminants

With the exception of some pesticides originating from agricultural runoff and carbonaceous particles originating from industrial coal processing, most organic contaminants are generated from point sources. However, recently there has been mounting evidence that many PAHs and PCBs can be found in areas far away from local point sources, indicating long-range transport as a significant source of forest soil contamination by organic compounds. Due to much higher concentrations of organic carbon in forest soils as compared to agricultural soils, organic contaminants originating from diffuse sources are usually found at much higher concentrations in forest soils. As previously mentioned, organic contaminants have a strong affinity for soil organic carbon.

Typical sources of organic contaminants include the combustion of organic materials such as coal, oil, or wood (PAHs), smelting processes (PCBs), pesticide production and application for agricultural, industrial, and residential pest control (dioxins, dichlorodiphenyltrichloroethane (DDT), chlorinated pesticides), accidental releases from oil producing facilities and during transportation of oil in tankers and (leaky) pipelines (petroleum hydrocarbons), wood treatment facilities (creosotes, pentachlorophenol (PCP)), production and use of explosives (cyclotetramethylenetrinitramine (RDX), trinitrotoluene (TNT), cyclotetramethylenetetranitramine (HMX)), and production and use of industrial solvents for dry-cleaning, degreasing, and plastics manufacturing (trichloroethylene (TCE), tetrachloroethylene (PCE), vinyl chloride).

Volatile organic compounds (VOCs), primarily in the form of BTEX (benzene, toluene, ethylbenzene, and xylene) compounds, are generally found in localized areas. Over two-thirds of sites regulated under Federal programs in the USA contain VOCs, which are also primary contaminants in many underground storage tank sites. Unless spills occur in or near forested sites, forest stands are rarely affected by VOCs. Nonhalogenated VOCs readily degrade under a variety of conditions, and are therefore prime candidates for bioremediation and/or natural attenuation. Halogenated VOCs (such as TCE, PCE, CCl_4) are also completely biodegradable, but require anaerobic conditions for the reductive dechlorination process to proceed.

Semivolatile organic carbons (SVOCs) include a large number of organic contaminants ranging from PAHs (such as naphthalene and pyrene), to PCBs (such as aroclors) to chlorobenzenes and chlorophenols, to pesticides and dioxins. There is a wide array of technologies available for the remediation of SVOCs, and with regard to contaminated forest soils, *in situ* biological approaches like bioremediation and phytoremediation appear to be the most applicable technologies.

Since the military uses large areas of land (quite often heavily forested as well) as military bases and for training purposes, these sites are greatly impacted by a wide variety of contaminants ranging from metals to solvents and explosives (including unexploded ordinance). More recently, perchlorate (ClO_4^-) has been identified as a major contaminant on virtually every military site where it has been included as a target analyte. Consequently, inorganic and organic contaminants in soils (and groundwater) are frequently commingled at these sites. This poses a significant challenge for remediation efforts since many cleanup technologies are specific to contaminants or groups of contaminants. For soil (and groundwater) remediation, the application of bioremediation (especially by creating reducing conditions) may be a feasible and cost-effective approach to simultaneously treat a variety of contaminants. However, highly contaminated (and toxic) areas containing nitroaromatics (i.e., explosives) and/or other organic contaminants may continue to require excavation and incineration.

Phytoremediation

A variety of *in situ* and *ex situ* remedial technologies are available to treat soils affected by the many contaminants described above. Environmental managers quite often prefer less invasive and more cost-effective approaches than excavation and disposal or incineration. Over the last two decades, phytoremediation has emerged as a feasible alternative to more active and costly technologies, especially for large areas with relatively low levels of contamination.

Phytoremediation – more recently, the term 'phytotechnologies' has been introduced since this remedial approach covers a number of technologies and applications – is the use of plants to remediate or contain contaminants in soil, groundwater, surface water, and sediments. The technology is rapidly gaining acceptance within regulatory agencies as well as the public. In general, six main mechanisms are involved in the application of phytotechnologies:

1. Phytostabilization (inorganic and organic contaminants) is the use of plants to immobilize contaminants in soil, sediments, and groundwater through the absorption and accumulation into the roots, the adsorption onto the roots, or the precipitation or immobilization within the root zone.
2. Rhizodegradation (organic contaminants) refers to the breakdown of contaminants in soil through the bioactivity that exists in the rhizosphere (an area about 1 mm away from a root surface).
3. Phytoaccumulation (inorganic contaminants) is the process of metal- or salt-accumulating plants to translocate and concentrate inorganic contaminants into the roots and aboveground biomass.
4. Phytodegradation (organic contaminants) refers to the uptake of organic contaminants from soil, sediments, and water with subsequent transformation by the plants.
5. Phytovolatilization (inorganic and organic contaminants) is the mechanism of uptake and translocation of the contaminant into the leaves with subsequent release to the atmosphere through transpiration.
6. Evapotranspiration of plants can be used to significantly affect the local hydrology through interception of rain on leaf surfaces and transpirational uptake by the plant root system.

The first five mechanisms have been successfully used to remediate or contain contaminated soils, while the use of evapotranspiration applies more to groundwater contamination. Contaminated forested areas are good candidates for the application of these technologies since they are generally impacted over large areas, but at relatively low concentrations. Phytoremediation is limited by the effective rooting depth of plants, as well as the phytotoxicity and/or plant-availability of contaminants. Quite often, only a fraction of the total concentration of a specific contaminant is in a potentially bioavailable form that is accessible for plant uptake. However, given that many regulated environmental sites are actually managed using a risk-based approach, it may be sufficient to remediate the bioavailable contaminant fraction rather than achieving a low total concentration of a specific contaminant.

See also: **Environment**: Impacts of Air Pollution on Forest Ecosystems; Impacts of Elevated CO_2 and Climate Change. **Health and Protection**: Biochemical and Physiological Aspects. **Silviculture**: Forest Rehabilitation. **Site-Specific Silviculture**: Reclamation of Mining Lands; Silviculture in Polluted Areas. **Soil Development and Properties**: Waste Treatment and Recycling.

Further Reading

Aamot E, Steinnes E, and Schmid R (1996) Polycyclic aromatic hydrocarbons in Norwegian forest soils: impact of long range atmospheric impact. *Environmental Pollution* 92(3): 275–280.

Adriano DC (2001) *Trace Elements in Terrestrial Environments: Biogeochemistry, Bioavailability, and Risks of Metals*, 2nd edn. New York: Springer-Verlag.

Adriano DC, Bollag JM, Frankenberger WT Jr., and Sims RC (1999) *Bioremediation of Contaminated Soils*. Agronomy Monograph no. 37. Madison, WI: American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America.

Bindler R, Brännvall ML, and Renberg I (1999) Natural lead concentrations in pristine boreal forest soils and past pollution trends: a reference for critical load models. *Environmental Science and Technology* 33: 3362–3367.

Federal Remediation Technology Roundtable (2003) *Remediation Technologies Screening Matrix and Reference Guide*, Version 4.0. Available online at http://www.frtr.gov/matrix2/top_page.html.

Horstmann M and McLachlan MS (1996) Evidence of a novel mechanism of semivolatile organic compound deposition in coniferous forests. *Environmental Science and Technology* 30(5): 1794–1796.

ITRC (2001) *Phytotechnology Technical and Regulatory Guidance Document*. Interstate Technology and Regulatory Cooperation Work Group. Available at: http://www.itreweb.org/PHYTO2.pdf/.

Markewitz D, Richter DD, Allen LH, and Urrego JB (1998) Three decades of observed soil acidification in the Calhoun Experimental Forest: has acid rain made a difference? *Soil Science Society of America Journal* 62: 1428–1439.

Matzner E and Murach D (1995) Soil changes induced by pollutant deposition and their implication for forests in Central Europe. *Water, Air and Soil Pollution* 85: 63–76.

US Environmental Protection Agency (1997) *Cleaning Up the Nation's Waste Sites: Markets and Technology Trends*, 1996 edn. EPA 542-R-96-005. Washington, DC: US Government Printing Office.

Van der Lelie D, Schwitzguébel JP, Glass DJ, Vangronsveld J, and Baker A (2001) Assessing phytoremediation's progress in the United States and Europe. *Environmental Science and Technology* 35(21): 447A–452A.

Waste Treatment and Recycling

W L Nutter, Nutter & Associates, Inc., Athens, GA, USA
L A Morris, University of Georgia, Athens, GA, USA

Introduction

Land treatment is the practice of applying waste to a vegetation–soil complex with the intention of further treatment or renovation. Land treatment is based on well-documented scientific concepts which have been used successfully for wastewater (i.e. liquid sewage effluent) treatment at thousands of sites throughout the world. Properly designed and managed, land treatment systems can enhance productivity of forest ecosystems and, at the same time, protect the quality of surface and groundwaters. Of the various methods of wastewater land treatment, spray irrigation (also referred to as slow rate), achieves the highest degree of renovation and beneficial reuse of nutrients and water. The US *EPA Process Design Manual – Land Treatment of Municipal Wastewater*, published in 1981, describes land treatment by spray irrigation as: the application of wastewater to a vegetated land surface with the applied wastewater being treated as it flows through the plant–soil matrix. A portion of the flow percolates to the ground water and some is used by the vegetation. Treated wastewater produced by municipalities must be disposed of and one way of providing further treatment and reaping some benefits is to apply the wastewater to land, of which forest land is often the most suitable from an environmental and public acceptance viewpoint.

Assimilative Capacity of Forests for Wastewater Renovation

Wastewater is applied to a land treatment system at a rate designed to optimize the renovative capacity of the soil–plant complex and to maximize the utilization of the available nutrients in the wastewater. Renovation of the wastewater is accomplished through degradation by microorganisms, chemical precipitation, ion exchange, biological transformation, and biological absorption through the soil and vegetative cover complex. Utilization of a vegetative cover is an integral part of the land treatment system and complements the soil microbiological and physicochemical systems. Vegetation is one of the most essential elements of the land treatment concept and provides for the maximum renovation capacity and durability of the system.

Wastewater irrigation in a properly designed and operated land treatment system is such that all the applied wastewater will enter the soil and no overland flow will occur. In this respect, forested sites are often better suited for land treatment than agricultural sites because undisturbed forest soils often have infiltration and percolation rates far in excess of normal hydraulic loading rates. Once in the soil, wastewater is renovated relatively quickly by the various chemical, physical, and biological processes. Chemical constituents of the wastewater such as dissolved salts, metals, phosphorus (P), and nitrogen (N) are considerably reduced in concentration. Organic compounds are usually not found in domestic wastewaters or are only present in small amounts and have not been found to be a limiting factor in the functioning of a land treatment system. Organic compounds are readily absorbed to the organic surfaces of the soil system and thus have limited mobility through the soil profile. Pathogens and viruses in wastewater are filtered out in the upper soil profile. Survival time for most microorganisms following land treatment is typically very short. Viability depends upon a variety of soil and climatic conditions including temperature, soil moisture, and pH. Most bacterial and viral pathogens will die off to negligible numbers within 2–3 months following application. Research has shown that in a properly designed and managed system these organisms remain in the surface soils for the duration of their survival period and do not leach through the soil profile.

The assimilative capacity of a land treatment site is the amount of wastewater, on a constituent by constituent basis, that can be optimally applied to the land. The basic environmental constraint of nondegradation is used to develop the assimilative capacity for each constituent. The nondegradation constraint is stated: each constituent is applied at a rate over a time period (mass of chemical species per unit area per unit time, i.e., $kg\,ha^{-1}\,year^{-1}$) that the land and water resources are not irreversibly converted to an unproductive condition or environmentally degraded. Use of such a strong constraint parallels environmental regulatory intent and provides for long-term and successful wastewater irrigation.

Wastewater Constituents and System Design

Land-applied wastewater constituents can be divided into three primary groups:

1. Those compounds that degrade or require plant uptake for assimilation in the plant–soil system (e.g., N, oil, organics).
2. Those mobile and nondegradative compounds that must be assimilated over land areas such that groundwater is not altered to a degree that would require further treatment to meet drinking water or other applicable standards (e.g., anionic species such as sulfate, chloride, boron, and fluoride).
3. Those compounds that are relatively immobile and nondegradative, and thus are permitted to accumulate in the soil to predetermined acceptable levels (e.g., trace metals). For calculation purposes, an operations period must be specified over which the total mass loading of constituents will be distributed.

Development of design criteria for a land irrigation system involves identification of the significant constituents of the waste stream, classification of each constituent into one of the above categories, and evaluation of the assimilative pathway(s) utilized for that constituent. The three principal components of assimilative pathways are the soil, vegetation, and groundwater. The land-limiting constituent (LLC), the waste constituent requiring the greatest land area, is determined from the assimilative capacities and wastewater characteristics. The LLC is determined by dividing the total mass of each constituent to be applied on an annual basis (kg $year^{-1}$) by the site assimilative capacity (kg ha^{-1} $year^{-1}$). Typically for municipal wastewater the LLC is either hydraulic loading or nitrogen.

The amount of wastewater irrigated is referred to as the hydraulic loading. Hydraulic loading must be balanced with vertical and lateral water movement in the soil, ground water movement, vegetation tolerances for soil wetness, and losses by evapotranspiration. Determination of hydraulic loading requires characterization of soil water movement to estimate the percolation rate, or rate of water movement through the hydraulically restrictive soil horizon (i.e., the first horizon encountered in the soil profile with a reduced permeability). This is accomplished by direct field testing of soil hydraulic conductivity. The irrigation system design and management is specified such that no overland flow of applied wastewater will occur, that is, all applied wastewater must infiltrate, or enter, the soil surface. Thus, the only pathways by which applied water may leave the site are evapotranspiration and percolation through the soil profile. Application of these principles in design and operation meets regulatory compliance for water quality and best management practices. Infiltrated wastewater that percolates through the soil profile (sometimes referred to as interflow) may emerge downslope in stream channels or seepage areas at the base of slopes as return flow, or percolate directly to groundwater and eventually to a stream channel or a regional groundwater aquifer. Residence time of water in the soil must be sufficient for all the physical, chemical, and biological renovation processes to occur and is controlled through timing of wastewater application and application rates. Typically, application rates are low (less than 6 mm h^{-1}) to achieve long residence times and slow rates of subsurface flow and, consequently slow return flow and/or percolation to groundwater. It is this long residence time and the high renovation capacity of the soil and vegetation complex which yields highly renovated subsurface flow (interflow) that emerges as return flow or percolates to groundwater. For most wastewater constituents, travel through only a few inches of soil and forest floor achieves 90–100% of the potential renovation. In humid regions, where rainfall exceeds evapotranspiration by 25–30%, strong development of subsurface flow and return flow in forested landscapes is a common occurrence, particularly during the wetter seasons of the year. Wastewater irrigation accentuates these processes such that they occur throughout the year.

The N cycle in a forest ecosystem is complex, dynamic, and varies with species, growth rates, soil morphology and fertility, climate, and other environmental factors. To determine the N assimilative capacity, a N budget is constructed to balance inputs with losses. All the N in municipal wastewater is typically plant available because the organic N will be readily mineralized to ammonia. Ammonia-nitrogen is not highly mobile, is retained within the soil complex, and is taken up by plants. Nitrate-nitrogen, on the other hand, is easily leached from the root zone and its assimilation is controlled through plant uptake and denitrification. Control of nitrate leaching is critical to maintain nitrate in groundwater at the drinking water standard (typically 10 mg l^{-1} nitrate-nitrogen). Nitrogen may be stored on the site as organic-nitrogen in bacterial cells as well as in living and dead plant material. It may also be stored as ammonia-nitrogen adsorbed on soil cation exchange surfaces. Ammonia-nitrogen may be volatilized to the atmosphere, transformed to nitrate-nitrogen by nitrifying bacteria, and/or taken up by vegetation. Nitrate-nitrogen may be taken up by vegetation, transformed to nitrogen gas by denitrifying bacteria, or leached to the groundwater. All of the N assimilative pathways occur simultaneously in natural systems. Nitrogen is removed primarily by crop uptake, which varies with the type of crop grown and the crop yield.

To remove the N effectively, the forest crop must be harvested periodically. Denitrification can also be significant, even if the soil is in an aerobic condition most of the time. Other N removal mechanisms include ammonia volatilization and storage in the soil.

Thus, N management in a land treatment system is achieved through management of vegetation and denitrification. Vegetation must be harvested and N removed in the biomass. Denitrification occurs naturally but can be enhanced by creating periodic soil saturation and providing available carbon. Irrigated wastewater and forest ecosystems have adequate supplies of organic carbon and management of hydraulic loading can create the requisite soil wetness. Management of denitrification is further enhanced in sloping sites because the infiltrated wastewater can move laterally through the soil profile maintaining the wet soils for the short periods required to drive the denitrification process.

Phosphorus added to the soil from wastewater undergoes a variety of biological and chemical reactions. The predominant phosphorus pool in the soil is in the inorganic form. That is, the P is physically part of the soil matrix. A much smaller pool of P is in the organic matter (organic phosphorus) and in a soluble form as part of the soil pore water. Soluble P is the only form that is available to the plant. Chemical fixation of P in the soil occurs under all soil pH ranges with the least occurring in the range of 5.8 to 6.8. The adsorption and precipitation processes at low soil pH are dependent on the amount of aluminum (Al), iron (Fe), and manganese (Mn) present. These elements are abundant in the highly weathered soils. Natural occurring P in geologic materials is also relatively low. Thus, acidic soil pH, abundant Al, Fe, and Mn, and low residual P levels in forest soils provide a high capacity for sequestration of P added from wastewater irrigation. A study of a forest wastewater irrigation site in north Georgia (southeastern USA) showed there was a residual P fixation capacity of over 100 years in the surface soils. The residual capacity of soils to chemically fix P is determined by laboratory determination on soil samples of adsorption and precipitation isotherms. Vegetation uptake and incorporation of organic P is minor compared to the capacity of the soil to fix and retain P. The residual forest floor (leaf litter and partially decomposed material) retains P also in a form that is largely unavailable to plant uptake or leaching. Phosphorus removal efficiencies are generally very high for spray irrigation systems and are more dependent on the soil properties than on the concentration of the P applied. Although P is held within the soil at different energy levels, little or no leaching occurs. This is demonstrated by groundwater concentrations beneath both natural and wastewater irrigation forested sites on the order of 0.01 to 0.1 mg l^{-1}. The principal nonpoint source of P to streams is runoff of soil and organic particles with 'attached' P.

Organics applied in the wastewater are reduced substantially within the top 1.5–2.5 cm of soil. Filtration and adsorption are the initial steps in biological oxygen demand (BOD) removal, but biological oxidation is the ultimate treatment mechanism. Filtration is the major removal mechanism for suspended solids. Residues remaining after oxidation and the inert solids become part of the soil matrix.

Metals, much like P, are retained in the soil complex and are immobile. Metals in municipal wastewater are rarely found in concentrations that result in any one becoming a land-limiting constituent.

Impacts of Wastewater Treatment: Case Study of Clayton County, Georgia, USA

Irrigation of secondary treated wastewater to a 1000 ha and mixed pine (*Pinus taeda*) and hardwood (*Quercus, Carya, Liquidambar*) forest site began in 1983 and continues to the present with an average flow of 0.85 $m^3\,s^{-1}$. Clayton County is located in the metropolitan Atlanta, Georgia area and has few heavy industry waste dischargers. Wastewater treatment by activated sludge occurs at two plants and the wastewater is combined and pumped 11 km to the land treatment site.

The site is within the headwaters of Pates Creek. The site is entirely forested and about 50 ha are harvested annually. Geologic structure is dominated by granitic gneiss with some fracturing and jointing. Groundwater occurs under water table conditions and most of the recoverable water is above the bedrock at depths of 3–25 m. Hydraulic conductivities of the saprolite overlying the bedrock are low, averaging 5×10^{-4} cm s^{-1}. Dominant soils are typic hapludults with A horizon textures ranging from fine sandy loam to sandy clay loam. The B horizon is argillic with sandy clay to clay textures. Depth of the A is shallow due to past erosion history and rarely exceeds 15 cm. B horizon hydraulic conductivities average 9×10^{-4} cm s^{-1}. Soils are classified as well drained except in alluvium along streams.

Wastewater loading is limited by nitrogen and water assimilative capacities of the site. Wastewater irrigation is limited to 6.3 cm water $week^{-1}$ which has resulted in maximum N applications of about 395 kg ha^{-1} $year^{-1}$. The irrigation system is solid-set buried PVC and ductile iron with galvanized steel risers and brass and plastic sprinklers. There are over 18 000 sprinklers and the pressure at the nozzles is about 345 kPa for an application rate of $5\,mm\,h^{-1}$. Storage equivalent to 12 days' flow is provided for flow equalization and inclement weather.

An intensive environmental monitoring program has been implemented at the Clayton County land treatment site that includes groundwater, surface water, soil, and vegetation. In addition numerous research projects have been undertaken that include changes in streamflow from the first order basins, changes in streamflow and water budget for the entire irrigated watershed, nitrogen gas evolution from the soil, earthworm populations, and soil hydraulic properties. Twenty-two groundwater wells as well as several private water supply wells in and around the site have been monitored. In the early years of operation, the wells were monitored monthly and as the project progressed and no significant impacts to water quality were demonstrated, the regulatory permit was modified to a mix of quarterly, semi-annual, and annual monitoring for different wells. The most frequent monitoring is conducted at wells located down gradient from the irrigation site. Surface water as it discharges from the site is monitored at Clayton County's water supply intake about 10 km downstream.

Groundwater quality has been monitored since 1979, over 4 years prior to commencement of wastewater irrigation. Initially, many inorganic parameters were monitored, including nitrate-nitrogen, phosphate, chloride, specific conductivity, a number of metals, and coliforms. Later, analysis of metal and coliforms was discontinued except for a few interior and down gradient wells on an annual basis.

Wells have been grouped by permit conditions as up gradient, interior, and down gradient. Considering the most mobile constituents monitored (chloride and nitrate-nitrogen) and specific conductivity, there have been increasing trends to what appears to be a plateau concentration for chloride and specific conductivity and an initial slight increase in nitrate-nitrogen with no long-term increasing trend since irrigation began in 1983. Chloride and nitrite-nitrogen concentrations and specific conductivity in the background (up gradient) wells average about $10\,mg\,l^{-1}$, $0.1\,mg\,l^{-1}$, and $80\,uS\,cm^{-1}$, respectively, and have remained somewhat constant since monitoring began in 1979. In contrast, chloride concentrations and specific conductivity in the down gradient wells (immediately outside the irrigation area) have steadily increased from 10 to $20\,mg\,l^{-1}$ and from 80 to $150\,uS\,cm^{-1}$, respectively. This represents a doubling in 12 years of irrigation. Both parameters, however, are well below the maximum contaminant level (MCL) for drinking water. Nitrate-nitrogen concentrations, on the other hand, in the down gradient well have increased to an average of $0.5\,mg\,l^{-1}$. Most of the increase in nitrate-nitrogen concentration came within 10 years of commencement of irrigation and has remained at the increased level since (**Figure 1**). Nitrate-nitrogen increases in the down gradient wells are not significantly different from preirrigation levels.

Monitoring also indicates that irrigated wastewater is percolating to the groundwater as evidenced by increases in chloride and specific conductivity. The interpretation drawn from the steadily increasing chloride and specific conductivity and no increasing trend in nitrate-nitrogen is that plant uptake and denitrification, which occurs at higher rates in irrigated areas than in nonirrigated forests (**Figure 2**), are occurring to the extent that little nitrate is reaching the groundwater.

About 8% of Pates Creek watershed above the drinking water supply reservoir is irrigated with wastewater. Water quality monitoring has been

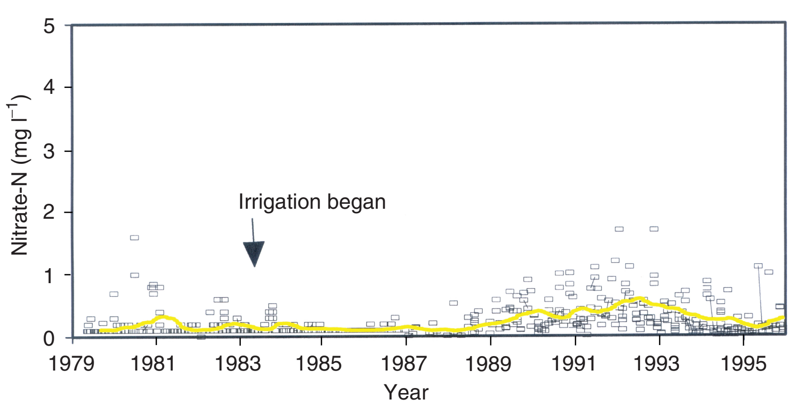


Figure 1 Trend of nitrate-nitrogen in the down gradient monitoring wells. The line is a moving mean and the symbols represent readings from five wells.

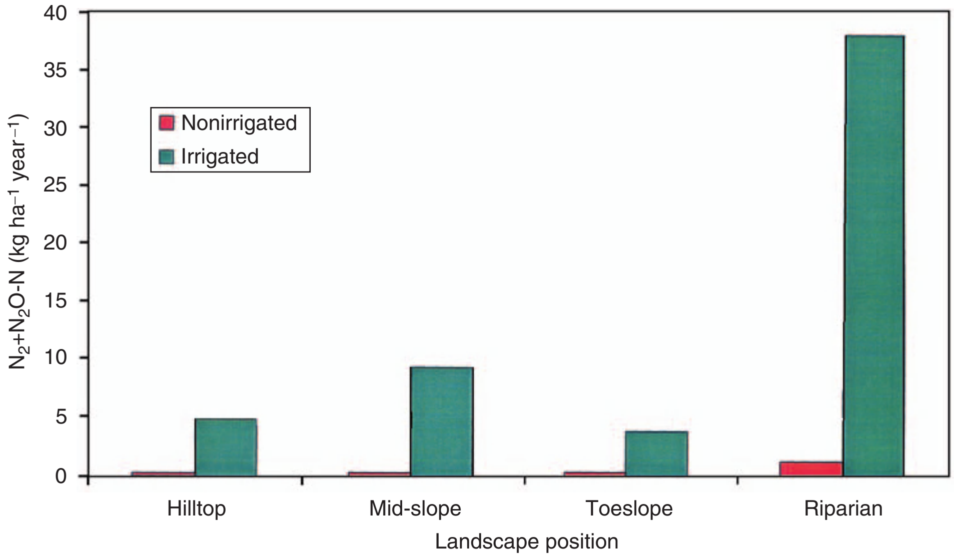


Figure 2 Annual denitrification in wastewater irrigated forests and adjacent nonirrigated forests in the Piedmont of the southeastern USA.

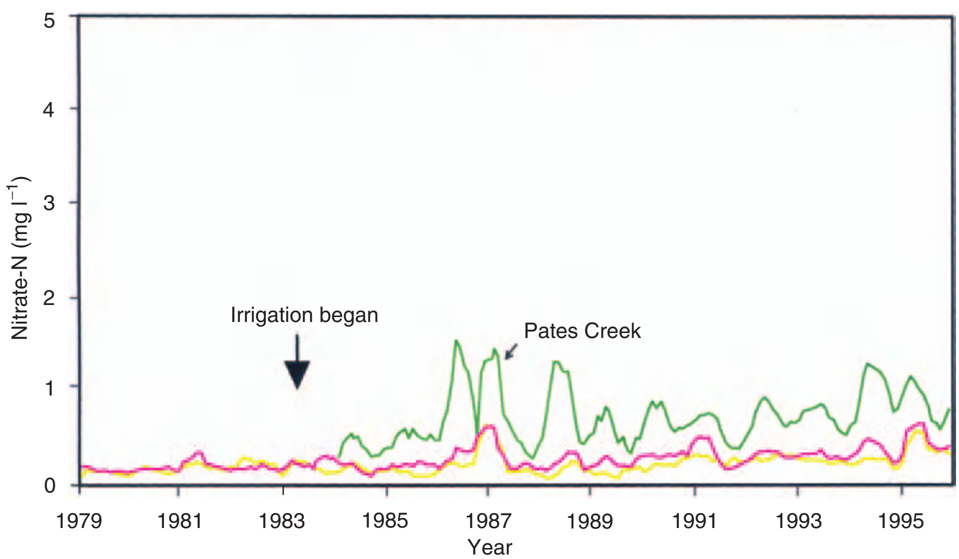


Figure 3 Trend of nitrate-nitrogen in Pates Creek draining the land treatment system compared to two nearby streams. Pates Creek flows directly to the drinking water reservoir.

conducted at the head of the reservoir and at two tributary streams that do not receive wastewater irrigation but are experiencing expanding urbanization. Pates Creek exhibits similar water quality changes that have occurred in the groundwater. Although there is greater variation in streamwater quality than groundwater quality, specific conductivity in Pates Creek has remained steady at an average of about $100\,\mathrm{uS\,cm^{-1}}$. Nitrate-nitrogen has also remained steady at about $1.0–1.5\,\mathrm{mg\,l^{-1}}$ (**Figure 3**) but chloride has steadily increased from an average of about $10–20\,\mathrm{mg\,l^{-1}}$. These later results are in direct correspondence with groundwater quality. Reeves Creek and Rum Creek, the two nonirrigated background monitored streams, have similar specific conductivity and nitrate-nitrogen concentrations as Pates Creek and chloride concentrations are similar to and unchanged from the initial preirrigation concentrations in Pates Creek.

Infiltration rates have remained high on the site due, in part, to the activity of earthworms, which occur in much higher numbers within irrigated forests than in nonirrigated forests. Tree growth and nutrient accumulation has been periodically assessed at Clayton County. In general, trees irrigated with wastewater have higher foliage nutrient concentrations and exhibit more rapid growth than trees grown on adjacent sites without irrigation.

Summary

1. The concept of land treatment of wastewater has a sound scientific and experience foundation which has proven that land can be used to renovate wastewater in a environmentally acceptable manner and that such land is not irreversibly withdrawn from any present or future societal use.
2. No human or animal health problems have been reported and studies have concluded that properly designed and operated wastewater irrigation systems are likely to pose less environmental health problems than most other wastewater treatment technologies.
3. Forests can be successfully used as the principal vegetative cover in a land treatment system. It has in fact a number of advantages over agronomic crops including greater flexibility to operate around climatic conditions, fewer interruptions to the irrigation schedule, and can be operated year-round.
4. The design of a forest system must be based on potential performance of the site to meet water quality performance criteria objectives including hydraulic capacity as well as nitrogen assimilative capacity. Both of these factors normally influence the total performance of the land treatment system.
5. Successful operation of the land treatment system is evaluated on the basis of performance standards established by water quality objectives.

See also: **Hydrology**: Impacts of Forest Conversion on Streamflow. **Silviculture**: Forest Rehabilitation. **Site-Specific Silviculture**: Silviculture in Polluted Areas. **Soil Development and Properties**: Water Storage and Movement. **Tree Breeding, Practices**: Nitrogen-fixing Tree Improvement and Culture.

Further Reading

Cole DW, Henry CL, and Nutter WL (eds) (1986) *The Forest Alternative for Treatment and Utilization of Municipal and Industrial Wastes*. Seattle, WA: University of Washington Press.

Hamsley WD (1979) *Estimation of Soil Phosphorus Fixation Capacity on a Forested Wastewater Land Treatment Site*. M.Sc. thesis, University of Georgia School of Forest Resources.

Henry CL, Harrison RB, and Bastian RK (eds) (2000) *The Forest Alternative: Principles and Practice of Residuals Use*, Proceedings of a Conference held at University of Washington, Seattle, July 14–16, 1997.

Iskander IK (1981) *Modeling Wastewater Renovation Land Treatment*. New York: John Wiley.

McKim HL, Sopper WE, Cole D, *et al*. (1982) *Wastewater Application in Forest Ecosystems*. CRREL Report no. 80-19. Hanover, NH: US Army Cold Regions Research and Engineering Laboratory.

Moffat AJ, Armstrong AT, and Ockleston J (2001) The optimization of sewage sludge and effluent disposal on energy crops of short rotation hybrid poplar. *Biomass and Bioenergy* 20(3): 161–169.

Nutter WL (1986) Forest land treatment of wastewater in Clayton County, Georgia: a case study. In: *The Forest Alternative for Treatment and Utilization of Municipal and Industrial Wastes*, pp. 393–405. Seattle, WA: University of Washington Press.

Nutter WL (2000) Implementation and operation of wastewater irrigation systems in forests. In: *The Forest Alternative: Principles and Practice of Residuals Use*, pp. 135–138. Proceedings of a Conference held at University of Washington, Seattle, July 14–16, 1997.

Nutter WL, Schultz RC, and Brister GH (1979) Renovation of municipal wastewater by spray irrigation on steep forest slopes in the Southern Appalachians. In: *Utilization of Municipal Sewage Effluent and Sludge on Forest and Disturbed Land*, pp. 77–85. Philadelphia, PA: Pennsylvania State University Press.

Overcash MR and Pal D (1979) *Design of Land Treatment Systems for Industrial Wastes: Theory and Practice*. Ann Arbor, MI: Ann Arbor Science.

Reed SC, Middlebrooks EJ, and Crites RW (1988) *Natural Systems for Waste Management and Treatment*. New York: McGraw-Hill.

US Environmental Protection Agency (1981) *Process Design Manual for Land Treatment of Municipal Wastewater*. EPA 625/1-81-013 (COE EM1110-1-501). Washington, DC: US Government Printing Office.

Water Storage and Movement

M Weiler, University of British Columbia, Vancouver, BC, Canada
J J McDonnell, Oregon State University, Corvallis, OR, USA

Introduction

Water storage and movement in forest soils is a key regulator for a variety of hydrological, physiological, and biogeochemical processes in a forest. The climate and geology controls on soils vary around the world; these can range from conditions of colluvial infilling of steep unstable hollows in and around the Pacific Rim, to till soils that develop on recently glaciated sites in Scandinavia, eastern Canada, and Russia, and deeper clay-rich soils in lower-latitude regions. While the physics of flow in porous media is the same regardless of land-use type, forest soils often have rather different depth-integrated and spatially variable properties relative to soils in agricultural or suburban areas. This entry considers a number of properties of forest soils as it relates to some of the basic definitions and physical processes governing water storage and movement. It then considers in detail the main processes of how water moves vertically and laterally through forest soils – from the plot scale, to hillslope scale, and catchment scale. Finally, influences of forest management and forest fires on water storage and movement are discussed. This entry focuses on some of the first-order controls common to most landscapes. The reader should consult material provided in the Further Reading section for a comprehensive review of water storage and movement in all climatic and physiographic regions of the world.

Soil Physics Terminology and Measurement

Soils, especially forest soils, are a complex mixture of organic and inorganic, living and dead, or solid, liquid, and gaseous materials. This complexity appears at first glance difficult to characterize; however, classifying soils into three phases – air, water, and solids – provides a convenient means to define the basic physical soil properties (**Figure 1**).

The particle density is equal to the ratio of mass to volume of solids. In contrast, the bulk density is the ratio of mass of solids to the total volume. The porosity is the proportion of pore space (air and water) in a given volume of soil. The water content of the soil is described in two ways, as the ratio of water to soil volume, if it is volumetrically defined, or mass, if it is gravitationally defined. Given the water content, the degree of saturation can be calculated as the ratio between volumetric water content and porosity. The water content is an

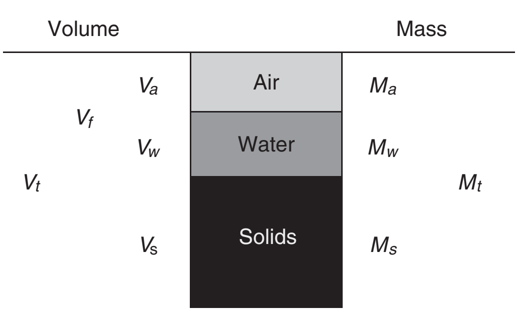


Figure 1 Soil and its three phases: air, water, and solids. V_t and M_t are totals.

important hydrological property of soils. It can be determined in the laboratory or using field methods. In the laboratory, one weighs a field-extracted intact core of known volume, dries it at 105°C for 24 h, and then weighs it again. The difference is used to compute the volumetric water content. In the field, water content is most often measured by time–domain reflectometry (TDR), although many investigators still use neutron probes, gypsum blocks, and capacitance techniques. TDR instruments operate by measuring the propagation velocity in the soil of an electric pulse that is related to the dielectric permittivity or dielectric constant, which is closely related to water content.

Energy State of Water in Soil

Knowing the temporal and spatial variation of water content in the soil is sufficient for determining the total soil water storage (usually expressed as a depth or volume per unit area). For measuring and defining the direction of water movement in soils, the energy state of soil water must be defined since differences in the energy state (potential) drive the direction of water movement. The total soil water potential is the sum of various forces acting on the soil water: gravitational potential, pressure potential, matric potential, and osmotic potential. The gravitational potential depends on the position in the gravitational force field relative to some reference level. Pressure potential is the hydrostatic pressure of the water column under saturation. The matric potential (also referred to as matric suction or capillary potential) is defined under unsaturated conditions, where capillary and adsorptive forces act to create a negative pressure (often called tension or suction). This is measured in soils relative to the external gas pressure. The osmotic potential is attributed to the presence of solutes in the soil water and only in arid environments significantly affects the water movement compared to pressure and matric potential. The primary effect of osmotic potential relates to the uptake of water by vegetation. In this case, the roots act as a membrane which regulates the movement of water as a function of osmotic potential, since water vapor pressure is lowered by the presence of solutes. The pressure potential of soil water is often measured with piezometers. Piezometers are tubes augered into the soil below the water table and only open at the bottom of the tube. Thus, the pressure potential at the bottom of the tube is reflected by the height of water rise in the standing water column within the tube. The soil matric potential is measured with porous cup devices called tensiometers that have a practical range from 0 to 800 cm (0–78 kPa). This range covers most of the naturally observed tensions in forest soils. For higher tensions, thermocouples, psychrometers, or gypsum electrical-resistance blocks are available.

Soil Moisture Characteristic Curve

The relationship between soil moisture and tension is called soil moisture characteristic curve (also soil moisture release curve, retention curve) and is an important property of unsaturated soil. This relationship strongly depends on the soil texture, but also on other soil properties like soil structure, organic matter, and bulk density. No universal theory yet exists to describe or predict the soil moisture characteristic curve (SMCC) from soil properties. In addition, the value of tension at a given water content is not unique, but depends on the soil history of wetting and drying. This hysteresis can have a significant influence on water movement, but is often not considered in describing water movement in hydrological models, since no unique functional relationship can be easily assumed.

The SMCC of forest soils is often highly nonlinear. **Figure 2** shows drying curves for forest soils in old-growth Douglas-fir at three soil depths. The water content decreases by 10–30% between saturation and 20–40 cm of tension. This typical 'drop' for many forest soils is related to soil structure and the macroporosity (large pore space) related to the effect of roots, especially in the topsoil. These macropores in the upper soil horizons drain water at a very low tension (low capillary). This nonlinearity often declines with soil depth (**Figure 2**) since the pore space often declines rapidly into the profile, with concomitant increases in bulk density.

Field Capacity and Permanent Wilting Point

Two points of the SMCC are particularly important: the field capacity and the permanent wilting point. Field capacity is the water content of a soil after gravitational drainage over approximately a day. The suction that defines this value varies from soil to soil, but is generally in the range of 10–33 kPa. Drainable porosity of a soil is defined as the water content between field capacity and saturation. The drainable porosity controls the transient water-table dynamic that often develops at the soil–bedrock interface or some zone of low permeability at depth (hardpan, duricrust, or other layer). The permanent wilting point is the water content at which plants start to wilt during daytime – indicating that they are no longer able to extract water from the soil. The suction at this point is very high, about 1470 kPa. The difference of water content between field capacity and permanent wilting point is often called the available water content.

Water Storage

Water storage in soils depends on the water balance of a soil pedon. The water balance represents one of the most basic equations in hydrology. The change in water storage is equal to the changes in input and output (**Figure 3**). The principal input flux in forest

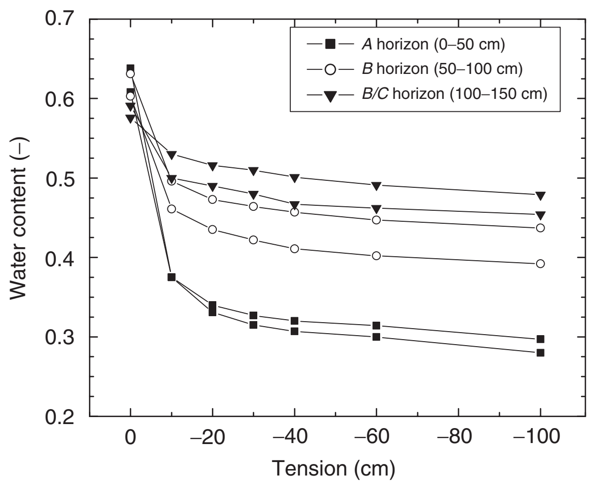


Figure 2 Soil moisture characteristic curves at three different depths of a forest soil (data from HJ Andrews Experimental Forest, Oregon, USA). Note the flattening of the curves deeper in the profile. These curves represent the trajectory of water content and water suction upon drying. Often, soils show differences in these curves during wetting. This difference, called hysteresis, can be significant for some forest soils.

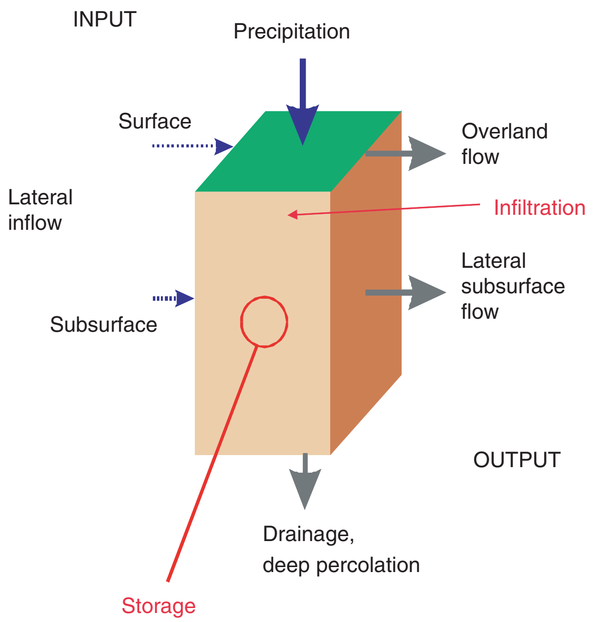


Figure 3 Water storage, input, and output fluxes for a soil column.

soils is precipitation. Only a proportion of total precipitation, termed throughfall, reaches the forest floor. The difference between total amount of precipitation and throughfall results from interception and storage by the forest canopy. Throughfall or snowmelt from snow accumulated above the forest floor infiltrates into the soil, flows over the soil surface, or is stored within surface depressions. While forest soil infiltration rates almost always exceed the precipitation input to the soil surface, 'excess water' may flow on the soil or decayed-leaf surfaces and become stored in small microtopographic depressions in the forest soil surface. Vertical inflow to the soil pedon may therefore originate as ponded overland flow or by lateral subsurface flow.

Three mechanisms act to deplete water in the soil pedon. The first includes direct evaporation from the soil surface and plant uptake in the rooting zone and then transpiration by plants. This loss is collectively termed evapotranspiration. The second is the vertical drainage into the underlying bedrock and possible recharge into underlying groundwater. The third mechanism is lateral subsurface flow within the soil. The dynamics of these fluxes in forest soils are unique as compared to soils under other land use. The modulation of the incoming precipitation by the canopy results in a reduction of both the rainfall intensity and the total amount of precipitation. In addition to trees, smaller plants (e.g., shrubs and bushes) as well as moss and the litter layer affect the disposition of incoming precipitation. Direct evaporation rates from the soil surface are generally lower than the transpiration rates by plants in forested settings. Since trees extract water from soil and have a deep root zone, the reduction of the water content with depth during dry periods is much more sustained in forest soils compared to soils under other land use. Alternatively, direct evaporation of water at the soil surface is reduced under the forest canopy. Water redistribution in forest soils by tree roots, especially by water uptake from the saturated zone (groundwater), and redistribution into the unsaturated zone is an important process, particularly in semi-arid climates.

Spatial Variability

The heterogeneous structure of forests, in combination with complex topography and soil heterogeneity, results in significant spatial variability of water storage within forest soils. The plant canopy modifies precipitation input and also produces a persistent spatial pattern of throughfall to the soil surface. Studies under coniferous canopies have shown up to 100% differences in throughfall application to the soil surface over distances of less than 1 m. In addition, flow down the tree stem (stem flow) further increases this variability of precipitation input to the soil. Snowmelt may produce a similar spatial variability through factors affecting the energy budget of the snow (e.g., slope aspect, inclination, and cover type). Lateral flow of water within the soil or upwards movement of groundwater into the soil profile is often described by topography. Thus, topographic position, local slope angle, and upslope contributing area are key variables to explain larger-scale spatial variability of soil water storage. These influences are most pronounced in areas with significant topographic relief, shallow lateral flow pathways, and under humid conditions. Finally, the variability of transpiration by trees and other plants may also affect a spatial variability of soil water storage within forests.

Water Movement

Hydrological Concepts – Runoff Generation Processes

Runoff generation processes during rainfall or snowmelt events are often separated into two classes: those processes which were relevant for generating overland and those processes that are relevant for generating lateral subsurface flow. Overland flow can be generated by infiltration excess (rainfall intensity is larger than the soil's infiltration capacity) or by saturation excess (where soils become saturated by a rising water table). In forest soils, overland flow is usually generated by the saturation excess mechanism. One exception is where infiltration excess overland flow may be produced on logging roads and other low-permeability areas (e.g., compacted soils) or on soils with seasonal water repellency due to fire (*see* **Health and Protection**: Forest Fires (Prediction, Prevention, Preparedness and Suppression)). Saturation overland flow is most common in areas where soils are often waterlogged (topographic confluence zones, near springs, and in riparian zones).

On steeper hillslopes, water infiltrating into the soil will either be stored in the soil or will continue moving vertically to recharge local groundwater or flow as lateral subsurface flow. This lateral subsurface flow (also called subsurface stormflow, interflow, and throughflow) are very common in forest soils since the lateral hydraulic conductivity and the gravitational gradients (in areas with a steep relief) are often high, and additional preferential flow pathways are present to enhance the downslope flow. Knowing the dominant runoff generation processes at a site is an important first step to understand runoff generation in a catchment, as well as flood generation, nutrient transport, and prediction of forest management practices on water quantity and quality.

Vertical Movement

Water movement in porous media like soils is often described based on the Darcy equation that flow is proportional to the hydraulic potential times the hydraulic conductivity:

$$q = -K\frac{\Delta H}{\Delta z}$$

where q is the water flow (length per time), K is the saturated hydraulic conductivity (length per time), ΔH is the hydraulic head difference, and Δz the distance. The saturated hydraulic conductivity (or permeability) is a spatially variable property of soils (over several orders of magnitude over short distances). Hence, it varies with the scale of measurement. It depends on the soil texture, but also on the soil structural features. Due to these structures, the saturated hydraulic conductivity of forest soils is usually much smaller in the vertical direction than in the horizontal direction (known as anisotropy). In addition, the hydraulic conductivity depends strongly on the degree of saturation and thus on the soil water tension. Based on this functional relationship, the Richards equation was developed by combining the Darcy equation with the continuity equation to describe flow in unsaturated porous media:

$$\frac{\partial\theta}{\partial t} = \frac{\partial}{\partial z}\left[K(h)\left(\frac{\partial h}{\partial z}+1\right)\right]$$

where $K(h)$ is the unsaturated hydraulic conductivity and θ the water content. Both equations are based on the capillary concept and work well in relatively homogeneous soils. However, in forest soils, the influence of plant roots, soil structure, burrowing animals, and worm casts creates a variety of larger pores (macropores) that water may follow preferentially (**Figure 4**). Due to these macropores, the unsaturated hydraulic conductivity relationship often shows a significant reduction (one to some orders of magnitude) at values near saturation. Thus, while macropores may comprise only a small part of the total soil porosity, they may control almost all the water flow at or near saturation within the profile. The water flow in these macropores is often turbulent and mostly driven by gravity. The resulting water movement in the soils is very heterogeneous and dry areas within the soil may be bypassed. These processes run counter to the Darcy and Richards formulations that rely exclusively on capillary-driven laws of fluid flow.

Water movement that may be influenced by preferential flow can be visualized by adding a dye tracer to the infiltrating water. **Figure 5** shows some experimental results where a food dye (Brilliant Blue FCF) was added to a simulated rainfall event. Soil profiles were excavated and pictures were taken from these vertical soil sections. **Figure 5** shows two examples of these dye patterns for forest soils in Oregon, USA. The patterns show that the soil surface itself may affect the disposition of infiltrating rainfall. The litter layer may be a significant generator of flowpath heterogeneity near the soil surface. Deeper in the soil profile, water flow may occur only in macropores, bypassing large dry areas of matrix in the soil profile. In contrast to homogeneous infiltration, the process of water flow into the macropores (initiation) and water flow from macropores into the surrounding soil matrix (interaction) mainly controls the vertical water movement of water in forest soils. In general, macropore flow results in a much faster flow and increased transport of solutes and nutrients.

Lateral Movement

Lateral water movement in the soil is an important process for redistribution of water, nutrients, and solutes in the environment. This process also controls the generation of storm runoff in many upland forested environments. Detailed process studies in forest soils in the last half-century have revealed a variety of flow pathways in forest watersheds. **Figure 4** illustrates the most important of these pathways. If the bedrock is relatively impermeable compared to the soil, infiltrating water perches on the soil–bedrock interface and flows laterally downslope along this interface. Since this interface is generally topographically 'rough' due to weathering and mass movement, water concentrates in hollows and depressions. The resulting channalized flow acts similarly to macropore flow whereas the average flow velocity increases and areas with a relatively higher soil–bedrock relief interface are bypassed. The lateral flow is less preferential if the soil–bedrock interface is more gradual in texture and where the hydraulic conductivity decrease with depth is more gradual. This gradual decline can be observed in soils developed from glaciated deposits (e.g. till).

Macropore flow is also a major control on lateral flow on forest hillslopes. Similar to the processes governing vertical flow in macropores, laterally oriented macropore flow may dominate in many forest environments where macropores are generated by plant roots and burrowing animals. These

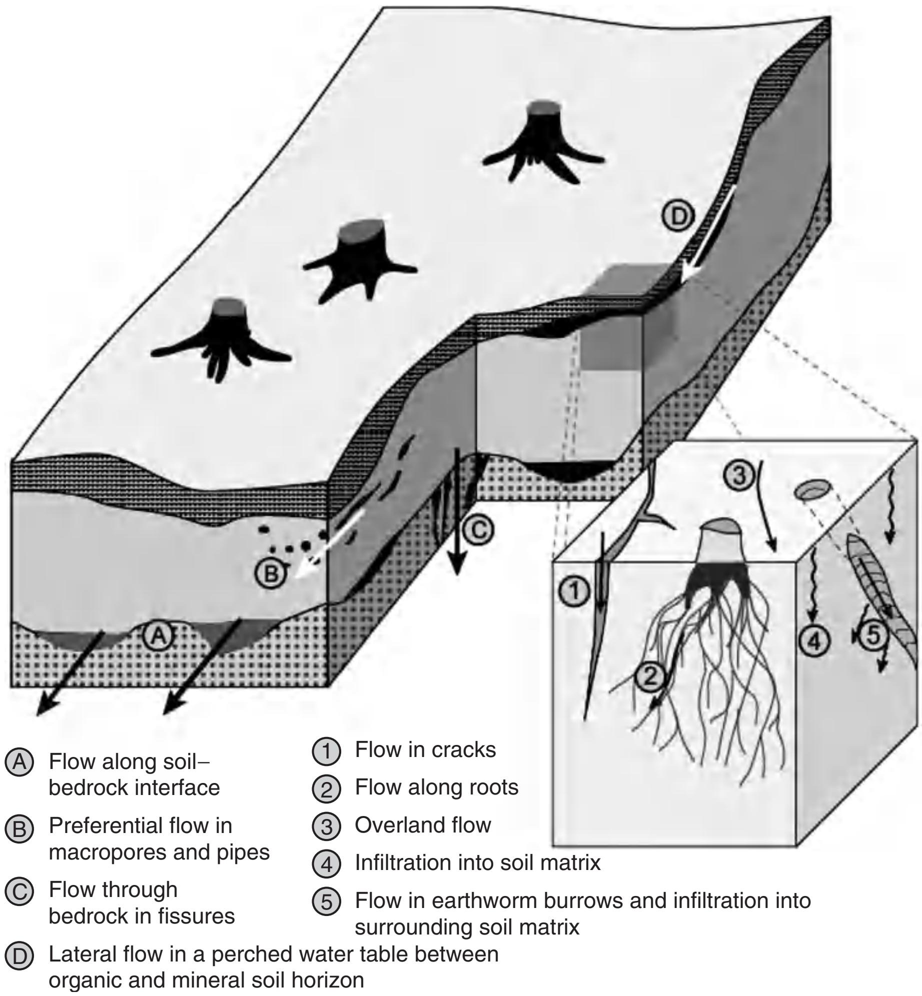


Figure 4 Water movement in forest soils: lateral flow pathways (A–D) and vertical flow pathways (1–5). Note the complexity of water flow pathways due to physical and biological agents acting on soil.

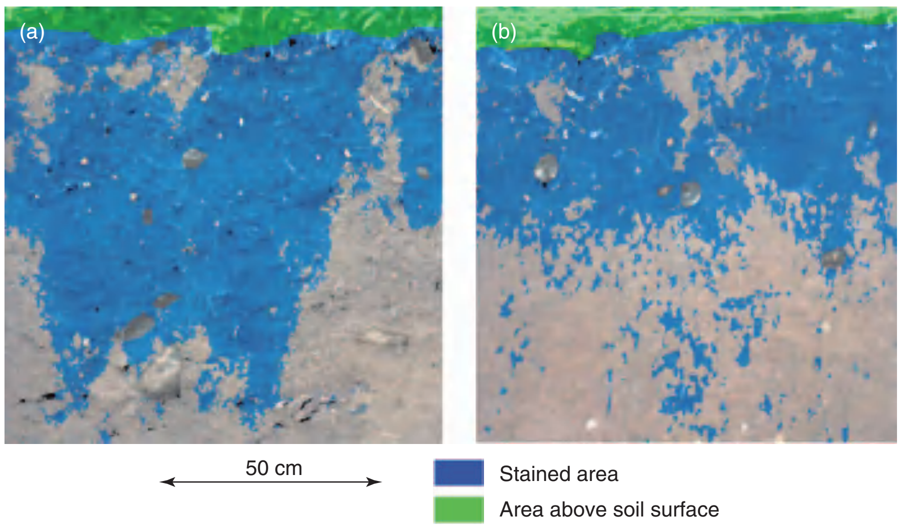


Figure 5 Dye patterns from two different forested sites: (a) HJ Andrews Experimental Forest, Oregon, USA; (b) Low Pass Area, Coastal Range, Oregon, USA. Note the spatial heterogeneity of dyed water and preferred nature of water flow vertically within the forest soil profile.

macropores are often termed soil pipes. If a connected network is developed due to internal erosion and connection of the macropores, piping can provide effective drainage augmentation to hillslopes. If the underlying bedrock is more permeable, water can infiltrate into the bedrock and then percolate vertically in fissures and cracks. The top soil layer (litter or organic layer) in forest soils includes a high proportion of organic material and roots that enhance the hydraulic conductivity. If the underlying mineral soil has a low hydraulic conductivity, a perched water table can sometimes develop during rainfall and snowmelt events within the organic horizon. Under these conditions, water may flow laterally within this layer.

Important Issues

Harvesting and Forest Management

Harvesting and forest management operations can strongly influence water storage and movement in soil. An important issue is soil compaction by using heavy machinery for timber harvesting. Depending on the soil texture, soil structure, and the soil moisture content during the operations, soil compaction can occur. Soil compaction is defined as an increase in bulk density and a decrease in soil porosity resulting from applied loads, vibration, or pressure. Compaction can reduce infiltration, leading to the development of areas that can produce infiltration excess and overland flow. Water storage capacity of the soil can also be reduced since the proportion of larger pore space may be reduced through compression. A specific feature of forest soils is the organic layer on top of the mineral soil. This organic layer modulates infiltration, reduces evaporation, and increases water storage. Removing this organic layer by forest management (mechanical removing and burning) often negatively changes the hydrological behavior of a site. While much progress has been made in forest operations in the developed world in reducing site disturbance associated with logging, poor logging practices can have deleterious effects on soil water storage and movement.

Fire

Forest fires may consume a large part of the forest floor, eliminating beneficial effects of the organic layer on soil properties. However, the effects of low-temperature fires (e.g., from controlled burning) are generally less than the effects from hot wildfires. The most pronounced impact of forest fires on soil properties is the reduction of infiltration rates due to water repellency. This reduced infiltration not only increases the amount of overland flow and thus soil erosion, but may further reduce the availability of soil water for plants, especially in semiarid regions. Water-repellent soils can develop from hydrophobic substances vaporized during burning of the surface litter layers. The degree and persistence of these hydrophobic substances depend not only on the temperatures during the fire but also on the timing, number, and magnitude of subsequent rainfall events on the burned site (as water repellency can decrease with time). In addition, drier soils show higher water repellency than wetter soils, which should be kept in mind considering these effects in different climate zones.

Measuring the effects of fire on water movement and storage in soils is difficult, and results from experimental studies concerning the effects of fire on changes in infiltration rate are equivocal. The major problem is to determine if small-scale effects due to hydrophobic substances translate into larger-scale (hillslope and watershed) behavioral changes. One possibility to explore the effects of forest fire on infiltration is to perform infiltration experiments in combination with dye patterns. **Figure 6** shows the impact of the water-repellent surface layer. Water was only able to infiltrate at few locations within the profile, coincident with local depressions or plant roots. Thus, the resulting dye pattern shows only a thin staining near the soil surface and some isolated ‘spots’ within the soil. Nevertheless, comprehensive analysis of the effects of fire on water storage and movement in forest soils on larger scales remain the topic of future research.

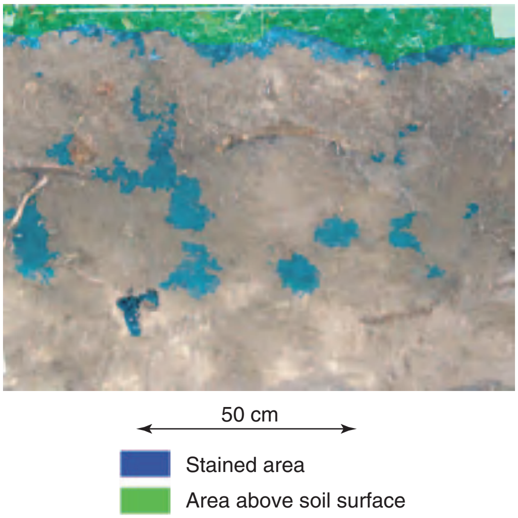


Figure 6 Dye pattern from a recently burned forest soil in the Western Cascades, Oregon, USA.

Summary

Water movement and storage in soils are regulated by a variety of temporally and spatially variable processes. This article presents an overview of the most important properties and processes influencing water movement and storage in forest soils. Soil water storage and movement are controlled by the size and spatial distribution of macropores, through which water can move rapidly but which drain under gravity, and micropores, through which water moves more slowly but can retain water against gravity. The relationship between water content and soil water tension is described by the soil moisture characteristic curve. Two points on this curve, field capacity and permanent wilting point, are particularly important as they describe storage of plant available water. Runoff from forests can be generated by overland flow and lateral subsurface flow. Overland flow usually only occurs on sites compacted by harvesting or which have water-repellent surfaces resulting from fire. Lateral subsurface flow is very common in forests since the lateral hydraulic conductivity and the gravitational gradients (in areas with a steep relief) are often high, and additional preferential flow pathways are present to enhance the downslope flow. The described processes of water storage and movement are applicable in various climates and geographical locations. However, certain processes dominate in certain locations – predicting and understanding water storage and movement in soils require one to use critical thinking to define the first-order controls at a particular site.

See also: **Ecology**: Forest Canopies; Natural Disturbance in Forest Environments. **Health and Protection**: Forest Fires (Prediction, Prevention, Preparedness and Suppression). **Hydrology**: Hydrological Cycle; Impacts of Forest Conversion on Streamflow; Impacts of Forest Management on Streamflow; Impacts of Forest Management on Water Quality. **Soil Biology and Tree Growth**: Soil Organic Matter Forms and Functions; Tree Roots and their Interaction with Soil. **Soil Development and Properties**: Forests and Soil Development; Landscape and Soil Classification for Forest Management; Nutrient Cycling; The Forest Floor.

Further Reading

Beven K (1989) Interflow. In: Morel-Seytoux HJ (ed.) *Unsaturated Flow in Hydrologic Modeling Theory and Practice*, pp. 191–219. Dordrecht, Germany: Kluwer Academic Publishers.

Beven K and Germann P (1982) Macropores and water flow in soils. *Water Resources Research* 18(5): 1311–1325.

Bonell M (1993) Progress in the understanding of runoff generation dynamics in forests. *Journal of Hydrology* 150: 217–275.

DeBano LF (2000) The role of fire and soil heating on water repellency in wildland environments: a review. *Journal of Hydrology* 231: 1–4.

Feddes RA, Kabat P, van Bakel PJT, Bronswijk JJB, and Halbertsma J (1988) Modelling soil water dynamics in the unsaturated zone – state of the art. *Journal of Hydrology* 100: 69–111.

Grayson R and Blöschl G (eds) (2000) *Spatial Patterns in Catchment Hydrology: observations and modeling*. Cambridge, UK: Cambridge University Press.

Hillel D (1998) *Environmental Soil Physics*. San Diego, CA: Academic Press.

Jury WA, Gardner R, and Gardner WH (1991) *Soil Physics*. New York: John Wiley.

Klute A (ed.) (1986) *Methods of Soil Analysis*, Part I, *Physical and Mineralogical Methods*. Madison, WI: American Society of Agronomy.

Kutílek M and Nielsen DR (1994) *Soil Hydrology*. Cremlingen-Destedt, Germany: Catena-Verlag.

McDonnell JJ (1990) A rationale for old water discharge through macropores in a steep, humid catchment. *Water Resources Research* 26(11): 2821–2832.

Pritchett WL and Fisher RF (1987) *Properties and Management of Forest Soils*. New York: John Wiley.

Weiler M and Naef F (2003) An experimental tracer study of the role of macropores in infiltration in grassland soils. *Hydrological Processes* 17(2): 477–493.

Weyman DR (1973) Measurements of the downslope flow of water in a soil. *Journal of Hydrology* 20: 267–288.

Youngs EG (1995) Developments in the physics of infiltration. *Soil Science Society of America Journal* 59: 307–313.

SOLID WOOD PROCESSING

Contents

Adhesion and Adhesives

C E Frazier, Virginia Technical Institute, Blacksburg, VA, USA

Introduction

Adhesion science and technology has developed since our earliest ancestors struggled to enhance their conditions. The struggle continues, and as with all modern technologies it is apparent that adhesion has evolved into a highly multi- and interdisciplinary activity. Three disciplines define the foundation of adhesion science and technology: chemistry, materials science, and mechanics of materials. It so happens that wood is a peculiar material with respect to each of these disciplines. The following discussion of wood adhesion touches upon the chemical and material sciences and is intended to direct the reader to the more complete treatments found in the recommendations for further reading. Afterwards, some of the more common wood adhesives are reviewed briefly.

Requirements for Adhesion

Adhesion is the process of 'making things stick.' By this definition, one appreciates that adhesive phenomena are widespread because sticky things and processes are all around us. However, this article focuses on applications in the forest products industry, a more narrow view because typical wood applications not only require 'stickiness,' but also structural integrity and long-term durability. There are three essential requirements for a durable, structurally sound adhesive bond:

1. Surface preparation.
2. Adhesive wetting.
3. Adhesive solidification.

While this seems like a simple plan, and it can be, each step is based upon numerous interacting variables. The highlights of each requirement follow.

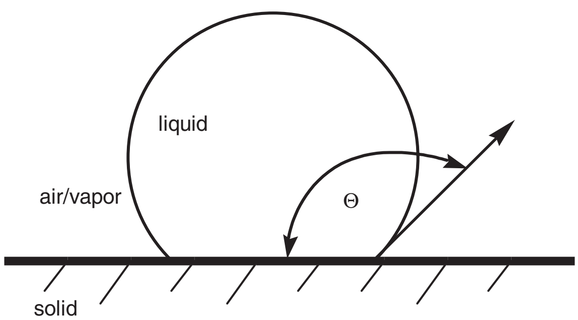
Surface Preparation

The preparation of bonding surfaces involves chemical and physical parameters. Physically, a clean bonding surface is required, devoid of loose particles and other weak boundary layers. For wood bonding, most desirable is a well-machined smooth surface with minimal cellular damage and compression. Machining processes such as knife planing and veneer slicing produce smooth surfaces with little damage, when the blades are sharp. In contrast, processes such as abrasive planing and sawing produce more cell damage and a weakened surface layer. Under loading, such defects may concentrate stress and promote bond failure. Understand that all machining processes cause some level of wood surface damage. But again, planing and slicing with sharp blades provides the smoothest and most structurally sound surface; this is generally best. However, contradictory findings exist. For example, there are times when wood surface roughening improves bond test-strengths. However, any benefits from wood surface roughening are difficult to reproduce due to changes in other influential parameters, such as adhesive layer thickness, physical interlocking of wood surfaces, and stress concentrations. Predicting when wood surface roughening may improve bond test-strength is difficult at best. Consequently, a safer approach is to machine a smooth, sound surface with minimal cellular damage.

The chemical aspects of wood surface preparation are also important, and this addresses the concept of surface energy. Surface energy is a chemical manifestation of solids and liquids. It reflects the nature of electrical charges present on the surfaces of all molecules. A higher surface energy reflects a higher degree of surface charge, lower surface energy, less charge. All molecules have surface charge, positive and negative, and all molecules tend to orient themselves in an attempt to neutralize this charge. This is the essence of adhesion; but these attractive adhesive forces act only over very small distances, under 10 nanometers, or on the order of molecular dimensions. This fact explains why all adhesives must be liquid at some stage, because only liquids can readily achieve intimate molecular contact over large bond areas. When liquid adhesives contact solid surfaces, the force of attraction depends upon the molecular surface charges, the surface energies of the liquid adhesive and the solid wood surface. Wood machining exposes 'fresh wood,' providing the highest possible surface energy which is very desirable for bonding. Unfortunately, there are many factors that tend to reduce the surface energy of wood, producing what is termed a deactivated or aged surface. These include: the simple deposition of airborne organic materials, ultraviolet radiation from the sun, excessive heat over time, and of course, dirt, grime and even oily human hands.

Adhesive Wetting

Wetting is the term used to describe how liquids adhere to solid surfaces. The quality of wetting, be it favorable or unfavorable, is a function of surface energy. This is why we are first concerned with surface preparation, and maximizing the wood surface energy. But we are also interested in the surface energy of the liquid adhesive. A relative measure of solid and liquid surface energy is observed through the 'contact angle,' as depicted in **Figure 1**. Also shown in **Figure 1** is the Young equation, which explains that the contact angle reflects the balance of surface energies (γ), that of the solid, the liquid, and the solid–liquid interface.



$$\gamma_{sv} = \gamma_{sl} + \gamma_{lv} \cos \Theta$$

Figure 1 Depiction of the contact angle of a liquid on a solid surface. Also shown is the Young equation which describes the balance of surface energy (γ) between the solid, liquid and vapor phases.

Arbitrarily, 'favorable wetting' is defined by a contact angle less than 90°. When the contact angle exceeds 90°, wetting is 'unfavorable.' When a liquid adhesive favorably wets the bonding surface, the attractive forces at the solid–liquid interface are greater than the cohesive forces acting within the liquid adhesive. Generally, favorable adhesive wetting provides good bonding, but there is no guarantee because good wetting is but one aspect of good bonding. On the other hand and invariably, unfavorable wetting will result in a poor adhesive bond. Consequently, the concepts of surface energy and wetting are critical aspects of adhesion.

Figure 2 depicts two strategies for controlling adhesive wetting. First, let us consider some unchanging solid surface, which is wetted by three different liquids. As the surface energy of the liquid is reduced, wetting becomes more favorable and the contact angle is reduced. For example, consider the wetting properties of two liquids, water and isopropanol (rubbing alcohol). Water is polar and has a high surface energy, whereas, isopropanol is less polar with a lower surface energy. (The term 'polar' also refers to molecular surface charge; polar

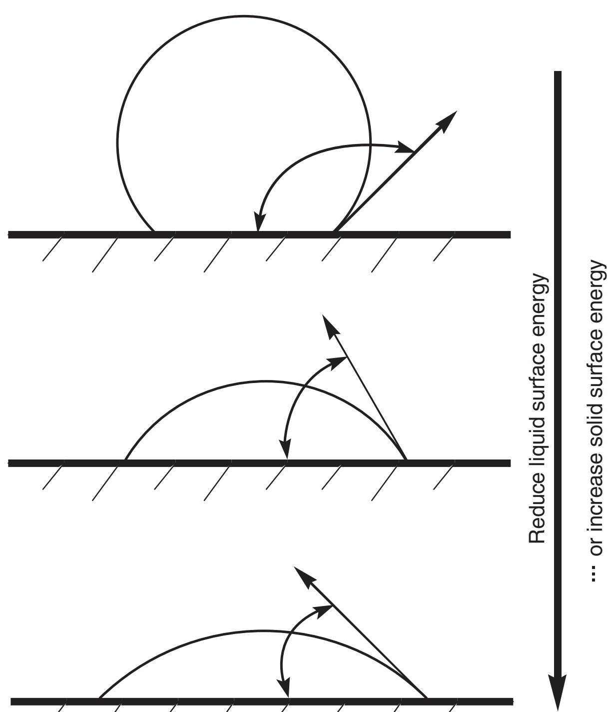


Figure 2 Illustration of two strategies for controlling the contact angle, or the wetting, of liquid adhesives on solid surfaces. Strategy 1: Three identical solid surfaces are contacted by three different liquids; wetting improves as the liquid surface energy is reduced. Strategy 2: Three different solid surfaces contacted by water in each case; water wetting improves as the solid surface energy is increased.

molecules have higher surface charge. Polarity and surface energy are generally related, but the terms should not be interchanged freely.) Isopropanol will wet any particular surface more favorably than will water. In other words, on a given surface the contact angle of isopropanol will be lower than that of water. Furthermore, one can improve the wetting of a liquid adhesive by simply reducing the surface energy of the adhesive. This is commonly achieved by adding wetting agents, chemicals that reduce the surface energy of aqueous solutions. Wetting agents are also referred to as surface active agents, or surfactants. Very small quantities of wetting agents dramatically reduce the surface energy of aqueous adhesives; wetting improves. Now look back at **Figure 2** as we discuss the second strategy to improve wetting.

If we consider a single unchanging liquid, we can improve the wetting of that liquid by increasing the wood surface energy. Imagine that **Figure 2** shows three different wood surfaces, each wetted by a drop of water. The topmost wood surface exhibits a low surface energy because the water contact angle is well over 90°. Likewise, the bottom surface has the highest surface energy, indicated by the lowest contact angle. The best bonds result from favorable wetting that is driven by a high wood surface energy. Unfortunately, we may not always control the wood surface energy. For example, remachining a deactivated wood surface immediately prior to bonding might not be feasible. One may then be forced to improve adhesive wetting by adding wetting agents. If given the choice, one should always achieve and maintain a high wood surface energy.

A simple test reveals differences in wood surface energy. One could measure the water contact angle on wood surfaces, but this is often impractical. However, it is easy to measure the time it takes a water drop to absorb into wood. If a water drop wets favorably, capillary forces rapidly draw the water into the wood. **Figure 3** shows data collected by a group of college students in the author's adhesion class. Water drops (10 μl in volume) were applied to red oak (*Quercus rubra*) samples having different surface treatments. The water absorption time is fastest on the freshly sanded surface; the sanded surface has the highest surface energy. Samples with the 'old surface' were stored in a plastic bag for 1 year, and they apparently lost surface energy because the absorption time is nearly doubled. The remaining samples were sanded and then heated at 185°C for 5 min, which caused a severe deactivation. Data on the far right of **Figure 3** demonstrate the power of wetting agents. In this case, the water drops contained 10% isopropanol, which causes a remarkable reduction in absorption time; wetting was improved. The broad variation in the absorption times is caused by the natural variability of wood.

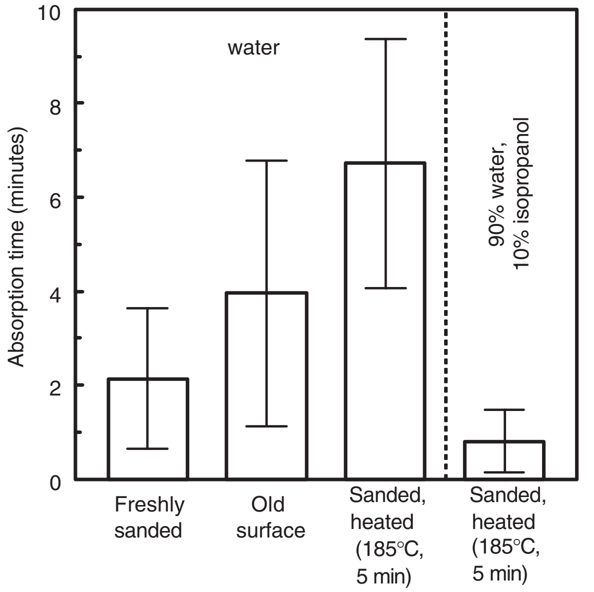


Figure 3 A simple method for comparing wood surface energies involves measuring the time it takes a 10 μl drop of water to absorb into the wood surface. The data shown are for red oak samples exposed to different surface treatments as described in the text.

Adhesive Solidification

Favorable wetting is required because it ensures strong and intimate molecular contact between wood and adhesive. However, favorable wetting is not enough. After wetting, the adhesive must solidify in order to transmit load. Through wetting we achieve intimate contact and adhesion, but through solidification the adhesive forces are essentially locked into a solid state having mechanical integrity. Small molecules like water do not solidify under convenient conditions. In contrast, the very large polymer molecules solidify into strong solids under desirable circumstances. This is why nearly all adhesives are polymeric. Polymeric molecules, polymers or macromolecules, are extremely large chainlike molecules that may be linear, branched, or crosslinked into network structures. There are three general mechanisms for adhesive solidification: (1) solvent loss, (2) chemical reaction or polymerization, and (3) cooling of a molten adhesive. In all three cases, we are manipulating an important physical parameter of the adhesive, and this is the temperature at which the adhesive changes from a liquid into a solid. For many adhesives, this temperature is referred to as the glass transition temperature, T_g. For other adhesives, hot melt adhesives in particular, this may be the melting temperature, T_m.

Certain adhesives are actually solutions of polymers in organic solvents. While dissolved in the solvent, the polymers are fluid, capable of flow and wetting. Afterwards, the solvent evaporates and/or absorbs into the wood. As the solvent evaporates, the adhesive polymers become less mobile, eventually transforming into a tough, solid adhesive layer (**Figure 4a**). Solvent loss also occurs for another common class of wood adhesive; these are latex adhesives, the water-based 'white glues.' Latex adhesives are actually water dispersions of soft microscopic polymer particles. The fluid latex wets and flows. As water is absorbed into the wood, the particles pack together and deform as they begin to coalesce. When completely dry, the particles have fused into a solid, tough and continuous adhesive film (**Figure 4b**). Adhesives that solidify through solvent loss are typically thermoplastic, meaning they will deform and flow under elevated temperatures. Such thermoplastic adhesives are not designated as structural adhesives because they may deform, or creep, under loading. Creep is avoided in adhesives that solidify through chemical reaction (polymerization) into rigid network structures. These adhesives are called thermosetting adhesives or resins. During application, thermosetting resins are chemically reactive fluid mixtures. While heated, they react into highly crosslinked, rigid network structures (**Figure 4c**). All wood adhesives that satisfy structural applications are thermosetting. Finally, hotmelt adhesives solidify by simply cooling from the molten state into a tough solid. The polymers in hotmelt adhesives are often semicrystalline. Semicrystalline polymers are typically linear and actually pack into three-dimensional crystal structures, or crystallites. Separate polymer chains pack into the crystallites and become 'physically crosslinked.' The hotmelt adhesive must be heated above the T_m of the crystallites, breaking the physical crosslinks and allowing the polymers to flow and wet. Upon

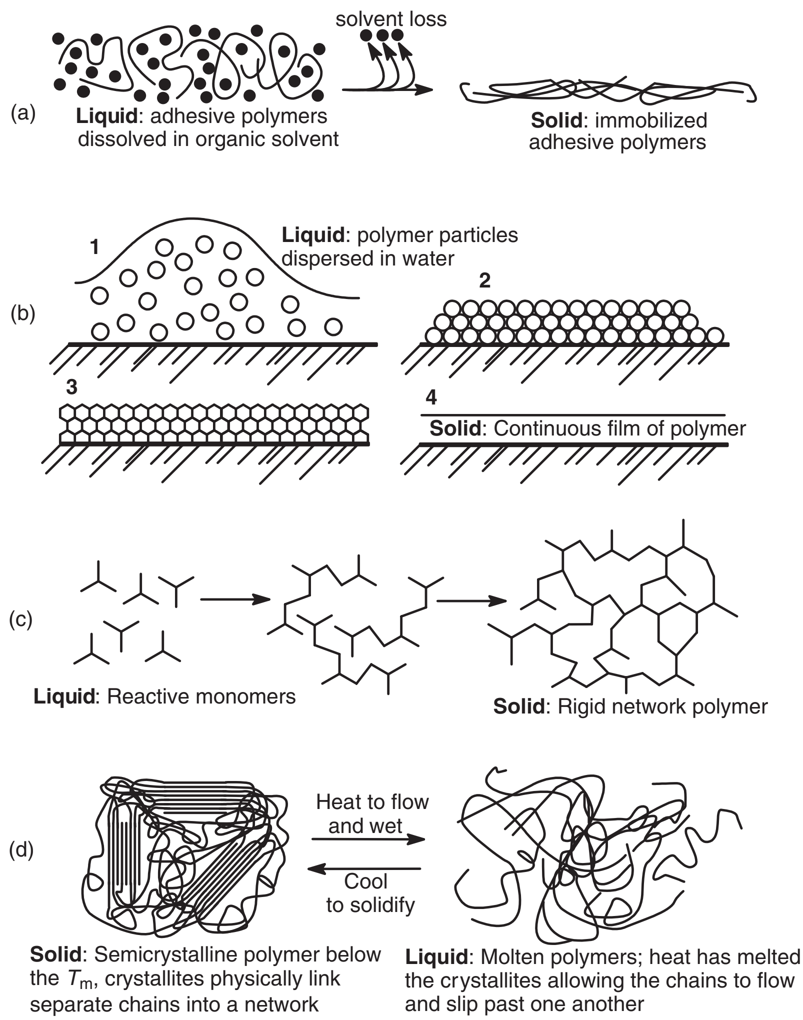


Figure 4 Illustration of four different ways that adhesives solidify to achieve structural integrity.

cooling, the crystallites reform and the adhesive is again a tough solid (**Figure 4d**).

Theories of Adhesion

There are generally five recognized mechanisms or theories of adhesion: (1) the theory of mechanical interlock, (2) the adsorption theory, (3) the covalent bonding theory, (4) the interdiffusion theory, and (5) the electronic theory. Not all of these theoretical mechanisms are important for wood bonding; we shall limit our attention to those that are. The reader interested in all theories should consult the recommendations for further reading.

Mechanical Interlock

The mechanical interlock theory states that adhesives must flow onto the bonding surfaces and into macro- and microscopic voids. After solidification, the adhesive and bonding surfaces are interlocked, or keyed, and capable of withstanding great shear forces. Of course, wood is porous and experience has shown that ideal performance results from adhesive penetration into the cell layers beneath the bonding surfaces. Consequently, it is clear that mechanical interlock contributes to wood adhesion. In the past some have argued that the interlocking mechanism is most important for wood adhesion. While mechanical interlocking is important, it cannot be described as the primary wood adhesive mechanism, for reasons that we shall discuss. Aside from the interlocking mechanism, one should appreciate that adhesive penetration reinforces the damaged surface cells, preventing crack initiation in the bondline.

Adsorption

We have already touched upon issues related to the adsorption theory; these are the concepts of surface energy and wetting. The adsorption theory states that adhesion results from intermolecular forces, also called secondary forces or secondary bonds, between the adhesive and substrate. The secondary forces are merely electrostatic attractions between complementary charges on molecular surfaces. All molecules possess positive and negative surface charge because atoms and molecules contain charged particles, the negative electrons and the positive protons. Depending upon the atomic elements and their molecular configuration, molecules may have permanent and relatively high-magnitude surface charge (polar molecules), or they may have temporary and lower-magnitude surface charge (nonpolar molecules). The secondary forces described in the adsorption theory are the simple electrostatic attractions between opposite charges on molecular surfaces. Collectively, these forces are referred to as the Van der Waals forces which includes the weak London, or dispersion, forces and the very strong hydrogen bond. Wood forms strong hydrogen bonds with water, and also with many types of adhesives. The adsorption theory is the most important adhesive mechanism for bonding all materials. So while mechanical interlock is important for wood bonding, adsorption and intermolecular forces are always dominant. Without favorable wetting and secondary forces, adhesive penetration is impaired and mechanical interlock becomes much less effective (**Figure 5**).

Covalent Bonding

The covalent bonding theory states that adhesion results from covalent, or primary, bonds between adhesive and substrate. Primary bonds are the very strong bonds that hold atoms together as molecules, and are an order of magnitude stronger than secondary bonds. Consequently, adhesion through covalent bonding is highly desirable because such bonds are not easily broken. In contrast, secondary bonds may be disrupted by water and/or elevated temperatures. Covalent bonding could be very important for wood adhesion because wood contains many chemically reactive sites that could provide strong covalent bonds to the adhesive. Not all adhesives possess the chemical properties that promote covalent bonding. Consequently, this adhesive mechanism is relatively specialized, but occasionally important for wood.

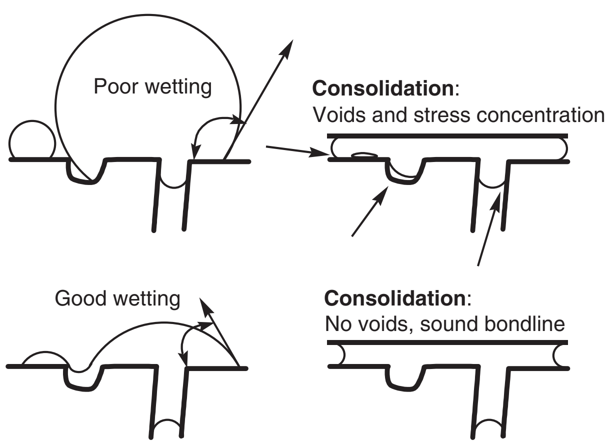


Figure 5 Illustration of the consequences of poor and good adhesive wetting on wood surfaces. Poor wetting promotes void formation by the inefficient coalescence of adjacent adhesive drops, and also by the inability to force air out of small crevices. Also, poor wetting inhibits adhesive penetration and promotes stress concentration. On the other hand, good wetting prevents these problems.

In summary, adsorption and mechanical interlock both contribute to wood bonding, and under special circumstances covalent bonding may also be important. While covalent bonding deserves special consideration, this adhesive mechanism does not improve the tested strength of wood bonds. Adhesion through adsorption and mechanical interlock produces very strong bonds that prove to be stronger than wood (depending upon the test method). However the special case of adhesion through covalent bonding would dramatically improve bond durability.

Wood-Related Factors that Impact Bond Performance

Wood Moisture Content

Wood is a hygroscopic material. Consequently, wood moisture content is determined by the prevailing environmental conditions (*see* **Wood Formation and Properties**: Formation and Structure of Wood; Physical Properties of Wood). Generally speaking, dry wood is easiest to bond, whereas very wet or green wood is difficult to bond for at least two reasons. The first is that wet wood is essentially encased in a layer of water; this prevents molecular contact. Secondly, as moisture is lost the wood shrinks, creating large bond stresses that may promote delamination. This is particularly troublesome when bonding cross-grain assemblies (**Figure 6**). The moisture-related dimensional change of wood in the longitudinal direction is quite small, whereas the same change in the radial and tangential directions is large. These dimensional changes oppose each other in cross-grain assemblies, creating potentially damaging bond stresses. The solution is to avoid cross-grain joints, use lower-density woods that exhibit less moisture-related dimensional change, and use compliant adhesives not brittle ones. Of course, each of these solutions entails a peculiar set of trade-offs.

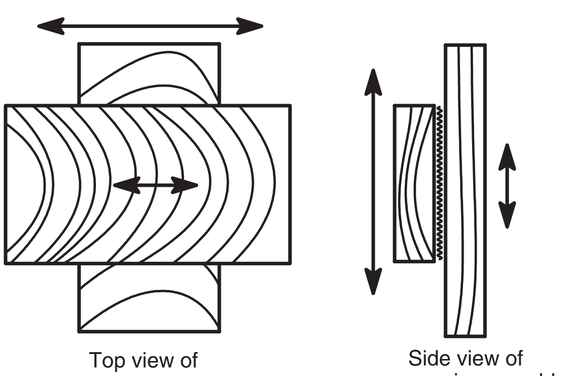


Figure 6 Illustration depicting the stresses that form in cross-grain assemblies, when solid wood is bonded such that the moisture-related dimensional changes in one piece oppose those in the other piece. The size of the double arrows indicates the relative degree of moisture-related dimensional change.

Another important aspect of wood moisture content impacts bond assembly with waterborne adhesives. Optimum bonding requires attention to consolidation pressure, adhesive viscosity and wood porosity; all of this controls penetration and bond thickness. Wood absorbs adhesive moisture, which rapidly changes the viscosity. If the bonded wood is excessively dry or wet, the adhesive will respectively dry out rapidly, or not at all. In either case, this influences how adhesive viscosity interacts with consolidation pressure and wood porosity to achieve the proper penetration and bond thickness.

Wood Density and Porosity

Dense woods have low porosity, and this often impairs adhesive penetration. Similarly, woods with uneven grain (nonuniform density from abrupt earlywood–latewood transitions), typically exhibit nonuniform penetration which can lead to undesirable stress concentrations. Likewise very-high-porosity, low-density woods may promote over penetration if the adhesive and consolidation parameters are not adjusted.

Very-high-density woods may also promote durability problems arising from moisture-related dimensional change, as mentioned previously. Higher-density woods shrink and swell to a greater degree, thus generating larger stresses on the bond. Regarding this point, also note that larger more massive wood components generate greater forces during moisture-related dimensional change, regardless of the wood density.

Extractives

Extractives are nonstructural organic molecules that result from primary and secondary metabolic functions in the living tree (*see* **Non-wood Products**: Chemicals from Wood. **Papermaking**: Paper Raw Materials and Technology. **Wood Formation and Properties**: Chemical Properties of Wood). This general term, extractives, represents a tremendous variety of chemical compounds. Collectively, the extractives are often cited as a major source of bonding problems. The resinous and fatty compounds are particularly troublesome because they may impair wetting by forming a nonpolar film on the wood surface. This process is often referred to as extractives migration, and is accelerated by heat. The loss of wood surface energy, or deactivation, caused by excessive thermal treatment is thought to arise from extractives migration to the wood surface.

Besides the lipid-like extractives, other extractive compounds may interfere with adhesives that cure under acidic or basic conditions. Certain acid and phenolic extractives influence the buffering capacity of wood, as discussed in the following section.

Wood Buffering Capacity

A buffer, or buffer solution, is an aqueous mixture that resists changes in pH. Different woods often behave as buffers and so may influence the cure of aqueous adhesives that polymerize under acidic or basic conditions. As with most properties, the buffering capacity is highly variable between woods. Within woods, there is often a marked difference between heart- and sapwood. Unfortunately, no commonality exists; in certain woods the heartwood is more buffering, while the sapwood is more so in other trees. When wood buffering is a problem, it either retards or accelerates cure. In the latter case, premature reaction is undesirable if it occurs prior to complete bond consolidation because adhesive flow and penetration may be impaired.

Drying and Surface Aging

This wood-related variable has been touched on previously. The vast majority of wood is dried prior to use, and so there is always an opportunity for surface deactivation. Recall that excessive heating may reduce the wood surface energy to the point that adhesive wetting is harmed. Drying will always reduce wood surface energy below its maximum, which is achieved after machining. However, only severe thermal treatments result in bonding problems. The sensitivity to thermal deactivation is highly variable among different woods.

Common Wood Adhesives

Phenol-Formaldehyde (PF) Resins

Thermosets made from phenol and formaldehyde (PF) are the first synthetic polymers to have been commercialized, which occurred early in the twentieth century. Two classes of PF resins exist: novolaks and resols. Novolaks function under acid conditions, and also require addition of formaldehyde 'hardeners' to cure. Resols operate under alkaline (basic) conditions, and only heat is required for cure. Of resols and novolaks, it is the resols that are preferred in the forest products industry, most commonly in liquid form. They are also prepared as powders and supported films.

PF resols are commonly used for the manufacture of structural composites such as oriented strandboard (OSB), plywood, parallel strand lumber, and laminated veneer lumber, and for nonstructural composites like hardboard. PF resins are highly durable and are exterior grade, weather-resistant structural thermosets. PF formulations vary widely according to application, i.e., hardboard resins versus plywood resins. PF resols are moderately priced compared to other wood adhesives, but they are probably the least expensive exterior grade wood adhesive.

Since PF resols contain formaldehyde, there is minor concern about the potential health risks of formaldehyde emissions. However, this concern exists only during wood composite manufacture where some free formaldehyde may emit during hotpressing. Any formaldehyde within composite products dissipates rapidly, so long-term formaldehyde emission is absent in PF-bonded wood products.

Urea-Formaldehyde (UF) Resins

Wood-bonding thermosets made from urea and formaldehyde (UF) are the largest production-volume wood adhesives in the world. UF resins are used for interior applications as in the case of particleboard, medium density fiberboard or decorative plywood. In other words, UF resins are not hydrolytically stable; moisture exposure causes adhesive degradation. UF resins are highly versatile and may be synthesized and formulated in many ways for a vast array of applications. Most UF resins are used in water-based liquid form, but they may also be produced as powders and films. In addition to their excellent performance, UF resins are very inexpensive.

While liquid PF resols are stored under alkaline conditions, liquid UF resins are stored very near neutral conditions ($pH \sim 7$). Liquid UF resins require an acid catalyst which is added immediately prior to cure. UF resin formaldehyde emission has received great research attention and regulation. Atmospheric moisture causes a very slow decomposition of the cured resin that causes long-term formaldehyde emissions in products like particleboard. To its credit, the UF resin industry has drastically reduced formaldehyde emissions while maintaining excellent performance. Formaldehyde emissions are controlled by manipulating the formaldehyde : urea mole ratio. This is accomplished by blending resins made with different mole ratios, or by adding formaldehyde scavengers such as urea.

Melamine-Formaldehyde (MF) Resins

Resins made from melamine and formaldehyde (MF) are similar to UF resins; however, they are superior to UF resins in many respects. MF thermosets are more durable and emit less formaldehyde than UF resins.

MF resins are used to produce plywood and particleboard for exterior or semiexterior applications. Melamine is a very expensive chemical, and so MF resins are commonly prepared with urea (MUF resins) to reduce costs.

A distinguishing characteristic of MF resins is chemical inertness, as well as hardness, lack of porosity and nonabsorbency in the cured state. These traits have provided endless lamination applications for MF resins. For example, paper sheets are impregnated with liquid MF and subsequently dried to produce supported, nontacky films that may be stacked and thermoformed onto various substrates including wood-based panels. Consequently, MF resins are commonly used for low- and high-pressure paper laminates and overlays, producing durable tabletops, industrial bench tops, etc.

Polymeric Methylenediphenyldiisocyanate (pMDI) Resins

Polymeric methylene bis(phenylisocyanate) is commonly referred to as pMDI or MDI, or even just as 'isocyanate.' Its use as a wood binder is relatively recent, growing in importance over the past 30 years. pMDI is commonly used for particulate wood-based composites such as OSB and laminated strand lumber. It is a highly durable, exterior grade structural thermoset. While formaldehyde is used in its preparation, pMDI resin does not emit formaldehyde, not at all. pMDI is more acutely toxic than the adhesives mentioned above. However, very standard precautions allow the safe and routine use of this material.

In a sense, pMDI is a two-part adhesive where the second component is wood moisture. This resin polymerizes by reacting with wood moisture. pMDI is hydrophobic (water insoluble), and therefore moisture tolerant, or insensitive to the steam that forms during hotpressing. This important property explains why pMDI resins are the only wood binders used for steam injection hotpressing. This is the purposeful injection of steam during panel hot compression, accelerating heat transfer in very thick panels, and also providing other product benefits.

Another significant characteristic of pMDI resins is their tendency to adhere to metal surfaces. This causes unacceptable problems during wood-based composite manufacture because the platens will adhere to the panel surface. Release agents (low surface-energy surface active molecules) applied to the platens will prevent this problem. Alternatively, a common practice is to use PF resins in the 'surface layers' and pMDI in the 'core layer,' as in OSB manufacture.

Resorcinol-Formaldehyde (RF) and Phenol-Resorcinol-Formaldehyde (PRF) Resins

Resorcinol-formaldehyde (RF) resins are generally considered to be the most durable and best-performing structural thermosetting wood adhesives. They are not commonly used for the production of wood-based composites such as plywood and OSB because the resin is very expensive. Resorcinol is very costly, and this fact led to the related adhesive in which some of the resorcinol is replaced by the much cheaper phenol molecule, producing the PRF adhesive. Resorcinol is highly reactive and so RF and PRF adhesives are two-part cold-setting resins. Typically, the resorcinolic liquid resin is mixed with a formaldehyde hardener and polymerization begins immediately, followed by solidification in 30–180 min after mixing. These adhesives are particularly well suited for structural wood-bonding applications in which the bonded assembly is not conveniently hotpressed, as in finger-jointed lumber, large laminated timbers, and wood-based I-beams.

Two-Part Isocyanate Curing Latex Adhesives (Emulsion Polymer Isocyanate, EPI)

Emulsion polymer isocyanate (EPI) adhesives are commonly used for the secondary assembly of a vast array of forest products, examples including finger-jointed lumber, furniture and wood lamination. This adhesive has two parts: a water-based latex that visually resembles the common 'white glue,' and pMDI, as in the wood binder mentioned above. As with RF and PRF adhesives, EPI is a cold-setting system that must be applied soon after mixing the latex and pMDI components. EPIs are durable exterior-grade structural thermosets that provide excellent performance.

Poly(vinyl Acetate) Latex (PVA)

Poly(vinyl acetate) latex (PVA) is a nonstructural thermoplastic latex adhesive which is familiar to many as the ubiquitous 'white glue.' PVA technology is extremely versatile because it is prepared in many ways and with a wide variety of monomers besides its namesake, vinyl acetate. PVA adhesives are commonly used for the assembly of many wood products such as furniture, window and door frames, and decorative panels. These waterborne adhesives are not weather durable; however, a common formulation includes comonomers and other additives that provide crosslinking. These more durable systems are referred to as crosslinking-PVAs. The crosslinking-PVAs also serve more demanding industrial applications where additional crosslinking is achieved by adding catalysts.

See also: **Non-wood Products**: Chemicals from Wood. **Papermaking**: Paper Raw Materials and Technology. **Solid Wood Products**: Glued Structural Members; Wood-based Composites and Panel Products. **Wood Formation and Properties**: Chemical Properties of Wood; Formation and Structure of Wood; Physical Properties of Wood. **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

Kendall K (2001) *Molecular Adhesion and Its Applications: The Sticky Universe*. New York: Plenum Press.

Kinloch AJ (1987) *Adhesion and Adhesives, Science and Technology*. London: Chapman & Hall.

Marra AA (1992) *Technology of Wood Bonding: Principles in Practice*. New York: Van Nostrand Reinhold.

Pizzi A (1994) *Advanced Wood Adhesives Technology*. New York: Marcel Dekker.

Pizzi A and Mittal KL (2003) *Handbook of Adhesive Technology*, 2nd edn. New York: Marcel Dekker.

Vick CB (1999) Adhesive bonding of wood materials. In: United States Department of Agriculture Forest Service, Forest Products Laboratory (eds) *Wood Handbook: Wood as an Engineering Material*, pp. 1–24. Madison, WI: US Department of Agriculture Forest Service.

Chemical Modification

R M Rowell, University of Wisconsin–Madison, Madison, WI, USA

Introduction

Wood is a hygroscopic resource that was designed to perform, in nature, in a wet environment. Nature is programmed to recycle wood in a timely way through biological, thermal, aqueous, photochemical, chemical, and mechanical degradations. In simple terms, nature builds wood from carbon dioxide and water and has all the tools to recycle it back to the starting chemicals. We harvest a green tree and convert it into dry products, and nature, with its arsenal of degrading reactions, starts to reclaim it at its first opportunity.

The properties of any resource are, in general, a result of the chemistry of the components of that resource. In the case of wood, the cell wall polymers (cellulose, hemicelluloses, and lignin) are the components that, if modified, would change the properties of the resource. If the properties of wood are modified, the performance of wood will be changed. This is the basis of chemical modification of wood to change properties and improve performance.

Wood changes dimensions with changing moisture content because the cell wall polymers contain hydroxyl and other oxygen-containing groups that attract moisture through hydrogen bonding. The hemicelluloses are mainly responsible for moisture sorption, but the accessible cellulose, noncrystalline cellulose, lignin, and the surface of crystalline cellulose also play major roles. Moisture swells the cell wall, and the fiber expands until the cell wall is saturated with water (fiber saturation point, FSP). Beyond this saturation point, moisture exists as free water in the void structure and does not contribute to further expansion. This process is reversible, and the fiber shrinks as it loses moisture below the FSP. The swelling pressures exerted when wood swells due to the uptake of water are very large. Stamm estimated these forces to be approximately 24 000 psi (165 MPa) but could only measure a swelling force of 12 000 psi (82.7 MPa). The ancient Egyptians split their large granite stones using the swelling forces of wood. They would chip rectangular holes (approximately 7×15 cm and 10 cm deep) into the rock the desired distance from the face of the mountain. They would then drive dry wooden stakes into the holes and wet them with water. The swelling forces would then split the granite stone from the face of the mountain.

Wood is degraded biologically because organisms recognize the carbohydrate polymers (mainly the hemicelluloses) in the cell wall and have very specific enzyme systems capable of hydrolyzing these polymers into digestible units. Biodegradation of the cell wall matrix and the high molecular weight cellulose weakens the fiber cell. Strength is lost as the cell wall polymers and matrix undergo degradation through oxidation, hydrolysis, and dehydration reactions.

Wood exposed outdoors undergoes photochemical degradation caused by ultraviolet radiation. This degradation takes place primarily in the lignin component, which is responsible for the characteristic color changes. The lignin acts as an adhesive in the cell walls, holding the cellulose fibers together. The surface becomes richer in cellulose content as the lignin degrades. In comparison to lignin, cellulose is much less susceptible to ultraviolet light degradation. After the lignin has been degraded, the poorly bonded carbohydrate-rich fibers erode easily from the surface, which exposes new lignin to further degradative reactions. In time, this 'weathering' process causes the surface of the composite to become rough and can account for a significant loss in surface fibers.

Wood burns because the cell wall polymers undergo reactions with increasing temperature to give off volatile, flammable gases. The hemicellulose and cellulose polymers are degraded by heat much before the lignin. The lignin component contributes to char formation, and the charred layer helps insulate the material from further thermal degradation.

This article discusses the concept of chemically modifying wood and then briefly reviews three types of treatments, monomer–polymer treatments, surface impregnation, and heat treatment for accomplishing chemical modification. The subject of cell wall bonded chemical modification is covered in more detail because of the large amount of interest in this subject. Typical uses for each of these modification technologies are also covered.

Chemical Modification

The term 'chemical modification' has been used to mean different things by different authors over the years. Here chemical modification will be defined as a chemical reaction between some reactive part of a lignocellulosic cell wall polymer and a simple single chemical reagent, with or without catalyst, to form a covalent bond between the two. This excludes chemical impregnation treatments (such as simple dip or pressure treatments with wood preservatives or fire retardants, or stains or penetrating oils), which do not form covalent bonds, monomer impregnation that polymerize *in situ* but do not bond with the cell wall, polymer inclusions, coatings (such as paints, varnishes, urethanes), or heat treatments. Wood finishes, preservatives, and adhesives are covered elsewhere (*see* **Solid Wood Processing**: Adhesion and Adhesives; Finishing; Protection of Wood against Biodeterioration). Other treatments that modify wood properties without bonding in the cell wall are described briefly. Many wood-based composites can be easily chemically modified (*see* **Solid Wood Products**: Wood-based Composites and Panel Products).

Monomer–Polymer Treatments

The objective of the monomer–polymer treatments is to produce a product with greatly enhanced physical properties. A monomer, such as an acrylic derivative dissolved in a suitable solvent, is impregnated into wood using a vacuum-pressure cycle. In most systems used today, the treating solution contains both a crosslinking agent and a catalyst. After treating with this solution, the treated wood is heated to a temperature where the catalyst becomes active and polymerization, *in situ*, takes place. In most cases, the polymer is located in the cell lumen but in cases (such as phenol-formaldehyde systems) where cell wall penetration takes place by the monomer, some of the polymer may reside in the cell wall. The final wood polymer composite (WPC) is much harder than the untreated wood and is mainly used as flooring where heavy wear is anticipated. A fire retardant can also be incorporated into the treating solution mixture to add fire retardance to the product as long as the fire retardant chemicals do not interfere with the polymerization.

Surface Impregnation

In the case of surface impregnation technology, this involves the treatment of wood with polymers that are too large to penetrate very far into the wood structure. This type of treatment is mainly done with epoxy resins that increase surface hardness and can also act as an adhesive. This technology is being used to make cold-molded boat hulls and in the preservation of degraded historical wooden objects. The object is treated with a diluted solution of the polymer (or in some cases, with an undiluted liquid polymer directly) where some surface penetration occurs.

Heat Treatment

In the heat treatments, the objective is to heat the wood to increase dimensional stability and moisture resistance. The mechanisms of the increased dimensional stability and reduced hygroscopicity achieved from high temperature treatment of wood may be a combination of one or more factors. These include:

1. Degradation of the hygroscopic hemicelluloses to form soluble sugars which may undergo reversion reactions to form less hygroscopic, highly branched polysaccharides.
2. Degradation of the hemicelluloses to form free sugars which, in turn, form furan intermediates that can undergo polymerization during hot-pressing resulting in the formation of an adhesive.
3. Thermal softening of the cell wall matrix, mainly lignin, to allow reformation of a new less stressed matrix after pressing.
4. Degradation of the hygroscopic hemicelluloses to form volatile break down products that are lost during hot-pressing.
5. Crosslinking between carbohydrate polymers and/or between lignin and carbohydrate polymers.
6. Densification of the wood resulting in a reduction of pore size and void volume which restricts the flow of moisture back into the pressed wood.
7. High temperature compression to increase cellulose crystallinity.

The temperature of treatment and the presence of oxygen are critical as heating at too high a temperature can cause great strength losses especially in the presence of oxygen. This technology is now being applied for both solid wood and wood composites. Heating wood fiber in a closed heated press, for example, at 200°C for 8 min, results in a fiberboard with an 80% reduction in dimensional instability.

Cell Wall Bonded Chemical Modification

For cell wall bonded chemical modification the chemicals to be used must be capable of reacting with wood cell wall hydroxyls under neutral, mildly alkaline or acid conditions at temperatures below 170°C. The chemical system should be simple and capable of swelling the structure to facilitate penetration. The complete molecule should react quickly with wood components yielding stable chemical bonds, and the treated wood must still possess the desirable properties of untreated wood. Many chemical reaction systems have been published for the modification of various agrofibers and these systems have been reviewed in the literature several times in the past. These chemicals include anhydrides such as phthalic, succinic, malaic, propionic and butyric anhydride, acid chlorides, ketene carboxylic acids, many different types of isocyanates, formaldehyde, acetaldehyde, difunctional aldehydes, chloral, phthaldehydic acid, dimethyl sulfate, alkyl chlorides, β-propiolactone, acrylonitrile, epoxides, such as, ethylene, propylene, and butylene oxide, and difunctional epoxides (see **Table 1**).

Acetylation Chemistry

While there has been much research on many different chemical reaction systems, the most research and interest, both in the past and the present, has been in the reaction of acetic anhydride with cell wall polymer hydroxyl groups to give an acetylated wood. The acetylation process has been applied to solid wood, veneers, and many different types of wood composites. For this reason, the acetylation of wood using new acetylation technology is reviewed in detail here. Application of this technology has mainly been considered for improving both dimensional stability and decay resistance.

The reaction of acetic anhydride with cell wall polymer hydroxyl groups is shown below. The anhydride reacts to form an ester with the wood hydroxyl group and the reminder of the molecule results in byproduct acetic acid.

$$\text{Cell Wall-OH} + CH_3C(=O) - O - C(=O) - CH_3 \rightarrow \text{Cell Wall} - O - C(=O) - CH_3 + CH_3C(=O) - OH$$

Properties of Acetylated Solid Wood

As the level of acetyl weight gain increases, the equilibrium moisture content (EMC) and FSP of control and acetylated pine and aspen goes down and the dimensional stability, as measured by antishrink efficiency (ASE), as calculated below, goes up.

$$S = \frac{V_2 - V_1}{V_1}$$

where S is volumetric swelling coefficient, V_1 is wood volume after wetting with liquid water, and V_2 is wood volume of ovendried wood before wetting.

Then:

$$\text{ASE} = \frac{S_2 - S_1}{S_1} \times 100$$

where ASE is antishrink efficiency resulting from a chemical modification, S_2 is reacted wood volumetric

Table 1 Dimensional stability and resistance to decay with a brown-rot and white-rot fungi achieved by various chemical reaction systems on pine wood

Chemical	*Weight percent gain (WPG) (%)*	*Antishrink efficiency (ASE) (%)*	*Weight loss after 12 weeks fungal test*	
			Brown-rot[a]	*White-rot*[b]
None	0	—	57.8	39.6
Methyl isocyanate	25	65	1.7	1.0
Butyl isocyanate	25	70	>3	>1
Acetic anhydride	20	75	>2	>1
Propylene oxide	28	65	32.8	4.8
Butylene oxide	25	70	2.0	1.8
Acrylonitrile	25	50	—	—
β-Propiolactone	30	60	—	—
Formaldehyde	10	85	>3	>2

[a] Brown-rot fungus: *Gloephyllum trabeum*.
[b] White-rot fungus: *Trametes versicolor*.

swelling coefficient, and S_1 is unreacted wood volumetric swelling coefficient.

Solid acetylated wood has been tested for resistance to several different types of organisms. In a 2-week termite test using subterranean termites (*Reticulitermes flavipes*), boards acetylated at 16 to 17 weight percent gain (WPG) were very resistant to attack, but not completely so. Control and acetylated pine were exposed to a 12-week soil block test using the brown-rot fungus *Gloeophyllum trabeum* and the white-rot fungus *Trametes versicolor*. All of the acetylated boards at a WPG over about 17 show good resistance to brown- and white-rot fungi.

Acetylated Composites

Wood veneers, chips, particles, and fibers can also be acetylated using the same chemistry. These acetylated materials can be formed into plywood, chipboard, particleboard, or fiberboard. Fibers, for example, can be formed into flexible fiber mats, which can be made by physical entanglement (carding), nonwoven needling, or thermoplastic fiber melt matrix technologies. In carding, the fibers are combed, mixed, and physically entangled into a felted mat. These are usually of high density but can be made at almost any density. A needle-punched mat is produced in a machine, which passes a randomly formed machine-made web through a needle board that produces a mat in which the fibers are mechanically entangled. The density of this type of mat can be controlled by the amount of fiber going through the needle board or by overlapping needled mats to give the desired density. In the thermoplastic fiber matrix, agricultural fibers can be held in the mat using a thermally softened thermoplastic fiber such as polypropylene or polyethylene.

These acetylated mats can then be used as geotextiles, oil sorbents, or filters, or can have an adhesive added and be formed into molded products. If a thermosetting resin is used, the composites can be used for structural applications. If the acetylated fiber is mixed with a thermoplastic, then the composites can be thermomolded into a large variety of shapes for nonstructural applications. Composites made from acetylated fiber have many of the same properties of solid wood, i.e., increased dimensional stability and improved biological resistance.

Thickness swelling and linear expansion at various levels of relative humidity are greatly reduced as a result of acetylation. Increasing the adhesive content can reduce the thickness swelling but not to the extent that acetylation does.

Biological resistance has also been demonstrated with acetylated composites using brown-, white-, and soft-rot fungi and tunneling bacteria in a fungal cellar. Nonacetylated (i.e., control) flakeboards were destroyed in less than 6 months while flakeboards made from acetylated flakes above 16 WPG showed no attack after 1 year. These data show that no attack occurs until swelling of the wood occurs. This is evidence that moisture content of the cell wall is critical before attack can take place. This fungal cellar test was continued for an additional 5 years with no attack at 17.9 WPG.

Table 2 Modulus of rupture (MOR), modulus of elasticity (MOE), and internal bond strength (IBS) of fiberboards made from control and acetylated pine fiber (10% phenolic resin)

Weight percent gain	*MOR (MPa)*	*MOE (GPa)*	*IBS (MPa)*
0	53	3.7	2.3
19.6	61	4.1	2.3
ANSI standard	31	—	—

Data from Simonson R and Rowell RM (2000) A new process for the continuous acetylation of lignocellulosic fiber. In: Evans PD (ed.) *Proceedings of the Fifth Pacific Rim Bio-Based Composite Symposium*, pp. 190–196. Canberra, Australia.

Table 2 shows data on strength properties of fiberboards made from both control and acetylated fiber. The board made from acetylated fiber has a higher modulus of rupture (MOR), modulus of elasticity (MOE), and equal internal bond strength (IBS) as compared to control boards.

Commercialization of Acetylated Wood Materials

In spite of the vast amount of research on the acetylation of both solid wood and wood composites, commercialization has been slow in coming. Two attempts, one in the USA and one in Russia, came close to commercialization but were discontinued presumably because they were not cost-effective. There are reports of a commercial acetylation plant for solid wood in Japan and a pilot plant for solid wood in the Netherlands but few details are available.

Two new processes are presently under way in Sweden to commercialize the acetylation of wood. One is a fiber process and the second a process to acetylate wood of large dimensions using microwave technology.

The Fiber Process

There is a pilot plant in Sweden with a capacity of approximately 4000 tonnes year^{-1} of acetylated fiber. **Figure 1** shows the schematic of the new continuous fiber acetylation process. The fiber is first dried in an optional dryer section to reduce the moisture content to as low a moisture content as is economically feasible realizing that the anhydride will react with water to form acetic acid and that a certain amount of acetic acid is needed to swell the fiber wall for chemical access.

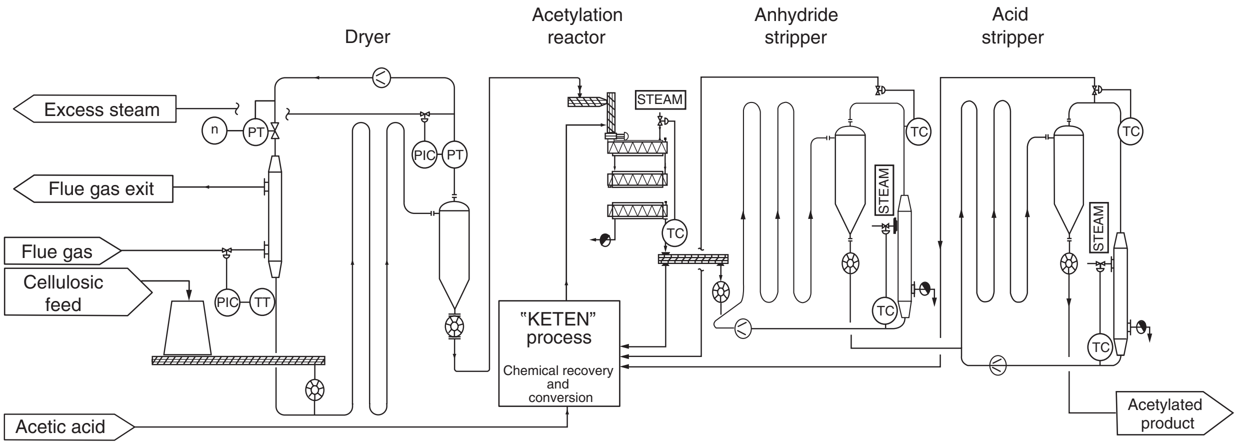


Figure 1 Schematic of the new fiber acetylation process. Reproduced with permission from Simonson R and Rowell RM (2000) A new process for the continuous acetylation of lignocellulosic fiber. In: Evans PD (ed.) *Proceedings of the Fifth Pacific Rim Bio-Based Composite Symposium*, pp. 190–196. Canberra, Australia.

The dried fiber is then introduced, by a screw feeder, into the reactor section and the acetylating agent is added. The temperature in this section is within the range of 110–140°C so the acetylating agent is in the form of a vapor/liquid mixture. Back flow of the acetylating agent is prevented by a fiber plug formed in the screw feeder. A screw-conveyor or similar device is used to move the material through the reactor and to mix the fiber–reagent mixture. During the acetylation reaction, which is exothermic, the reaction temperature can be maintained substantially constant by several conventional methods. The contact time in the reactor section is 6–30 min. The bulk of the acetylation reaction takes place in this first reactor.

The resultant acetylated fiber from the first reactor contains excess acetylating agent and forms acetic acid as it is fed by a star feeder into the second reactor, designed as a long tube and working as an anhydride stripper. The fiber is transported through the stripper by a stream of superheated vapor of anhydride and acetic acid. The temperature in the stripper is preferably in the range of 185–195°C. The primary function of this second step is to reduce the content of the unreacted acetylating medium remaining in the fiber emerging from the first reactor. An additional acetylation of the fiber is, however, also achieved in this step. The residence in this step is relatively short and normally less than 1 min. After the second reactor (stripper), superheated vapor and fiber are separated in a cyclone and part of the superheated vapor is recirculated after heating to the stripper fiber inlet and part is transferred to the system for chemical recovery.

The acetylated fiber from the second reactor may still contain some anhydride and acetic acid that is sorbed or occluded in the fiber. In order to remove remaining chemicals and the odor from them, the acetylated fiber is introduced into a second stripper step also acting as a hydrolysis step. The transporting medium in this step is superheated steam, and any remaining anhydride is rapidly hydrolyzed to acetic acid, which is evaporated. The acetylated fiber emerging from the second stripper is essentially odor-free and is completely dry. The acetylated fiber can as a final treatment be resinated for fiberboard production or conditioned and baled for other uses as desired. The steam and acetic acid removed overhead from this step is processed in the chemical recovery step.

The preferred recovery of chemicals includes separation of acetic anhydride from acetic acid by distillation, and conversion of acetic acid, recovered as well as purchased, by the ketene process into anhydride. The raw materials entering the production site is thus fiber and acetic acid to cover the acetyl groups introduced in the fiber. This minimizes the transportation costs and the chemical costs and makes the process much more cost effective.

The plant was built during the spring of 2000, taken apart, and reassembled in Kvarntorp, Sweden in the summer. The designated production rate is 500 kg h^{-1} or 12 tonnes day^{-1} or about 4000 tonnes - $year^{-1}$ of acetylated wood fiber. The process can be applied to any lignocellulosic fiber and fibers other than wood will be used.

Solid Wood Microwave Process

Microwave energy has been shown to heat acetic anhydride and acetic anhydride impregnated wood. The absorption of microwave energy in acetic anhydride impregnated wood is preferred over other methods of heating since it heats less of the wood, provides some self-regulation of the overall temperature rise, and promotes a more uniform heating pattern. Acetic anhydride is supplied to the reactor, under vacuum, then a pressure is applied for a short time, and then another vacuum step to remove excess anhydride is used. Microwave energy is then applied to heat the anhydride soaked wood.

The penetration depth of the microwaves at 2450 MHz is approximately 10 cm, which means this technology can be used to acetylate large wood members. The variation in acetyl content, both within and between samples, is less than 2%. Microwave energy can also be used to remove the excess acetic anhydride and by-product acetic acid after acetylation.

One of the concerns about the acetylation of lignocellulosics, using acetic anhydride as the reagent, has been the by-product acetic acid. Many attempts have been made for the 'complete removal' of the acid to eliminate the smell, make the process more cost effective, and to remove a chemical potentially causing ester hydrolysis. Complete removal of by-product acetic acid has now been achieved in both the fiber process and the solid wood microwave process.

See also: **Solid Wood Processing**: Adhesion and Adhesives; Finishing; Protection of Wood against Biodeterioration; Wood-based Composites and Panel Products. **Wood Formation and Properties**: Chemical Properties of Wood; Formation and Structure of Wood.

Further Reading

Larsson Brelid P, Simonson R, and Risman PO (1999) Acetylation of solid wood using microwave heating. *Holz als Roh- und Werkstoff* 57: 259–263.

Rowell RM (1983) Chemical modification of wood: a review. *Commonwealth Forestry Bureau, Oxford, England* 6(12): 363–382.

Rowell RM (1984) *The Chemistry of Solid Wood*. Advances in Chemistry Series no. 207. Washington, DC: American Chemical Society.

Rowell RM, Young RA, and Rowell JK (1996) *Paper and Composites from Agro-Based Resources*. Boca Raton, FL: CRC Press.

Stamm AJ (1964) *Wood and Cellulose Science*. New York: Ronald Press.

Protection of Wood against Biodeterioration

T P Schultz and D D Nicholas, Mississippi State University, MS, USA

Introduction

Wood and wood composites are degraded by many organisms, including brown, white and soft rot fungi, termites and other insects, bacteria, and marine borers. Traditionally, the wood protection industry has relied on a few preservatives which have a broad range of activity, with cost and efficacy being the major considerations. However, governmental regulations, public perceptions, and environmental and disposal issues have resulted in rapid and profound changes. Further compounding the difficulty for industry is the relatively low market value for wood-preserving biocides, about US$200 million in direct sales annually worldwide in 2000, two-thirds of that in North America. Other problems are that the cost of the biocide is only a small fraction of the total value of the treated wood product, but biocide failure will entail replacement of the entire product (i.e., the biocide has a relatively low value but carries a high liability potential), and the long service life expected of treated wood products.

Biocides

Wood can be colonized and degraded by a variety of organisms. In addition, a preservative must be effective for many years during which the biocide level can be reduced by leaching, evaporation, and/or degradation. Thus, biocides for preservatives must be thoroughly tested by lengthy outdoor exposure. Even after years of testing and commercial use, unforeseen problems may arise. Also important is the biocide level required to protect wood adequately for a particular application and location. Warm and moist climates generally have greater decay and/or insect hazard than cool and/or dry locations and, thus, require higher biocide levels. Generally, biocide levels vary for different applications such as above-ground, ground-contact/residential, ground-contact/industrial, and marine exposure. For example, retentions for chromated copper arsenate (CCA) treated southern pine wood in the United States are 4.0, 6.4, 9.6 or 12.8, and 24 or 40 $kg\,m^{-3}$ for the above applications, respectively.

All biocides must be registered with the appropriate governmental agency which ensures that all products are safe; in the United States the agency is the Environmental Protection Agency (EPA) under the Federal Insecticide, Fungicide and Rodenticide Act, with other possible additional requirements by individual state agencies. Other countries have similar agencies and requirements. Use of a registered bioactive compound still carries some inherent health risk, however. To register a compound, a company must conduct extensive testing on the toxicological and other health effects, environmental fate, etc. Once registered the company then develops a 'label' which, after acceptance by the appropriate regulatory agency, clearly lists the specific applications and quantifies the amounts for which the formulated biocide product can be legally used; use of a registered biocide for any nonlabeled application is not permitted. Additional nonlabeled applications for a registered compound can be proposed following further testing, termed supplemental labeling or label expansion.

The 'traditional' wood preservatives are creosote oil, oilborne pentachlorophenol (penta), and waterborne arsenicals. These three systems effectively and economically control many of the fungi, insects, and marine borers that attack wood. Arsenicals, principally CCA, currently are, or were, the major preservatives in many countries. For example, in 1997 CCA was used for about 80% of all wood treated in the United States. However, recent public concerns about arsenic have led to restrictions that will reduce CCA usage by about 70% in the United States as CCA is delabeled (no longer approved) for residential applications by 2004. Most European countries have already limited or totally banned CCA with further restrictions likely, and Japan has almost entirely converted to preservatives without arsenic or chromium. Use of alternative copper : organic systems is expanding, but these copper-rich second-generation systems may also be restricted in the future with totally organic preservatives mandated; this trend is already apparent in some European countries.

Commercial Wood Preservatives

Biocides that are commercially used at this time to protect wood are discussed below and shown in **Table 1**, starting with the three traditional systems and then listing the 'newer' systems alphabetically, with potential biocides then discussed and shown in **Table 2**.

Chromated copper arsenate/arsenicals Of the arsenicals, CCA is unquestionably the principal wood preservative in many countries. CCA is very effective, economical, dependable, waterborne and leaves lumber with a clean and nonoily surface. Thus, CCA usage has greatly increased in the past 30 years, especially for residential applications. About 75 000 tonnes (oxide basis) was consumed in 2000 in North America and about 15 000 tonnes in Europe, but

Table 2 Biocides with the potential to protect wood, pending further development

Common name	*Chemical name*
Chlorothalonil	2,4,5,6-Tetrachloroisophthalonitrile
CDDC	Copper(II) mono(dimethyldithiocarbamate)
Dichlofluanid, DCFN	1,1-Dichloro-*N*-[(dimethylamino) sulfonyl]-1-fluoro-*N*-phenylmethanesulfenamide
Imidacloprid	1-[(6-chloro-3-pyridinyl) methyl]-*N*-nitro-2-imidazolidinimine
Fipronil	5-Amino-1-[2,6-dichloro-4-(trifluoromethyl)phenyl]-4-[(trifluoromethyl)sulfinyl]-1*H*-pyrazole-3-carbonitrile
Kathon 930™	4,5-Dichloro-2-n-octyl-4-isothiazolin-3-one
PXTS	Polymeric xylenol tetrasulfide
TCMTB, Busan 30™	2-(Thiocyanomethylthio) benzothiazole

Table 1 Biocides and biocide combinations used commercially as wood preservatives

Common name(s)	*Chemical name*
Arsenicals (CCA)[a]	Chromated copper arsenate, CuO, CrO_3, As_2O_5
Creosote	Creosote, Coal tar distillate
Penta, PCP	Pentachlorophenol
Azoles (Tebuconazole)[a]	(3*RS*)-5-(4-chlorophenyl)-2, 2-dimethylethyl-3-1*H*-[1,2,4-triazole)methyl]-3-pentanol
Borates, Timbor™, DOT	Disodium octaborate tetrahydrate
Copper/chromium systems (CCB)[a]	Chromated copper borate, CrO_3, CuO, $B(OH)_3$
Copper azole, CA, CBA	Copper(II) + tebuconazole + [boron]
Cu-HDO	Copper(II) bis-*N*-cyclohexyldiazeniumdioxy + CuO + boric acid
Copper citrate, CC	Ammoniacal copper(II) citrate
Copper quats, ACQ	Alkaline copper(II) quats, CuO + quats
Oxine copper, copper-8	(bis)Copper-8-quinolinolate
Copper naphthenate	Copper(II) naphthenate
IPBC, Polyphase™	3-Iodo-2-propynlbutyl carbamate
Quats (DDAC)[a]	Quaternary ammonium compounds (didecyldimethylammonium chloride)
Synthetic pyrethroids (Permethrin)[a]	Cyclopropanecarboxylic acid, 3-(2,2- dichloroethenyl)-2, 2-dimethyl-(3-phenoxyphenyl) methyl ester
TBTO	Tributyltin oxide
Zinc borate	Boric acid + zinc salt, 2 : 3

[a] A class of compounds, of which several individual compounds are used to protect wood. An example of one compound is shown.

usage will shortly be dramatically lower. Formulations with different ratios of chromium, copper, and arsenic are available; in the United States CCA-type C is used which contains 18.5% copper (as CuO), 47.5% chromium (as CrO_3), and 34.0% arsenic (as As_2O_5). CCA is effective against a wide variety of wood-consuming fungi, insects, and marine borers, but ineffective against the small fraction of insects, marine borers, and stain/mold fungi that inhabit but do not consume wood as a food source. Waterborne, CCA becomes fixed by a complex series of redox, complexing and precipitation reactions with wood and, once fixed, resists leaching. CCA-treated softwoods perform extremely well, but CCA-treated hardwoods can sometimes fail due to poor microdistribution. Another arsenical preservative is ammoniacal copper zinc arsenate (ACZA). ACZA is limited to treating refractory (difficult to treat) species, such as those present in western North America where the alkaline solution provides better penetration, but it is not as highly fixed as CCA.

Creosote Creosote is a preservative oil that has been used for more than 150 years. It is a coal tar distillation product, and is mainly composed of a complex mixture of polyaromatic hydrocarbons. It is sometimes combined with coal tar, especially for marine systems. Creosote is a thick black tar which is generally heated prior to impregnation into the wood. It is effective against a variety of wood-colonizing organisms and used to treat railroad ties, utility poles, and pilings, accounting for about 10% of the treated wood volume in North America. Recent concerns over possible mutagenic properties have reduced usage in some countries. A pigmented and emulsified formulation (PEC) is available in Australia, but treatment problems have arisen and interest has waned. An emulsion system is being examined in Europe.

Pentachlorophenol Pentachlorophenol (penta, PCP) is effective against a variety of wood-destroying organisms and stain and mold fungi, is inexpensive and readily soluble in hydrocarbons. Thus, penta has replaced creosote in many industrial applications. However, due to environmental concerns many countries have reduced or banned penta. It is currently used in about 10% of all treated wood in North America, primarily for utility poles. It can be formulated with a variety of heavy or light organic solvents, and salt and emulsion water-based systems are also possible. Poor performance can occur with some light solvent, emulsion, and salt-based systems because of inadequate distribution and/or leaching.

Azoles The azoles, or more properly triazoles, include cyproconazole (1*H*-1,2,4-triazole-1-ethanol, α-(4-chlorophenyl)-α-(1-cyclopropylethyl)), propiconazole ((2*RS*, 4*RS*)-2-(2,4-dichlorophenyl)-2-[1-1*H*-(1,2,4-triazole)methyl]-4-propyl-1,3-diaxolane), and tebuconazole ((3*RS*)-5-(4-chlorophenyl)-2,2-dimethylethyl-3-(1*H*-[1,2,4-triazole]methyl)-3-pentanol). They are highly active against wood-decaying fungi, readily soluble in hydrocarbon solvents, and exhibit good stability and leach resistance in wood. Although azoles are expensive, their high activity makes them relatively cost effective. Disadvantages include minimal or no activity against sapstains, molds, and insects/termites. Thus, azoles are usually combined with other fungicides and/or termiticides. Copper azoles (CA), and other commercial preservatives in Europe based on an azole combined with another biocide, are discussed below.

Borates Borates (borax, boric acid, disodium octaborate tetrahydrate (DOT), sodium borate) are inorganic boron-based biocides, generally formulated as a mixture of borax and boric acid. Borates have extremely low toxicity to mammals and a broad range of activity against decay fungi and insects, and are inexpensive and readily soluble in water. However, water solubility limits applications to those with minimal or no leaching exposure. Borates are used as a sole biocide in many countries. Borates are also a component in some newer nonarsenical copper : organic systems, but the boron is highly susceptible to leaching. Borates are also used as a diffusible biocide for the remedial treatment of millwork and related applications in many countries. Studies examined treating wood by a vapor process with trimethyl borate, which then reacts with the residual water in lumber to form boric acid. Several groups have examined compounds which form complexes with borates, or the use of water repellents, to reduce leaching.

Copper/chromium systems Chromated copper borate (CCB) and related copper/chromium systems are used in Europe, but environmental concerns may limit future applications of these systems. In the United States acid copper chromate (ACC) is listed in the American Wood-Preservers' Association (AWPA) Standards and, while not commercially used for some time, is being reconsidered. However, ACC is weak against copper-tolerant fungi and future disposal might be regulated.

Copper azole Copper azole, either with (CBA) or without added boron (CA), consists of the biocides copper(II), boron, and tebuconazole (or propiconazole). CBA is one of the newer nonarsenical water-based preservatives for aboveground and ground-contact applications in Europe, the United States, and Asia. CBA is listed in the AWPA Standards as CBA-type A, with a copper : boric acid : tebuconazole composition of 49 : 49 : 2. A modified formulation without boron (CA-type B) has just been introduced in the United States. CAs are formulated with relatively expensive ethanolamine to minimize metal corrosion at treating facilities and improve penetration and distribution of the biocide within wood.

Cu-HDO The copper bis-(*N*-cyclohexyldiazeniumdioxy) system (Cu-HDO, CX) consists of the biocides Cu-HDO, additional uncomplexed copper (II), and boron. The Cu-HDO portion exhibits good stability, but the borate component can quickly leach and the uncomplexed copper is also subject to some leaching. A water-based Cu-HDO standard has just been developed by the AWPA for aboveground applications, CX-type A, and which may be available once Cu-HDO is registered by the EPA. It is formulated with an organic amine having 93.6% of the copper as copper(II) carbonate and the remaining 6.4% copper as Cu-HDO, with a CuO : boric acid : HDO ratio of 4.38 : 1.75 : 1. A similar product is one of the major preservatives in Europe for aboveground and ground-contact applications.

Copper citrate Copper citrate (ammoniacal copper citrate (CC)) is formed by the combination of copper and citric acid. It is effective against most wood-destroying fungi and insects but weak against copper-tolerant fungi and susceptible to copper leaching. Thus, CC may be best suited for aboveground applications. Only small amounts are available in North America.

Copper quaternary ammonium compounds Copper quats (alkaline copper quat (ACQ), amine copper quat, ammoniacal copper quat) combine the biocides copper(II) and one of the quaternary ammonium compounds (quats) discussed below, usually with a CuO : quat ratio of 2 : 1. These are formulated in aqueous solutions using ammonia or a relatively expensive organic amine. Three types of ACQ are available in North America, with various formulations and types of quat. ACQ has been available in the United States and Australia for about 10 years and even longer in Europe and Japan. ACQ may soon be one of the major preservatives in North America.

Oxine copper (Bis)-copper-8-quinolinolate (oxine copper, copper-8, Cu-8) is an organometallic with very low acute toxicity to mammals, excellent stability and leach resistance, broad activity against decay fungi and insects, and has been used for minor applications for over 30 years. It is insoluble in water and most organic solvents and thus difficult to formulate. An oil-soluble formulation uses relatively expensive nickel-2-ethylhexoate as a cosolvent. A water-soluble form is made with dodecylbenzene sulfonic acid, but the solution is highly corrosive to metals. Cu-8 is currently the only biocide listed in the AWPA Standards for treating wood that comes in contact with foodstuffs. A small volume of Cu-8 is used in the United States for aboveground applications and for sapstain and mold control, and minor amounts are sold as a brush-on preservative. The mono form of Cu-8 is being studied.

Copper naphthenate Copper naphthenate is an organometallic biocide made by combining copper (II) with naphthenatic acid mixtures. Copper naphthenate is relatively low cost and has been used for over 50 years for various applications in North America, including treating wood during World War II. It has low toxicity to mammals, broad activity against decay fungi and insects, is readily soluble in hydrocarbons, and has good stability and leach resistance. Since the 1990s some utility poles have been treated with copper naphthenate in North America. Another commercial product used in several countries is the combination of copper naphthenate, borate, water, and a thickening agent, with the mixture applied as a remedial ground treatment to utility poles followed by a tarpaper or plastic wrap. Small amounts of copper naphthenate are also sold over the counter to homeowners. Copper naphthenate imparts a green color to wood; for applications where color is objectionable the slightly less effective zinc naphthenate can be used. A water-based system is available in North America for brush-on (nonpressure) applications, and may be available soon for pressure treating.

Polyphase™ 3-Iodo-2-propynylbutyl carbamate (IPBC, Polyphase™) is an organic biocide with low toxicity to mammals, is readily soluble in hydrocarbon solvents, has a broad range of activity against decay and mold fungi, but has no activity against insects and may be slowly degraded. In the United States, as a sole biocide IPBC is currently used for millwork-type applications, and IPBC was combined with the insecticide chlorpyrifos as an oilborne treatment for aboveground beams, etc. A formulation containing IPBC, propiconazole, and tebuconazole has recently been introduced as a millwork preservative in the US. In Europe many combinations of IPBC and propiconazole, or IPBC, propiconazole and tebuconazole, solvent- or waterborne, are used in aboveground applications. IPBC is the active ingredient in many brush-on systems sold in North America, and the combination of IPBC and DDAC is used for sapstain and mold control.

Quaternary ammonium compounds Several quaternary ammonium compounds (quats) are available, including didecyldimethylammonium chloride (DDAC, Bardac 22^{TM}) and other similar dialkydimethylammonium chlorides with C_8–C_{14} alkyls, and the alkyldimethylbenzyl ammonium chlorides (alkyl benzyldimethylammonium chlorides, benzalkonium chlorides, ABACs, ADBACs), usually sold as a mixture with C_{12}–C_{18} alkyl groups. The quats have very low toxicity to mammals, are relatively inexpensive, have broad activity against decay fungi and insects, are soluble in both water and hydrocarbon solvents, and exhibit excellent stability and leach resistance due to ion exchange fixation reactions with wood. However, their efficacy is only moderate and when used alone may not be adequate. Another disadvantage is that quats, as surfactants, make exposed wood wet more easily. Due to their surfactant properties and low cost quats are often combined with other biocides. For example, copper and quats are the active ingredients in ACQ, discussed above, and DDAC plus IPBC is a commercial sapstain and mold agent. Quats will undoubtably continue to be considered in the development of new preservative systems.

A relatively new quat analog is an oligomer of alternating quat and borate ether units, commonly called polymeric betaine (didecyl-bis(2-hydroxyethyl) ammonium borate or didecylpolyoxethylammonium borate). Both the quats and borate ethers can bind to wood and, thus, the structure of the active ingredient changes when exposed to wood. The oligomeric structure makes the borate relatively less susceptible to leaching. Being composed of both quats and borates, polymeric betaine is active against both decay fungi and insects. Several water-based polymeric betaine systems are commercially available in Europe, including systems with polymeric betaine alone or combined with an insecticide for above-ground use, or with co-added copper for ground-contact applications.

Synthetic pyrethroids The synthetic pyrethroids (Permethrin, Bifenthrin, Cypermethrin, Cyfluthrin, and Deltamethrin), analogs of chrysanthemum-derived terpenoid pyrethrins, have low toxicity to mammals, exhibit good efficacy against insects (but are not fungicidal), and are soluble in many hydrocarbon solvents. (Only the structure of Permethrin is shown in **Table 1**.) In the United States research on the combination of a synthetic pyrethroid and fungicide has been conducted but no commercial applications currently exist. In Europe several combinations of a synthetic pyrethroid and other biocide(s) are available, including the quat benzalkonium chloride combined with permethrin and tebuconazole, or a cypermethrin and tebuconazole mixture.

Tributyltin oxide Tributyltin oxide (TBTO) is an organometallic biocide which exhibits good activity against fungi and insects, is soluble in most hydrocarbons, and has good leach resistance. It is used as an aboveground treatment for millwork and related applications in many countries. However, it undergoes slow dealkylation which reduces its fungicidal properties. Consequently, TBTO has been used for reduced decay applications such as millwork in Europe and the US.

Biocides with the Potential to Preserve Wood

Some biocides are being evaluated for wood preservation. Most of these are already registered and labeled for non-wood agricultural applications. Examining the potential of registered agrochemicals to protect wood has the advantage that the cost of label expansion is less than the expenditure required to develop, test, then register and label an entirely new biocide developed for only the relatively small wood preservation market. Potential biocides shown in **Table 2** are briefly discussed below.

Chlorothalonil Chlorothalonil (2,4,5,6-tetrachloroisophthalonitrile) is an organic biocide with very low toxicity to mammals, broad activity against decay fungi and insects, relatively low cost, and good stability and leach resistance in wood. A major research effort in the 1990s examined chlorothalonil as an alternative for penta. However, the poor solubility of chlorothalonil in most organic solvents made formulation difficult and interest has waned.

Copper bis(dimethyldithiocarbamate) Copper bis (dimethyldithiocarbamate) (CDDC), with the mono form preferred, is formulated with copper(II), ethanolamine, and sodium dimethyldithiocarbamate (SDDC). Since copper reacts rapidly with SDDC to form an insoluble complex, a two-step treating process is required. This results in a stable preservative with good activity against most wood-destroying organisms, but the dual treatment increases the cost.

Dichlofluanid Dichlofluanid (1,1-dichloro-*N*-[(dimethylamino)sulfonyl]–1- fluoro -*N*-phenyl-methanesulfenamide (DCFN)) is a fungicide used in paints and stains in Europe, and which may have potential as a fungicide in wood preservative systems.

Kathon 930™ The isothiazolone 4,5-dichloro-2-n-octyl-4-isothiazolin-3-one (Kathon 930™) is a biocide with moderately low toxicity to mammals and broad activity against decay fungi and termites. It is readily soluble in hydrocarbons, and exhibits excellent stability and leach resistance in wood. Research has shown that Kathon 930 effectively protects wood in both aboveground and ground-contact applications, but no commercial formulations are currently available. Other isothiazolone analogs are used for short-term control of mold and sapstain fungi on wet, freshly treated lumber.

Fipronil Fipronil (5-amino-1-[2,6-dichloro-4-(trifluoromethyl)phenyl]-4-[(trifluoromethyl)sulfinyl]-1*H*-pyrazole-3-carbonitrile) is an α-phenyl pyrazole-type insecticide. When combined with a fungicide it has been examined as a wood preservative.

Imidacloprid Imidacloprid (1-[(6-chloro-3-pyridinyl)methyl]-*N*-nitro-2-imidazolidinimine) is a neonicotinoid insecticide. Field tests in the United States showed that imidacloprid had much greater efficacy than chlorpyrifos in protecting wood against termite attack, but it may be degraded relatively rapidly.

Polymeric xylenol tetrasulfide Polymeric xylenol tetrasulfide (PXTS) is an oligomer consisting of a mixture of alkylphenols linked by 2-10 sulfurs, with a low degree of polymerization. This biocide has many of the same characteristics and efficacy as creosote so far in marine and ground-contact tests currently under way. Being an oligomer PXTS should have minimal leaching, which would reduce the retention necessary for long-term protection and be suitable for environmentally sensitive applications. PXTS has exhibited low toxicity to mammals in tests to date.

2-(**Thiocyanomethylthio) benzothiazole** 2-(Thiocyanomethylthio) benzothiazole (TCMTB, Busan 30™) is an organic biocide with a broad range of activity against both fungi and insects. It is readily soluble in hydrocarbons and exhibits good leach resistance in wood, but it is susceptible to biodegradation.

Trends in Biocides Used to Preserve Wood

Wood preservation is rapidly changing. In North America CCA is currently the most important preservative–by far–for residential applications, and penta, creosote, and CCA are used for industrial applications. However, CCA will be restricted to industrial applications starting in 2004 in North America, and residential lumber will be treated with alternative second-generation waterborne copper: organic systems which are copper-rich and possibly the older ACC system. ACQ, CA, Cu-HDO, copper and polymeric betaine, and possibly CCB and related copper/chromium systems, will probably be the main systems in Europe, Japan, and/or North America for the next several years. The newer preservatives are relatively expensive, more corrosive to metal fasteners, and apparently leach more copper than CCA-treated lumber. While these problems are avoided by the copper/chromium systems such as CCB and ACC, disposal concerns may soon lead to restrictions on chromium-containing systems. Another problem is that all lumber which has been treated with a waterborne preservative system and not yet redried (including wood treated with CCA) is susceptible to growth of molds and sapstains on the lumber surface, but the organic amine in many of the new copper-based preservatives may exacerbate mold growth. (Many preservative formulations also contain a biocide for short-term control of molds and sapstains on wet, freshly treated lumber.) New preservatives may also require more attention in the treating plant than CCA; indeed, many new systems have initial problems. Copper has some environmental and disposal concerns, and systems with relatively low copper levels plus one or more organic cobiocides might be eventually required. Alternatively, totally organic biocides might be mandated, a trend already happening in some European countries. Borates are being used to a greater extent for nonleaching residential applications.

Disposal of treated wood is, or will shortly be, a major issue in many countries and could be a principal factor determining which biocides are permitted. An intriguing possibility being studied in Europe is to utilize organic biocides which slowly degrade, and would protect wood for a specified time but then allow the product to be safely disposed of. The recycling of treated wood, such as grinding CCA-treated lumber into particles for particleboard furnish, may prove difficult due to liability concerns.

Many new organic biocides are extremely effective against some, but not all, wood-destroying organisms. Thus, future totally organic preservatives will likely consist of a combination of biocides, possibly including other nonbiocidal additives such as water repellents, to enhance the biocide's efficacy. Any synergism observed by combining multiple biocides would be a bonus. A preservative system used to treat lumber for residential construction will likely be water-based, but most organic biocides are not water soluble. Consequently, stable emulsions must be developed. Another problem is that organic biocides can be degraded by various chemical, biological, thermal, and/or photolytic mechanisms and thus rendered inactive; in contrast, the inorganic metals, such as the components in CCA, are 'permanent' and will only undergo a change in oxidation state. Thus, developing economical and effective totally organic systems, especially for locations with severe decay and/or termite conditions, will be a difficult, long-term, and costly process. At the present time no totally organic, aqueous-based system capable of protecting ground-contact wood for residential applications in the United States has even been proposed to a regulatory agency.

The high cost of new biocides, along with environmental concerns, will undoubtedly result in efforts to reduce the biocide level in totally organic systems to about 0.4% to 0.01% mass per mass of wood. By contrast, the traditional CCA and penta systems use about 1% mass per mass. Since wood is inherently variable this results in lumber from one commercial treating charge having a wide range of within- and among-board biocide retentions. With the highly effective traditional systems biocide retention variability is not serious, but it may become an important factor with the newer systems which have lower retention levels, and possibly less efficacy, than CCA or penta.

The total yearly cost to US homeowners due to fungal and termite attack is estimated at about US$5 billion. Some of these costs could be avoided by better design and construction techniques, but wood preservatives will still be needed for many applications.

Formulations

Once a particular biocide(s) has been selected it must be formulated into a preservative system suitable for commercial applications, in which the active ingredient (the biocide) is combined with various inactive compounds. For treating solid wood and many composites, the biocide must be dissolved in a solvent (the carrier) or an emulsion developed. For industrial applications a heavy or light organic solvent, or water, can be used. Better efficacy with organic biocides is usually obtained with heavy oils, which by themselves often exhibit some biocidal activity and impart water repellency. For residential applications most systems are water-based; a light hydrocarbon is feasible but not likely due to cost and solvent emission issues. Since most organic biocides are not soluble in water an economical and stable oil-in-water emulsion must be developed.

Other characteristics of a viable preservative formulation, especially for residential applications, include:

- low cost
- good efficacy
- broad activity
- good permanence under long-term use
- no significant effect on wood strength
- low or no odor
- not corrosive to metal fasteners
- good penetration
- safe to handle and use
- leaves wood paintable and with an attractive appearance
- allows the wood to be disposed of or recycled at the end of the product's life
- capable of being concentrated (for shipment)
- formulated using only registered biocides.

Standards and Organizations that Set Specifications

Once a preservative system formulation has been developed it is subjected to various tests with the results submitted to the appropriate standard-producing organization. Many organizations worldwide help set standards. In the United States over 10 organizations are involved to some degree in wood preservation; the major US organizations which develop standards are the AWPA and the American Society for Testing Materials (ASTM). The AWPA and/or ASTM Standards specify the formulations and retentions of various preservative systems for a wide variety of applications, as well as penetration requirements, treating processes, analysis procedures, laboratory and outdoor efficacy evaluation tests, etc.

A proposal of a new wood preservative system submitted to the AWPA for standardization typically includes the exact formulation, safety and health aspects, and results from various laboratory and field tests on corrosion, leaching, efficacy, etc., with the proposal listing the desired application(s) and retentions. The proposal is subjected to a peer review process by various industrial, governmental, and academic professionals, with an initial period of back-and-forth written questions followed by oral discussion at an AWPA meeting and then further time for additional written comments. If the proposal is accepted AWPA Technical Committees develop specifications that list the minimum requirements covering specific wood products recommended for a given preservative. Sponsors of the preservative system are required to submit periodic updates of long-term efficacy data generated in outdoor exposure trials. Standard development by organizations in other countries may follow a different format, but all are designed to ensure that the consumer obtains a reliable and safe product.

Treatment Processes

Over-the-counter wood preservatives are generally brushed on by homeowners and only provide short-term protection. Control of sapstain and mold in green (never dried) lumber is accomplished by dip- or spray-treating with aqueous formulations. Millwork is generally treated by dipping or spraying dried wood. Most wood products are treated by a vacuum/pressure process, which gives the high loading and uniform penetration necessary for good quality control and long-term performance. In this process the wood product is usually first dried so that some or all of the free water in the cell lumen is replaced with air. The dried wood is placed in a pressure-treating cylinder, a vacuum drawn, then the preservative solution added to the cylinder so that the wood is fully immersed. Pressure is then applied to force the solution into the porous wood, with the preservative solution filling some or all of the lumen air-void volume; a vacuum may be drawn as a final step. The pressure treatment processes have basically remained the same for many years.

Preservation of Wood Composites

Most preservatives are used to treat solid wood products such as lumber, ties, poles, etc., but the protection of wood composites is increasingly important. The treatment of composites involves special considerations. Generally, the furnish used to make wood composites is either treated with a biocide prior to manufacturing (preprocess) or a biocide is added during manufacture (in-process), or the composite is treated after manufacture (postprocess). The particular method and biocide system depends on the composite.

An example of a preprocess method is gluing lumber, which had been previously treated with CCA, into glulam beams. This process is only used with a few wood composites, using preservatives that do not negatively affect the adhesive. Postprocess treatment of an already manufactured composite is used where treatment will not adversely affect the product, and usually involves composites manufactured from lumber or veneer. In-process, where the biocide is added to the furnish just before mat formation and/or pressing occurs, is used where a postprocess treatment will cause undesired swelling and/or delamination of the composite and is usually practiced with composites manufactured from flakes, particles, or fibers. Postprocess treatments use standard preservative systems, are relatively easy and require no modification of the manufacturing process, but can result in only the outer shell being treated and some dimensional changes and strength loss. The in-process method gives protection throughout the composite, but the preservative can interfere with the adhesive and thermal degradation of organic biocides might occur during hot-pressing.

Because of its low cost, relatively good leaching properties, broad activity against a wide range of wood-destroying organisms, low toxicity to mammals, and good thermal stability, zinc borate has become one of the principal biocides used to treat in-process composites. Wax-based water repellents, either alone or in combination with a biocide, are also used.

Naturally Durable Woods

The heartwood of some woods is naturally resistant to biodegradation. Commercially available durable woods include western red cedar, redwood, and cypress in North America, larch and pine heartwood in Europe, some woods from tropical forests, some eucalypts in Australia, etc. A major drawback is that most of these woods are not highly durable and may have a relatively short service life in certain applications or locations. Also, the availability of durable woods is not equal to the volume of pressure-treated wood produced in North America. Finally, some lumber with nondurable sapwood can be mixed in, durability varies greatly among and within trees, and the heartwood extractives which impart durability are often toxic or irritants.

Nonbiocidal Additives to Enhance Biocide Efficacy

In addition to protecting wood, an ideal wood preservative system should improve the weathering characteristics by reducing water sorption. Consequently, the addition of water repellents to wood preservative systems is desirable. Besides improved weathering, durable water repellents enhance the biocide's efficacy by reducing leaching and lowering the moisture content of exposed wood. Water repellents are usually benign and can be extremely cost-effective. For example, most water repellents are wax- or oil-based and, on a weight basis, are about 100-fold cheaper than most organic biocides.

Lumber treated with several water repellent and preservative combinations is available in North America, and linseed oil-treated wood is being studied in Europe.

It is well known that decay fungi utilize free radicals generated by metals and/or organometallics to degrade wood. This, and the knowledge that extractives in durable woods have excellent antioxidant and metal chelating properties, suggested that antioxidants and/or metal chelators might help protect wood against fungal attack. Laboratory experiments have shown that antioxidants or metal chelators alone provide little protection to wood, but when combined with organic biocides enhance the efficacy of all biocides studied. Ground-contact and aboveground outdoor exposure trials are now under way and results so far are promising. This approach will likely be suitable only with totally organic systems.

Other possible additives include the in situ polymerization of nonbiocidal monomers. A portion of the monomers may covalently bond to the wood structural components to make the wood both more hydrophobic and impervious to enzymatic degradation. A similar concept involves reagents which form ester or ether linkages with the polysaccharide hydroxyls. Alternately, a resin could be impregnated into wood followed by polymerization. However, these treatments are expensive and require careful control and monitoring and so far have limited applications.

Thermal Modification of Wood

In the past decade European researchers have reexamined the thermal modification of wood. As a result several processes have been developed and commercial production of heat-treated wood is growing rapidly. Generally, lumber is heated to at least 180°C in a nonoxidizing atmosphere. This causes some chemical degradation of the wood and, consequently, the wood has some decay resistance but mechanical properties are reduced. Also, greatly reduced hygroscopicity gives the lumber improved weathering characteristics. Although the durability of heat-treated wood is not equivalent to pressure-treated wood, it is suitable for low-hazard, nonstructural, above-ground applications.

Biocontrol

Another biocide-free approach is to use microorganisms that are antagonistic to wood-degrading fungi and insects. This bioprotectant approach has been marketed in Europe to a limited degree, but there are some concerns about long-term effectiveness. Based on research to date, it appears that the most promising use for this concept is to control sapstain and mold fungi where only short-term protection is required.

See also: **Pathology**: Heart Rot and Wood Decay; Insect Associated Tree Diseases. **Wood Formation and Properties**: Biological Deterioration of Wood.

Further Reading

Anonymous (2002) *American Wood-Preservers' Association Standards 2002*. Granbury, TX: American Wood-Preservers' Association.

Barnes HM (2001) Wood: preservative treated. In: *Encyclopedia of Materials: Science and Technology*, pp. 9683–9688. London: Elsevier Science.

Barnes HM and Murphy RJ (1995) Wood preservation: the classics and the new age. *Forest Products Journal* 45(9): 16–26.

Eaton RA and Hale MDC (1993) *Wood: Decay, Pests and Protection*. London: Chapman & Hall.

Edlund M-E and Jermer J (2002) *Evaluation of Wood Preservatives for Nordic Wood Preservation Class AB*, Paper IRG/WP no. 02-30297. Stockholm, Sweden: International Research Group on Wood Preservation.

Goodell B, Nicholas DD, and Schultz TP (2003) *Wood Deterioration and Preservation: Advances in our Changing World*, ACS Symposium Series no. 845. Washington, DC: American Chemical Society.

Morrell JJ and Morris PI (2002) *Methods for Improving Preservative Penetration into Wood: A Review*, Paper IRG/WP no. 02-40227. Stockholm, Sweden: International Research Group on Wood Preservation.

Nicholas DD (ed.) (1973) *Wood Deterioration and Its Prevention by Preservative Treatments*, vols. 1 and 2. Syracuse, NY: Syracuse University Press.

Nicholas DD (2001) The preservation of wood. In: Hon DN-S and Shiraishi N (eds) Wood and Cellulosic Chemistry, 2nd edn, pp. 795–806. New York: Marcel Dekker.

Preston AF (2000) Wood preservation: trends of today that will influence the industry tomorrow. *Forest Products Journal* 50(9): 12–19.

Rapp AO (ed.) (2001) *Review of Heat Treatments of Wood*, COST Action E22, Report EUR 19885. Brussels: *European Commission*.

Suttie ED, Bravery AF, and Dearling TB (2002) *Alternatives to CCA for Ground-Contact Protection of Timber: A Perspective from UK on Performance and Service Life Expectations*, Paper IRG/WP no. 02-30289. Stockholm, Sweden: International Research Group on Wood Preservation.

Wilkinson JG (1979) *Industrial Timber Preservation*. London: Associated Business Press.

Zabel RA and Morrell JJ (1992) *Wood Microbiology: Decay and Its Prevention*. New York: Academic Press.

Protection from Fire

C R McIntyre, McIntyre Associates, Walls, MS, USA

Introduction

Wood has been an excellent building material for many centuries; however, its ability to ignite and burn has limited its use in many applications. Applications of various fire retardant chemicals has expanded the use of wood and provided significant safety to occupants of wooden buildings. The fire-retardant systems used for wood generally contain nitrogen, boron, and phosphorus chemicals. The properties of specific formulations and their advantages and disadvantages are discussed in this article, and the modes of action and testing procedures for fire retardants are also given.

History of Fire Retardants

Although various chemicals were utilized through history, the modern use of fire retardants for wood stems from 1820 when Gay-Lussac developed treatments with ammonium phosphates and borax. The full impact of this invention can be gauged by the realization that systems similar to this are still in use today. But there have been many other inorganic chemicals investigated as fire retardants in the intervening years. Around 1900, formulations based on silicates, sulfates, borates, phosphates, zinc, tin, and calcium were in vogue and by 1915, ammonium chlorides, phosphates, and sulfates were known to be effective for wood.

From 1930 to 1935, researchers at the US Department of Agriculture Forest Products Laboratory (FPL) reported on investigations of about 130 different inorganic fire retardant formulations. It was found that diammonium phosphate was the most effective for reducing flame spread while monoammonium phosphate, ammonium chloride, ammonium sulfate, borax, and zinc chloride were also active. However, many of the chemicals in this test program had associated problems of high cost, corrosion, hygroscopicity, strength reduction, or glow promotion. Therefore, other approaches such as *in situ* polymerizations or reactions of retardants with wood components were investigated.

By the 1950s, there were several formulations in commercial use for pressure treating wood. (Fire retardant coatings were also being investigated but, as discussed later, their acceptance and regulation lagged that of pressure treated products.) The American Wood-Preservers' Association (AWPA) listed four formulations and the US Navy allowed several others for shipboard use (**Table 1**). All of these formulations were inorganic combinations blended to achieve a reasonable compromise of cost and acceptable performance. However, in the 1960s, three formulations similar to the four AWPA formulations had supplanted the previous ones and were by far the dominant retardants (**Table 2**).

In the late 1960s, formulations were introduced in the USA and Canada that protected exterior products such as shingles, shakes, and siding or scaffold planking that are exposed to the elements. These systems typically injected the precursors to a nitrogenous polymer system such as urea-formaldehyde or melamine-formaldehyde along with phosphoric acid into the wood. Then a special kiln cycle was used to effect an *in situ* polymerization that encapsulated the phosphoric acid and rendered it

Table 1 1950s formulations for five retardants

AWPA formulation ingredients	*Percent*
1. Chromated zinc chloride (CZC)	
$ZnCl_2$	>77.5
$Na_2Cr_2O_7.2H_2O$	>17.5
2. Chromated zinc chloride FR	
CZC (above)	80
H_3BO_3	10
$(NH_4)_2SO_4$	10
3. Minalith	
$(NH_4)_2SO_4$	60
H_3BO_3	20
$(NH_4)_2HPO_4$	10
$Na_2B_4O_7$	10
4. Pyresote	
$ZnCl_2$	35
$(NH_4)_2SO_4$	35
H_3BO_3	25
$Na_2Cr_2O_7.2H_2O$	5
Other formulation ingredients	
5.	
$(NH_4)_2SO_4$	>78
$NH_4H_2PO_4$ or $(NH_4)_2HPO_4$	>19
6.	
$Na_2B_4O_7$	60
H_3BO_3	40
7.	
$Na_2B_4O_7$	67–70
$NH_4H_2PO_4$	33–30
8.	
$ZnCl_2$	54
$NH_4H_2PO_4$	46

Source: Prepared from AWPA and other documents cited.

Table 2 Interior formulations from the 1960s and 1970s

Formulation ingredients	*Percent*
1.	
$(NH_4)_2SO_4$	50
$NH_4H_2PO_4$	41
$Na_2B_4O_7$	7
Moldicide	2
2.	
$(NH_4)_2SO_4$	45
$NH_4H_2PO_4$	45
$Na_2B_4O_7$	6
H_3BO_3	4
3.	
$NH_4H_2PO_4$	65
H_3BO_3	35

Source: Prepared from AWPA and other documents cited.

leach resistant. The kiln cycle called for moderate temperatures (70°C) for 2–3 days or until the wood was below 25% moisture content and then elevation of the kiln temperature to 100°C for up to 24 h to complete the reaction.

The use of fire retardants climbed very slowly in the USA until the 1960s (**Figure 1**). Then from 1960 to 1970, the use quadrupled as new formulations became available that expanded the useful applications for fire retardants. There was also an increased awareness of the considerable safety benefits of fire retardants. However, the emergence of corrosion, hygroscopicity, and strength problems began to plague the industry and the market grew only slightly until 1980. Building code changes were implemented in the late 1970s that opened up a major new end use for roof framing and sheathing (predominately plywood) in buildings that otherwise were required to be constructed from noncombustible materials. At about that time, replacements for the above first-generation retardant systems were also being developed.

In the early 1980s, second-generation fire retardants were introduced to address the corrosion and hygroscopicity problems of the first-generation inorganic formulations. One new product was an 'organic' that was a blend of guanylureaphosphate (GUP, formed by the reaction of dicyandiamide with phosphoric acid) with boric acid. There were several other second-generation formulations that were based on ammonium polyphosphates with or without various additives in small quantities. The additives included boric acid, borax, moldicides, and the like.

However, in the late 1980s, reports began to surface that some of the second-generation formulations were experiencing strength loss in high temperature applications such as roof sheathing. After

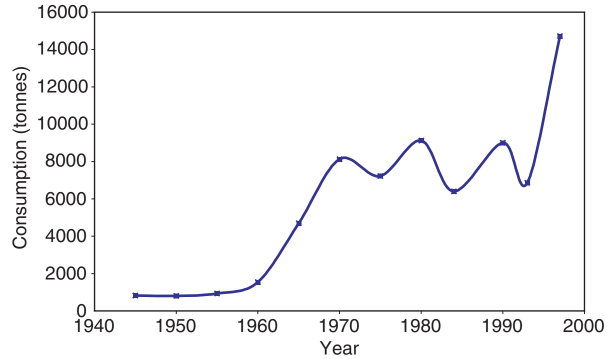


Figure 1 US consumption of fire retardants for wood. Prepared from AWPA publications.

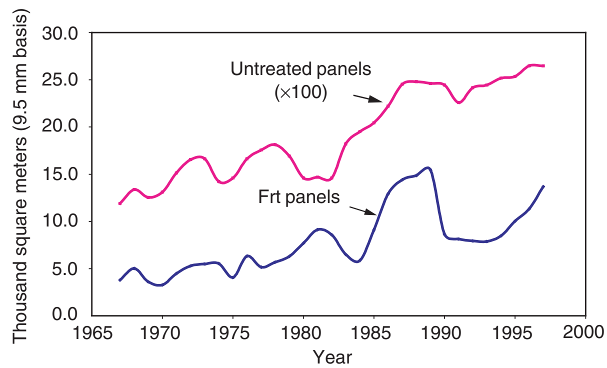


Figure 2 Annual production in the USA of fire retardant treated and untreated panels. Prepared from AWPA and FPL publications.

the initial concern that all second-generation products were involved, it was found that problems were occurring with only some formulations. Multiple lawsuits occurred and further investigations revealed that high humidity conditions frequently existed in problem installations. Numerous causes were alleged for the strength problems and the end result was that the overall market for fire retardants was severely impacted.

Prior to these problems, the market had accepted the second-generation products and growth in treated panels had matched that of untreated panels (**Figure 2**), but the threat of litigation soon caused a steep decline in volume in the early 1990s. Most of the ammonium polyphosphate containing products were removed from the market as well.

At the onset of the heat degradation problem, researchers at the FPL and elsewhere began investigating the issue. During the next several years a series of publications delineated that certain combinations of fire retardant ingredients with elevated temperatures and humidities would cause liberation of acidic moieties that in turn attacked certain components of the wood. Without these components, the wood quickly lost its strength. Throughout this work, various laboratory tests were performed for exposure periods of up to 5 years at elevated temperatures and strength testing was done on the aged wood. These results led to development of test protocols for evaluating strength properties of fire retardant wood.

In particular, two organizations, ASTM International (American Society for Testing and Materials, ASTM) and AWPA, were very active in developing new test procedures and standards to address strength issues. In the late 1980s when the apparent strength problem was first becoming known, ASTM issued an emergency standard that addressed strength losses for plywood exposed at elevated temperatures and humidities. In this emergency standard, which later became ASTM D5516, plywood is exposed for at least 60 days at temperatures of 77°C and 50% relative humidity. The strength reductions from exposure can then used to develop design adjustment factors for the fire retardant formulation using a computer based modeling approach detailed in ASTM D6305 that considers climatic data. Similar testing procedures and design adjustment methodology for fire retardant lumber are detailed in D5664 and D6841. The AWPA have revised their standards related to fire retardants to require strength testing by the above ASTM procedures and incorporated recommended minimum acceptable levels of strength loss.

These actions have given specifiers the needed confidence to again use fire retardant treated wood without fear of premature strength loss. These tests were quickly adopted by building codes and other regulators with the result that several products are currently available that give excellent strength performance. Corrosion and hygroscopicity concerns that had plagued the first-generation products have also been addressed. Today's products are no more corrosive than untreated wood and do not display any significantly different moisture content up to 92% relative humidity.

The significant commercial formulations now accepted in the US and Canada are the GUP/BA combination, a similar urea-boric acid combination, a nonphosphate containing mixture of nitrogen and borate compounds, and a combination of diammonium phosphate and boric acid where sufficient boric acid is available to buffer any free phosphate acids produced. The market has readily accepted the current formulations and substantial growth has occurred in the last decade (**Figure 1**).

Testing of Fire Retardants

Commercial Testing

For commercial purposes, the dominant test for fire retardant treated wood is the measurement of surface flame spread by use of ASTM E84. In this test, the treated material forms the roof of a 24-ft long (7.3 m) tunnel and the wind-aided spread of flame is tracked for 10 min. For all structural applications of fire retardant treated wood, building codes require that the test duration be extended an additional 20 min without significant progressive combustion. A standard ignition flame is used and the tunnel is calibrated to have a flame spread rating of 0 using an inert cement board and a rating of 100 using red oak flooring. The flame spread of the test product is determined under these standard conditions and flame spread ratings for fire retardant treated and untreated wood are discussed later. A smoke rating is also obtained during the tunnel test and most uses allowed in the building codes require a smoke level of less than 450.

Typically, a supplier of a fire retardant formulation will contract with a testing laboratory such as Underwriters Laboratory (ULI) to conduct the testing on a number of species of lumber. Various plywood species and grades may also be tested. The testing laboratory monitors all phases of the preparation of the test material. Upon completion of successful testing, the laboratory then lists the materials as acceptable in their publications and issues identification stamps or labels that are used to indicate to others that the material passes recognized testing protocols.

The building codes classify materials in broad ranges of flame spread based on the first 10 min of test: Class I or A has a flame spread of 0–25, Class II or B is 26–75, and Class III or C is 76–200. Class I material can be used in more critical applications such as on the walls of exit corridors while the others are used in less critical applications where there is less risk to human life if a fire occurs. For structural uses of fire retardant treated wood where the E-84 test is extended for an additional 20 min of flame there cannot be any sign of significant progressive combustion as defined in the standard.

When treated with fire retardants, structurally qualified species have a 10-min rating of less than 25 and there is no significant progressive combustion when the test is extended to a 30-min total burning time. All of the commonly available lumber species and plywood sizes are available with this classification. Understandably, the flame spread ratings of untreated wooden commodities lie near 100 since the tunnel is calibrated at that value for red oak. A number of important species and materials have been tested and the flame-spread values for the untreated wood are given in **Table 3**. Note though that some species such as southern pine (*Pinus*) can have a much higher flame spread than the others when untreated due to their higher resin content.

Table 3 Flame spread indices for untreated wood

	Flame spread index
Lumber	
Western redcedar	70
Douglas-fir	70–100
Maple (flooring)	105
Oak, red	100
Pine, white	75–85
Pine, southern yellow	130–195
Redwood	70
Spruce, Sitka	75
Plywood	
Softwood	
Douglas-fir (10 mm)	110–150
Southern pine (10 mm)	100–105
Hardwood	
Birch (6 mm)	115–185
Lauan (6 mm)	100–140
Oak (6 mm)	125–185

Source: Prepared from American Wood Council *Flame Spread Performance of Wood Products*. Available online at http://www.awc.org.

Spray or brush applied fire retardant coatings for wood differ significantly from pressure treated formulations in that they are only tested for 10 min total and then assigned a flame spread rating. Thus, they do not have the additional structural designation. Also, coatings are limited to only one species, Douglas-fir (*Pseudotsuga menziesii*), and are not available for a wide variety of products.

Other important tests for commercial fire retardants include measuring:

- heat release rate
- smoke density
- lateral spread of flame
- smoke toxicity
- ancillary properties: corrosion, hygroscopicity, strength.

There are a number of test procedures used to document the above properties and specific protocols can be found in ASTM, AWPA, Factory Mutual (FM), International Standards Organization (ISO), and ULI documents. It should be noted that in recent years, the fire research community has expended great effort to harmonize the North American and ISO standards on fire testing. However, many differences still exist in the standards and one should not assume interchangeability of the standards from different organizations.

There are also applications where the fire resistance properties of fire retardant wood are more important than the surface spread of flame. For these tests, the ability of wood to resist burn through is challenged and typically these tests are done on large assemblies such as walls or doors. In these cases, the fire retardant wood contributes a portion of the total assembly properties.

Historically, in Europe, fire resistance properties have been more important than flame spread and the test procedures produce ratings based on measuring resistance. Imparting resistance requires significantly higher retentions of fire retardants wood and this leads to higher costs. Therefore the use of fire retardants in Europe has lagged behind that of North America.

In recent years, there has been an increasing use of fire retardants in Europe for nonstructural products such as wall linings and siding (cladding). There is still only limited use in structural applications. However, there are a number of modified protocols being proposed and/or accepted as part of the European Union process so current affairs in Europe regarding fire retardants for wood are in a state of flux. Presumably these changes will lead to further increases in use.

Laboratory Testing

A number of testing techniques are used for the development of fire retardant formulations. In the past, the fire tube test (ASTM E69), 2-ft (60 cm) tunnel, and other small-scale fire tests were used. However these tests were frequently misleading in that their reproducibility is relatively poor. Consequently, in recent years most researchers have migrated to thermal analysis and other more sophisticated test equipment such as the cone calorimeter.

For fire retardants, the two most important thermal tests are thermogravimetric analysis (TGA) and differential thermal analysis (DTA). TGA measures weight loss as the sample is heated while DTA measures exothermic or endothermic reactions that occur as the sample is heated. Most modern thermal analysis equipment can provide TGA and DTA data simultaneously and the combination can help guide the researcher. The testing can be done in an inert gas atmosphere so that pyrolysis occurs or in oxygen so that combustion occurs. Although the chemical processes for pyrolysis and combustion are similar, the relative degree of formation of various products can greatly differ.

Typical TGA curves are shown in **Figure 3** for untreated and wood treated with two different commercial fire retardant formulations. Note that the dominant effect of the fire retardants is to reduce the onset of decomposition to around 200°C and to increase the amount of residue (char) from 1–2% to about 20% when the TGA furnace reached 500°C.

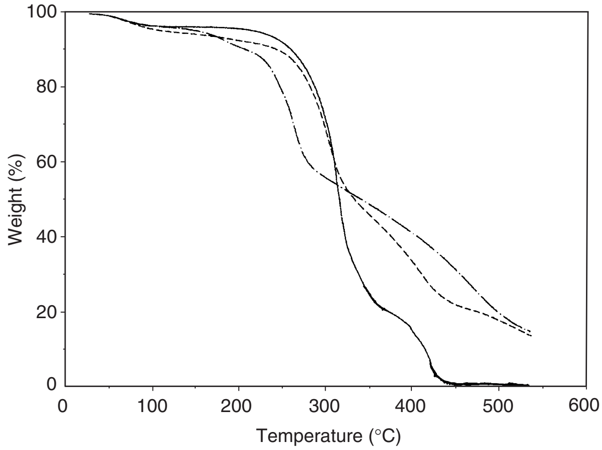


Figure 3 Typical thermogravimetric analyses of fire retardant treated and untreated wood. Solid line, untreated wood; dashed line, commercial formula A; dash–dot line, commercial formula B.

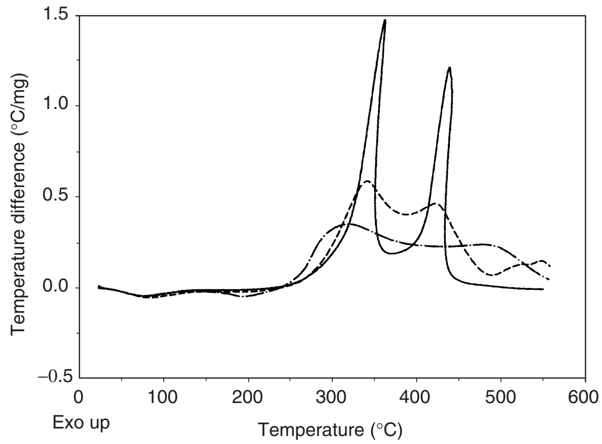


Figure 4 Typical differential thermal analyses of fire retardant treated and untreated wood. Solid line, untreated wood; dashed line, commercial formula A; dash–dot line, commercial formula B.

The DTA curves that correspond to these samples are shown in **Figure 4**. In these cases, most of the samples absorb small amounts of energy (i.e., are slightly endothermic) up to about 250°C and then liberate that energy (i.e., become exothermic) during the later stages of heating. The extent and location of the various thermal events guide the development researcher in the search for fire retardant formulations. Successful laboratory candidates are further tested with the commercial procedures discussed above.

Pricing of Fire Retardant Wood

For most species, the pressure treatment process must leave 32–48 kg m^{-3} retention of the fire retardant formulation in the wood to achieve a Class I flame spread rating of 25 or less. This degree of protection costs about US\$50–60 m^{-3} for the chemicals alone and there is additional cost of about US\$30 m^{-3} for the processing. In addition, building codes require redrying after treatment which generally costs at least US\$40 m^{-3}. Thus, most commercial fire retardants add nearly US\$140 m^{-3} to the untreated price of the wood.

Mechanism of Fire Retardant Action

A number of mechanisms through which fire retardants exert their influence on the combustion of wood have been proposed over the years. For combustion to occur, the larger polymeric molecules in wood must be broken down into small, volatile fragments. This breakdown can occur in a variety of ways and it is recognized that combinations of the various mechanisms actually occur during combustion. For convenience though, the various mechanisms can be grouped into six different theories.

Increased Char Formation Theories

In this theory, the fire retardant chemicals dominant influence is on the various chemical mechanisms that promote char formation while liberating small, highly oxidized fragments of the polymers in wood. Typically, these mechanisms are of the decarboxylation, decarbonlylation, and dehydration types where, say, cellulose is transformed into levoglucosan which further degrades to char and small volatiles. (A somewhat simplistic way of thinking of this is to say that the carbon framework of wood is largely charred in place while small fragments such as water, carbon dioxide, and carbon monoxide are liberated.)

Reduced Volatiles Formation Theories

An adjunct to the increased char theory is the reduced volatile theory that in fact means that the heat content of the volatile products is reduced. Since there is less heat generated by the combustion of the volatiles, the propensity for self-sustaining burning is reduced.

Coating or Barrier Theories

It is thought that some fire retardants create physical barriers such as glasses or rigid foams that inhibit oxygen transport necessary to support combustion. The barriers can also provide thermal insulation to prevent heat transfer. Many fire retardant formulations for wood intumesce or swell when heated and this mechanism may be important for these types.

Gas Theories

The gas theories state that fire retardants cause dilution of the combustible gases with noncombustible gases during the early stages of pyrolysis and this inhibits subsequent combustion. In effect, there is a gaseous barrier to combustion.

Free Radical Inhibition Theories

This theory proposes that fire retardants act as traps to inhibit free radical propagations. Thus the various radicals formed by scission mechanisms are not available and subsequent combustion is retarded.

Thermal Theories

The thermal theories predict that fire retardants reduce the capacity of the wood to absorb heat. Consequently, they limit the amount of heat available for pyrolysis reactions.

The first two theories above seem especially important for fire retardants for wood since effective agents demonstrate the two properties of increased char and decreased combustible volatiles over and over again. Many authors have proposed specific chemical mechanisms for the pyrolysis and burning of wood and the interaction of fire retardants with these mechanisms. However these detailed discussions are beyond the scope of this article and the interested reader is directed to the Further Reading section below.

See also: **Solid Wood Processing**: Protection of Wood against Biodeterioration. **Solid Wood Products**: Structural Use of Wood; Wood-based Composites and Panel Products. **Wood Formation and Properties**: Chemical Properties of Wood; Physical Properties of Wood.

Further Reading

Browne FL (1963) *Theories of the Combustion of Wood and Its Control*. US Department of Agriculture Forest Products Laboratory Report no. 2136. Madison, WI: US Department of Agriculture Forestry Service.

Goldstein IS (1973) Degradation and protection from thermal attack. In: Nicholas DD (ed.) *Wood Deterioration and Its Prevention by Preservative Treatments*, vol. I, pp. 307–339. Syracuse, NY: Syracuse University Press.

Holmes CA (1977) Effect of fire-retardant treatments on performance properties of wood. In: Goldstein IS (ed.) *Wood Technology: Chemical Aspects*. Washington, DC: American Chemical Society. Available online at http://www.fs.fpl.fed.us/publications

Levan SL (1984) Chemistry of fire retardancy. In: Rowell RM (ed.) *The Chemistry of Solid Wood*, pp. 531–574. Washington, DC: American Chemical Society. Available on line at http://www.fs.fpl.fed.us/publications.

Lyons JW (1987) *The Chemistry and Uses of Fire Retardants*. Malabar, FL: Robert E. Krieger.

Shafizadeh F (1984) The chemistry of pyrolysis and combustion. In: Rowell RM (ed.) *The Chemistry of Solid Wood*, pp. 489–529. Washington, DC: American Chemical Society. Available online at http://www.fs.fpl.fed.us/publications.

Shafizadeh F, Sarkanen KV, and Tillman DA (eds) (1976) *Thermal Uses and Properties of Carbohydrates and Lignins*. New York: Academic Press.

Winandy JE (2001) Thermal degradation of fire-retardant-treated wood: predicting residual service life. *Forest Products Journal* 51(2): 47–54.

Recycling

J I Zerbe, Madison, WI, USA

Introduction

Paper has been the mainstay of recycling efforts for many years, but other forest products are making increasingly larger impacts on recycling. This means a growing contribution to environmental benefits from conserving resources and energy as well as reducing the need for landfill space.

Other forest products for recycling include wood in many forms from construction sites to 55-m depths in Lake Superior, from logs with fine-textured growth that are much sought after to much more common products that clutter and are sometimes hazardous, and from spruce milled from the millennium Christmas tree on the White House lawn to live oak from the U.S.S. *Constitution* that was launched in 1797.

Recycled wood is converted into products from fuel to fine furniture, and from carvings and sculpture to composites with plastics and concrete.

Recycling

Problems in Recycling Wood

Major sources of wood for recycling are used pallets from commodity distribution channels and all types of wood from municipal solid waste collection sites. Pallets during their lifetimes could have carried hazardous materials, and there could have been spills of undesirable substances onto pallet frames. However the likelihood of such occurrences is remote.

Similarly municipal solid waste may have unknown constituents that could impact adversely on derived products that find their way into processing and use streams. Panel products containing adhesives that were formulated with formaldehyde, wood containing preservatives to protect against insects and decay, painted wood from older structures that were painted with paint containing lead, and wood that emits volatile organic compounds to the air or produces ash with undesirable components on burning must all be handled and used judiciously.

On 12 February 2002 manufacturers of chromated copper arsenate (CCA)-treated wood products reached a voluntary agreement with the US Environmental Protection Agency to stop the use of these products in residential applications by the end of 2003. This could lead to a massive disposal problem when existing CCA-treated products reach the end of their service lives, or if they are replaced sooner with products such as copper-based preservatives with organic biocides that do not contain arsenic. But consumers can benefit from safe recycling of these and other contaminated products through such approaches as safe combustion of hazardous waste for fuel or reconstituting the wood products for other nonresidential applications such as marine pier pilings and highway sound barriers.

Despite some recognized problems in recycling wood products, with proper attention to circumventing the potential dangers, recycled wood is gaining momentum and increasingly contributing to the overall conservation of material and energy.

Recovery of Wood from New Building Sites

In the USA wood is a favorite material for residences. Single family detached homes usually have some wood building components. Wood framing is common for walls, and almost universal for roofs. Ideally wood components would be furnished to these construction sites so that they could be fastened together without waste. But this is rarely the case except for manufactured homes. Most housing construction sites are a treasure trove of sawn ends and other trimmings of clean wood in various forms that are well suited for recycling.

Recovery of Wood from Building Demolition and Restoration

Other building sites also have wood suitable for recycling, but the residues from these sites are less advantageous. Where buildings are being demolished to free land for other purposes, or, to some degree, where buildings are being renovated, wood is generally available. However often it is in admixtures with other contaminating materials such as gypsum wallboard, plaster, carpeting, plastics, steel, and concrete.

Deconstruction of Buildings

Deconstruction of wood construction components in buildings that are being renovated or razed is often a good source of high-quality forest products for reuse. Planned disassembly to yield wood without attachment to other materials is a means of avoiding problems in recycling such are normally encountered with wood from demolished buildings.

But there are other problems. While larger timbers command a high price and are regularly recycled wood members of smaller cross-section are seldom reused. One reason is because such lumber often sustains some consequential damage in both the construction and deconstruction processes that makes it less competitive with new products such as low-cost studs for house wall construction.

In a study to determine strength properties and market value of timbers deconstructed from buildings at military bases, researchers at the US Forest Products Laboratory found some reduction in comparison with new timbers. As a result of damage, the quality of lumber from nonindustrial military buildings was found to average one grade lower than that of freshly sawn lumber. Types of damage included holes resulting from nails or bolts, splits resulting from factors other than drying, saw cuts, notches, decay, and mechanical damage (such as gouges and broken ends).

Recovery of Wood from Municipal Solid Waste

In 1998, 16.9% of municipal solid waste generated in the USA was solid wood. This amounted to 37 009 000 short tons (33 575 000 metric tonnes). Of this amount 11 700 000 tons (10 611 000 metric tonnes) were recovered, 7 025 000 tons (6 373 000 metric tonnes) were combusted, 6 096 000 tons (5 530 000 metric tonnes) were not usable, and 12 191 000 tons (11 060 000 metric tonnes) were available for recovery (**Figure 1**). Wood that is recovered from the waste stream for recycling is economically sound, conserves natural resources, and benefits the environment by reducing requirements for landfill space and by reducing the accumulation of greenhouse gases in the atmosphere.

Recovery of Wood from Industrial Sites

Industrial sites are other sources of wood for recycling. Large components of industrial waste are railroad ties, used pallets, reels, and containers.

Nationally there are 750 million railroad ties in the USA and Canada, and approximately 12 million of these ties, or 1.6%, are replaced annually. Throughout North America, 62% of used ties are sold to contractors who sell them to commercial landscapers

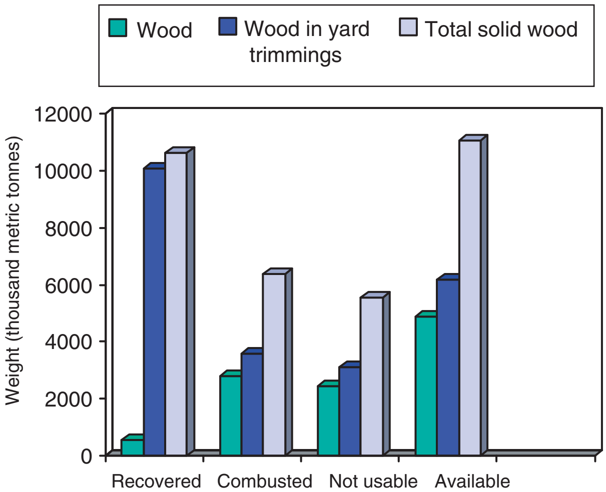


Figure 1 Wood in municipal solid waste (MSW) in 1998 in the USA.

or lumberyards. One-fifth of old ties are landfilled, 15% are sold to cogeneration facilities, and 3% are stored.

Some used pallets, reels, and containers are constituents of municipal waste streams, but often they are disposed through other means. Industry data in the USA indicate that the wood pallet, reel, and container manufacturing industry produces nearly 500 million new units per year and uses over 9 million tons of wood (based on dry moisture content). About half of these units are returnable and are reused as is or they are reused after undergoing repair, but they must all be disposed after a few to several service cycles. Wood pallet suppliers are often asked to provide pick-up and disposal service for broken pallets.

Millions of wood electric and telephone utility cable reels weighing from 22.7 to 227 kg (50 to 500 pounds) each, and a much larger number of smaller plywood reels are discarded each year.

Wood shipping crates used for crating machinery, machinery spare parts and other items are handled and disposed of daily by tens of thousands of manufacturing plants across the USA.

Recycling of Wood from Brush and Tree Trimmings and Tree Removals

The waste stream from brush and tree trimmings and tree and stump removals results from residential tree pruning, street clean-up after storm damage, diseased tree removal, clearings for new construction, and tree pruning along utility rights of way. This wood is often available chipped and used for fuel. Some can be used in papermaking. Some is used as a bulking agent in yard waste composting, and some is screened for landscaping and architectural mulch. For these purposes it may be blended with other wood or manufacturing wood waste such as cedar, and be dyed in various colors. Clean wood fines can be used in animal bedding, or wood flour, and animal feed.

Recycled Products

Products from Used Pallets

Once pallets are recovered from the waste stream, they are most likely to be repaired and reused for their original purpose. Of the wood contained in pallets recovered by the industry in the USA in 1995, 87% was used again in other pallets.

It was estimated that one in four wood pallets sold by firms in the industry consisted of recovered material. About 10% of the wood (by volume) from used pallets was ground or chipped. Tub grinders facilitated separation and removal of nails in recycling pallets. Chipped and ground material was used for products such as animal bedding, mulch, and composite products. Some of the better wood from pallets could also be used for higher-value products such as flooring, paneling, or furniture.

Shop-Fabricated Specialized Retail Sale Items

Sometimes pallet lumber and other reclaimed wood material is made for market sale items. An example is box shapes for purposes that include flower boxes, planters, bird houses and feeders, and storage chests. One manufacturer made fine-quality jewelry boxes from high-quality recycled lumber. Other popular fabricated products from recycled wood are folding chairs.

Unique Products that Use High-Quality Characteristics of Certain Woods Advantageously

Sometimes recycled wood is imbued with desirable characteristics inherent in wood harvested from virgin forests that are difficult to find in second-growth material which is typical of new lumber on the market today. Or lumber takes on desirable properties as a result of its service life in buildings or other applications.

After years of aging, wood takes on a patina that can be pleasing and desirable for specialty products such as flooring. Floors made from recycled pine often have a natural beauty of distinctive coloring together with other special features such as knots and worm and nail holes, and occasional plugged bolt holes. Sometimes the source of older material is not from previous construction, but from logs salvaged from river bottoms. In Kentucky desirable white oak wood from used whiskey barrels is available. In

California deconstruction of sawmills yields old fine grain timbers of Douglas fir, sugar pine, and incense cedar that may be used for fine millwork and other purposes.

In Pennsylvania old barns are disassembled piece by piece to save the flooring, siding, windows, doors, roofing, beams, joists, and even contents such as hog troughs. Deconstruction can take considerably longer than standard demolition by heavy equipment, but deconstruction costs much less than demolition. People who own old barns often want to keep them looking like they did 150 or 200 years ago. If a barn is not structurally suited for reconstruction, its materials are used for repair parts, new construction, siding, flooring, or structural or decorative beams.

Sunken Logs from Lake Superior as a Source for Recycled Wood Products

In Chequamegon Bay on the Wisconsin shore of Lake Superior a company recovers sunken logs from a depth of 18.3 m (60 feet). Because the logs have been in cold water from as long ago as the 1880s to as recently as the 1930s they are well preserved. Logs are sold at premium prices to furniture makers, architects, contractors, and instrument makers in the USA and Japan. The wood includes 12.2-m (40-foot) lengths of red oak and other logs of white pine, richly figured maple, hemlock, yellow birch, and red elm. Because this maple wood is so fine grained, compared to wood from the remaining forest, it is highly valued for specialty purposes such as violin making. All of the woods are highly prized by artisans, custom furniture makers, and makers of other musical instruments.

The recycled red oak was used for paneling in the dome where the Calgary Flames ice hockey team plays. Other orders have come from the Getty Museum in Los Angeles, the Boeing Company in Seattle, and the William Gates residence in Seattle.

Composite Products from Recycled Wood

In addition to about 19.7% wood in municipal solid waste from wood and yard trimmings categories in the USA there is about 38% paper and paperboard and close to 10% plastics (**Figure 2**). These three sources of material offer opportunities for recycling into wood fiber–plastic composites.

Laboratory research has demonstrated that with air-laid composite technology composites very similar to commercial composites could be made from demolition wood waste and waste plastic from milk bottles (polyethylene) and beverage bottles (polyethylene terephthalate). Waste materials consisting of waste paper, polyethylene from milk bottles, and polypropylene from automobile battery cases or ketchup bottles could be melt-blended into promising products. Generally the properties of the recycled composite products are comparable to those of the original plastics.

A composite wood–concrete wall forming system has performed successfully on the international market. The original insulated concrete form has been manufactured in Canada since 1953. The low-density cement-bonded wood fiber composite is made from postindustrial recycled waste lumber and Portland cement. The product is resistant to fire, mold, and decay.

At an international builders' show in Atlanta, Georgia in February 2002, a large US forest products company demonstrated new composite decking

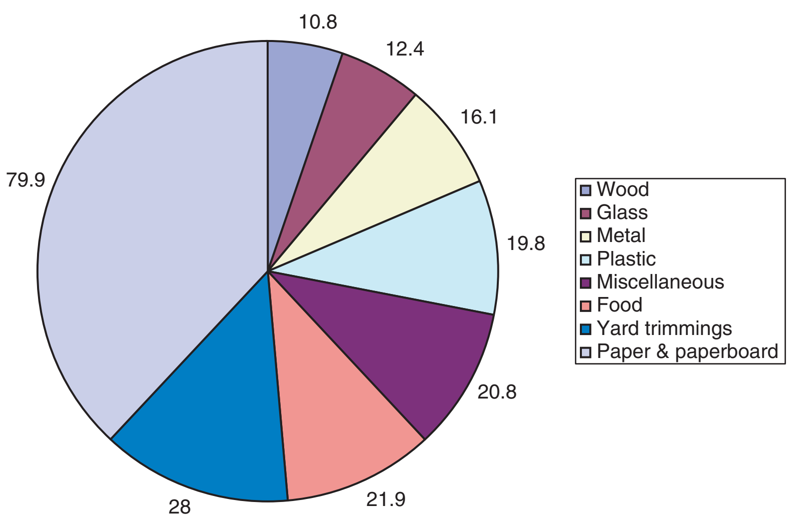


Figure 2 Categories of municipal solid waste (MSW) generated in the USA in 1996.

manufactured from polyethylene plastic and wood fiber residues. It has been marketed throughout the US through a major home-building products chain since March 2002.

The termite-proof material is marketed as not susceptible to decay, splintering, swelling, twisting, or warping. It is specially designed to acquire the weathered look of natural wood, and it is slip-resistant when wet. It is marketed as a system with other composite accessories. Consumers may choose spindles or square balusters and choices of rails, post caps, and post collars. The decking may be installed with nails or screws, and painting of the surface is not required.

Recycling into Mulch, Compost, Wood Flour, Chips, and Shavings

Mulch Mulch is commonly composed of recycled wood particles that are used in landscaping around plants, shrubs, and trees to retain moisture and suppress weeds. Some companies manufacture a blend of recycled wood and paper fibers as a mulch to enhance seed germination and minimize erosion on revegetation projects. These products soak up water, allowing seed and fertilizer to form a homogeneous slurry that enables a uniformly distributed stand of grass, suitable for turf lawns and all general-purpose planting.

Wood chips make excellent mulch that resists compaction, remains in place, and weathers to an attractive silvery-gray color. Sawdust is often readily available and may be helpful in acidifying the soil around rhododendrons and other acid-loving plants. Sawdust, however, tends to cake, making it harder for water to soak into the ground. Sawdust is low in nitrogen, so it robs nitrogen from the soil as it decomposes. Therefore, more nitrogen fertilizer may be needed. A 7–15-cm (3- to 6-inch) layer of sawdust does work well, however, for mulching pathways.

Mulches colored with natural colorants are popular for landscaping and special uses such as ground covering under playground equipment.

Compost Compost from recycled wood is a blend of chips mixed with other organic materials such as horse, chicken, and turkey manures. Compost keeps the soil loose and allows more retained moisture. Compost materials are decomposed and composted to create a dark product that is commonly used for potting plants and adding nutrients to the soil. During composting, microorganisms (bacteria, fungi, actinomycetes) from the soil eat the organic (carbon-containing) waste and break it down into its simplest parts. This produces a fiber-rich, carbon-containing humus with inorganic nutrients like nitrogen, phosphorus, and potassium.

Wood chips, sawdust, and bark are used as bulking materials in composting sewage sludge, although some governmental jurisdictions may have regulations against this practice.

Wood flour Wood flour is a by-product of wood processing. It consists of fine screened wood particles that are dried to an unusually low 6–8% moisture content.

Wood flour is commonly used as a filler material. One major outlet has been for mixing with glues and adhesives. More recently wood flour is used as a filler with plastics. A manufacturer in Wisconsin makes automotive interior panels such as side door panels with polypropylene and 40–55% wood flour. A large millwork manufacturer in Minnesota makes door sills and windows with waste polyvinyl chloride and wood flour. Plastic lumber is another product that may use wood flour. A company in Billingfors, Sweden makes a recycled wood flour–polyethylene plastic compound for use in further processing to plastic products.

Chips By far, the primary use of wood residue is burning for energy, and chips are a convenient form for use in combustors of advanced design. Wood chips from slabs, edgings, and trim ends are also often used for pulp to make paper. Some wood chips are pyrolyzed to make extenders that can substitute for up to 50% of the phenol in phenolic resin adhesives.

Shavings Shavings often result from turning poles on a lathe as in the manufacture of logs for rustic building construction. These residues often are used to advantage for higher moisture content fuel. Planer shavings from millwork, molding, and other product manufacture make good dry fuel.

Compressed Logs, Charcoal, Wood Briquettes, and Wood Pellets

Compressed logs Fireplace logs made from wood residues are popular retail items in areas where fireplaces are common. They may be made entirely of wood, or use wood in combination with 50% or more wax. The use of wax detracts from the environmental advantages gained as a result of displacing nonrenewable fossil fuels, but wax logs do burn with fewer emissions to the air.

Wood briquettes Wood briquettes are usually made in the same machines that are used to make all-wood fireplace logs. They are used primarily as stoker-fed fuel for industrial boilers.

Wood charcoal Charcoal briquettes have limited markets in the USA, but they can be readily manufactured from waste wood. A disadvantage is the difficulty in preventing high rates of air pollution in charcoal manufacture.

Wood pellets Wood pellets are made from dry wood residues, and, optimally, they are made from wood with a minimum of bark. Pellets are a desirable form of wood fuel, and modern stoves and furnaces for burning pellets have automatic feed and control modules. Pellets may therefore be burned without undue exertion. Moreover they are usually cost-effective, and the combustion units are reliable. Usually there is little ash, especially if excessive amounts of bark in pellet manufacture are avoided.

Animal Bedding

When wood is placed in contact with soil, the action of bacteria in the decomposition of the soil traps much of the soil nitrogen. This can cause a condition known as 'nitrogen starvation' for plants growing in the soil. An attractive solution for this problem is to use the wood as animal bedding prior to spreading it on the soil. Wood bedding reduces manure runoff and helps to control odors.

Dry wood, especially that from planer shavings, tends to get dusty and is good for poultry bedding and some other domestic animal bedding.

Although the smell of cedar makes it a preferred species for use in home pet care, other species may be used. The freedom from splinters and the clean smell of aspen and cottonwood make them desirable for some animals, including mink that are raised for fur production.

See also: **Non-wood Products**: Energy from Wood. **Packaging, Recycling and Printing**: Paper Recycling Science and Technology. **Wood Use and Trade**: Environmental Benefits of Wood as a Building Material.

Further Reading

Bratkovich SM (2001) *Utilizing Municipal Trees: Ideas from Across the Country*, Report no. NA-TP-06-01. St Paul, MN: Northeastern Area State and Private Forestry.
Bush RJ, Araman PA, and Reddy VS (1997) Pallet recycling and material substitution: how will hardwood markets be affected? In: Wiedenbeck J (ed.) *Eastern Hardwoods: Resources, Technologies, and Markets*, pp. 67–73. Madison, WI: Forest Products Society.
Denison RA and Ruston J (1990) *Recycling and Incineration: Evaluating the Choices*. Washington, DC: Island Press.
Falk RH (1999) The properties of lumber and timber recycled from deconstructed buildings, Research Bulletin no. 212. In: Walford GB and Gaunt DJ (eds) *Proceedings of the Pacific Timber Engineering Conference*, pp. 255–257. Rotorua, New Zealand: New Zealand Forest Research Institute.
Ince PJ (1994) *Recycling and Long-Range Timber Outlook*, Background Research Report 1993 RPA Assessment Update, US Department of Agriculture Forest Service, Technical Report no. FPL-RP-534. Madison, WI: US Forest Products Laboratory.
Jones CH (ed.) (1996) *National Wood Recycling Directory*. Washington, DC: American Forest and Paper Association.
Rosenberg N (1976) *Perspectives on Technology*. Cambridge, UK: Cambridge University Press.
Sherwood GE (1984) *Renovate an Old House*? US Department of Agriculture, Forest Service Home and Garden Bulletin no. 212. Washington, DC: US Government Printing Office.
US Department of Agriculture (1991) *Agriculture and the Environment: The 1991 Yearbook of Agriculture*. Washington, DC: US Government Printing Office.
US Department of Agriculture (1992) *New Crops, New Uses, New Markets – Industrial and Commercial Products from US Agriculture: The 1992 Yearbook of Agriculture*. Washington, DC: US Government Printing Office.
US Environmental Protection Agency (1995) *Manufacturing from Recyclables: 24 Case Studies of Successful Recycling Enterprises*, EPA-R-95-001. Washington, DC: US Government Printing Office.
Youngquist JA, Myers GE, Muehl J, Krzysik A, and Clemons CC (1993) *Composites from Recycled Wood and Plastics*, Report no. IAG DW12934608-2. Cincinnati, OH: Environmental Protection Agency.

Drying

M R Milota, Oregon State University, Corvallis, OR, USA

History of Wood Drying

Evidence exists in furniture, carvings, and artwork that survive from millennia ago that the importance of drying and how wood responds to changing ambient conditions has long been recognized. Until the turn of the twentieth century, however, only limited quantities of wood were artificially (kiln) dried. Natural (air) drying was generally sufficient because the practice of heating all rooms in a house was not common. The smoke kiln was developed in Europe 200 to 250 years ago. As the name implies, a fire burned under a perforated floor and the wood was stacked above the floor. In the late nineteenth century, humidity was added to help control the drying rate. A few smoke kilns were still in use in the United States in 1926, but they had disappeared in Europe.

The lumber dry kiln as we know it today has its origins in the late nineteenth and early twentieth century. By the time of World War I, drying methods had been established and texts from the 1920s have much the same basic information as those written today. Since that time our understanding of what happens at the cellular level has advanced, improvements have been made in the equipment, and techniques have been developed for many species. The advancement of other types of dryers, for example veneer and particle dryers, was in parallel with the development of these industries during the twentieth century.

Why Wood is Dried

It is generally desirable for the shrinkage associated with moisture loss to occur before products are produced. For example, furniture parts will not fit together if they change moisture content after manufacturing. It is most desirable to dry the wood to the moisture content it will eventually achieve in service. This depends on relative humidity at the location of installation and varies from summer to winter, but ranges from 5% to 15% for indoor applications. In temperate climates, 7% to 9% is a common indoor equilibrium moisture content.

As wood dries, some defects such as splitting and warping are likely to happen in some pieces. It is desirable for these to occur prior to using the wood in an appearance application.

In some cases wood is dried to improve its ability to accept adhesives, paints, preservative treatments, or finishes. Moisture content is critical for adhesive penetration and most surface coatings need to be applied over dry wood. The quality of a machined surface will not be good if the moisture content is not correct for the machine tools. The strength of wood increases as it is dried. This allows dry wood to be assigned higher strength properties than green wood in some applications. If green wood is used at the dry wood design values, excessive deflection or even failure might result before it has a chance to dry in service.

When sufficiently high temperatures are used, insects and their eggs are killed as are some fungi. The temperatures normally used in kiln drying are sufficient to accomplish this as well as set the pitch. When the wood is at 20% or less in moisture content, fungal attack is prevented and most insects lose interest in the wood. Setting the pitch means that the wood resins no longer flow at in-service temperatures. For some species the drying process gives a desirable color to the wood, for example in walnut (*Juglans* spp.), maple (*Acer* spp.), and red alder (*Alnus rubra*). Drying also reduces the shipping weight.

How Water Moves in Wood

For wood with a wet surface, a boundary layer of air near the surface of the wood limits the drying rate. Increased airflow reduces the thickness of the boundary layer and lower relative humidity increases the driving force for mass transfer across it. This boundary layer is most important for small pieces of wood, such as particles or veneer, for which the internal resistance to drying is minimal and when the moisture content is high.

Moisture moves from wetter areas to dryer areas. Within the wood, free (liquid) water can move through the capillary structure if the wood is permeable enough. This can keep the surface wet and the drying rate high. This mode of mass transfer is important in fast-drying woods such as the pines (*Pinus* spp.). Capillary forces, and to a certain extent heating of the wood, cause pressure gradients which result in free water movement. Smaller capillaries tend to pull water from large capillaries so that evaporation from pits near the surface can pull water from the interior of the wood. Once some cells lose most of the free water, a continuous pathway of water is no longer present and moisture cannot move as a liquid.

Water can also diffuse through the wood as a vapor or in the bound state. Vapor diffusion requires a continuous gaseous pathway such as open vessels or cell lumens connected by unaspirated pits. Bound water diffusion occurs through the cell wall material. While vapor diffusion coefficients are much greater than bound water diffusion coefficients, the pathways for vapor diffusion are small compared with those for bound water. Therefore, bound water diffusion dominates moisture movement at low moisture contents. The difference between the equilibrium moisture content and the wood moisture content is often used as the driving force for diffusion at moisture contents below fiber saturation. Diffusion rates increase with increasing temperature, moisture content, and wood permeability. High temperatures (70°C and higher) are used as the wood gets low in moisture content to prevent prolonged drying times.

All modes of moisture movement may be occurring simultaneously at different locations within a piece of wood. Near the center of a piece the moisture content might be high enough for free water movement to occur. At some plane the moisture content is too low to support free water movement and the liquid water evaporates. From there it can move to the surface in the vapor or bound phase.

Lumber

Lumber refers to wood that is typically greater than 5 mm in thickness and sawn. It is either air dried, kiln dried, or dried by a sequence of these. In either type of drying the wood is stacked so that there is airflow around each piece. In developing regions, lumber may be air dried by leaning the pieces almost vertically against a support. In industrial facilities, it is common to lay the pieces horizontally and use narrow strips of dry wood as spacers (**Figure 1**). These are called stickers or fillets. Almost all kiln drying is done on stickers which range from 12 to 24 mm in thickness and 36 to 100 mm in width. Wider stickers are used on heavy woods with low basic density to reduce crushing. The wood is stacked in cuboid packages so the air can move horizontally, perpendicular to the long axis of the wood.

Quality Considerations

Maintaining product quality is a major concern in lumber drying. Stains (chemical or biological) need to be prevented by rapid drying; however, slow drying is often needed to prevent structural damage. Water evaporating from the surface can create enough capillary force to cause the cells to collapse early in the drying process (**Figure 2**). As the surface dries below the fiber saturation point and shrinks, surface checks may appear on the face of the board. These are splits which may be from one to several centimeters in length and from very narrow to a millimeter or two in width (**Figure 3**). The likelihood of surface checking decreases as the wood gets drier. They are most likely to appear in the rays on the bark side of wide, flat sawn pieces.

Early in drying while the shell of the wood has tensile stress, the core of the piece has compressive stress. The tension in the shell prevents it from shrinking as much as a stress-free section. The compression in the core causes it to decrease slightly

Figure 1 Lumber is stacked in cuboid packages with the layers separated by stickers so air can move between the layers.

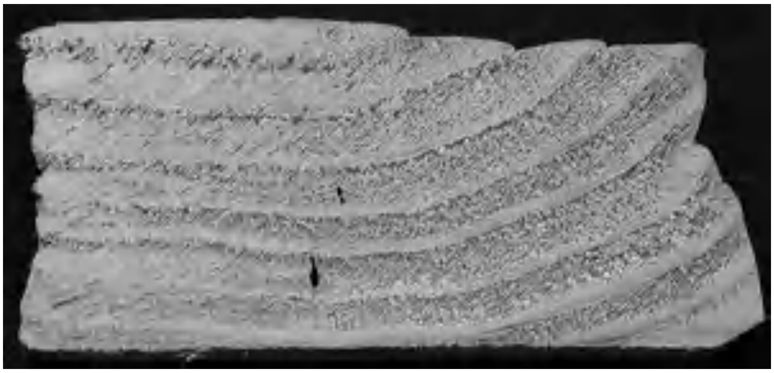


Figure 2 Capillary forces, especially in low density species with high moisture content, can result in collapse. Wood can be steamed to recover minor collapse if no cracks have occurred.

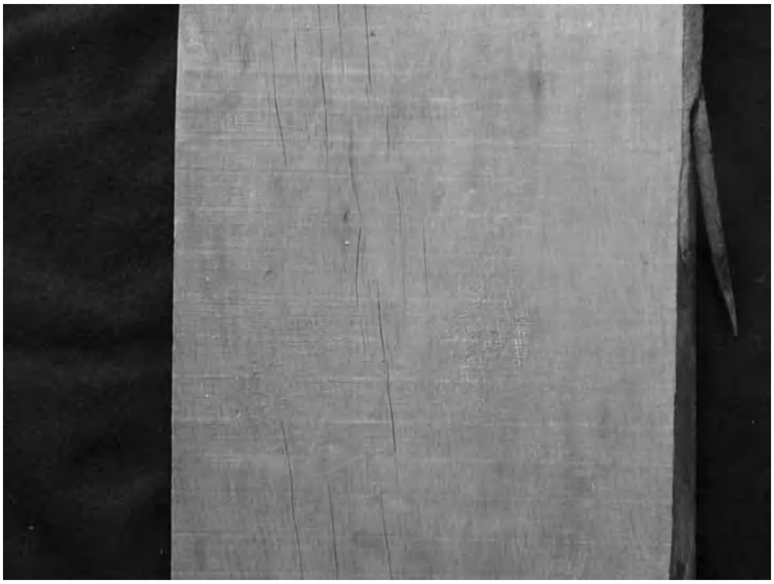


Figure 3 Surface checks can occur if the surface of the board shrinks too much or too quickly compared to the center. This can happen early in lumber drying and the checks close part way through the drying cycle. They are still considered a defect after they close.

in size due to creep and mechanosorptive effects. Later in drying, the core begins to dry below the fiber saturation point and shrink. However, it has already changed size somewhat and the additional size change due to shrinkage causes the stress state in the wood to reverse. After the core begins to shrink there is tensile stress in the core and a compressive stress in the shell. Surface checks close and internal checks, called honeycomb, can form on the inside of the piece (**Figure 4**).

At the end of drying, even if there is no moisture content difference between the shell and the core, there is still tensile stress in the core and compressive stress in the shell. The term 'casehardening' has been applied to this even though the shell is no harder than the core. If the lumber is not resawn or machined extensively, this is not a defect. In many products, however, internal stress will cause warp in pieces that are resawn or machined. Casehardening is relieved at the end of drying with a conditioning step, a process in which the moisture content of the wood is raised by exposing it to using a high relative humidity at a high enough temperature ($>70^\circ C$). The degree of casehardening in wood is determined by the prong test or a similar method (**Figure 5**). The prong test should be evaluated 24 h after cutting to allow for moisture and mechanical equilibrium.

Pieces of lumber can change shape during drying (**Figure 6**). The difference in tangential and radial shrinkage results in diamonding and cup. Differences in longitudinal shrinkage from one side or face of the board to the other results in crook or bow. Spiral grain in the tree leads to twist in lumber. These defects are worsened by drying to low moisture

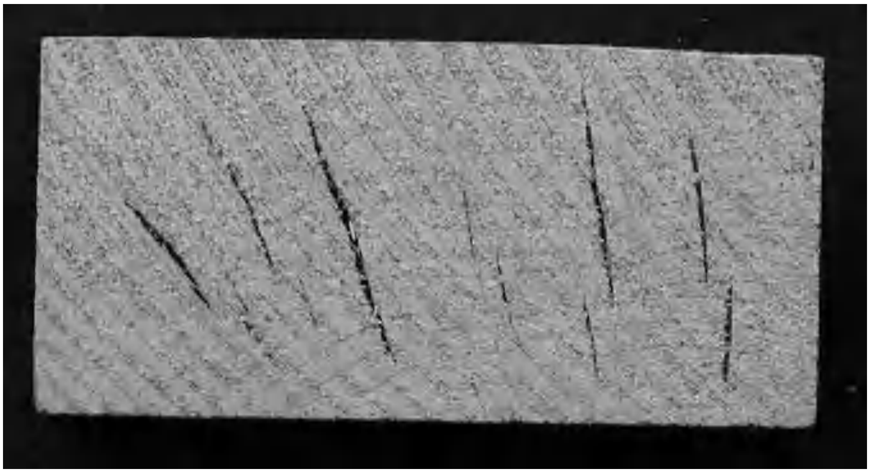


Figure 4 Honeycomb can occur if the internal tensile stress is high enough. This occurs when the core of the piece is near or below the fiber saturation point. These cracks would not be visible on the end of the piece.

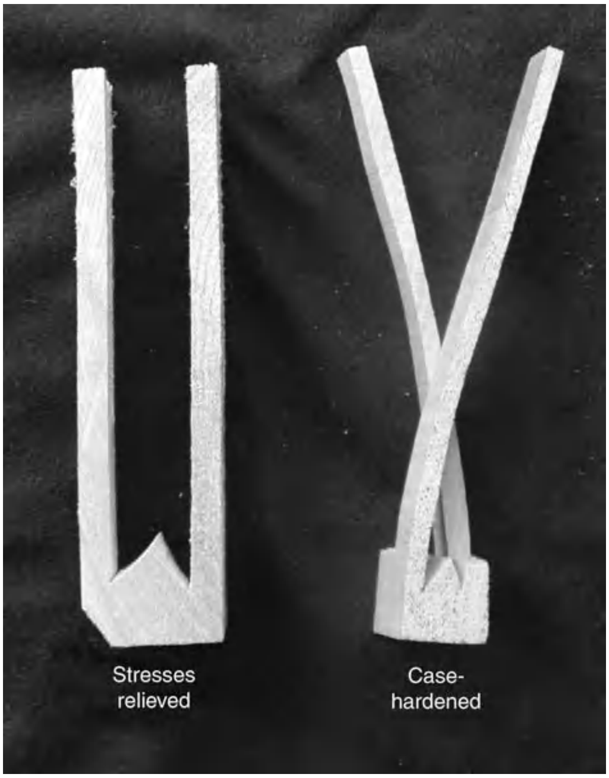


Figure 5 Casehardening can be detected by the prong test. In some regions it is more common to saw the board into two pieces rather than cutting prongs.

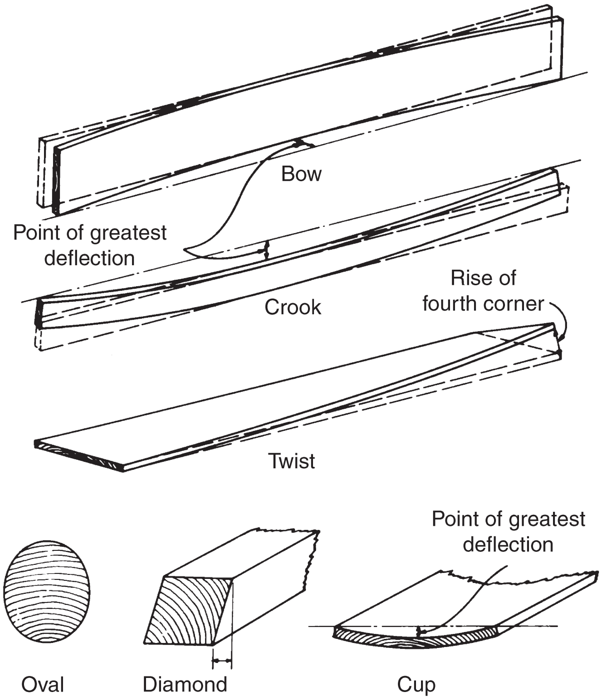


Figure 6 Lumber can distort due to differences in the amount of shrinkage in different locations of directions. From Simpson WT (ed.) (1991) *Dry Kiln Operator's Manual*. US Department of Agriculture.

contents. Stacking boards so they are restrained by the boards above them helps to minimize warp. In some regions it is common to put concrete or steel weights on top of the stacks to reduce warp.

Air Drying

Air drying is used on woods that need to be dried slowly to avoid defects such as collapse and surface checks. To dry slowly in a kiln is very expensive from a capital investment and energy standpoint. During air drying the wood is exposed to uncontrolled conditions and large losses in wood value can occur. For example, one day of hot, windy, dry, weather can cause oak (*Quercus* spp.) to check so badly that it cannot be used for a high-quality product. Conversely, extended humid weather with little wind can result in lumber that is stained.

Air drying is done in open areas with good airflow. The package arrangement is a trade-off to achieve good airflow, forklift access, and to maximize solar gain to promote faster drying. When slower drying is desired, the piles might be covered with a porous cloth to reduce airflow. In rare cases, water mists are used to raise the relative humidity so freshly sawn lumber does not dry too fast. Drier lumber is sometimes placed on the windward side of the yard and the fresh, wetter lumber on the cooler, more humid leeward side to reduce the drying rate and avoid degrade. The inventory in an air yard must be controlled so wood is removed when it reaches the appropriate moisture content.

For some outdoor applications, air drying alone is sufficient. However, the lowest moisture content that can be achieved is about 12% in most regions. This is too high for applications such as furniture and flooring. Also, as the wood approaches the ambient equilibrium moisture content it dries very slowly which would result in large inventories and much land area for drying. Therefore air drying is often followed by kiln drying.

Kiln Drying

Kiln drying occurs in a building with a way to control the temperature, humidity, and airflow (**Figure 7**). The temperature most often is controlled by steam in pipes or coils. The humidity is controlled by limiting how much water leaves the building through vents. If the wood is not losing moisture fast enough, live steam or a water mist might be used to raise the humidity. The air is circulated with fans. Modern kilns use electronic instrumentation and controls; however, pneumatic instrumentation is the norm in many parts of the world.

The packages of wood are loaded into the kiln by forklift (package kilns) or rolled in on tracks (track kilns). Package kilns are more common for species with longer drying times, making the turn around time between charges less important. Package kilns occupy less land area. Track kilns are more common for softwoods. There are some semicontinous track kilns; however, almost all kiln drying is done as a batch process. That is, the kiln is loaded with a charge of wet lumber, it is dried, then removed.

Lumber is kiln dried using a set of environmental conditions called a schedule (**Figure 8**). The schedule is highly dependent on the species and thickness and somewhat dependent on the width and the eventual product. The purpose of the schedule is to minimize defects in the product while also minimizing drying time and cost. Published schedules are available for most species and thicknesses of wood; however, in practice most mills have their own schedules.

While the wood is at high moisture content, the temperature in the kiln is kept low and the relative

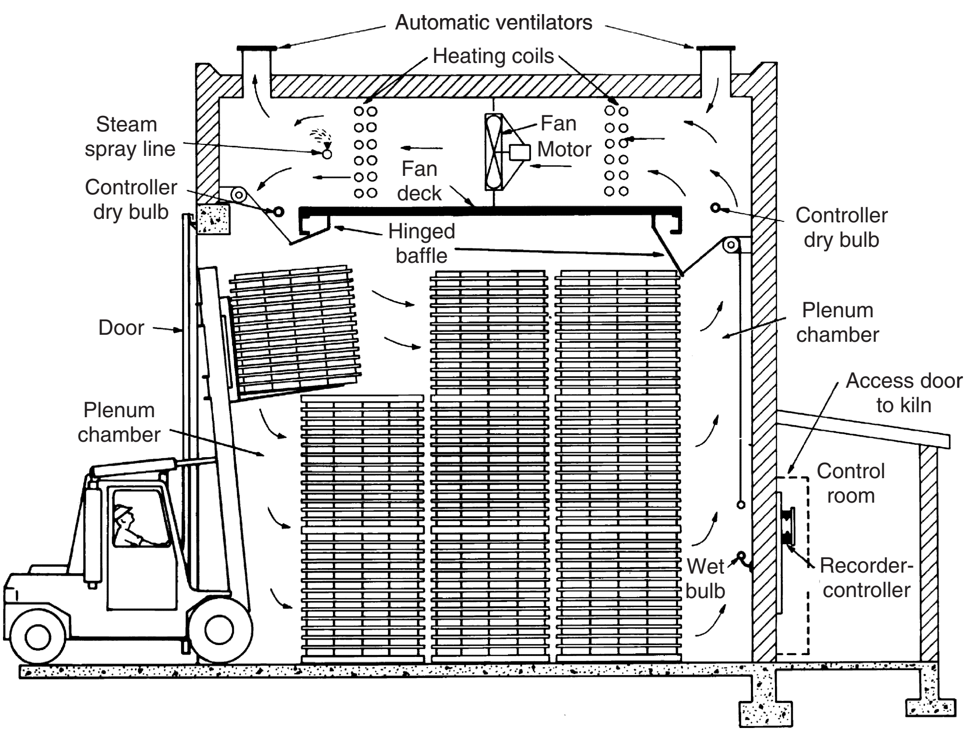


Figure 7 Package lumber kiln. From Simpson WT (ed.) (1991) *Dry Kiln Operator's Manual*. US Department of Agriculture.

Moisture content-based drying schedule					
Step	MC, %	T_{db}, °C	T_{wb}, °C	EMC, %	RH, %
1	above 35	43.3	41.1	17.6	87
2	35 – 30	43.3	40.6	16.3	84
3	30 – 25	48.8	44.4	13.5	77
4	25 – 20	54.4	46.6	10.1	65
5	20 – 15	60.0	43.3	5.8	38
6	15 – dry	82.2	60.0	3.5	26
Equalize and condition as necessary					

Time-based drying schedule					
Step	Time, hrs	T_{db}, °C	T_{wb}, °C	EMC, %	RH, %
1	0 – 12	76.7	73.3	14.1	86
2	12 – 24	76.7	71.1	11.4	78
3	24 – 48	79.4	71.1	9.1	69
4	48 – 72	82.2	71.1	7.7	62
5	72 – dry	82.2	60.0	4.5	36
Equalize and condition as necessary					

Figure 8 Drying schedules. The upper schedule is based on the moisture content of the wood in the kiln. The lower schedule is based on time. Moisture-based schedules are used for species that are difficult to dry. Time-based schedules are used for species that are easy to dry. EMC, equilibrium moisture content.

humidity high to restrict the drying rate. After the surface has dried and the wood has lost about one-third of its moisture, the relative humidity is gradually lowered. When the free water has evaporated from the center of the piece, the temperature is raised and the relative humidity reduced further. After some of the pieces reach the desired moisture content, the humidity is raised to prevent the driest pieces from getting even drier while the wetter pieces continue to lose moisture. This is known as an equalization step. Finally, after the moisture content distribution among the pieces is acceptable, a conditioning step may be employed to eliminate internal stress. The acceptable moisture content distribution depends on final moisture content and end use. For furniture, 7% plus or minus 0.5% to 1% might be necessary whereas for structural lumber 15% plus or minus 2% to 4% or more may be acceptable.

The above schedule description is for species that are prone to defects which result from fast drying, such as oak and eucalyptus (*Eucalyptus* spp.). Many species dry quite easily and the drying schedules are very simple. For example, *Pinus taeda* and *P. radiata* can be dried rapidly with little defect. In easy-to-dry species the kiln is often brought up to the final temperature as rapidly as practical, then the relative humidity is lowered to achieve a high drying rate.

Initial kiln conditions for difficult-to-dry woods may be as low at 35°C with a relative humidity of 85% while easy-to-dry species may be dried with initial temperatures of 120°C or occasionally higher. At the end of drying and before equalization, most dry kiln schedules for difficult-to-dry species call for a temperature greater than 70°C but generally not higher than 85°C. Air velocity varies from 2 to $8\,m\,s^{-1}$ through the sticker spaces with the greater values used for rapid drying. Kiln drying takes from 16 h to 60 days, depending on the species and thickness.

Sorting the lumber into groups with similar drying properties is desirable prior to drying. Wood is almost always sorted by species and thickness. Some other possible sorting criteria include: initial moisture content, length, width, heartwood content, sawing pattern, or grade. The equipment at the mill and the number of kilns limit how much sorting can practically be accomplished. It is also possible to sort wet pieces after drying and before planing and redry them. This reduces the overall kiln time required to produce a given quantity of dry lumber, reduces the number of overdried pieces, and eliminates the problem of wet pieces in the final product.

Veneer

Veneer is cut with a knife and ranges from 1 to 5 mm in thickness. Some veneer, most likely from a slicing process, is dried in the same manner as lumber, i.e., placed on stickers and loaded into a kiln. Several veneer layers are left together when dried in this way.

More commonly, however, veneer is dried in a conveyor dryer. The veneer is placed on rollers or wire mesh at one end of the dryer and moves through. There may be multiple decks of veneer vertically and three to five zones of different temperature along the dryer length. Rolls or mesh hold the veneer flat and play a significant role in heat transfer to the wood. A moisture meter at the end of the dryer automatically identifies wet pieces which are then redried. The moisture meter is also used to control the speed of the veneer through the dryer and hence its moisture content.

The airflow in older veneer dryers, called longitudinal dryers, is parallel to the surface veneer. Because veneer is thin, the external boundary layer is more significant than internal resistance to moisture movement and newer dryers (called jet or impingement dryers) have manifolds above and below the veneer that direct the airflow perpendicular to it. The temperatures in veneer dryers are limited to approximately 200–260°C because visible hydrocarbon emissions would be generated at higher temperatures. The highest temperatures are found in the early zones where evaporation keeps the wood cool. High wood temperature can inactivate the veneer's surface and prevent the adhesive from wetting the wood and penetrating. Overdried pieces may reach too high a temperature and show surface inactivation. The relative humidity is necessarily low because the dryers are operated at ambient pressure and well above the boiling point of water. Because of this, an attempt is made to minimize the amount of intake air and operate with a high absolute humidity.

Particles

Rotary dryers are often used for particulate material. Particles and hot air are continually fed to the drum. These large rotating drums have lifting flights which carry the particles upward as the drum rotates. The particles leave the lifting flight near the top of the drum and fall through the air stream. Heat is transferred to the particles both from the air and from contact with the dryer. The drums may have concentric sections so that the particles and air traverse the length of the drum up to three times. Residence time is on the order of minutes. Friable material, such as wafers or flakes, may be dried on trays or belts instead of in drums. Very fine material, such as fiber board furnish, might be dried in a tube dryer in which the air carries the fiber through the tube in seconds.

Moisture Content Measurement

Measuring moisture content is an important part of the drying process. Green lumber is sometimes sorted based on moisture content by simply weighing the pieces, measuring their size, and calculating a green density. In this case, accuracy is not critical and it is simply assumed that basic density does not vary among the pieces. At this point, no other good automated way exists to estimate the moisture content of green wood.

Hand-held meters (**Figure 9**) are used to measure the moisture content of dry wood. Conductance-type moisture meters have needles that are pressed or pounded into the wood and the electrical conductivity of a circuit including the pins and the wood is measured. The pins are about 3 cm apart and put into the wood to the depth at which the reading is desired. Pins up to 100 cm long are available for thick lumber while 0.5-cm needles might be used for veneer. Hand-held capacitance-type moisture meters are used by placing the meter on the surface of the wood. The meter generates an electric field into the wood to a depth of 2–3 cm. Based on the energy lost to the wood, moisture content is estimated. Several frequencies might be used simultaneously to reduce the effects of temperature and basic density. Pin-type moisture meter readings are corrected for species and temperature. Capacitance-type moisture meter readings are corrected for basic density and temperature. In modern meters these corrections are internal to the meter with user input for species, temperature, and/or density. Hand-held meters work well up to about 25–30% moisture content.

A capacitance-type moisture meter is often used in production to check the moisture content of each piece of dry lumber. If done before planing, the meter can be used to sort wet pieces for redrying. For veneer, the production line meter is often of conductance type with metal brushes instead of pins. It is located at the outfeed of the dryer. In particle

Figure 9 Pin-type (left) and capacitance-type (right) hand-held moisture meters.

operations, an infrared sensor is used to measure the moisture content of furnish as it moves along a belt.

Inside veneer and particle dryers, there is no moisture content measurement. The traditional method in lumber kilns is to weigh 0.5–1-m-long samples of the wood being dried (**Figure 10**). Approximately six to 12 samples are used to monitor a kiln charge. These samples are intended to represent the wettest (or slowest to dry) lumber and driest (or fastest to dry) lumber in the charge. The wettest pieces will control the schedule because these are most likely to surface check, collapse, and honeycomb. The driest pieces tell the operator when to start the equalization step. This technique is well developed and described in many texts. Variations on this technique include putting pins in the samples to measure conductance or having load cells inside the kiln to weigh the samples without the operator entering the kiln.

Some in-kiln systems utilize metal capacitance plates inserted into the lumber stack. Recently developed in-kiln meters can give a moisture content from about 60% to 80% to dryness and are accurate enough that operators typically do not enter the kiln with a hand-held meter. In-kiln will probably become standard for easy-to-dry species; however, for difficult-to-dry species operators want to know the variability and especially the moisture content of the wetter pieces. Therefore, acceptance into the hardwood industry is uncertain. Any of the in-kiln systems can be integrated with the kiln controller so that the schedule can be advanced based on the moisture content or the rate of moisture content change.

Energy and Environmental Considerations

Drying is a very energy-intensive process and uses up to 85% of the manufacturing energy. Energy use varies greatly, depending on dryer conditions. Difficult-to-dry products require more energy, 7–9 MJ per kilogram of water removed, because more make-up air is required due to the low temperature and humidity. Easy-to-dry products might require 3–6 MJ per kilogram of water removed with particles being on the low end of this range. Of this, approximately 2.3 MJ is used to evaporate each kilogram of water and the remainder consumed by heating make-up air, the kiln structure, the wood and water, by heat transfer through the structure, and electrical inefficiencies. Some dryers are equipped with heat exchangers to recover some of the energy in the vent gas. They have the greatest potential on low temperature dryers with large make-up air requirements. Fan speeds are reduced later in drying in lumber kilns to reduce consumption of electricity when high air velocities are not needed.

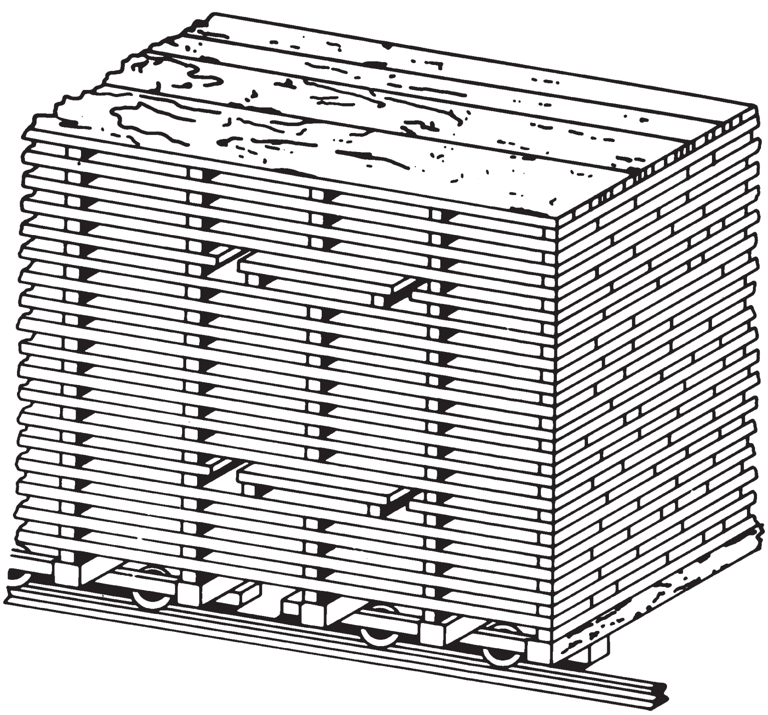


Figure 10 Lumber stack showing placement of kiln moisture samples. Six to 12 samples are weighed and selected to represent the moisture content range in the kiln and are used for determining the step in moisture content-based drying schedules. From Simpson WT (ed.) (1991) *Dry Kiln Operator's Manual*. US Department of Agriculture.

Perhaps the greatest environmental impact of drying is generating energy, either at the on-site boiler or off-site electrical power supplier. Additionally, the exhaust from wood dryers contains a small amount of organic material. Most of this is from volatile material in the wood, such as terpenes, and ranges from 0.1 to $3\,g\,kg^{-1}$ (grams emitted per kilogram of oven-dry wood processed). Release of some organic compounds may be the result of breakdown of the wood, especially at high temperatures. The main breakdown product with toxicity is methanol which is emitted in quantities from less than 0.01 to $0.3\,g\,kg^{-1}$. Methanol generation is very dependent on temperature and the moisture removed. A small amount of liquid effluent may come from some kilns, particularly if they are poorly insulated.

Other Technologies

Dehumidification kilns utilize heat pumps to remove water and recover energy. They are very energy efficient, consuming 1.4–2.3 MJ of electrical energy per kilogram of water removed. The operating cost is higher due to electrical energy costs; however, they offer an attractive alternative for low-volume producers because there is no boiler and the initial capital cost is low. An atmospheric pressure steam generator is sometimes added to these kilns to relieve stress. The effluent is water and must be treated prior to being released into the environment.

Solar kilns are used in tropical and even temperate regions. The slow drying and diurnal changes in temperature and humidity can produce lumber with minimal internal stress. Enough solar energy can be collected to evaporate about 5 kg of water per square meter of collector area per day.

Vacuum kilns operate at a pressure below atmospheric. This lowers the boiling point of water so that wood can be dried quickly at lower temperature. The wood remains stronger at lower temperature and fewer defects develop. Besides the cost of the vessel, a disadvantage of this method is that heat does not transfer in a vacuum and conductive metal blankets or electromagnetic energy is used to heat the wood. Rapid drying rates can be achieved when radio-frequency energy is combined with a vacuum. A variation on the vacuum kiln that has gained popularity is the superheated steam kiln. A partial vacuum is drawn and the remaining gas is circulated with fans. As water vapor is removed, the remaining gas becomes almost all water vapor and total pressure and temperature are used to control the drying rate. High air velocity, $10–20\,m\,s^{-1}$, is needed for adequate heat transfer because of the low air density.

See also: **Solid Wood Processing**: Machining. **Solid Wood Products**: Lumber Production, Properties and Uses; Wood-based Composites and Panel Products. **Wood Formation and Properties**: Physical Properties of Wood. **Wood Use and Trade**: Environmental Benefits of Wood as a Building Material.

Further Reading

Boone RS, Kozlik CJ, Bois PJ, and Wengert EM (1988) *Dry Kiln Schedules for Commercial Woods: Temperate and Tropical*, General Technical Report no. FPL-GTR-57. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory. (Available through Forest Products Society: www.forestprod.org)

Denig J, Wengert EM, and Simpson WT (2000) *Drying Hardwood Lumber*, General Technical Report no. FPL-GTR-118. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory.

Forest Products Laboratory (1999) *Air Drying of Lumber*, General Technical Report no. FPL-GTR-117. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory.

Mujumdar AS (1987) *Handbook of Industrial Drying*. New York: Marcel Dekker.

Siau JF (1984) *Transport Processes in Wood*. New York: Springer-Verlag.

Simpson WT (ed.) (1991) *Dry Kiln Operator's Manual*. Agriculture Handbook no. AH-188. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory. (Available through Forest Products Society: www.forestprod.org)

Skaar C (1988) *Wood–Water Relations*. New York: Springer-Verlag.

Wengert EM and Toennisson RT (1998) *Lumber Drying Sourcebook: 40 Years of Experience*. Madison, WI: Forest Products Society.

Finishing

W C Feist, Middleton, WI, USA

Introduction

Like other biological materials, wood is susceptible to environmental degradation. When exposed outdoors above ground, a complex combination of chemical, mechanical, and light energy factors contribute to what is described as weathering. Weathering is detrimental to the surfaces and appearance of wood. Thus, weathering must be taken into account when considering the protection of outdoor wood but not indoor wood. Weathering of wood is not to be confused with wood decay (rot), which results from fungal organisms acting in the presence of excess moisture and air for an extended period. Under conditions suitable for decay, wood can deteriorate rapidly, and the result is far different from that observed for natural outdoor weathering.

The wide range of wood and wood-based materials and the variety of paints, stains, varnishes, and other finishes available provide a great latitude and flexibility for protecting and beautifying wood and wood structures both indoors and outdoors (interior and exterior). Indoors, many finishes can be used to provide a range of appearance to any wood product. Outdoors, there are stricter requirements for the finish since exposure to the weather (water and sunlight) can severely damage any sensitive finish. Thus, many finishes suitable for indoor use are not at all suitable outdoors. The choice of finishes outdoors must be made in concert with the design, good understanding of the wood materials being used, and knowledge about the weather conditions that will affect the structure.

Exterior Wood Finishes

The main function of any outdoor wood finish is to protect the wood surface, and secondarily, help maintain a certain appearance, and provide a cleanable surface. Although wood can be used both outdoors and indoors without finishing, unfinished wood surfaces exposed outdoors to the weather change color, are roughened by photodegradation and surface checking, and erode slowly. Unfinished wood surfaces exposed indoors may also change color; moreover, unfinished wood is more difficult to clean than is finished wood.

Wood and wood-based products in a variety of species, grain patterns, textures, and colors can be finished effectively by many different methods. Selection of a finish will depend on the appearance and degree of protection desired and on the substrates used. Because different finishes give varying degrees of protection, the type of finish, its quality and quantity, and the method used to apply the finish must be considered when finishing or refinishing wood and wood products.

Protective finishes and coatings for wood used indoors can perform for many years without refinishing or severe deterioration. The durability of finishes on wood exposed outdoors to natural weathering processes, however, depends first of all on the wood itself. Other factors that contribute are the nature and the quality of the finish used, application techniques, the time between refinishings, the extent to which the surfaces are sheltered from the weather, and climatic and local weather conditions.

The primary function of any outdoor wood finish is to protect the wood surface from natural weathering processes (sunlight and water), and help maintain appearance. Weathering erodes and roughens unfinished wood. Despite this, wood can be left unfinished to weather naturally, and such wood can often provide for extended protection of the structure.

The protection that surface treatment provides against light and water will be affected by the weather resistance of the bonding agents used in the finish (e.g., drying oils, synthetic resins, and latexes), as these agents are subject to some degree of photolytic degradation. The mechanism of failure of paints and other finishes has been described in great detail and will not be discussed further here. Protection of wood exposed outdoors by various finishes, by construction practices, and by design factors to compensate for effects of weather has also been addressed in great detail by others.

A variety of finishes can be applied to outdoor wood. These include clear finishes, which reveal and accentuate the natural beauty of wood; stains, which impart a rustic appearance; and paint or solid-color stains, which can be obtained in a multitude of colors. Finishes or coatings are applied to exterior wood surfaces for a variety of reasons. The particular reason will determine the type of finish selected and subsequently the amount of protection provided to the wood surface as well as the life expectancy for the finish. Finishes can be divided into two general categories: (1) film-forming opaque coatings, such as paints and solid-color stains, and (2) natural finishes, such as film-forming varnishes, and penetrating (nonfilm-forming) water repellents, water-repellent preservatives, oils, and penetrating semi-transparent stains.

Film-Forming Opaque Finishes

Paints Paints are common film-forming coatings used on wood that provide the most protection against surface erosion by weathering and against wetting by water. They are also used for esthetic purposes and to conceal certain defects. Paints contain substantial quantities of pigments, which account for the wide range of colors available. Some pigments will essentially eliminate ultraviolet light degradation of the wood surface. Oil-based or alkyd-based paints are a suspension of inorganic pigments in a resin vehicle and a petroleum or turpentine solvent that helps carry the pigment particles and the bonding agent (resin) to the wood surface. Latex paints are likewise a suspension of inorganic pigments and various latex resins, but the solvent or dispersant in this case is water. Paint lifetimes up to 10 years are possible with good-quality paints applied as two coats over a coat of primer paint.

Oil-based paint films usually provide the best shield from liquid water and water vapor. However, they are not necessarily the most durable because they become brittle over time. No matter how well sealed, wood still moves with seasonal humidity, thus stressing and eventually cracking the brittle paint. On the other hand, latex paint films, particularly the acrylic paints, remain more flexible with age. Even though latex paints allow some water vapor to pass through (thus they are sometimes erroneously described as 'breathable'), they hold up better than oil-based paints by swelling and shrinking with the wood. They are also less prone to mildew growth and discoloration from dirt collection.

Paints perform best on edge-grained lumber of low-density wood species such as redwood and cedar. Paints are applied primarily to the wood surface and do not penetrate the wood deeply. Rather, the wood grain is completely obscured and a surface film is formed. This film can blister or peel if the wood is wetted or if inside water vapor moves through the house wall and wood siding because of the absence of a vapor barrier. Original and maintenance costs are often higher for a paint finish than for a nonfilm-forming water-repellent preservative or penetrating stain finish.

Solid-color stains Solid-color stains (sometimes called hiding, heavy-bodied, or opaque stains) are opaque, film-forming finishes that come in a wide range of colors and are essentially thin paints. Solid-color stains are made with a higher concentration of pigment than are the semitransparent penetrating stains discussed below, but a somewhat lower concentration of pigment than that of standard paints. As a result, solid-color stains obscure the natural wood color and grain, and they can also be applied over old paints or solid-color stains. However, surface texture is retained and a flat-finish appearance normally results. Like paints, solid-color stains protect wood against ultraviolet light degradation. Lifetimes of 3 to 7 years can be expected for two-coat applications. Solid-color stains can be both alkyd and latex based; they form a thin film much like paint and consequently can also peel loose from the substrate. They are often used on textured surfaces and panel products such as hardboard and plywood.

Transparent Natural Finishes

Varnishes and varnish stains Varnishes are composed primarily of resins or drying oils dissolved in a suitable solvent. The clear coatings of conventional spar, urethane, or marine varnish, which are film-forming finishes, are not generally recommended for exterior use on wood unless the finished wood is protected by a suitable roof or overhang. Ultraviolet light from the sun penetrates the transparent film and degrades the wood under it. Regardless of the number of coats applied, the finish will eventually become brittle as a result of exposure to sunlight, develop severe cracks, and peel, often in less than 2 years.

A finish that forms a thin, erodable film is popular in Europe and has had some limited success in the United States. This finish is sometimes called a varnish stain or a nearly film-forming stain. The film of varnish stain is thicker than that provided by a semitransparent stain, but thinner than that provided by a conventional film-forming varnish. Varnish stains contain a water repellent, special transparent iron oxide pigments, and mildewcides. The surface coating is designed to slowly erode and can be refinished more easily than a coating provided by a conventional varnish. Varnish stains are usually applied initially as two- or three-coat systems and may last 2 to 4 years.

Water-repellent preservatives Water-repellent preservatives contain a fungicide, a small amount of wax as a water repellent, a resin or drying oil, and a suitable solvent. Some contain ultraviolet light stabilizers. The wax reduces the absorption of liquid water by the wood, and the preservative prevents wood from darkening (graying) by inhibiting the growth of mildew and other staining organisms. Some waterborne or water-dispersed formulations are also available.

A penetrating water-repellent preservative may be used as a natural wood finish. These finishes have minimal protection for wood and may last only 1 to 2 years depending on exposure. The treatment reduces warping and checking, prevents water staining at the edges and ends of wood siding, and helps control mildew growth. Paintable water-repellent preservatives are available and may be used as a treatment for bare wood before priming and painting or in areas where old paint has peeled, exposing bare wood, particularly around butt joints or in corners. This treatment keeps rain or dew from penetrating the wood, especially at joints and on end grain, thus decreasing the shrinking and swelling of the wood. As a result, less stress is placed on the paint film, and its service life is extended. These treatments are nonfilm-forming and do not protect wood from water vapor.

Oils Many penetrating oil or oil-based natural wood finish formulations are available for finishing exterior wood. The most common drying oils used are based on linseed and tung. However, these oils may serve as a food source for mildew if applied to wood in the absence of a mildewcide. The oils will also perform better if a water repellent is included in the formulation. All these oil systems will protect wood, but their average lifetime may be only as long as that described for the water-repellent preservatives. Some oil finishes also contain alkyd resins.

Semitransparent penetrating stains Semitransparent penetrating stains are moderately pigmented water repellents or water-repellent preservatives, often containing higher amounts of drying oil or other resin. These penetrating stains are oil based (or alkyd based), and some may contain a fungicide (preservative or mildewcide), ultraviolet light stabilizer, or water repellent. Finish lifetimes may vary from 2 to 6 years depending on wood surface texture and quantity of stain applied.

The solvent-borne stains (alkyd or oil based) penetrate the wood surface to a degree, are porous, and do not form a surface film like paint. Thus, they do not totally hide the wood grain and will not trap moisture that may encourage decay. As a result, the stains will not blister or peel even if moisture penetrates the wood. Latex-based (waterborne) stains are also available, but they do not penetrate the wood surface as do their alkyd- or oil-based counterparts. Newer latex formulations are being developed that may provide some penetrating characteristics.

Lacquers and shellac Lacquers and shellac are often used as indoor finishes. However, they are not suitable for exterior application, even as sealers, because these resins in these coatings have little resistance to moisture. These finishes are also normally brittle and thus crack and check easily. However, specialty pigmented knot-sealer primers based on shellac are available for specific exterior applications.

Preservatives Although not generally classified as wood finishes, preservatives do protect wood against weathering and decay, a great quantity of preservative-treated wood being exposed without any additional finish. There are three main types of wood preservative: (1) preservative oils (e.g., coal-tar creosote), (2) organic solvent solutions (e.g., pentachlorophenol), and (3) waterborne salts (e.g., chromated copper arsenate). These preservatives can be applied in several ways, but pressure treatment generally gives the greatest protection against decay. Greater preservative content of pressure-treated wood generally results in greater resistance to weathering and improved surface durability. The chromium-containing preservatives also protect against degradation by ultraviolet light.

Wood treated with waterborne preservatives, such as chromated copper arsenate, can be painted or stained if the wood is clean and dry. Wood treated with a water-repellent preservative, by vacuum-pressure or dipping, is paintable. Wood treated with coal-tar creosote or other dark oily preservatives is generally not paintable.

Special Applications

Although general wood-finishing procedures are applicable to typical situations, some applications deserve special mention. These include the application of finish to decks and porches, fences, wood roofs, log structures, and structures in marine environments. Wood used in all of these applications is usually exposed to particularly harsh weathering conditions. Special consideration must be given to finish selection and application. Log structures need special consideration because of the large amounts of end grain exposed and the deep checking associated with large timbers as well as small, round logs.

Compliance of VOC Finishes with Pollution Regulations

Volatile organic compounds (VOCs) are those organic materials in finishes that evaporate as the finish dries and/or cures. These compounds are regarded as potential air pollutants, and the amount that can be released for a given amount of solids (for example, binder, pigments) in the paints is now regulated in many areas. Regulations that restrict the amount of VOCs in paints have been enacted in many states, including California, New York, Texas, Massachusetts, New Jersey, and Arizona, and legislation is pending in many others.

The existing and pending regulations are a serious concern throughout the United States because many traditional wood finishes may no longer be acceptable, including oil- and alkyd-based semitransparent stains, oil- and alkyd-based primers and top coats, solvent-borne water repellents, and solvent-borne water-repellent preservatives. Many current wood finishes, including some latex-based materials, may need to be reformulated. These changes could affect the properties of the finish, application, interaction with the wood (for example, adhesion, penetration, moisture-excluding effectiveness), and possibly durability.

Many penetrating finishes, such as semitransparent stains, have low solids content (pigment, oils, polymers) levels and are being reformulated to meet low-VOC regulations. To meet the VOC requirements, these reformulated finishes may contain higher solids content, reactive diluents, new types of solvents and/or cosolvents, or other nontraditional substituents. There is little information about the way these new penetrating finishes interact with the substrate to protect the wood or about the degradation mechanisms of these finishes when exposed to various outdoor conditions.

Interior Wood Finishes

Interior finishing differs from exterior finishing chiefly in that interior woodwork usually requires much less protection against moisture and ultraviolet light, but more exacting standards of appearance and cleanability. A much wider range of finishes and finish methods are possible indoors because weathering does not occur. Good finishes used indoors should last much longer than paint or other coatings on exterior surfaces.

Much of the variation in finishing methods for wood used indoors is caused by the wide latitude in the uses of wood – from wood floors to cutting boards. There is a wide range of finishing methods for just furniture. Factory finishing of furniture is often proprietary and may involve more than a dozen steps.

Color changes on wood surfaces can sometimes cause problems when wood is used indoors, particularly if the wood is finished to enhance its natural appearance with transparent finishes. This color change is a natural aging of the newly cut wood, and little can be done to prevent it, except, of course, to keep the wood in the dark. The color change is caused by visible light, not the ultraviolet light radiation associated with outdoor weathering, and by oxygen in the air. Most of this color change occurs within 2 to 3 months, depending on the light intensity, although some slight color changes due to visible light and air can slowly occur over 1 or 2 years.

Film-Forming Opaque Finishes

Interior surfaces may be easily painted by procedures similar to those for exterior surfaces. As a rule, however, smoother surfaces, better color, and a more lasting sheen are demanded for interior woodwork, especially wood trim; therefore, enamels or semigloss enamels are often used rather than flat paints.

Imperfections such as planer marks, hammer marks, and raised grain, are accentuated by enamel finish. Raised grain is especially troublesome on flat-grained surfaces of the denser softwoods because the hard bands of latewood are sometimes crushed into the soft earlywood in planing, and later expand when the wood changes moisture content.

To effectively finish hardwoods with large pores, such as oak and ash, the pores must be filled with wood filler. After filling and sanding, successive applications of interior primer and sealer, undercoat, and enamel are used. Knots in the white pines, ponderosa pine, or southern pine should be sealed with shellac or a special knot-sealer before priming. A coat of pigmented shellac or special knot-sealer is also sometimes necessary over white pines and ponderosa pine to retard discoloration of light-colored enamels by colored matter present in the resin of the heartwood of these species.

Transparent Natural Finishes

Transparent finishes are often used on most hardwood and some softwood trim and paneling. Most finishing consists of some combination of the fundamental operations of sanding, staining, filling, sealing, surface coating, or waxing. Before finishing, planer marks and other blemishes on the wood surface that would be accentuated by the finish need to be removed.

Stains Both softwoods and hardwoods are often finished without staining, especially if the wood has a pleasing and characteristic color. When stain is used, however, it often accentuates color differences in the wood surface because of unequal absorption into different parts of the grain pattern. With hardwoods, such emphasis of the grain is usually desirable; the best stains for the purpose are dyes dissolved either in water or solvent. The water stains give the most pleasing results, but raise the grain of the wood and require an extra sanding operation after the stain is dry.

The most commonly used stains are the ‘nongrain-raising’ ones in solvents which dry quickly, and often approach the water stains in clearness and uniformity of color. Stains on softwoods color the earlywood more strongly than the latewood, reversing the natural gradation in color unless the wood has been sealed first with a wash coat. Pigment-oil stains, which are essentially very thin paints, are less subject to this problem and are therefore more suitable for softwoods. Alternatively, the softwood may be coated with penetrating clear sealer before applying any type of stain to give more nearly uniform coloring.

Fillers In hardwoods with large pores (e.g., oak and ash), the pores must be filled, usually after staining and before varnish or lacquer is applied, if a smooth coating is desired. The filler may be transparent and without effect on the color of the finish, or it may be colored to contrast with the surrounding wood. A filler may be a paste or liquid, natural or colored.

Birch has pores large enough to take wood filler effectively when desired, but small enough as a rule to be finished satisfactorily without filling. Hardwoods with small pores may be finished with paints, enamels, and varnishes in exactly the same manner as softwoods.

Sealers Sealers are thinned varnish, shellac or lacquer and are used to prevent absorption of surface coatings and also to prevent the bleeding of some stains and fillers into surface coatings, especially lacquer coatings. Lacquer and shellac sealers have the advantage of being very fast drying. Sealers are sometimes used as final finishes, often when applied in two or more coats.

Film-forming surface coatings Transparent surface coatings may be gloss varnish, semigloss varnish, shellac, nitrocellulose lacquer, conversion varnishes, wax, or similar finishes. Wax provides protection without forming a thick coating and without greatly enhancing the natural luster of the wood. Coatings of a more resinous nature, especially lacquer and varnish, accentuate the natural luster of some hardwoods and seem to permit the observer to look down into the wood. Shellac applied by the laborious process of French polishing probably achieves this impression of depth most fully, but the coating is expensive and easily marred by water. Rubbing varnishes made with resins of high refractive index for light (ability to bend light rays) are nearly as effective as shellac. Lacquers have the advantages of drying rapidly and forming a hard surface, but require more applications than varnish to build up a lustrous coating.

Varnish and lacquer usually dry with a highly glossy surface. To reduce the gloss, the surfaces may be rubbed with pumice stone and water or polishing oil. Waterproof sandpaper and water may be used instead of pumice stone. The final sheen varies with the fineness of the powdered pumice stone; coarse powders make a dull surface and fine powders produce a bright sheen. For very smooth surfaces with high polish, the final rubbing is done with rottenstone and oil. Varnish and lacquer made to dry to semigloss or satin finish are also available.

Flat oil finishes commonly called 'Danish oils' are also very popular interior wood finishes. This type of finish penetrates the wood and forms no noticeable film on the surface. Two or more coats of oil are usually applied, which may be followed with a paste wax. Such finishes are easily applied and maintained but are more subject to soiling than a film-forming type of finish. Simple boiled linseed oil or tung oil dissolved in a solvent are also used extensively as wood finishes. They are applied in excess and then wiped for a soft sheen surface appearance.

See also: **Solid Wood Processing**: Machining. **Wood Formation and Properties**: Chemical Properties of Wood; Formation and Structure of Wood; Mechanical Properties of Wood; Physical Properties of Wood.

Further Reading

Allen S (1995) *Classic Finishing Techniques*. New York: Sterling Publishing.

Carter D (1996) *The Complete Paint Book*. London: Conran Octopus.

Cassens DL and Feist WC (1991) *Exterior Wood in the South: Selection, Applications and Finishes*, General Technical Report no. FPL-GTR-69. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory.

Feist WC (1990) Outdoor wood weathering and protection. In: Rowell RM (ed.) *Archaeological Wood: Properties, Chemistry, and Preservation*, pp. 263–298. Washington, DC: American Chemical Society.

Feist WC (1996) *Finishing Exterior Wood*. Blue Bell, PA: Federation of Societies for Coatings Technology.

Feist WC (2000) Wood: finishes and coatings. In: Beall F (ed.) *Encyclopedia of Materials: Science and Technology*, vol. 3, *Wood*, pp. 1–5. London: Elsevier Science.

Flexner B (1994) *Understanding Wood Finishing*. Emmaus, PA: Rodale Press.

Gorman TM and Feist WC (1989) *Chronicle of 65 Years of Wood Finishing Research of the Forest Products Laboratory*, General Technical Report no. FPL-GTR-60. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory.

McDonald KA, Falk RH, Williams RS, and Winandy JE (1996) *Wood Decks: Materials, Construction, and Finishing*, Publication no. 7298. Madison, WI: Forest Products Society.

Satas D and Tracton AA (eds) (2001) *Coatings Technology Handbook*. New York: Marcel Dekker.

Tichy RJ (1997) *Interior Wood Finishing: Industrial Use Guide*, Publication no. 7288. Madison, WI: Forest Products Society.

Williams RS (1991) Effects of acidic deposition on painted wood: a review. *Journal of Coatings Technology* 63(800): 53–73.

Williams RS (1999) *Finishing of Wood*. In: *Wood Handbook: Wood as an Engineering Material*, Publication no. 7269, pp. 15-1–15-37. Madison, WI: Forest Products Society.

Williams RS, Knaebe MT, and Feist WC (1996) *Finishes For Exterior Wood: Selection, Application, and Maintenance*, Publication no. 7291. Madison, WI: Forest Products Society.

Machining

R Szymani, Wood Machining Institute, Berkeley, CA, USA

Introduction

Wood machining can be defined as the application of energy to sever the workpiece at a chosen internal surface. The purpose of wood machining is to produce a desired shape and dimension with requisite accuracy and surface quality in the most economical way. Major developmental trends in wood machining involve: attempts to reduce material losses in both the machined material and the cutting tools; improvement of the quality of machined products by attaining necessary accuracy of shape and dimensions as well as surface quality of the workpiece; increasing production output and minimizing cost; improvement of worker safety by machine guarding; and controlling generation of noise and dust.

Machining processes in the manufacture of wood products may be classified as follows: sawing; peeling and slicing; planing, molding, shaping, and routing; turning and boring; sanding; and nontraditional machining processes such as cutting with laser beam and high-energy liquid jet.

Wood as a Material to be Cut

Wood is anisotropic and a heterogeneous material. The structural nature of wood, in terms of its three-dimensional properties, is very important in wood machining, particularly the relationship between the strength of wood parallel and perpendicular to the grain. As indicated in **Figure 1**, the cutting force of birch wood is about two to four times as high across grain as along it.

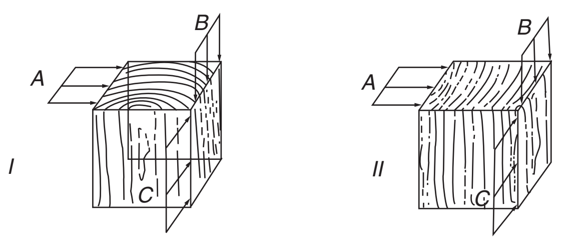
Wood strength and cutting resistance are dependent on specific gravity, moisture content, and temperature during processing as well as growth-related characteristics of wood such as spiral or interlocked grain, presence of knots, growth stresses, reaction wood, and drying stresses.

Sawing Technology

Sawing is the most important frequent cutting process. Sawing machines are classified according to the basic machine design; that is, sash gang saws (reciprocating, multiple blade frame saws), circular saws, band saws, and chain saws. Circular saws are designated ripsaws if they are designed to cut solid wood along the grain, as bucking or trim saws if they are designed to cut across the grain, or as combination saws if designed to cut along and across the grain, as well as at a certain angle to the grain (e.g., miter saws). Sawing machines are further classified according to their use. For example, a bucking saw is used for cutting logs to length, a headrig for primary log breakdown, a resaw for resawing cants into boards, an edger for edging boards, a trimmer for cutting boards to length, table saws for ripsawing and crosscutting of solid wood, panel saws for cutting plywood, fiberboards and particleboards, and a scroll saw for general-purpose cutting of intricate patterns.

In general, saw blades are made from cold-rolled, hardened, and tempered steel. For band saws a high carbon content, nickel-alloyed saw steel has been used in most cases (e.g., Uddelhom Steel UHB 15 N_2O:0.75% C and 2.0% Ni). Other saw steel alloys may contain manganese, chromium, and vanadium. With the gradual transition from swaged saw teeth to Stellite-tipped saws, saw blade manufactures such as Uddeholm and Sandwik have developed special band saw steels. The Uddeholm ANKAR-R steel, formulated for Stellite tipping, has improved stability of tensioning stresses, welding properties, and mechanical strength. The Sandvik Multishift steel increased fatigue resistance and the capacity to operate at higher strain rates.

Circular saw blades made from stainless steel were recently introduced by California Saw and Knife Works to bring under control the problems associated with corrosion-initiated material loss in guided saws. Other benefits are attributed to thermal and mechanical properties which make stainless-steel saws stiffer when cutting, and which allow them better to retain their original flatness compared to saws made from alloy saw steels.



Main cutting direction	Main cutting force F_1 kgf cm^{-1} A	B	C
Cutting instance *I*	7.75	2.90	1.65
Cutting instance *II*	8.35	3.15	1.85

Figure 1 Schematic illustration of main cutting directions in respect to the annual rings and values of the main cutting force obtained with a work-sharp normal knife and 0.1 mm chip thickness. The specific gravity of the birch used for the tests is 0.64 and moisture content 12%.

Circular saws typically range from 1.0 to 5.0 mm in thickness and from 150 to 1800 mm in diameter. The thickness of a bandsaw may range from 0.4 to 2.1 mm. Bandsaw width ranges from 60 to 360 mm for saws used in lumber manufacturing, and 6 to 50 mm for the narrow bandsaws used in furniture manufacturing and for portable sawing machines. As a rule, the saw blade thickness should not exceed 0.1% of the wheel diameter, and the bandsaw width should not be greater than wheel width plus gullet depth and an additional 5 mm. The typical sash gang saws used for primary wood processing are 2.0 mm in thickness and approximately 175 mm in width.

Saws vary considerably with regard to tooth and gullet design. The primary design considerations include tooth strength and gullet loading capacity, the function of the gullet being sawdust removal. Other important factors are tooth wear and noise generation. The typical bandsaw tooth geometry is described by specifying rake and clearance angle as depicted in **Figure 2**. If the saw tooth has a face and/or top bevel, those angles should also be specified. The optimum tooth geometry, as determined from the measurement of cutting forces and power requirements, mainly depends upon cutting direction, wood species, density, and moisture content. Tooth geometry may vary considerably: for example, the rake angle for crosscut circular saws ranges from $+10^\circ$ to -30°. In the case of circular ripsaws and band saws, the rake angle will vary from 10° for high-density hardwoods to 30° for softwood species. The top clearance angle may range from 8° for dense hardwoods to approximately 10° for softwoods. Many sawmills in the USA and Canada are currently using variable sawtooth spacing in order to reduce the problem of 'washboarding' during sawing.

The side clearance for wide bandsaws, which is required to reduce friction between the saw blade and generated surface, may range from 0.30 to 0.35 mm for hardwoods and from 0.50 to 0.60 mm for softwoods. Certain specialty circular saws such as miter saws can be tapered (hollow ground) to provide side clearance.

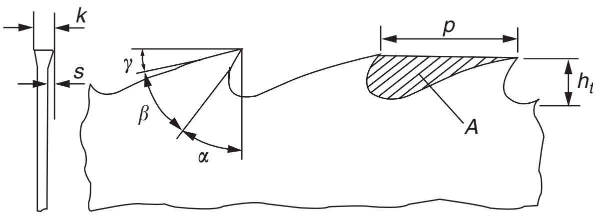


Figure 2 Bandsaw tooth geometry. α, rake or hook angle; p, pitch or tooth spacing; β, sharpness angle; h_t, depth of gullet or tooth height; γ, clearance angle; A, gullet area; k, kerf width (theoretical); s, side-clearance. Reproduced with permission from *The Wood Bandsaw Blade Manual* (1993), Uddeholm Strip Steel AB, Munkfors, Sweden.

The purpose of tipping saw teeth with hard alloys is to increase their wear resistance, which prolongs the useful life of the blade. Most bandsaws are Stellite-tipped, while circular saws in addition to Stellite are tipped with tungsten carbide and polycrystalline diamond (PCD) tips. Optimizing the relationship between the saw-tipping material properties and the cutting edge geometry is a precondition for high performance of circular and bandsaws.

Each single tooth will remove a certain volume of wood given by the feed per tooth and the cutting height. This volume should correspond to the chosen gullet capacity $V = 0.5\,A$ up to $0.75\,A$. The feed per tooth t is given by $t = p\ (F/C)$ where p is the pitch (mm), F is the feed rate (m min^{-1}), and C is the cutting speed (m min^{-1}). The average blade velocity C is about 3000 m min^{-1}.

The use of thin-kerf circular saws (thickness of cut 3 mm or less) has proved to be very beneficial to industry in the reduction of kerf losses, as long as saw stability is maintained. One of the principal manifestations of circular-saw instability is standing-wave resonance. The rotation speed, at which a standing wave is formed, is called the critical speed. All in-plane or membrane stresses (i.e., stresses due to temperature gradients, rotation, cutting forces, and tensioning or prestressing) shift the saw natural frequencies and alter its critical speed accordingly. Computer programs such as CSAW are available for estimating the critical speed of circular saws based on design and operation variables. The operating speed, for saws clamped in the center, should be at least 15% below their critical speed. The sawing accuracy improves with the increase of the critical speed margin. In the case of bandsaws, currently available computer programs can be used to evaluate bandsaw design relative to band vibration and stability. The effective stiffness and stability of circular saws can be increased by introducing radial slots, by prestressing or tensioning, by using guiding systems, by online cooling near the cutting edge, and by heating near the center (i.e., thermal tensioning). Radial slots in circular saws reduce compression hoop stresses at the saw periphery due to temperature gradients, introduce asymmetry into the saw-blade design and consequently reduce transverse vibration and reduce noise. The application of various guiding systems in conjunction with the use of splined-arbor saws, which can float on the arbor, is a common and particularly effective method used for stability control of thin-kerf circular saws. Most sawmills in North America resaw cants with spline arbor saw blades with fluid-lubricated guides which generally work better than clamped saws. Circular saw guides serve to position the saw blade relative to the workpiece, to lubricate and cool the saw blade, to stiffen the saw blade against the transverse forces generated during sawing, and to dampen saw vibrations. This sawing system allows the use of thin saw blades having a kerf width as small as 1.8 mm at a cutting depth of 140 mm and feed rate of 30 m min^{-1}.

In the case of bandsaws, in addition to prestressing and the use of saw-guiding systems, the type of straining mechanism for providing axial tension and its response will significantly affect saw stability and consequently sawing accuracy. The saw blade must operate under maximum applied tension force, consistent with the endurance strength of the saw blade material, in order to maximize stiffness and critical edge-buckling load.

The general practice in the industry has been to select saws on the basis of past experience or by an expensive trial-and-error process. Due to extensive research on saw dynamics, however, it is now possible to design both circular and bandsaws on the basis of sound engineering principles.

Regardless of the operating conditions, the stress level in saw blades must be kept constant. The online control of circular and bandsaw stability basically consists of either modifying the forces exciting the blade or altering the effective saw-blade stiffness and damping to reduce vibration. This can be achieved, for example, by online thermal tensioning of circular saws, i.e., introduction of thermal stresses beneficial to saw stability. At present, the trend is to use online monitoring of bandsaw displacements and measurement of sawing accuracy, and online control of feed speed.

Veneer Peeling and Slicing

Rotary cutting (peeling) and slicing of wood are used in the manufacture of veneer. At least 95% of veneer is produced by peeling, for which a veneer lathe is used, and about 5% by slicing, for which a horizontal or vertical slicer is used. The primary components of any lathe or slicer are the knife and pressure flat nose bar or powered roller nose bar. They are similar in both machines and perform the same function. The cross-section of a typical lathe presented in **Figure 3** illustrates the position of the knife and the pressure nose bar. The most common knife thickness for a lathe is 16 mm, and, for the face veneer slicer, 15–19 mm. The knife's Rockwell hardness on the C scale may vary from 56 to 60.

While the knife severs the veneer from the bolt or flitch, the pressure nose bar compresses the wood and thus reduces splitting of wood ahead of the knife.

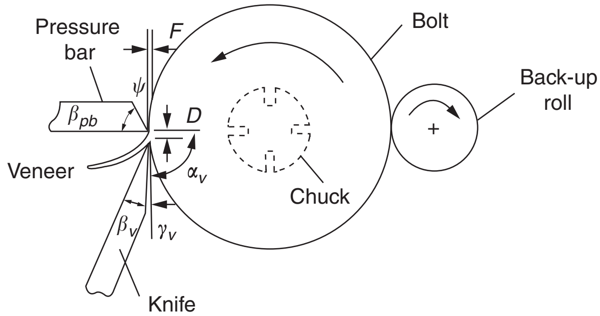


Figure 3 Cross-section of a veneer lathe with fixed pressure bar. α_v, knife angle; β_v, knife bevel angle; γ_v, clearance angle; D, lead or vertical gap; β_{pb}, pressure-bar bevel angle; ψ, pressure-bar compression angle; F, gap (horizontal gap).

The amount of compression depends on wood density and will vary from species to species. For Douglas-fir, it is about 15% of the veneer thickness; for western white spruce about 8%. In both lathe and slicer, the wood compression is important in controlling roughness, depth of checks, and thickness of the veneer. The slicer has a fixed nose bar while the lathe may have either a fixed nose bar or a rotating roller bar. The flitch on a slicer is backed by the flitch table while support for a veneer bolt may be provided by a powered back-up roll on a veneer lathe. Full-length powered back-up rolls reduce spin-outs, and prevent the bolt from flexing during peeling. For maximum yield of rotary peeled veneer it is essential that bolts are chucked in the geometric center. Laser scanning and computerized centering systems are currently used with modern *X-Y* lathe chargers, which allow determination of chucking centers for best yield of each individual block. Other developments in veneer manufacturing equipment include high-speed veneer lathes having spindle speeds of 500 rpm and over, digital carriage drive which eliminates the mechanical clutch assembly, hydraulic powered back-up rolls, and dual hydraulic spindles.

The production of high-quality veneer requires proper pretreatment of the wood prior to cutting. This is done by heating green wood in water or steam. Heating wood above 50°C makes it more plastic and reduces veneer checking during peeling or slicing. The recommended peeling temperature ranges from 50° to 90°C and will vary with the average specific gravity of the species.

Planing, Molding, Shaping, and Routing

Planing refers to the peripheral milling of wood. Its purpose is to smooth one or more surfaces of the workpiece and at the same time bring the workpiece to some predetermined dimension. The machinery used for planing operations includes: (1) surfacers designed to smooth one or two sides of the workpiece and reduce it to a predetermined thickness; and (2) planers and matchers defined as double surfacers which are further equipped with two opposed profile side heads that can simultaneously machine the two edges to the desired pattern or profile.

The molding operation aims to machine lumber into forms of various cross-sectional shapes, such as picture-frame moldings. Both planing and molding machines employ rotating cutterheads. By definition, a molder differs from a planer in that the molder side heads are staggered instead of directly opposed. The typical operating speed for multiknife cutter heads ranges from 3600 to 6000 rpm. The number of spindles may range from one to 10. Molding machines can be equipped with variable feed rate typically ranging from 6 to 60 $\mathrm{m\,min^{-1}}$.

Shaping involves machining an edge profile or edge pattern on the side and/or periphery of a workpiece. The basic types of shapers include single and double spindle shapers, double head automatic shaper, and center profiler. The shaper spindle speeds range from 7200 to 10 000 rpm.

Routing is similar to the shaping operation. While a shaper always shapes the periphery, a router is used to make a variety of cuts such as mortises, irregularly shaped holes, and three-dimensional plunge cuts using computer numerical control (CNC). Most router spindle speeds are from 10 000 to 30 000 rpm, depending on the diameter of the cutter. When machining abrasive composite wood products, there is a trend to use PCD cutting tools in routing and shaping operations.

In all three operations, it is of prime importance to adjust the operating conditions and knife geometry so that machining defects are minimized. The most commonly encountered defects are torn or fuzzy grain, raised and loosened grain, and chip marks. These defects are caused by improper cutting angles, chip thickness which is too large, dull knives, low-density species, and often the presence of reaction wood. In the case where the torn-grain defect is highly probable, the most important variable is the number of marks per centimeter or inch (reciprocal of the feed per cutter). The marks per centimeter should be between three and five for rough planing operations and between five and six for finishing cuts. The clearance angle should in all cases exceed a value of 10°. The optimum cutting angle (angle between the knife face or knife bevel and a radius of the cutter head) lies between 20° and 30° for most planing situations; however, in the cases of interlocked or wavy grain, it may be necessary to reduce the cutting angle to 15° or even 10°.

Turning and Boring

Turning of wood is a machining process for generating cylindrical forms by removing wood, usually with a single-point cutting tool. The turning machines include single- and multiple-spindle lathes. The tools used for turning on the lathe perform operations primarily directed to machining the outer surfaces of the workpiece. From practical experience and experimental investigations, lathe clearance angles between 12° and 18° offer optimum cutting conditions. In practice, a lip or wedge angle between 20° and 30° is recommended for softwoods, the wedge angle corresponding to the sharpness angle in the case of saw teeth and to the knife bevel angle in the case of a veneer knife. For hardwoods, wedge angles between 50° and 60° are recommended. The quality of surfaces of most turned-wood articles is of the utmost importance, for example, for tool handles. The roughness perpendicular to the grain increases with the feed speed. The specific pressure of the tool on the turned surface also has a remarkable influence on the roughness.

Most machines which will perform turning operations can also perform boring operations, although machines are available which will perform boring, drilling, and other related operations. Boring machines can have many configurations, ranging from the simple vertical single-spindle boring machine to complex transfer machines involving multiple vertical, horizontal, and angular spindles. There are many specialized boring-bit designs in use. The common bit types include: (1) double-spur, double-lip solid-center bit on which the spurs cut ahead of the lips; (2) double-spur, double-twist bit on which the spurs cut after the lips; and (3) twist drill. The first is a fast-boring general-purpose bit; the second bit is particularly suited for boring to extreme depth. The twist drill is frequently used on machine boring equipment for drilling in end grain and for boring dowel holes. The quality of finish produced by a twist drill may be inferior to that produced by a bit equipped with spurs.

Sanding Technology

Sanding is the abrasive machining of wood surfaces to obtain a smooth surface quality. The abrasive tool consists of a backing material to which abrasive grains are bonded by an adhesive coat. The abrasive or sanding tool is specified by the sanding and backing materials. Sanding materials vary according to type, size, and form of grain. Typical abrasive materials for wood-working applications are garnet, aluminum oxide, and silicon carbide. Garnet is the most commonly used because of its low cost and acceptable working qualities. It is used with all types of machines for sanding softwoods. Aluminum oxide abrasives are used extensively for sanding hardwood, particleboard, and hardboard. Silicon carbide abrasive is used for sanding and polishing between coating operations and for sanding softwoods where the removal of raised fibers is a problem. The size of the abrasive particles is specified by the mesh number (i.e., the approximate number of openings per linear inch in the screen through which particles will pass); mesh numbers range from about 600 to 12.

Backing materials vary according to the strength, flexibility, and required spacing of the sanding tool and are made of paper, cotton, or polyester cloth, or cloth–paper combinations. Bonding materials are generally animal glues, urea resins, or phenolic resins. The choice of these materials depends upon the required flexibility of the tool and the work rate required of the tool. Animal-glue bonds are the most flexible, whereas resin bonds are harder, more moisture- and heat-resistant, and have superior grain retention.

Sanding machines include multiple-drum sanders, wide-belt sanders, automatic-stroke sanders, and contact wheel disk sanders. The drum sander is probably the oldest of all the wood-working machines using coated abrasive, and it is used in solid-wood furniture manufacturing.

The drum sanding machine is used following the planer or veneer press. Multiple-drum sanders are of the endless-bed or roll-feed type and have from two to six drums. The abrasive is usually a heavy paper-backed aluminum oxide product. In very heavy sanding operations, a fiber-backed abrasive is recommended. A sequence of 60, 80, and 100 mesh abrasive is frequently used on a three-drum endless-bed sander.

Wide-belt sanders use an abrasive belt at least 30 cm wide and are commonly used on panels (plywood, particleboard, hardboard). Silicon carbide is normally used as the abrasive. They have higher production rates and greater accuracy than multiple-drum sanders.

Heavy-duty high-speed (up to $600\,\mathrm{m\,min^{-1}}$ feed rate) wide-belt sanders are called abrasive planers when used for dimensioning and surfacing. Abrasive planers are used for dimensioning of accurately sawn, kiln-dried lumber, plywood and particleboard, and for furniture production. In comparison with the knife planer, the abrasive planer has in general higher production rates, a lower noise level, and virtually no machining defects. New developments in wide-belt sanding include the use of antistatic belts and sanding with aerostatic (air cushion) supported belts. It is critical when using sanders and abrasive planes to have an adequate dust removal system.

Surface finish during the sanding process is for the most part independent of pressure and cutting speed. The optimum belt speed as determined by the specific quantities of abrasion is about $30\,\mathrm{m\,s^{-1}}$ for particle size 60 and slightly less than $30\,\mathrm{m\,s^{-1}}$ for particle size 120.

Automatic-stroke sanders use a narrow abrasive belt and a reciprocating shoe which creates contact between the abrasive and the workpiece. This sanding machine is commonly used in furniture plants for final sanding operations and touch-up sanding.

The contact-wheel sander also uses a narrow abrasive belt. Contact wheels normally range from 150 to 350 mm in diameter. A typical application is the sanding head on an edge banding machine where the edging tape is given a finish after application to the board. Cloth belts are usually preferred because of their durability.

The disk sander consists of a revolving back plate to which a coated abrasive disk of paper or cloth is attached by an adhesive. It usually incorporates a tilting action for angle or miter sanding. The major disadvantage of this method is a pattern of circular scratches which have to be removed by other means before finishing.

Nontraditional Machining Processes

Various new cutting techniques have been investigated during the last 40 years for possible use in the wood industry in an effort to reduce or eliminate kerf losses. These include the laser beam and the high-energy water jet. Major advantages of a laser beam and water jet include the ability to cut intricate patterns, high cutting accuracy, and the possibility of numerical control.

A wide variety of materials can be cut using a continuous carbon dioxide laser. The laser beam produces a very narrow kerf, in most cases approximately 1 mm. The major disadvantages of cutting wood and wood-based panels with the laser are low feed rate, resulting in high cost per unit of lineal cut, and the charring of the generated surface. Therefore, the application of laser machining, most economically justified, includes laser engraving, automatic preparation of wooden die blocks for the folding-carton industry, cutting chair backs, and veneer inlays in furniture industry.

Cutting with abrasive liquid jet has been useful for a wide variety of materials but has rather limited application in the wood industry. The application of the liquid jet as a cutting tool depends on the availability of high-pressure pumping equipment capable of generating a high-velocity continuous jet. For the generation of a high-energy continuous flow, a pressure level of about $4100\,\mathrm{kp\,cm^{-2}}$ (60 000 psi) is required. The nozzles range from 0.1 to 0.4 mm in diameter and are made from ruby or sapphire. The liquid jet, like the laser, approaches the ideal single-point cutting tool, which can follow highly complicated patterns. It eliminates crushing or deformation of the material such as corrugated paper board and generation of dust. Water jet technology reduces cutting noise significantly and offers the ability to cut without high temperatures. The greatest use of liquid-jet cutting is in the paper and paper-board industry where it has been quite successful in cutting laminated paperboard into upholstery frames. In the paper industry liquid-jet slitting systems are used to cut paper at higher speeds than with a mechanical knife – as high as 3200 m min^{-1}.

See also: **Solid Wood Processing**: Finishing. **Solid Wood Products**: Construction; Logs, Poles, Piles, Sleepers (Crossties); Lumber Production, Properties and Uses; Structural Use of Wood. **Wood Formation and Properties**: Formation and Structure of Wood; Mechanical Properties of Wood; Physical Properties of Wood. **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

Baldwin RF (1975) *Plywood Manufacturing Practices*. San Francisco, CA: Miller Freeman.
Effner J (1992) *Chisel on the Wheel: A Comprehensive Reference to Modern Woodworking Tools and Materials*. Ann Arbor, MI: Prakken.
Ettelt B (1987) *Sawing, Milling, Planing, Boring: Wood Machining and Cutting Tools* (in German). Stuttgart, Germany: DRW-Verlag.
Handbook for Woodworking Machine Tools (2001) *The Leitz Lexicon*, 3rd edn. Oberkochen, Germany: Leitz.
Koch P (1985) Machining. In: *Utilization of Hardwoods Growing on Southern Pine Sites*, pp. 1687–2281. Washington, DC: Government Printing Office.
Lutz JF (1978) *Wood Veneer: Log Selection, Cutting and Drying, Technical bulletin* no. 1577. Madison, WI: US Department of Agriculture Forest Products Laboratory.
Maier G (1987) *Woodworking Machines: Requirements, Concepts, Machine Elements, Construction* (in German). Stuttgart, Germany: DRW-Verlag.
Mote CD Jr, Schajer GS, and Wu WZ (1982) Band saw and circular saw vibration and stability. *Shock Vibration. Digest* 14(2): 19–25.
Stephenson E (2001) *Circular Saws*. Hertford, UK: Stobart Davies.
Szymani R (1986) Status report on the technology of saws. *Forest Products Journal* 36(4): 15–19.
Szymani R (ed.) (2001) *Proceedings of SawTech 2001: The 7th International Conference on Sawing Technology*, November 8–9, 2001. Seattle, Washington.
Szymani R (ed.) (2001) *Proceedings of the 15th International Wood Machining Seminar*, July 31–August 2, 2001, Los Angeles, CA.
Wijesinghe R (1998) *The Bandmill Book: The Complete Guide to your Industrial Bandmill and Bandsaw.* North Vancouver, Canada: Tech Pubs, Western Technigraphics.
Willard R (1980) *Production Woodworking Equipment*, 4th edn. Raleigh, NC: North Carolina State University.
Williston EM (1989) *Saws: Design, Selection, Operation, Maintenance*, 2nd edn. San Francisco, CA: Miller Freeman.

SOLID WOOD PRODUCTS

Contents

Glued Structural Members

J A Youngquist, Forest Products Consultant, Verona, WI, USA
R Youngs, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

Published by Elsevier Ltd., 2004

Introduction

The material in this article is adapted from the Forest Products Laboratory *Wood Handbook*, which is especially concerned with use of wood as an engineering material in the USA. However, the use of wood in laminated form is common worldwide and the same principles apply. Glued structural members are manufactured in a variety of configurations. Structural composite lumber (SCL) products consist of small pieces of wood glued together into sizes common for solid-sawn lumber. Glued-laminated timber (glulam) is an engineered stress-rated product that consists of two or more layers of lumber in which the grain of all layers is oriented parallel to the length of the lumber.

Glued structural members also include lumber that is glued to panel products, such as box beams and I-beams, and structural sandwich construction.

Structural Composite Lumber

Structural composite lumber (SCL) was developed in response to the increasing demand for high-quality lumber at a time when it was becoming difficult to obtain this type of lumber from the forest resource. SCL products are characterized by smaller pieces of wood glued together into sizes common for solid-sawn lumber. SCL is a growing segment of the engineered wood products industry. It is used as a replacement for lumber in various applications and in the manufacture of other engineered wood products, such as prefabricated wood I-joists, which take advantage of engineering design values that can be greater than those commonly assigned to sawn lumber.

Types

One type of SCL product is manufactured by laminating veneer with all plies parallel to the length. This product is called laminated veneer lumber (LVL) and consists of specially graded veneer. Another type of SCL product consists of strands of wood or strips of veneer glued together under high pressures and temperatures. Depending upon the component material, this product is called laminated strand lumber (LSL), parallel strand lumber (PSL), or oriented strand lumber (OSL) (**Figure 1**). These types of SCL products can be manufactured from raw materials, such as aspen (*Populus* spp.) or other underutilized species, that are not commonly used for structural applications. Different widths of lumber can be ripped from SCL for various uses. Production of LVL uses veneers 3.2–2.5 mm thick, which are hot pressed with phenol-formaldehyde adhesive into lengths from 2.4 to 18.3 m or more. The veneer for the manufacture of LVL must be carefully selected for the product to achieve the desired engineering properties and is often sorted using ultrasonic testing. End joints between individual veneers may be staggered along the product to minimize their effect on strength. These end joints may be butt joints, or the veneer ends may overlap for some distance to provide load transfer. Some producers provide structural end joints in the veneers using either scarf or fingerjoints. LVL may also be made in 2.4-m lengths, having no end joints in the veneer; longer pieces are then formed by end-jointing these pieces to create the desired length. Sheets of LVL are commonly produced in 0.6–1.2-m widths in a thickness of 38 mm. Continuous presses can be used to form a potentially endless sheet, which is cut to the desired length. Various widths of lumber can be manufactured at the plant or the retail facility.

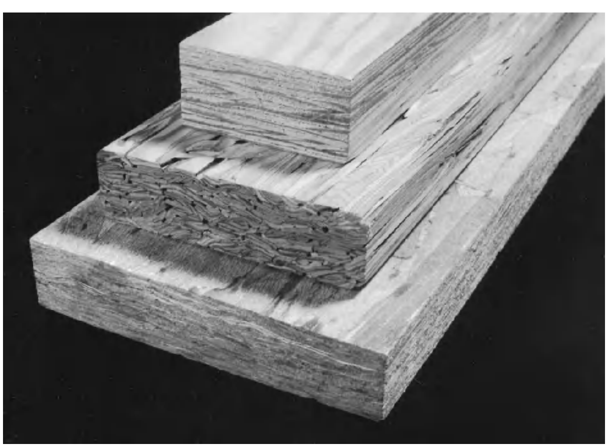


Figure 1 Examples of three types of SCL (top to bottom): laminated veneer lumber (LVL), parallel strand lumber (PSL), and oriented strand lumber (OSL).

Parallel strand lumber (PSL) is defined as a composite of wood strand elements with wood fibers primarily oriented along the length of the member. The least dimension of the strands must not exceed 6.4 mm, and the average length of the strands must be a minimum of 150 times the least dimension. PSL is manufactured using veneer about 3 mm thick, which is then clipped into strands about 19 mm wide. These strands are commonly at least 0.6 m long. The manufacturing process was designed to use the material from roundup of the log in the veneer cutting operation as well as other less than full-width veneer. Thus, the process can utilize waste material from a plywood or LVL operation. Species commonly used for PSL include Douglas-fir (*Pseudotsuga menziesii*), southern pines (*Pinus palustris*, *P. echinata*, *P. taeda*, and *P. elliottii*), western hemlock (*Tsuga heterophylla*), and yellow-poplar (*Liriodendron tulipifera*), but there are no restrictions on using other species. The strands are coated with a waterproof structural adhesive, commonly phenol-resorcinol formaldehyde, and oriented in a press using special equipment to ensure proper orientation and distribution. The pressing operation results in densification of the material, and the adhesive is cured using microwave technology. Billets larger than those of LVL are commonly produced; a typical size is 0.28 by 0.48 m. This product can then be sawn into smaller pieces, if desired. As with LVL, a continuous press is used so that the length of the product is limited by handling restrictions.

Laminated strand lumber (LSL) and oriented strand lumber (OSL) products are an extension of the technology used to produce oriented strandboard

(OSB) structural panels. One type of LSL uses strands that are about 0.3 m long, which is somewhat longer than the strands commonly used for OSB. Waterproof adhesives are used in the manufacture of LSL. One type of product uses an isocyanate type of adhesive that is sprayed on the strands and cured by steam injection. This product needs a greater degree of alignment of the strands than does OSB and higher pressures, which result in increased densification.

Advantages and Uses

In contrast with sawn lumber, the strength-reducing characteristics of SCL are dispersed within the veneer or strands and have much less of an effect on strength properties. Thus, relatively high design values can be assigned to strength properties for both LVL and PSL. Whereas both LSL and OSL have somewhat lower design values, they have the advantage of being produced from a raw material that need not be in a log size large enough for peeling into veneer. All SCL products are made with structural adhesives and are dependent upon a minimum level of strength in these bonds, and are made from veneers or strands that are dried to a moisture content that is slightly less than that for most service conditions. Thus, little change in moisture content will occur in many protected service conditions. When used indoors, this results in a product that is less likely to warp or shrink in service. However, the porous nature of both LVL and PSL means that these products can quickly absorb water unless they are provided with some protection.

All types of SCL products can be substituted for sawn lumber products in many applications. Laminated veneer lumber is used extensively for scaffold planks and in the flanges of prefabricated I-joists, which take advantage of the relatively high design properties. Both LVL and PSL beams are used as headers and major load-carrying elements in construction. The LSL and OSL products are used for band joists in floor construction and as substitutes for studs and rafters in wall and roof construction. Various types of SCL are also used in a number of nonstructural applications, such as the manufacture of windows and doors.

Glulam

Structural glued-laminated timber (glulam) is one of the oldest glued engineered wood products. Glulam is an engineered, stress-rated product that consists of two or more layers of lumber that are glued together with the grain of all layers, which are referred to as laminations, parallel to the length. Glulam is defined as a material that is made from suitably selected and prepared pieces of wood either in a straight or curved form, with the grain of all pieces essentially parallel to the longitudinal axis of the member. The maximum lamination thickness permitted is 5 mm and the laminations are typically made of standard 25- or 50-mm thick lumber. Because the lumber is joined end to end, edge to edge, and face to face, the size of glulam is limited only by the capabilities of the manufacturing plant and the transportation system.

Douglas-fir, larch (*Larix occidentalis*), southern pine, western hemlock, firs (*Abies lasiocarpa*, *A. magnifica*, *A. grandis*, *A. procera*, *A. amabilis*, and *A. concolor*), spruce (*Picea rubens*, *P. glauca*, and *P. mariana*), and pine (*Pinus monticola*) are commonly used for glulam in the USA. Nearly any species can be used for glulam timber, provided its mechanical and physical properties are suitable and it can be properly glued. Industry standards cover many softwoods and hardwoods, and procedures are in place for including other species.

Advantages

Compared with sawn timbers as well as other structural materials, glulam has several distinct advantages in size capability, architectural effects, seasoning, variation of cross-sections, grades, and effect on the environment.

Glulam offers the advantage of the manufacture of structural timbers that are much larger than the trees from which the component lumber was sawn. By combining the lumber in glulam, the production of large structural elements is possible. Straight members up to 30 m long are not uncommon and some spans up to 43 m with sections deeper than 2 m have been used. Thus, glulam offers the potential to produce large timbers from small trees.

By curving the lumber during the manufacturing process, a variety of architectural effects can be obtained that are impossible or very difficult with other materials. The degree of curvature is controlled by the thickness of the laminations. Thus, glulam with moderate curvature is generally manufactured with standard 19-mm thick lumber. Low curvatures are possible with standard 38-mm lumber, whereas 13 mm or thinner material may be required for very sharp curves. As noted below, the radius of curvature is limited to between 100 and 125 times the lamination thickness.

The lumber used in the manufacture of glulam must be seasoned or dried prior to use, so that the effects of checking and other drying defects are minimized. In addition, design can be on the basis of seasoned wood, which permits greater design values than can be assigned to unseasoned timber.

Structural elements can be designed with varying cross sections along their length as determined by strength and stiffness requirements. The beams in **Figure 2** show how the central section of the beam can be made deeper to account for increased structural requirements in this region of the beam. Similarly, arches often have varying cross-sections as determined by design requirements.

One major advantage of glulam is that a large quantity of lower-grade lumber can be used within the less highly stressed laminations of the beams. Grades are often varied within the beams so that the highest grades are used in the highly stressed laminations near the top and bottom and the lower grade for the inner half or more of the beams. Species can also be varied to match the structural requirements of the laminations.

Much is being written and discussed regarding the relative environmental effects of various materials. Several analyses have shown that the renewability of wood, its relatively low requirement for energy during manufacture, its carbon storage capabilities, and its recyclability offer potential long-term environmental advantages over other materials (*see* **Wood Use and Trade**: Environmental Benefits of Wood as a Building Material). Although aesthetic and economic considerations usually are the major factors influencing material selection, these environmental advantages may increasingly influence material selection.

The advantages of glulam are tempered by certain factors that are not encountered in the production of sawn timber. In instances where solid timbers are available in the required size, the extra processing in making glulam timber usually increases its cost above that of sawn timbers. The manufacture of glulam requires special equipment, adhesives, plant facilities, and manufacturing skills, which are not needed to produce sawn timbers. All steps in the manufacturing process require care to ensure the high quality of the finished product. One factor that must be considered early in the design of large straight or curved timbers is handling and shipping.

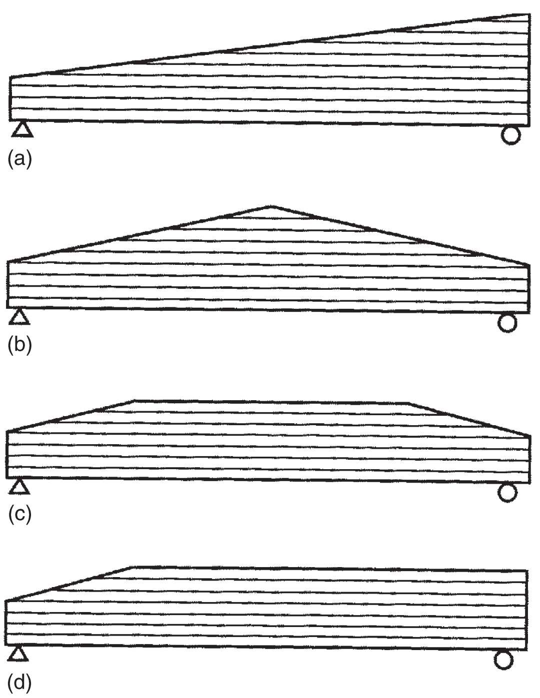


Figure 2 Glulam timbers may be (a) single tapered, (b) double tapered, (c) tapered at both ends, or (d) tapered at one end.

Types of Glulam Combinations

The configuring of various grades of lumber to form a glulam cross-section is commonly referred to as a glulam combination. Glulam combinations subjected to flexural loads, called bending combinations, were developed to provide the most efficient and economical section for resisting bending stress caused by loads applied perpendicular to the wide faces of the laminations. This type of glulam is commonly referred to as a horizontally laminated member. Lower grades of laminating lumber are commonly used for the center portion of the combination, or core, where bending stress is low, while a higher grade of material is placed on the outside faces where bending stress is relatively high. To optimize the bending stiffness of this type of glulam member, equal amounts of high quality laminations on the outside faces should be included to produce a ‘balanced’ combination.

Glulam axial combinations were developed to provide the most efficient and economical section for resisting axial forces and flexural loads applied parallel to the wide faces of the laminations. Members having loads applied parallel to the wide faces of the laminations are commonly referred to as vertically laminated members. Unlike the practice for bending combinations, the same grade of lamination is used throughout the axial combination. Axial combinations may also be loaded perpendicular to the wide face of the laminations, but the nonselective placement of material often results in a less efficient and less economical member than does the bending combination. As with bending combinations, knot and slope-of-grain requirements apply based on the intended use of the axial member as a tension or compression member.

Efficient use of lumber in cross-sections of curved glulam combinations is similar to that in cross-sections of straight, horizontally laminated combinations. Tension and compression stresses are analyzed as tangential stresses in the curved portion of the member. A unique behavior in these curved members is the formation of radial stresses perpendicular to the wide faces of the laminations. As the radius of curvature of the glulam member decreases, the radial stresses formed in the curved portion of the beam increase. Because of the relatively low strength of lumber in tension perpendicular-to-the-grain compared with tension parallel-to-the-grain, these radial stresses become a critical factor in designing curved glulam combinations.

Glulam beams are often tapered to meet architectural requirements, provide pitched roofs, facilitate drainage, and lower wall height requirements at the end supports. The taper is achieved by sawing the member across one or more laminations at the desired slope. It is recommended that the taper cut be made only on the compression side of the glulam member, because violating the continuity of the tension-side laminations would decrease the overall strength of the member. Common forms of straight, tapered glulam combinations include: (1) single tapered, a member having a continuous slope from end to end on the compression side; (2) double tapered, a member having two separate slopes sawn on the compression side; (3) tapered at both ends, a member with slopes sawn on the ends, but the middle portion remaining straight; and (4) tapered at one end, similar to (3) with only one end having a slope. These four examples are illustrated in **Figure 2**.

Glued Members With Lumber and Panels

Highly efficient structural components can be produced by combining lumber with panel products through gluing. These components include box beams, I-beams, 'stressed-skin' panels, and folded plate roofs.

These highly efficient designs, although adequate structurally, can suffer from lack of resistance to fire and decay unless treatment or protection is provided. The rather thin portions of the cross-section (the panel materials) are more vulnerable to fire damage than are the larger, solid cross-sections.

Box beams and I-beams with lumber or laminated flanges and structural panel webs can be designed to provide the desired stiffness, bending, moment resistance, and shear resistance. The flanges resist bending moment, and the webs provide primary shear resistance. Proper design requires that the webs must not buckle under design loads. If lateral stability is a problem, the box beam design should be chosen because it is stiffer in lateral bending and torsion than is the I-beam. In contrast, the I-beam should be chosen if buckling of the web is of concern because its single web, double the thickness of that of a box beam, will offer greater buckling resistance.

In recent years, the development of improved adhesives and manufacturing techniques has led to the development of the prefabricated I-beam industry. This product is a unique type of I-beam that is replacing wider lumber sizes in floor and roof applications for both residential and commercial buildings (**Figure 3**). Significant savings in materials are possible with prefabricated I-beams that use either plywood or oriented strandboard (OSB) for the web material and small-dimension lumber or SCL for the flanges. The high-quality lumber needed for these flanges has been difficult to obtain using visual grading methods, and both mechanically graded lumber and SCL are being used by several manufacturers. The details of fastening the flanges to the webs vary between manufacturers; all must be glued with a waterproof adhesive. Prefabricated I-beams are becoming popular with builders because of their light weight, dimensional stability and ease of construction. Their accurate and consistent dimensions, as well as uniform depth, allow the rapid creation of a level floor. Utility lines pass easily through openings in the webs.

Constructions consisting of structural panel 'skins' glued to wood stringers are often called stressed-skin panels. These panels offer efficient structural constructions for floor, wall, and roof components. They can be designed to provide desired stiffness, bending moment resistance, and shear resistance. The skins resist bending moment, and the wood stringers provide shear resistance.

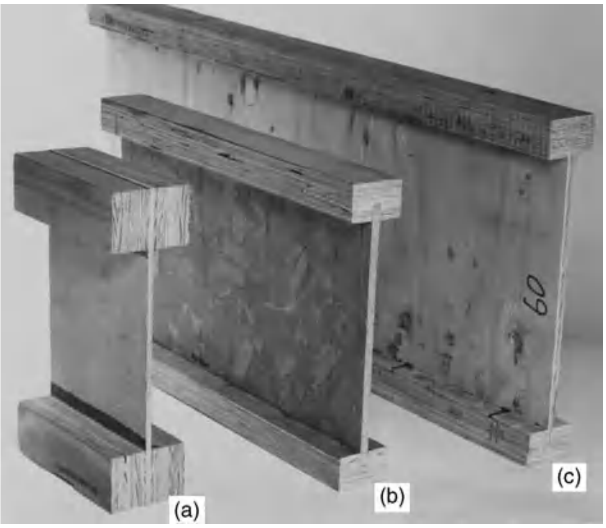


Figure 3 Prefabricated I-beams with laminated veneer lumber flanges and structural panel webs. (a) one experimental product has a hardboard web. The other two commercial products have (b) oriented standboard and (c) plywood webs.

Structural Sandwich Construction

Structural sandwich construction is a layered construction formed by bonding two thin facings to a thick core (**Figure 4**). The thin facings are usually made of a strong and dense material because they resist nearly all the applied edgewise loads and flatwise bending moments. The core, which is made of a weak and low-density material, separates and stabilizes the thin facings and provides most of the shear rigidity of the sandwich construction. By proper choice of materials for facings and core, constructions with high ratios of stiffness to weight can be achieved. As a crude guide to the material proportions, an efficient sandwich is obtained when the weight of the core is roughly equal to the total weight of the facings. Sandwich construction is also economical because the relatively expensive facing materials are used in much smaller quantities than are the usually inexpensive core materials. The materials are positioned so that each is used to its best advantage.

Specific nonstructural advantages can be incorporated in a sandwich construction by proper selection of facing and core materials. An impermeable facing can act as a moisture barrier for a wall or roof panel in a house; an abrasion-resistant facing can be used for the top facing of a floor panel; and decorative effects can be obtained by using panels with plastic facings for walls, doors, tables, and other furnishings. Core material can be chosen to provide thermal insulation, fire resistance, and decay resistance. Because of the light weight of structural sandwich construction, sound transmission problems must also be considered in choosing sandwich component parts.

Methods of joining sandwich panels to each other and other structures must be planned so that the joints function properly and allow for possible dimensional change as a result of temperature and moisture variations. Both structural and nonstructural advantages need to be analyzed in light of the strength and service requirements for the sandwich construction. Moisture-resistant facings, cores, and adhesives should be used if the construction is to be exposed to adverse moisture conditions. Similarly, heat-resistant or decay-resistant facings, cores, and adhesives should be used if exposure to elevated temperatures or decay organisms is expected.

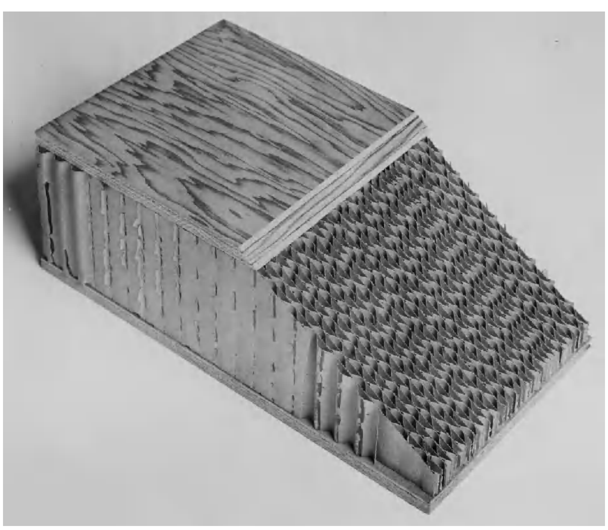


Figure 4 Cutaway section of sandwich construction with plywood facings and a paper honeycomb core.

See also: **Solid Wood Processing**: Adhesion and Adhesives; Machining; Protection from Fire. **Solid Wood Products**: Lumber Production, Properties and Uses; Wood-based Composites and Panel Products. **Wood Formation and Properties**: Physical Properties of Wood. **Wood Use and Trade**: Environmental Benefits of Wood as a Building Material.

Further Reading

Forest Products Laboratory (1999) *Wood Handbook – Wood as an Engineering Material*. General Technical Report FPL-GTR-113. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory.
Smulski S (ed.) (1997) *Engineered Wood Products: A Guide to Specifiers, Designers and Users*. Madison, WI: Product Fabrication Services Research Foundation.
US Department of Agriculture (1999) *Wood Handbook*: *Wood as an Engineering Material*. General Technical Report no. FPL-GTR-113. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory.

Structural Use of Wood

S Smulski, Wood Science Specialists Inc., Shutesbury, MA, USA

Introduction

Wood is an indispensable structural material worldwide and has been so since antiquity. The global prominence of wood as a construction staple is owed not only to its desirable attributes, but also to the fact that the forest resources from which it is derived are universally distributed, abundant, and renewable. Whether in the form of traditional solid-sawn lumber or a modern engineered wood I-joist, wood is unique among load-bearing building products. The only structural material of biological origin, wood has a high strength-to-weight ratio, is easily cut to size and shape with simple tools, is readily joined with fasteners or adhesives to produce strong joints, and is prized for its natural beauty. The perceived limitations of wood as a structural material – combustibility and degradation by decay fungi and insects – were overcome long ago with advances in building design, construction practice, and the advent of preservative and fire-retardant treatments.

North America is both the world's largest producer and consumer of structural wood products. The majority of the structural wood products manufactured in the USA and Canada is used domestically to build more than 1 million single-family houses annually as well as thousands of other wood-frame structures of all kinds. The balance of North America's output of structural wood products is exported to Asia, Europe, and Australia and, more recently, to South America, where it is utilized for much the same purposes, but to a much lesser extent. While nearly all residential structures in North America are framed with wood, concrete and masonry dominate house building in Asia, Europe, and South America. Traditional on-site stick-building of houses is the norm in North America, but off-site factory-assembly predominates in Japan and Europe. Virtually all North American dimension lumber is made from softwoods, while much of Australia's native structural framing is manufactured from hardwoods. Wood-frame buildings in North America seldom exceed four stories in height, but those in Europe increasingly rise to six stories. Despite these and other regional differences, similar structural wood products are used for similar applications worldwide. It is for these reasons that the focus here is on the structural use of wood in North America, and by extension, around the globe.

Today, structural wood products are available in a wide array of forms useful in a broad spectrum of applications. The decision to use traditional solid-sawn products or modern engineered products is made based on the kind of structure under consideration, the distances to be spanned, the magnitude of the loads to be supported, and the desired aesthetics. Solid-sawn options are boards, dimension lumber, timbers, poles, piles, and construction logs. The choice of engineered wood products presently includes glue-laminated timber, laminated veneer lumber, wood I-joists, parallel strand lumber, laminated strand lumber, metal plate connected trusses, and panel products plywood and oriented strand board.

Structural Wood Product Allowable Design Values

Historically, the size of the solid-sawn lumber and timber needed to frame a structure was chosen based on rules of thumb borne from past success. This educated-guess approach of choosing structural wood products that are 'big enough' and thus 'strong enough' for the task at hand is still used locally in some parts of the world. In almost all industrialized nations, however, solid-sawn and engineered wood products intended for use in structural applications are stress-rated to ensure that they will safely support the loads imposed on them in service. This means that they have been assigned allowable design values for various mechanical properties such as modulus of elasticity in bending, extreme fiber stress in bending, tension, compression, and shear, based on the results of destructive tests conducted on full-size members. As a consequence of the built-in safety factor, the actual breaking strength of a structural wood product is four to five times greater than its allowable design value. All wooden structures are designed such that the stresses induced in the structural members by in-service loads are less than the allowable design values.

Allowable design values must sometimes be adjusted as part of the design process to account for the effect on member stiffness and strength of duration of loading, in-service conditions of use, and postgrading treatment. This is true for both solid-sawn and engineered wood products, although the adjustment factors for each type of member may differ. Published allowable design values apply to so-called normal load duration, which is the load that fully stresses a member to its allowable design value, intermittently or continuously, for a cumulative period of 10 years. Because wood can carry much higher loads for shorter periods of time than it can for longer periods, allowable design values for members subject to short-term, high-magnitude loads such as those imposed by snow, wind, and earthquakes must be adjusted for duration of loading. Modification of allowable design values is required whenever wood will experience sustained exposure to temperatures of 38–66°C (100–150°F) and whenever its in-service moisture content will exceed 19% for prolonged periods. Interaction between the chemicals in certain preservatives and fire retardants and heat during the treating process and posttreatment kiln-drying reduces wood's stiffness and strength. Because such formulations are proprietary, allowable design values for treated members must be altered as per the recommendation of the formulator or treater. Depending on the type of member and how it will be used, additional refinements to allowable design values for size, flat use, repetitive use, and curvature may also be warranted.

Solid-Sawn Wood Products

Boards, Dimension Lumber, and Timbers

Sawed directly from logs in an essentially finished form, boards, dimension lumber, and timbers are the oldest and still most widely used structural wood products. The three are differentiated on the basis of their nominal thickness (i.e., their smallest rough dimension as sawed from the log), not their actual thickness (i.e., their smallest finish dimension after surfacing). Boards are less than 38 mm (2 in.) thick; dimension lumber is 38 mm (2 in.) to, but not including, 127 mm (5 in.) thick; and timbers are 127 mm (5 in.) or more in thickness. Within each of the three nominal thickness classifications there are width categories, use categories, and grades. The names of the width and use categories indicate the intended application. Those for dimension lumber, for example, are light framing, stud, structural light framing, and structural joists and planks. Within width and use categories there are grades. Boards, dimension lumber, timbers, poles, piles, and construction logs are predominantly visually graded according to a set of rules that specify the natural and processing characteristics permitted in each grade. The higher the grade, the fewer and smaller the characteristics that are permitted and the higher the allowable design values. The grade names for dimension lumber structural joists and planks, for instance, are select structural (highest grade), no. 1, no. 2, and no. 3 (lowest grade). Dimension lumber used for fabricating trusses and glue-laminated timber, however, is graded mechanically and identified in the grade stamp as machine stress-rated or MSR.

The grade stamp printed on boards, dimension lumber, and timbers identifies the species, grade, and moisture condition of the member when it was machined to finish size. Knowledge of the moisture condition is especially useful in minimizing shrinkage, warpage, splitting, and other moisture-related problems that can arise after a member is placed in service. Solid-sawn products are either green (i.e., water-saturated) or dry (i.e., maximum 19% moisture content) when surfaced to finish dimensions. Most boards and dimension lumber are air- or kiln-dried to 19% moisture content or less prior to surfacing and thus shrink minimally after installation. Timbers are almost always green when surfaced because it is physically and economically impractical to kiln-dry members larger than 102 × 102 mm (4 × 4 in.). Consequently, the sometimes considerable postinstallation initial shrinkage of timbers must be accounted for during the design process. Attention must also be given to the initial shrinkage of boards and dimension lumber pressure-treated with water-borne preservatives. These products are saturated with water during treatment and seldom redried afterwards.

Boards Compared with dimension lumber and timbers, stress-rated boards are of minor importance and see limited use. Employed occasionally for wall and roof sheathing, subflooring, collar ties, diagonal bracing, and decking, most are made from the pines, spruces, true firs, and other softwoods. Boards are manufactured in 25-mm (1-in.) increments from 51 to 305 mm (2 to 12 in.) wide; wider boards are made but difficult to find. Most boards are 1.8–6.1 m (6–20 ft) in length, in multiples of 0.3 m (1 ft).

Dimension lumber By far the most widely used solid-sawn structural product, dimension lumber is routinely used for sill plates, wall studs, floor and ceiling joists, roof rafters, ridge boards, purlins, door and window headers, decking, and site-built nail-laminated girders. Manufactured in increments of 51 mm (2 in.) in width and thickness and in 0.6-m (2-ft) multiples in length beginning at 2.4 m (8 ft), virtually all dimension lumber is made from softwoods such as the pines, spruces, true firs, hemlocks, larches and Douglas-fir. Dimension lumber up to 305 mm (12 in.) wide and 4.9 m (16 ft) long is still readily available. Larger members are increasingly scarce because the inventory of large-diameter trees has essentially been depleted. Where wider or longer members are required, engineered wood products are used instead. Two engineered wood substitutes are themselves made from dimension lumber: metal plate connected trusses and glue-laminated timber.

Timbers Made primarily from high-density softwoods and hardwoods such as the hard pines, Douglas-fir and the oaks, timbers are subdivided into two use and width categories: beams and stringers, which are plainly rectangular, and posts and timbers, which are essentially square. The nominal width of beams and stringers is more than 51 mm (2 in.) greater than their nominal thickness, while that of posts and timbers is 51 mm (2 in.) or less. Timbers are sawed in multiples of 51 mm (2 in.) in width and thickness and 0.3 m (1 ft) in length, starting at 1.8 m (6 ft) and ranging to 12.2 m (40 ft) and longer. As the name implies, beams and stringers are used as beams, stringers, girders, sills, purlins and other horizontally oriented primary and secondary supporting members. Posts and timbers are mainly employed as primary vertical supports such as posts and columns. Timbers of both width categories are widely used in pedestrian and vehicular bridges; piers, seawalls and other freshwater and marine structures; and as chords and webs in heavy timber trusses. Rough-sawn timbers are often employed in the construction and renovation of concrete and steel structures as temporary shoring and bracing.

Round Timbers

Poles Essentially tree-length logs shaved of their bark, poles are 127–762 mm (5–30 in.) in diameter at the butt and 6.1–36.6 m (20–120 ft) in length. Because straightness is important, virtually all poles are made from softwood trees whose excurrent form (i.e., a single, tapering main stem) is well suited for this purpose. Utility poles and utility pole structures carry electric power distribution wires and communications cables. Construction poles serve as both the foundation and main vertical supports in pole buildings and highway sound barriers. Often, a narrow flat plane extending from groundline to tip is machined on one face of construction poles to remove taper and facilitate attachment of framing, sheathing, and siding. Because the butt is embedded in the ground, both utility and construction poles function as cantilever beams. As such, they are stress-rated according to their allowable extreme fiber stress in bending. Utility and construction poles are routinely pressure-impregnated with a preservative such as creosote, pentachlorophenol, or chromated copper arsenate because of the decay hazard imposed by soil contact.

Piles Manufactured in the same manner and in essentially the same sizes as poles, piles are used in foundations under buildings and bridges. Most are made from softwoods such as the hard pines and Douglas-fir, although some are oak. End-bearing piles are driven down to bedrock so that the weight of the structure is transferred along the pile to this immovable base. Friction piles are used where soil is so deep that bedrock is inaccessible. So-called skin friction that develops between the wood and the surrounding soil prevents the pile from slipping downward under the load exerted by the structure. Because piles are loaded axially both when hammered into the ground and in service, they are stress-rated according to their allowable compression strength parallel to grain. Straightness is of utmost importance in minimizing pile breakage during driving. Often, the butt end of a pile embedded in soil is above the water table or even partially exposed above ground and thus vulnerable to decay fungi and insects. The submerged portion of piles supporting piers and other marine structures is susceptible to marine borers, while the above-water segment is threatened by decay fungi and insects. For these reasons, piles are routinely pressure-treated with the same preservatives as poles.

Construction logs Stacked vertically to form the walls of log buildings, construction logs are typically 203–305 mm (8–12 in.) in diameter and 2.4–9.1 m (8–30 ft) long. Virtually all construction logs are milled from softwoods such as the cedars and pines. They are made by passing tree-length logs or rough-sawn timbers through a four-sided cutterhead that machines the member to a circular or rectangular profile that is uniform along its length. A construction log's vertical faces, which are rounded or flat with beveled edges, become the exterior and interior surfaces of the wall. A system of tongues and grooves or grooves and splines is milled on the top and bottom faces so that construction logs interlock when stacked. Construction logs made from softwoods that lack natural decay resistance are treated by nonpressure dipping or spraying with a waterborne borate preservative to deter decay fungi and insects. Milled when green, construction logs shrink considerably in diameter after erection. Door and window openings in log buildings must be designed to accommodate this shortening of wall height.

Engineered Wood Products

During the last four decades of the twentieth century, traditional solid-sawn boards, dimension lumber, timbers, poles, piles, and construction logs were joined by numerous structural-engineered wood products made by gluing together small pieces of wood with a waterproof structural adhesive. The roster continues to expand as new products are introduced, but currently includes glue-laminated timber, laminated veneer lumber, wood I-joists, parallel strand lumber, laminated strand lumber, and panel products plywood and oriented strand board. Metal plate connected wood trusses are the nonglued exception.

Engineered wood products will eventually supplant the larger sizes of high-grade solid-sawn dimension lumber and timbers. A nonrenewable resource in truth, the old-growth forests from which large, high-grade dimension lumber and timbers were sawed are almost gone. Most of what is left has been set aside in national parks, wilderness areas, and other holdings that prohibit harvesting. Today's forest resources consist primarily of second- and third-generation trees managed under sustainable forestry practices for harvesting on 30–80-year rotations. Trees are thus smaller in diameter when felled, and the dimension lumber and timbers sawed from them contain more natural characteristics such as knots and juvenile wood that affect strength and in-service performance. While smaller sizes of dimension lumber (up to 51 × 254 mm (2 × 10 in.))

and timbers (up to 254 × 254 mm (10 × 10 in.)) will always be plentiful, the future availability of larger members, especially in the higher grades, is arguably uncertain. For these reasons, glue-laminated timber, laminated veneer lumber, wood I-joists, parallel strand lumber, laminated strand lumber, metal plate connected trusses, plywood, and oriented strand board represent the future of structural wood products. All of these engineered wood products can be made from trees no larger than 305 mm (12 in.) in diameter or from dimension lumber no wider than 102 mm (4 in.), and in lengths substantially longer than can be sawed from today's logs. Because knots and other natural strength-reducing characteristics are restricted to a single lamination, veneer, or strand, they are smaller and harmlessly dispersed throughout the product's volume. As a result, the range of stiffness and strength among individual pieces of engineered wood products is considerably narrower than that of solid-sawn dimension lumber and timbers. Allowable design values are consequently higher, as is the predictability of in-service performance.

Except for plywood and oriented strand board, which are commodity products, engineered wood products and their allowable design values are proprietary. This means that the allowable design values for an otherwise identical product made by two different manufacturers will almost certainly differ. As such, a wood I-joist fabricated by one manufacturer cannot necessarily be substituted for that made by another simply because both are the same depth. Because of the complications that arise from this present situation, some voices in the construction community have called for the production of commodity-engineered wood products that share the same allowable design values and are thus interchangeable. Whether this happens remains to be seen.

With the exception of trusses, engineered wood products are manufactured from wood kiln-dried to a moisture content of 12% or less, which is well below the 19% typical of boards and dimension lumber. Consequently, they shrink, warp, and split much less than solid-sawn boards, dimension lumber, and timbers after being installed. Fastener pops, floor squeaks, drywall cracks, and other shrinkage-related problems are virtually eliminated. Camber is routinely built in to nonpanel-engineered wood products to counter dead load deflection and creep (i.e., progressive sagging of a member under sustained load over a very long time).

Glue-laminated timber Glue-laminated timber or glulam is made by face-laminating softwood dimension lumber that has been finger-jointed end-to-end. With this method, beams and columns that are longer, wider, and deeper than sawn timbers can be fabricated, as can curved members and arches. Lengths up to 30.5 m (100 ft) are common, as are depths and widths of 0.3 (1 ft) to several meters (feet). While small stock sizes are manufactured for residential use, the majority of glulams are custom-made. Efficient use of wood is made when designing glulams by strategically placing the highest-grade laminations where in-service stresses are highest, then filling out members with lower-grade laminations where stresses are lower. Glulams are used in structures where long, clear spans and/or appearance are of primary importance, such as factories, warehouses, sports arenas, aircraft hangars, churches, auditoriums, and large office, hotel, retail, and institutional buildings. Preservative-treated members are utilized in bridges, piers and other freshwater and marine structures, power transmission towers, and as the main vertical supports in postframe buildings. Due to their large size, connections between members are made with through-bolts and steel gusset plates and framing anchors. Because glulam is made from dimension lumber at 12% moisture content, initial shrinkage after installation is small. However, connections must be designed so that members can shrink and swell freely in-service without overstressing the surrounding wood (**Figure 1**).

Laminated veneer lumber Composed of multiple sheets of veneer bonded together such that the grain of each ply is parallel to the product's length, laminated veneer lumber (LVL) is essentially reconstituted

Figure 1 Glue-laminated timbers provide both structural support and pleasing aesthetics for this curling rink. Courtesy of APA – The Engineered Wood Association.

dimension lumber. Like glulam, veneers are graded for stiffness and strength, then strategically positioned within the product to maximize allowable design values. Manufactured in the same and slightly larger thicknesses as dimension lumber, but in greater widths and in lengths up to 24.4 m (80 ft), LVL is widely used in residential and commercial construction for beams, girders, headers, joists, purlins, posts, and columns. LVL is also used extensively for scaffold planks and for the flanges of wood I-joists. Most is made from high-density softwoods such as the hard pines and Douglas-fir, and medium-density hardwoods like yellow poplar. LVL pressure-treated with waterborne preservatives and fire retardants is available (**Figure 2**).

Wood I-joists I-shaped in cross-section and light in weight, wood I-joists come in many depths and flange widths and in lengths up to 24.4 m (80 ft). Flanges are LVL or dimension lumber, while webs are plywood, oriented strand board, and sometimes, dimension lumber. As their name suggests, most I-joists are used for framing floors in houses and low-rise office, hotel, retail, and institutional buildings. The small mass and long span typical of an I-joist floor system occasionally interact to produce annoying vibrations underfoot. Blocking, cross-bracing, and strongbacks are needed to stiffen these floor systems and dampen vibrations. Increasingly, I-joists are being utilized as rafters and purlins in residential and commercial roofs. Because of their unique cross-section, the proper way of designing and building with wood I-joists may not be apparent to those accustomed to using boards, dimension lumber, and timbers. As such, I-joist manufacturers supply design manuals and software to ensure their correct use (**Figure 2**).

Figure 2 Engineered wood products such as wood I-joists (far left), laminated strand lumber (left, right), laminated veneer lumber (center), and parallel strand lumber (far right) are replacing the larger sizes and higher grades of solid-sawn dimension lumber. Courtesy of TrusJoist A Weyerhaeuser Business.

Parallel strand lumber Offering the highest allowable design values of today's engineered wood products, parallel strand lumber (PSL) competes for the same applications as timber and glulam. Because of its pleasing appearance, PSL beams, stringers, girders, headers, purlins, posts, and columns are typically left exposed. Composed of long, narrow strips of Douglas-fir, larch, hard pine, and yellow-poplar veneer bonded together and oriented parallel to the product's length, PSL is available in lengths up to 21.3 m (70 ft) and in widths and thicknesses ranging from 102 to 508 mm (4 to 20 in.). PSL readily treats with preservatives and fire retardants (**Figure 2**).

Laminated strand lumber The most recent engineered wood innovation, laminated strand lumber (LSL) consists of short, thin strands of underutilized, fast-growing mixed softwoods and hardwoods consolidated with heat and pressure into dimension lumber-sized products. To date, its use is limited to rim joists, studs, blocking, and light-duty headers in residential construction (**Figure 2**).

Metal plate connected wood trusses The dimension lumber chords and webs of metal plate connected wood trusses are joined not with adhesive, but with toothed metal plates pressed into the wood. Routinely used for framing roofs of virtually any shape in residential construction, trusses are commonly utilized in many types of commercial, industrial, and agricultural buildings as well. Lengths range from 4.6 to 24.4 m (15 to 80 ft) and more, with truss height dictated by roof pitch. Stock roof trusses are fabricated for residential use, but most trusses are designed to order using sophisticated engineering software. Because dimension lumber grade is matched to in-service stresses on a chord-by-chord and web-by-web basis, trusses make especially efficient use of wood. Where a conventionally framed roof might use 51×203 mm (2×8 in.) rafters spaced 406 mm (16 in.) on-center, for instance, trusses for the same roof, made from members 51×102 mm (2×4 in.) and spaced 610 mm (24 in.) apart, use 15–25% less wood. More and more, floors and low-slope roofs in nonresidential buildings are being built with parallel chord trusses whose open webs simplify and speed the placement of piping, ductwork, and wiring. Where spans and/or in-service loads are very large or appearance is important, heavy timber trusses are employed. Made from timber, glulam, or PSL, the chords and webs of these heavy-duty trusses are joined with through-bolts inserted into steel gusset plates, framing anchors, split-ring connectors or shear plate connectors. Depending upon their configuration, these massive trusses may span up to 90 m (300 ft) (**Figure 3**).

Plywood and oriented strand board Two structural panel products – plywood and oriented strand board – are routinely used in all types of wood-frame buildings. Most plywood is made from softwood veneer, while oriented strand board consists of small, thin strands of mixed softwoods and hardwoods. Both panels are cross-laminated such that the grain of each layer is perpendicular to that of adjacent layers. Most commonly manufactured in 1.2×2.4 m (4×8 ft) sheets 12.7–38.1 mm (0.5–1.5 in.) thick, plywood and oriented strand board are employed as roof and wall sheathing, subflooring, and underlayment. Special grades of both panels are made for use in engineered applications such as diaphragms and shearwalls in wind- and earthquake-resistant structures, as well as in stressed skin panels. Plywood is widely utilized for concrete formwork, while oriented strand board is the preferred facing for foam-core structural insulated panels. Plywood and oriented strand board panels intended for structural use are selected according to the span rating and exposure durability class found in the grade stamp. The span rating is a two-number code such as 812/406 (32/16). The number on the left is the maximum recommended on-center spacing in millimeters (inches) for framing when the panel is used as roof sheathing. The right-hand number is the maximum recommended on-center spacing of framing when the panel is used as subflooring. In all cases, panels are to be installed with their long dimension perpendicular to framing and across three or more supports.

Exposure durability class indicates a panel's ability to resist the damaging effects of exposure to the weather or to moisture. Panels marked exterior or marine are the only choice for those that will be permanently exposed to the elements or to high moisture. Exposure 1 panels are intended for applications where long delays in construction or high moisture in service is possible. Interior panels are meant for dry, protected uses. Fire retardant-treated plywood is readily available, as is the preservative-treated plywood used in permanent wood foundations. Because treatment reduces plywood's stiffness and strength, the appropriate adjustment factors must be obtained from the formulator or treater. With oriented strand board, strands are treated before consolidation, so no adjustment is needed (**Figure 4**).

Wooden Structures

While the number of potential structural applications for wood is limited only by the imagination, the majority of structural wood products are used in constructing buildings and bridges. Wood-frame buildings are classified according to the size of the members used and the geometry of the structural skeleton they form. Five basic types are light-frame, log, post-frame, pole, and heavy timber. In addition, many very large, special-purpose buildings such as domed and arched sports arenas are constructed with solid-sawn and engineered wood products. The fundamental types of wooden bridges – beam, deck, truss, arch, and suspension – are named after the

Figure 3 Roofs of virtually any shape can be framed with metal plate connected wood trusses fabricated from dimension lumber. Courtesy of the Wood Truss Council of America.

Figure 4 Plywood and oriented strand board are routinely used for roof and wall sheathing in all types of residential and commercial construction. Courtesy of APA – The Engineered Wood Association.

configuration of their superstructure. Variations on these five archetypal designs abound.

Wood-Frame Buildings

Light-frame buildings By far the most common wood-frame structure, light-frame buildings are constructed largely from dimension lumber, wood I-joists, and roof and floor trusses spaced 406 or 610 mm (16 or 24 in.) on-center and sheathed with plywood or oriented strand board. Examples include single-family houses; garages and outbuildings; apartment and condominium buildings; and low-rise office, hotel, retail, and institutional buildings. The traditional method of stick-building – framing a structure on-site member-by-member – is gradually yielding to automated building in which structures are made from factory-fabricated subassemblies that are joined on-site. Leading this trend are panelized buildings made from preframed and sheathed wall, floor, and roof subassemblies and modular buildings consisting of three-dimensional boxes that are stacked on-site. Greater control over the quality of assembly, more efficient use of materials, freedom from the vagaries of weather, rapid on-site erection, and reduced on-site generation of construction waste are driving the switch (**Figure 5**).

Log buildings The walls of log buildings are made from construction logs, and sometimes profiled timbers, that are stacked vertically. Floors and roofs are framed with dimension lumber, wood I-joists, trusses, or exposed construction logs. Most log buildings are single-family dwellings, although many are park structures and retail shops where this rustic look is appropriate. Virtually all log buildings are sold as kits, with each log precut to length and marked for sequential stacking on-site. Typically, all other materials needed to complete the shell such as roof framing, sheathing, shingles, and doors and windows are included (**Figure 6**).

Post-frame buildings Construction of a post-frame building begins with embedding in the ground preservative-treated nail-laminated dimension lumber, timber, or glulam posts, also known as wall columns. Horizontal wall girts of dimension lumber are then fastened to the posts, and plywood or oriented strand board sheathing and/or siding is affixed to the wall girts. This framework is capped with metal plate connected roof trusses installed on 1.2–3.6-m (4–12-ft) centers, with dimension lumber purlins spanning across or between trusses to support plywood or oriented strand board sheathing, and/or metal roofing. Formerly used only for livestock barns, equipment sheds and other agricultural structures, post-frame buildings are today erected for use as retail shops, warehouses, factories, fire stations, commercial garages, and recreational facilities (**Figure 7**).

Pole buildings The forerunner of post-frame buildings, pole buildings have declined markedly in popularity. Constructed in virtually the same manner as post-frame buildings, pole buildings are occasionally erected for agricultural use and as bulk storage sheds for road deicing chemicals. Structures supported by poles such as highway sound barriers and billboards, however, are common.

Heavy timber buildings
Timber frame buildings Timber frame construction represents the oldest formal use of wood as a

Figure 5 Light-frame buildings constructed from dimension lumber and plywood or oriented strand board sheathing such as these houses are the most common wood-frame structures. Courtesy of APA – The Engineered Wood Association.

Figure 6 Typically sold as kits, modern log buildings are increasingly complex in design. Courtesy of Original Lincoln Logs Ltd. and Craig Murphy Photography.

structural material. For over 20 centuries, timbers have been employed as the structural framework for all types of buildings. Members were connected with mortise and tenon joints pegged with wooden dowels called trunnels to prevent the tenon from pulling out. These same joints are still used today, especially where appearance is important, although mechanical fastening is increasingly common. While most timber frame buildings utilize timber, glulam usage is growing. The skeleton of a modern timber frame building differs little from that of its ancestors, but the walls and roof are now made of structural insulated panels. Applied to the outside of the timber frame, these energy-efficient panels have a foam core sandwiched between oriented strand board faces. Floor decks and interior partitions are typically built with dimension lumber. Although many types of modern buildings are of timber frame construction, including office, hotel and retail complexes, most are single-family residences (**Figure 8**).

Figure 7 Diagonal bracing holds the dimension lumber walls and roof trusses of this post-frame building plumb and square before sheathing is applied. Courtesy of National Frame Builders Association.

Figure 8 Diagonal braces lend rigidity to the timber frame of this future retail shop. Courtesy of Bensonwood Homes.

Mill buildings Infrequently constructed today, mill buildings have a masonry exterior and an interior framework of timber beams and columns. Floor and roof decking is usually tongue-and-groove dimension lumber. Originally built as factories and warehouses, thousands of nineteenth- and twentieth-century mill buildings have been renovated in the last few decades into retail and office complexes, and apartments and condominiums.

Wooden Bridges

Contemporary beam, deck, truss, arch, and suspension wooden bridges are used almost exclusively on secondary and rural roads where traffic volume and vehicular weights are relatively low. Components of the superstructure, which consists of the primary longitudinal supports, bracing, floor decking, railings, and other minor members, are preservative-treated timber or glulam. PSL and LVL are beginning to be used as well. Concrete abutments and intermediate supports of concrete or treated wooden piles form the underlying substructure. Beam bridges consist of longitudinal main carrying members with timber or glulam decking laid perpendicular to them. Spans are limited to about 7.6 m (25 ft) with timber supports, while 30 m (100 ft) or more can be achieved with glulam. The superstructure of a deck bridge is dimension lumber, timber, or glulam placed on edge and nail-laminated or, more commonly, drawn tightly together with threaded metal through-rods in a process known as stress-laminating, into a massive plate that doubles as both main support and decking. Because of the composite action that develops, deck bridges can span up to 11 m (36 ft). Parallel chord or bowstring trusses of timber or glulam form the sides and main supports of truss bridges. Bowstring trusses permit spans up to 30 m

Figure 9 Hinged glue-laminated timbers support the deck of this graceful arch bridge. Courtesy of APA – The Engineered Wood Association.

(100 ft), while 75 m (250 ft) is possible with parallel chord trusses. The familiar railroad trestle bridge is actually a beam, deck, or truss superstructure supported on wooden piles. Arch bridges have a timber or glulam deck that is supported by glulam arches. These graceful structures can span up to 60 m (200 ft) (**Figure 9**). The longest spans are achieved with suspension bridges, virtually all of which, however, are for pedestrian use only. Consisting of a timber or glulam deck hanging from wire rope cables, these bridges are up to 150 m (500 ft) long.

See also: **Solid Wood Products**: Construction; Logs, Poles, Piles, Sleepers (Crossties); Glued Structural Members; Lumber Production, Properties and Uses; Wood-based Composites and Panel Products. **Wood Use and Trade**: Environmental Benefits of Wood as a Building Material.

Further Reading

American Forest and Paper Association (1987) Permanent Wood Foundation System Design, Fabrication and Installation Manual. Washington, DC: AF&PA.

American Forest and Paper Association (1996) Load and Resistance Factor Design Manual for Engineered Wood Construction. Washington, DC: AF&PA.

American Forest and Paper Association (1997) National Design Specification for Wood Construction. Washington, DC: AF&PA.

American Forest and Paper Association (1997) Supplement National Design Specification for Wood Construction. Washington, DC: AF&PA.

American Institute of Timber Construction (1994) Timber Construction Manual., 4th edn. Englewood, CO: AITC.

Canadian Wood Council (1991) Wood Reference Handbook. Ottawa, Canada: CWC.

Canadian Wood Council (1993) Wood Building Technology. Ottawa, Canada: CWC.

Faherty K and Williamson T (1989) Wood Engineering and Construction Handbook. New York, NY: McGraw-Hill.

Forest Products Laboratory (1999) Wood Handbook. Wood as an Engineering Material. Madison, WI: Forest Products Society.

Goldstein E (1999) Timber Construction for Architects and Builders. New York, NY: McGraw-Hill.

Hoyle R and Woeste F (1989) Wood Technology in the Design of Structures., 5th edn. Ames, IA: Iowa State University Press.

National Frame Builders Association (2001) Post-Frame Building Design Manual. Lawrence, KS: NFBA.

National Institute of Standards and Technology (1999) American Softwood Lumber Standard DOC PS 20-99. Gaithersburg, MD: NIST.

Sherwood G and Stroh R (1989) *Wood-Frame House Construction*. USDA Forest Service Agriculture Handbook 73. Washington, DC: US Superintendent of Documents.

Smulski S (ed.) (1997). Engineered Wood Products. A Guide for Specifiers, Designers and Users. Madison, WI: PFS Research Foundation.

Williamson T (ed.) (2002) APA Engineered Wood Handbook. New York, NY: McGraw-Hill.

Wood Truss Council of America (1997) Metal Plate Connected Wood Truss Handbook. Madison, WI: WTCA.

Lumber Production, Properties and Uses

F G Wagner, University of Idaho, Moscow, ID, USA

Lumber production or sawmilling is the process of sawing and/or chipping logs to form rectangular pieces of wood (lumber, cants, or timbers) for buildings, packaging, furniture, and many other applications. Lumber production may have begun in Egypt as early as 6000 BC, where handsaws and planes were utilized to fashion small volumes of crude lumber. Today, facilities for lumber production (sawmills) range from those with one or two slow-simple machines powered by electric motors or internal-combustion engines to those with many high-speed computerized machines powered by electric motors and hydraulic pumps. Some modern high-speed sawmills are capable of producing as much as 2000 m^3 (1 million board feet) of lumber per day. Sawmills often also include equipment for drying and shaping the sawn lumber into finished products. Properties important to lumber products include strength, stiffness, straightness, appearance, and proportion of clear wood. Standards have been established for grading lumber based on these properties.

Log Supply

Lumber manufacturing begins in the forest. Many large lumber-producing companies own forest land, and they obtain at least a portion of their log supply from that land. Other lumber-producing companies purchase logs or standing trees (stumpage) from private forest landowners or government agencies. Independent logging contractors are often hired to harvest and transport logs to the sawmill. In other cases, logs (gate wood) are purchased from individuals who deliver noncontracted logs to the sawmill. Logs may be cut to lumber lengths plus trim allowance, multiple lumber lengths (multisegment logs) plus trim allowance, or tree length. The trim allowance is a small amount of extra log length that allows lumber end trimming during manufacture. Logs may be as small as 10 cm in diameter, or they may be greater than 1 m in diameter.

Logs are purchased by weight or by log scale. If logs are purchased by weight, log trucks are weighed both loaded and empty to calculate the weight of the logs. Mathematical formulae are often used to convert weight to cubic or lumber volume.

Log scale is an estimate of the volume of lumber that is expected to be sawn from the logs. If logs are purchased by log scale, an experienced individual measures the diameter and length of logs, calculates gross lumber volume based on a scale stick or portable computer, and subtracts scale volume for defects that may reduce the volume of lumber sawn from the logs.

Logs are usually delivered to sawmills on log trucks or railcars. They are unloaded with large specially designed lift trucks or overhead cranes, and they are placed on a log yard. Logs are often sorted on the yard based upon species, species group, and diameter of the logs. It is important that enough logs be stored on the log yard to supply the sawmill during interruptions in log deliveries. Log deliveries may be interrupted because of wet weather, lags in log purchases, equipment breakdowns, or a number of other factors. Therefore, logs are sometimes stored for a year or more before they are sawn into lumber. If logs are stored for an extended period of time during warm weather (above 10°C), they must be protected from stain fungi, decay fungi, insects, and drying (*see* **Solid Wood Processing**: Protection of Wood against Biodeterioration. **Wood Formation and Properties**: Biological Deterioration of Wood). Protection is often accomplished by spraying the logs with water. The wet log surfaces provide an anaerobic environment in which most fungi and insects cannot survive, and it prevents drying of the logs. Environmental–government agencies often require that water sprayed on logs be captured at the sawmill site and reused. This prevents chemicals leached from the wood and bark of the logs from entering streams and other estuaries. If these chemicals enter streams and estuaries at high levels, they may be toxic to fish and other marine life.

Lumber Production

Stored logs are eventually transported to the sawmill by lift trucks or overhead cranes. Logs may then be moved by conveyor to a debarker where bark is detached from the logs. Debarkers are usually electrically powered machines that scrape or rub bark from the logs. Bark often contains soil and small rocks that become embedded during log harvest or storage. Thus, removing bark from logs helps prevent dulling of cutting tools in the sawmill. Removing bark from logs also separates bark from the outer portion of logs that often becomes pulp chips during the sawmill process. Bark and sawdust from the sawing processes are often burned to provide energy for lumber drying.

Either before or after the logs are debarked, multisegment logs and tree-length logs are crosscut (bucked) to lumber lengths plus trim allowance. Logs that were bucked to lumber lengths during the harvest process bypass this step. In large sawmills, logs are transported to the log-bucking station via conveyor where they are bucked to length with large circular saws or chainsaws powered by electric motors. At small sawmills, logs may be bucked to length with manually operated gasoline-powered chainsaws.

Logs are next processed by a machine called a headrig. A headrig is the first machine in a sawmill where longitudinal cuts are sawn or chipped on the log (*see* **Solid Wood Processing**: Machining). Every sawmill has one or more headrigs. Many different types of headrig are used worldwide, but most utilize one or more band saws, circular saws, and/or chipping heads to make longitudinal cuts. Logs may be completely sawn into lumber or timbers at the headrig, or they may be sawn into some combination of lumber, timbers, and cants. Cants are logs with one or more sawn or chipped faces. Some lumber may be produced with two sawn wide faces and wane (absence of wood) at the narrow faces (flitches). Flitches may be edged at an edger in the sawmill where the wane is sawn or chipped away. In the case of some hardwoods, flitches may also be sold to other manufacturers for further processing.

The speed of processing at headrigs is quite variable. At some small sawmills, only a few logs may be sawn on the headrig each hour. These are usually headrigs with many manual functions. At modern high-speed small-log sawmills, as many as 25 logs per minute may be processed. These are usually headrigs with scanners and computers that automatically determine the log size and shape, make sawing decisions, and perform many of the sawing functions. Many headrigs have chipping canters that chip a flat face on the side of logs. If the headrig does not have a chipping canter, flat faces are produced with the headrig saws, and the portion removed (slabs) is chipped at another location. Chips (small rectangular pieces of wood) produced at the headrig and at other machine centers in the sawmill are usually sold to pulp companies.

Various sawing methods may be used at headrigs and resaws. Sawn faces may be parallel to the log taper (follow the slope of the outside of the log from the small end to the large end of the log). This sawing method is termed 'taper sawing.' Logs may also be sawn parallel to the centerline of the log, which is termed split taper sawing. In addition, three different sawing patterns may be used. Logs may be completely sawn into lumber on the headrig with all saw lines parallel (live-sawing pattern). Alternatively, lumber and cants may be sawn on a headrig, and the cants may be transported to a resaw where sawn faces are made perpendicular to the sawn faces made at the headrig (cant-sawing pattern). A grade-sawing pattern is also sometimes used where the sawyer makes sawing decisions based upon defects in the log. In grade sawing, the sawyer attempts to improve the grade of the sawn lumber by first sawing the worst face. The log is then rotated to the best face, and the sawyer saws additional lumber from that face until grade declines. The sawyer then rotates the log 90° and continues to saw until the log is completely sawn into lumber.

If cants are produced at the headrig, they are further sawn into lumber at a resaw. Resaws often have multiple circular or band saws, and they may saw cants into lumber in one pass. Lumber produced at a headrig or resaw containing excess wane (absence of wood for any reason but usually due to sawing to the outside of the log) may be edged at an edger. An edger is a machine with saws or chipping heads that produce acceptably square narrow faces on each piece. Lumber is usually fed through an edger lengthwise. Typically some wane may be left on lumber if the amount of wane is not expected to lower the grade. Resaws and edgers may be operated manually, or they may be operated by scanning and computer systems. Chips are produced from the edges of wide faces.

At many sawmills, lumber trimsaws are used to trim one or both ends of lumber. Ends are trimmed to make the ends more square, to make the lumber consistent lengths for further processing, and to remove excess wane or other defects at one or both ends. Trimsaws typically have multiple circular saws that are set at specified distances apart. Lumber usually moves through trimsaws sidewise, and the appropriate saw is lowered to crosscut the lumber to length. Trimsaws may be operated manually, or they may be operated by scanning and computer systems. Short trim ends produced at the trimsaw may be chipped and sold to pulp companies.

Sawmill Performance

The principal measures of sawmill performance are lumber production and lumber recovery. Profitability of a sawmill is closely linked to lumber production. Because some costs at a sawmill are fixed (buildings, machines, and labor), higher lumber production results in lower fixed cost per unit of lumber. Many sawmills set goals or standards of production for a shift, day, week, month, or year. Sometimes bonuses are paid to sawmill workers if production standards are met or exceeded.

Lumber recovery is a measure of the proportion of lumber produced to the volume of logs processed. Lumber recovery is extremely important to the profitability of a sawmill because approximately 75% of the total manufacturing cost of lumber is the cost of logs. Therefore, even small improvements in recovery can greatly reduce manufacturing costs. Lumber recovery may be expressed in terms of percent cubic recovery, volume of lumber to cubic volume or weight of logs, or volume of lumber to log scale. When sawmill recovery is high, 50% or more of the log will become lumber. The rest of the log will become green sawdust and bark, which is often burned to produce energy for dry kilns, chips which are usually sold to pulp manufactures, and dry sawdust and planer shavings which are often sold to particleboard manufactures or burned to produce energy for the kilns. At most sawmills, 100% of the log is utilized.

One method of maintaining high lumber recovery is to have a quality-control program at the sawmill. Sawmill recovery is usually highest when log diameter is large, logs are straight with little taper, saw kerf (width of cut made by saws) is narrow, sawing variation (thick and thin lumber) is low, lumber products are wide and thick, equipment is well maintained, sawing decisions are good, and lumber is carefully dried to the correct moisture content. Therefore quality-control programs often collect and analyze data related to each of these factors. Measurements are taken on a regular basis within the sawmill, and statistics are used to determine whether established standards are being met and manufacturing processes are in control.

Lumber Drying

After trimming, lumber is sorted for thickness, width, and length to accommodate lumber drying and finishing. Lumber may be sorted manually by individuals who pull lumber from a slowly moving chain (green chain) and stack the lumber in an appropriate compartment. Lumber may also be sorted automatically by a large machine that drops lumber into compartments or slings according to thickness, width, and length. In these machines, sort decisions are often based upon limit switches placed along the length of the machine, or they may be based upon a scanning and computer system at the trimsaw.

Lumber may be sold in a rough-green condition, finished (planed) and sold in a dressed-green condition, dried and sold in a rough-dry condition, or dried, finished, and sold in a dry-dressed condition. Hardwood lumber is often sold in the rough-green or rough-dry conditions, and softwood lumber is often sold in the dressed-green or dressed-dry conditions. If lumber is dried at the sawmill, it is dried in an air-drying yard or in a dry kiln (*see* **Solid Wood Processing**: Drying). In the case of hardwoods, lumber may also be partially air-dried and then kiln-dried. Lumber is dried to reduce weight for shipping, to make the wood more dimensionally stable, and to comply with grade standards.

To prepare lumber for drying, it is usually stacked in layers with narrow pieces of lumber (stickers) placed perpendicular to the length of the lumber. This separates each layer of lumber in a stack, and allows air to flow through the stack and dry the lumber. Stacking may be done manually, or it may be done by machine. Softwood structural lumber is typically dried to 15% or 19% moisture content, and hardwood furniture lumber may be dried to 6–8% moisture content.

Lumber dried in an air-drying yard may take several months to reach desired moisture content. However, lumber may sometimes be dried in a dry kiln in as little as a few hours. A dry kiln is a chamber where temperature and relative humidity are closely monitored. Dry kilns are heated with steam or direct-combustion systems. As previously mentioned, heat is often produced by burning bark and sawdust. The heat provides energy for evaporation of water from the wood. Regulation of relative humidity helps control the rate of drying. It is important to control the rate of drying because some types of lumber may be damaged if dried too fast. Regulation of relative humidity within the kiln is achieved by opening vents to exhaust water vapor and reduce relative humidity and by spraying water or steam into the kiln to increase relative humidity. Temperatures within commercial dry kilns may be as high as 125°C.

After drying, lumber may be graded and packaged for sale. It may also be finished (planed) to a smooth surface, graded, and packaged for sale (*see* **Solid Wood Processing**: Machining). Lumber is often planed on four faces, and sometimes a pattern is machined into one or more faces. Lumber planers are usually composed of a lumber feed mechanism and planer heads with planning knives. As lumber is transported through a planer, the planing knives remove a small amount of wood on each planed surface. This provides a smooth surface, and it reduces variation in thickness and width.

Lumber Grading, Properties, and Uses

Lumber is then graded to separate lumber according to the level of quality needed for its intended use. Softwood structural lumber (lumber used for framing buildings) is usually graded based upon visual defects that detract from strength, stiffness, and utility. Structural lumber is graded on both faces for the presence of knots, excess wane, warp (deviation from straight), and other defects. It may also be machine stress-rated by passing each piece of lumber through a machine that bends the lumber flat-wise and measures resistance to bending. Almost all species of softwood trees are manufactured into structural lumber. However, where high strength and stiffness are needed, such as in roof trusses, those softwood species with high density (e.g., Douglas-fir: *Pseudotsuga menziesii*) are often preferred. Dry-dressed softwood structural lumber is typically 38–100 mm thick and 100–300 mm wide. Structural lumber thicker than 125 mm is often defined as timbers. Structural lumber and timbers often range in length from 2.4 to 6.1 m. However, longer lengths are sometimes produced.

Appearance-grade lumber (lumber used for trim and other nonstructural applications in building construction) is usually graded for appearance of the best face and for utility. Appearance lumber is graded on the best face, because often the best face is the only face that will be seen when the lumber is in service. This type of lumber may be painted or finished with a transparent material. Some defects that reduce the grade of appearance lumber are knots, stain, streaks, warp, and other defects. Since high strength is not required, low-density softwood species (e.g., Ponderosa pine (*Pinus ponderosa*) and spruce (*Picea* sp.)) are often preferred for appearance lumber. Dry-dressed appearance-grade lumber is often 19 mm thick and 100–300 mm wide. Lengths often range from 2.4 to 6.1 m.

Factory and shop lumber (lumber used for furniture and millwork) is graded based upon the proportion and size of clear area on the worst face of the lumber. This lumber is often sold to furniture or millwork plants where it will be sawn into parts for furniture, windows, doors, and other applications. Many species of hardwood logs are sawn into factory lumber for furniture production. However, the most popular species groups are white oak and red oak (*Quercus* spp.). Furniture manufacturers often prefer lumber produced from species with high strength and stiffness, attractive appearance, and good machining properties. Lower grades of hardwood factory lumber are sometimes used to manufacture pallets. Pallets are support structures used to ship numerous manufactured products. Rough (undressed)-dry hardwood factory lumber often ranges from 25 to 50 mm thick and may be almost any width 100 mm or greater. Lengths are usually from 2.4 to 4.9 m.

Softwood shop lumber is often used to manufacture furniture or millwork for wood doors and windows. As with hardwood factory lumber, softwood furniture and millwork lumber are often sawn into clear parts. Therefore, the size and proportion of clear-lumber area are important to the grade. Softwood furniture and millwork producers often prefer species with low density and good machining properties (e.g., Ponderosa pine and radiata pine (*Pinus radiata*)). Dry-dressed softwood shop lumber is usually 19 or 29 mm thick and 100–300 mm wide. Lengths often range from 2.4 to 6.1 m.

All types of lumber are graded by experienced sawmill employees who follow grade standards established by grade agencies. These grade standards specify the size, spacing, and/or volume of defects for each size and grade of lumber. Softwood structural lumber and softwood appearance lumber are stamped showing the grade, moisture content, supervising grade agency, and sawmill number. Supervising grade agencies provide training to sawmill graders, and inspect random packages of lumber for conformance to grade standards. They may also settle grade disputes between the sawmill and lumber customers. Hardwood factory lumber and softwood shop lumber usually do not carry a grade stamp. Rather, whole packages of lumber containing the same grade, species, and size are packaged and sold to experienced manufacturers of furniture, millwork, windows, doors, and other products.

Following grading, lumber is packaged and shipped to customers via truck, rail, barge, or ship. If lumber is to be transported over long distances and there is a chance that dry-lumber packages will encounter rain, the packages may be wrapped with a water-resistant covering. In other cases, packages are simply banded with steel bands and shipped without a covering.

See also: **Solid Wood Processing**: Drying; Machining; Protection of Wood against Biodeterioration. **Solid Wood Products**: Construction; Logs, Poles, Piles, Sleepers (Crossties); Structural Use of Wood. **Wood Formation and Properties**: Biological Deterioration of Wood; Formation and Structure of Wood.

Further Reading

Haygreen JG and Bowyer JL (1996) Lumber. In: *Forest Products and Wood Science*, 3rd edn, pp. 303–330. Ames, IA: Iowa State University Press.

Simpson WT (1991) *Dry Kiln Operators Manual*. Madison, WI: Forest Products Society.

Steele PH (1984) *Factors Determining Lumber Recovery in Sawmilling*. Madison, WI: USDA Forest Products Laboratory.

Williston EM (1981) *Small Log Sawmills: Profitable Product Selection, Process Design and Operation*. San Francisco, CA: Miller Freeman.

Williston EM (1988) *Lumber Manufacturing: The Design and Operation of Sawmills and Planer Mills*. San Francisco, CA: Miller Freeman.

Construction; Logs, Poles, Piles, Sleepers (Crossties)

J A Youngquist, Verona, WI, USA
R Youngs, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

Published by Elsevier Ltd., 2004

Introduction

The material in this article is adapted from the Forest Products Laboratory *Wood Handbook*, which is especially concerned with use of wood as an engineering material in the USA. However, the use of wood in log or timber form is common worldwide and the same principles apply. Such applications were among the first uses of wood by primitive people, because the material was available and could be used without further processing, except to cut to size. It was used to make homes, buildings of many types, and fortifications, as well as weapons and means of transport. The concepts developed through experience were carried on and improved over thousands of years, appearing today in homes, barns, bridges, and other structures of many kinds. Use of timber as sleepers (crossties) made possible the development of railroads in many parts of the world and continues as a major element in transportation systems. Poles for electric power transmission lines have developed with the industry and provide essential structures as electricity is generated and distributed to the far corners of the world.

Wood in the form of timbers and poles for construction has been an essential element in the development of civilization and continues in that role today.

Material Requirements

Round timber and tie material requirements vary with intended use. Most uses involve exposure to harsh environments. Thus, in addition to availability, form, and weight, durability is an important consideration for the use of round timbers and ties. Availability reflects the economic feasibility of procuring members of the required size and grade. Form or physical appearance refers to visual characteristics, such as straightness and occurrence of knots and spiral grain. Weight affects shipping and handling costs and is a function of volume, moisture content, and wood density. Durability is directly related to expected service life and is a function of treatability and natural decay resistance. Finally, regardless of the application, any structural member must be strong enough to resist imposed loads with a reasonable factor of safety. Material specifications available for most applications of round timbers and ties contain guidelines for evaluating these factors.

Availability

Material evaluation begins with an assessment of availability. For some applications, local species of timber may be readily available in an acceptable form and quality. However, this is not normally the case. Pole producers and tie mills are scattered throughout heavily forested regions. Their products are shipped to users throughout North America.

Most structural applications of poles require timbers that are relatively straight and free of large knots. Poles used to support electric utility distribution and transmission lines (**Figure 1**) range in length from 6 to 38 m (20–125 ft) and from 0.13 to 0.76 m (5–30 in.) in diameter, 1.8 m (6 ft) from the butt. Poles used to support local area distribution lines are normally <15 m (<50 ft) long and are predominantly southern pine.

Hardwood species can be used for poles when the trees are of suitable size and form; their use is limited, however, by their weight, by their excessive checking, and because of the lack of experience in preservative treatment of hardwoods. Thus, most poles are softwoods.

The southern pine lumber group (principally loblolly (*Pinus taeda*), longleaf (*P. palustris*), shortleaf (*P. echinata*), and slash (*P. elliottii*)) accounts for roughly 80% of poles treated in the USA. Three traits of these pines account for their extensive use: (1) thick and easily treated sapwood; (2) favorable strength properties and form; and (3) availability in popular pole sizes. In longer lengths, southern pine poles are in limited supply, so Douglas fir, and to some extent western red cedar, Ponderosa pine, and western larch, are used to meet requirements for 15-m (50-ft) and longer transmission poles.

Figure 1 Round timber poles form the major structural element in these transmission structures. Courtesy of Koppers Co.

Douglas-fir (*Pseudotsuga menziesii*) is used throughout the USA for transmission poles and is used in the Pacific Coast region for distribution and building poles. Because the heartwood of Douglas fir is resistant to preservative penetration and has limited decay and termite resistance, serviceable poles need a well-treated shell of sapwood that is free of checking. To minimize checking after treatment, poles should be adequately seasoned or conditioned before treatment. With these precautions, the poles should compare favorably with treated southern pine poles in serviceability.

A small percentage of the poles treated in the USA are of western redcedar (*Thuja plicata*), mostly produced in British Columbia. The number of poles of this species used without treatment is not known but is considered to be small. Used primarily for utility lines in the northern and western USA, well-treated redcedar poles have a service life that compares favorably with poles made from other species and could be used effectively in pole-type buildings.

Lodgepole pine (*Pinus contorta*) is also used in small quantities for treated poles. This species is used for both utility lines and for pole-type buildings. It has a good service record when well treated. Special attention is necessary, however, to obtain poles with sufficient sapwood thickness to ensure adequate penetration of preservative, because the heartwood is not usually penetrated and is not decay-resistant. The poles must also be well seasoned prior to treatment to avoid checking and exposure of unpenetrated heartwood to attack by decay fungi.

Western larch (*Larix occidentalis*) poles produced in Montana and Idaho came into use after World War II because of their favorable size, shape, and strength properties. Western larch requires full-length preservative treatment for use in most areas and, as in the case of lodgepole pine poles, must be selected for adequate sapwood thickness and must be well seasoned prior to treatment. Other species occasionally used for poles are listed in the American National Standards Institute (ANSI) O5.1 standard. These minor species make up a very small portion of pole production and are used locally.

Glued-laminated, or glulam, poles are also available for use where special sizes or shapes are required. The ANSI standard O5.2 provides guidelines for specifying these poles.

Material available for timber piles is more restricted than that for poles. Most timber piles used in the eastern half of the USA are southern pine, while those used in western USA are coast Douglas fir. Oak, red pine, and cedar piles are also referenced in timber pile literature but are not as widely used as southern pine and Douglas fir.

Round timbers have been used in a variety of structures, including bridges, log cabins, and pole buildings. Log stringer bridges (**Figure 2**) are generally designed for a limited life on logging roads intended to provide access to remote areas. In Alaska, where logs may exceed 1 m (3 ft) in diameter, bridge spans may exceed 9 m (30 ft). Building poles, on the other hand, are preservative-treated logs in the 0.15–0.25-m (6–10-in.) diameter range. These poles rarely exceed 9 m (30 ft) in length. Although poles sold for this application are predominantly southern pine, there is potential for competition from local species in this category. Finally, log cabin logs normally range from 0.2 to 0.25 m (8–10 in.) in diameter, and the availability of logs in this size range is not often a problem. However, because logs are not normally preservative-treated for this application, those species that offer moderate to high natural decay resistance, such as western red cedar, are preferred. Pole buildings, which incorporate round timbers as vertical columns and cantilever supports, require preservative-treated wood. Preservative-treated poles for this use may not be readily available.

Figure 2 Logs are used to construct logging bridges in remote forest areas.

The most important availability consideration for railroad crossties is quantity. Ties are produced from most native species of timber that yield log lengths >2.4 m (8 ft) with diameters >0.18 m (7 in.). The American Railway Engineering Association (AREA) lists 26 US species that may be used for ties. Thus, the tie market provides a use for many low-grade hardwood and softwood logs.

Form

Natural growth properties of trees play an important role in their use as structural round timbers. Three important form considerations are cross-sectional dimensions, straightness, and the presence of surface characteristics such as knots.

Standards for poles and piles have been written with the assumption that trees have a round cross-section with a circumference that decreases linearly with height. Thus, the shape of a pole or pile is often assumed to be that of the frustum of a cone. Actual measurements of tree shape indicate that taper is rarely linear and often varies with location along the height of the tree. Guidelines to account for the effect of taper on the location of the critical section above the groundline are given in ANSI O5.1. The standard also tabulates pole dimensions for up to 15 size classes of 11 major pole species.

Taper also affects construction detailing of pole buildings. Where siding or other exterior covering is applied, poles are generally set with the taper to the interior side of the structures to provide a vertical exterior surface (**Figure 3**).

Another common practice is to modify round poles by slabbing to provide a continuous flat face. The

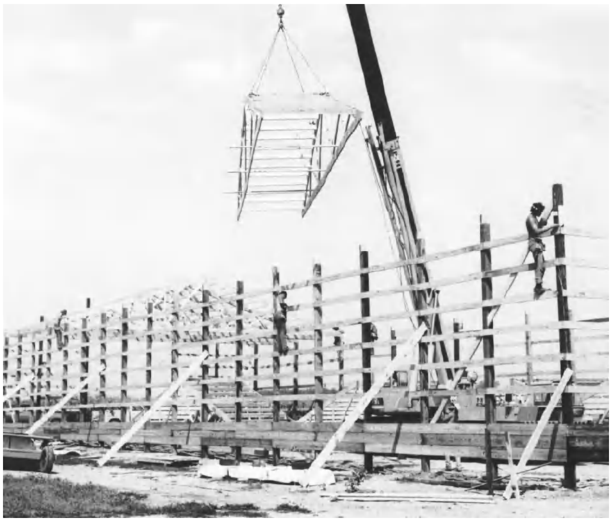


Figure 3 Poles provide economical foundation and wall systems for agricultural and storage buildings.

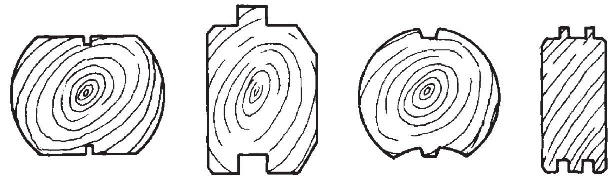


Figure 4 Construction logs can be formed in a variety of shapes for log homes. Vertical surfaces may be varied for aesthetic purposes, while the horizontal surfaces generally reflect structural and thermal considerations.

slabbed face permits more secure attachment of sheathing and framing members and facilitates the alignment and setting of intermediate wall and corner poles. The slabbing consists of a minimum cut to provide a single continuous flat face from the groundline to the top of intermediate wall poles and two continuous flat faces at right angles to one another from the groundline to the top of corner poles. However, preservative penetration is generally limited to the sapwood of most species; therefore slabbing, particularly in the groundline area of poles with thin sapwood, may result in somewhat less protection than that of an unslabbed pole. All cutting and sawing should be confined to that portion of the pole above the groundline and should be performed before treatment.

The American Society for Testing and Materials (ASTM) D25 standard provides tables of pile sizes for either friction piles or end-bearing piles. Friction piles rely on skin friction rather than tip area for support, whereas end-bearing piles resist compressive force at the tip. For this reason, a friction pile is specified by butt circumference and may have a smaller tip than an end-bearing pile. Conversely, end-bearing piles are specified by tip area and butt circumference is minimized.

Straightness of poles or piles is determined by two form properties: sweep and crook. Sweep is a measure of bow or gradual deviation from a straight line joining the ends of the pole or pile. Crook is an abrupt change in direction of the centroidal axis. Limits on these two properties are specified in both ANSI O5.1 and ASTM D25.

Logs used in construction are generally specified to meet the same criteria for straightness and knots as poles and piles (ASTM D25). For log stringer bridges, the log selection criteria may vary with the experience of the person doing the selection but straightness, spiral grain, wind shake, and knots are limiting criteria. Although no consensus standard is available for specifying and designing log stringers, the *Design Guide for Native Log Stringer Bridges* was prepared by the US Department of Agriculture Forest Service.

Logs used for log cabins come in a wide variety of cross-sectional shapes (**Figure 4**). Commercial cabin logs are usually milled so that their shape is uniform along their length. The ASTM D3957 standard, a guide for establishing stress grades for building logs, recommends stress grading on the basis of the largest rectangular section that can be inscribed totally within the log section. The standard also provides commentary on the effects of knots and slope of grain.

Railroad ties are commonly shaped to a fairly uniform section along their length. The AREA publishes specifications for the sizes, which include seven size classes ranging from 0.13×0.13 m (5×5 in.) to 0.18×0.25 m (7×10 in.). These tie classes may be ordered in any of three standard lengths: 2.4 m (8 ft), 2.6 m (8.5 ft), or 2.7 m (9 ft).

Tables for round timber volume are given in the American Wood Preservers Association (AWPA) standard F3. The volume of a round timber differs little whether it is green or dry. Drying of round timbers causes checks to open, but there is little reduction of the gross diameter of the pole.

Wood density also differs with species, age, and growing conditions. It will even vary along the height of a single tree. Average values, tabulated by species, are normally expressed as specific gravity (SG), which is density expressed as a ratio of the density of water (*see* **Wood Formation and Properties**: Physical Properties of Wood). For commercial species grown in the USA, SG varies from 0.32 to 0.65. If you know the green volume of a round timber and its SG, its dry weight is a product of its SG, its volume, and the unit weight of water ($1000\,\mathrm{kg\,m^{-3}}$ ($62.4\,\mathrm{lb\,ft^{-3}}$)). Wood moisture content can also be highly variable. A pole cut in the spring when sap is flowing may have a moisture content (MC) exceeding 100% (the weight of the water it contains may exceed the weight of the dry wood substance). If you know the MC of the timber, multiply the dry weight by (1 + MC/100) to get the wet weight.

Finally, in estimating the weight of a treated wood product such as a pole, pile, or tie, you must take into account the weight of the preservative. By knowing the volume, the preservative weight can be approximated by multiplying volume by the recommended preservative retention.

Durability

For most applications of round timbers and ties, durability is primarily a question of decay resistance. Some species are noted for their natural decay resistance; however, even these may require preservative treatment, depending upon the environmental conditions under which the material is used and the required service life. For some applications, natural decay resistance is sufficient. This is the case for temporary piles, marine piles in fresh water entirely below the permanent water level, and construction logs used in building construction. Any wood members used in ground contact should be pressure-treated, and the first two or three logs above a concrete foundation should be brush-treated with a preservative-sealer.

Federal Specification TT-W-571 (US Federal Supply Service (USFSS)) covers the inspection and treatment requirements for various wood products, including poles, piles, and ties. This specification refers to the AWPA standards C1 and C3 for pressure treatment, C2 and C6 for treatment of ties, C8 for full-length thermal (hot and cold) treatment of western red cedar poles, C10 for full-length thermal (hot and cold) treatment of lodgepole pine poles, and C23 for pressure treatment of construction poles. The AREA specifications for crossties and switch ties also cover preservative treatment. Inspection and treatment of poles in service has been effective in prolonging the useful life of untreated poles and those with inadequate preservative penetration or retention.

Service conditions for round timbers and ties vary from mild for construction logs to severe for crossties. Construction logs used in log homes may last indefinitely if kept dry and properly protected from insects. Most railroad ties, on the other hand, are continually in ground contact and are subject to mechanical damage.

The life of poles can vary within wide limits, depending upon properties of the pole, preservative treatments, service conditions, and maintenance practices. In distribution or transmission line supports, however, service life is often limited by obsolescence of the line rather than the physical life of the pole.

It is common to report the average life of untreated or treated poles based on observations over a period of years. These average life values are useful as a rough guide to the service life to be expected from a group of poles, but it should be kept in mind that, within a given group, 60% of the poles will have failed before reaching an age equal to the average life.

Early or premature failure of treated poles can generally be attributed to one or more of three factors: (1) poor penetration and distribution of preservative; (2) an inadequate retention of preservative; or (3) use of a substandard preservative. Properly treated poles can last 35 years or longer.

Western red cedar is one species with a naturally decay-resistant heartwood. If used without treatment, however, the average life is somewhat less than 20 years.

The expected life of a pile is also determined by treatment and use. Wood that remains completely submerged in water does not decay although bacteria may cause some degradation; therefore, decay resistance is not necessary in all piles, but it is necessary in any part of the pile that may extend above the permanent water level. When piles that support the foundations of bridges or buildings are to be cut off above the permanent water level, they should be treated to conform to recognized specifications such as Federal Specification TT-W-571 and AWPA standards C1 and C3. The untreated surfaces exposed at the cut-offs should also be given protection by thoroughly brushing the cut surface with coal-tar creosote. A coat of pitch, asphalt, or similar material may then be applied over the creosote and a protective sheet material, such as metal, roofing felt, or saturated fabric, should be fitted over the pile cut-off in accordance with AWPA standard M4. Correct application and maintenance of these materials are critical in maintaining the integrity of piles.

Piles driven into earth that is not constantly wet are subject to about the same service conditions as apply to poles but are generally required to last longer. Preservative retention requirements for piles are therefore greater than for poles. Piles used in salt water are subject to destruction by marine borers, even though they do not decay below the waterline. The most effective practical protection against marine borers has been a treatment first with a waterborne preservative, followed by seasoning with a creosote treatment. Other preservative treatments of marine piles are covered in Federal Specification TT-W-571 and AWPA standard C3.

The life of ties in service depends on their ability to resist decay and mechanical destruction. Under sufficiently light traffic, heartwood ties of naturally durable wood, even if of low strength, may give 10 or 15 years of average service without preservative treatment; under heavy traffic without adequate mechanical protection, the same ties might fail in 2 or 3 years. Advances in preservatives and treatment processes, coupled with increasing loads, are shifting the primary cause of tie failure from decay to mechanical damage. Well-treated ties, properly designed to carry intended loads, should last 25–40 years on average. Records on life of treated and untreated ties are occasionally published in the annual proceedings of AREA and AWPA.

Strength Properties

Allowable strength properties of round timbers have been developed and published in several standards. In most cases, published values are based on the strength of small clear test samples. Allowable stresses are derived by adjusting small clear values for effects of growth characteristics, conditioning, shape, and load conditions, as discussed in applicable standards. In addition, published values for some species of poles and piles reflect the results of full-sized tests.

Most poles are used as structural members in support structures for distribution and transmission lines. For this application, poles may be designed as single-member or guyed cantilevers or as structural members of a more complex structure. Specifications for wood poles used in single-pole structures have been published by ANSI in standard O5.1. Guidelines for the design of pole structures are given in the ANSI National Electric Safety Code (NESC) (ANSI C2). The ANSI O5.1 standard gives values for fiber stress in bending for species commonly used as transmission or distribution poles. These values represent the near-ultimate fiber stress for poles used as cantilever beams. For most species, these values are based partly on full-sized pole tests and include adjustments for moisture content and pretreatment conditioning. The values in ANSI O5.1 are compatible with the ultimate strength design philosophy of the NESC, but they are not compatible with the working stress design philosophy of the National Design Specification (NDS). Reliability-based design techniques have been developed for the design of distribution–transmission line systems. This approach requires a strong database on the performance of pole structures. Supporting information for these design procedures is available in a series of reports published by the Electric Power Research Institute (EPRI).

Bearing loads on piles are sustained by earth friction along their surface (skin friction), by bearing of the tip on a solid stratum, or by a combination of these two methods. Wood piles, because of their tapered form, are particularly efficient in supporting loads by skin friction. Bearing values that depend upon friction are related to the stability of the soil and generally do not approach the ultimate strength of the pile. Where wood piles sustain foundation loads by bearing of the tip on a solid stratum, loads may be limited by the compressive strength of the wood parallel to the grain. If a large proportion of the length of a pile extends above ground, its bearing value may be limited by its strength as a long column. Side loads may also be applied to piles extending above ground. In such instances, however, bracing is often used to reduce the unsupported column length or to resist the side loads. The most critical loads on piles often occur during driving. Under hard driving conditions, piles that are too dry ($<18\%$ moisture content at a 51-mm (2-in.) depth) have literally exploded under the force of the driving hammers. Steel banding is recommended to increase resistance to splitting, and driving the piles into predrilled holes reduces driving stresses. The reduction in strength of a wood column resulting from crooks, eccentric loading, or any other condition that will result in combined bending and compression is not as great as would be predicted with the NDS interaction equations. This does not imply that crooks and eccentricity should be without restriction, but it should relieve anxiety as to the influence of crooks, such as those found in piles. There are several ways to determine the bearing capacity of piles. Engineering formulae can estimate bearing values from the penetration under blows of known energy from the driving hammer. Some engineers prefer to estimate bearing capacity from experience or observation of the behavior of pile foundations under similar conditions or from the results of static-load tests. Working stresses for piles are governed by building code requirements and by recommendations of ASTM D2899. This standard gives recommendations for adjusting small clear strength values listed in ASTM D2555 for use in the design of full-sized piles. In addition to adjustments for properties inherent to the full-sized pile, the ASTM D2899 standard also provides recommendations for adjusting allowable stresses for the effects of pretreatment conditioning. Design stresses for timber piles are tabulated in the NDS for wood construction. The NDS values include adjustments for the effects of moisture content, load duration, and preservative treatment. Recommendations are also given to adjust for lateral support conditions and factors of safety.

Design values for round timbers used as structural members in pole or log buildings may be determined following standards published by ASTM and the American Society of Agricultural Engineers (ASAE). The ASTM standard refers pole designers to the same standard used to derive design stresses for timber piles (D2899). The ASAE standard (EP388), which governed the derivation of construction poles for agricultural building applications, is being revised. The future revision will be designated EP560 and will only deal with round wood poles. Derivation of design stresses for construction logs used in log homes is covered in ASTM D3957, which provides a method of establishing stress grades for structural members of any of the more common log configurations. Manufacturers can use this standard to develop grading specifications and derive engineering design stresses for their construction logs.

Railroad cross and switch ties have historically been overdesigned from the standpoint of rail loads. Tie service life was largely limited by deterioration rather than mechanical damage. However, because of advances in decay-inhibiting treatment and increased axle loads, adequate structural design is becoming more important in increasing railroad tie service life. Rail loads induce stresses in bending and shear as well as in compression perpendicular to the grain in railroad ties. The AREA manual gives recommended limits on ballast bearing pressure and allowable stresses for crossties. This information may be used by the designer to determine adequate tie size and spacing to avoid premature failure due to mechanical damage. SG and compressive strength parallel to the grain are also important properties to consider in evaluating crosstie material. These properties indicate the resistance of the wood to both pull-out and lateral thrust of spikes.

See also: **Solid Wood Products**: Lumber Production, Properties and Uses. **Wood Formation and Properties**: Formation and Structure of Wood; Physical Properties of Wood.

Further Reading

ANSI (current edition). ANSI O5.1. *Specifications and Dimensions for Wood Poles*. ANSI C2. *National Electrical Safety Code*. ANSI O5.2. *Structural Glued Laminated Timber for Utility Structures*. New York, NY: American National Standards Institute.

AREA (1982) Ties and wood preservation. In: *Manual for Railway Engineering*. Washington, DC: American Railway Engineering Association.

AREA (1982) Timber structures. In: *Manual for Railway Engineering*. Washington, DC: American Railway Engineering Association.

Armstrong RM (1979) Structural properties of timber piles. In: *Behavior of Deep Foundations*, pp. 118–152. ASTM STP670. Philadelphia, PA: American Society for Testing and Materials.

ASTM (current edition) *Standard Test Methods for Establishing Clear Wood Strength Values*. ASTM D2555. West Conshohocken, PA: American Society for Testing and Materials.

ASTM (current edition) ASTM D3200. *Standard Specification and Methods for Establishing Recommended Design Stresses for Round Timber Construction Poles*. ANSI/ASTM D1036-58. *Standard Methods of Static Tests of Wood Poles*. West Conshohocken, PA: American Society for Testing and Materials.

ASTM (current edition) ASTM D25. *Standard Specification for Round Timber Piles*. ASTM D2899. *Establishing Design Stresses for Round Timber Piles*. West Conshohocken, PA: American Society for Testing and Materials.

ASTM (current edition) *Standard Methods for Establishing Stress Grades for Structural Members Used in Log Buildings*. ASTM D3957. West Conshohocken, PA: American Society for Testing and Materials.

AWPA (current edition) *Book of Standards*. (American Wood-Preserver's Bureau official quality control standards.) Bethesda, MD: American Wood-Preservers' Association.

AWPI (1969) *Pile Foundations Know-How*. Washington, DC: American Wood Preservers Institute.

Carson JM and Dougherty M (eds) (1997) *Post-Frame Building Handbook: Materials, Design Considerations, Construction Procedures*. Ithaca, NY: Northeast Regional Agricultural Engineering Service.

Engineering Data Management and Colorado State University (1989–1998) *International Conference – Wood Poles and Piles*. Conference proceedings. Fort Collins, CO: Engineering Data Management and Colorado State University.

EPRI (1981) *Probability-Based Design of Wood Transmission Structures*, vols. 1–3. Palo Alto, CA: Electric Power Research Institute.

EPRI (1985) *Wood Pole Properties*, *vol. 1*, *Background and Southern Pine Data*. Palo Alto, CA: Electric Power Research Institute.

EPRI (1986) *Wood Pole Properties*, *vol. 2*: *Douglas Fir Data*. *vol. 3*: *Western Redcedar*. Palo Alto, CA: Electric Power Research Institute.

Forest Products Laboratory (1999) *Wood Handbook – Wood as an Engineering Material*. General Technical Report FPL-GTR-113. Madison, WI: US Department of Agriculture, Forest Service, Forest Products Laboratory.

Morrell JJ (1996) *Wood Pole Maintenance Manual*. Corvallis, OR: College of Forestry, Forest Research Laboratory, Oregon State University.

Muchmore FW (1977) *Design Guide for Native Log Stringer Bridges*. Juneau, AK: US Department of Agriculture, Forest Service, Region 10.

NFPA (current edition) *National Design Specification for Wood Construction*. Washington, DC: National Forest Products Association.

NRAES (1997) *Post-Frame Building Construction*. Ithaca, NY: Northeast Regional Agricultural Engineering Service.

USFSS (current edition) *Poles and Piles*, *Wood*. Federal specification MM-P-371c-ties, railroad (cross and switch); Federal Specification MM-T-371d-wood preservation: treating practice; Federal Specification TT-W-571. Washington, DC: US Federal Supply Service.

Wood-based Composites and Panel Products

F A Kamke, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

Introduction

Wood-based composites consist of wood elements, such as veneer, fibers, particles, or strands, which are bonded together to collectively perform some function. These wood elements may be bonded with natural adhesives (such as starch or protein from plant or animal sources) or synthetic adhesives (usually derived from petroleum). The classification of wood-based composites is inexact, but may be grouped as panels or composite lumber. The panels may be further divided into veneer (such as plywood) or particulate (such as particleboard) composites. Another means of categorizing the wood-based composites is by function, i.e., structural (building components) and nonstructural (furniture and cabinet applications). Examples of commercially available wood-based composites are shown in **Figure 1**. While endless combinations of wood elements, and indeed wood and other materials, could be used to produce a vast array of products, this article will focus on the major wood-based composites produced commercially.

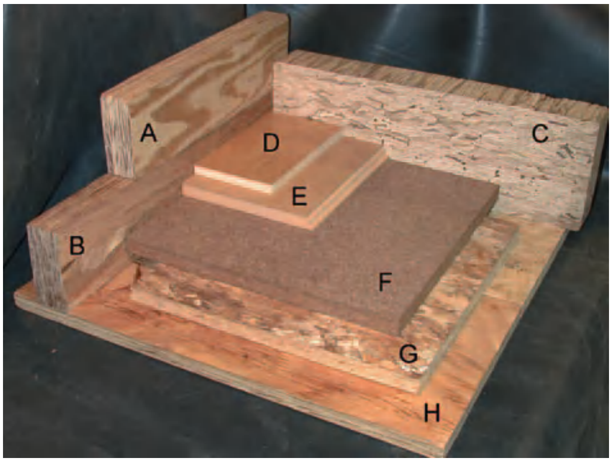


Figure 1 Examples of commercially available wood-based composites. (A) Laminated veneer lumber (LVL); (B) laminated strand lumber (LSL); (C) parallel strand lumber (PSL); (D) nonstructural plywood; (E) medium density fiberboard (MDF); (F) particleboard; (G) oriented strand board (OSB); (H) structural plywood.

History

The event of the first composite produced from wood is probably unknown. The simple act of adhesively bonding together two or more pieces of wood is a composite manufacturing process. Paper is a composite of wood fibers, which utilizes the natural lignocellulosic compounds present in wood to bond the fibers. The Chinese, during the early second century, are believed to have produced the first paper from wood pulp. The ancient Egyptians, prior to 1400 BC, developed the art of bonding wood veneers for decorative articles. A type of wood fiberboard was patented in the USA by Lyman in 1858. This was followed by a high-density version of fiberboard, known today as hardboard, which was called Masonite by its inventor William Mason in 1924. Structural plywood was introduced to the USA in 1905 by the Portland Manufacturing Company in Oregon. Particleboard had its origin in Germany, with early references to Ernst Hubbard in 1887. The first commercial manufacturing facility for particleboard is thought to be one opened in Bremen, Germany in 1941. The growth of the modern wood-based composites industry was made possible with the development of synthetic adhesives during the 1930s. Thermosetting adhesives, such as urea-formaldehyde and phenol-formaldehyde, greatly accelerated the manufacturing process, improved performance, and reduced costs. The latter part of the twentieth century saw the development of structural lumber composites, including laminated veneer lumber, parallel strand lumber, and laminated strand lumber.

Manufacture of wood-based composites is now a worldwide industry. **Table 1** shows the world production of wood composite panels and laminated veneer lumber in 2001. Production has increased each year since the introduction of these products. Structural plywood, oriented strand board, and structural lumber composites are primarily North American products, due to preference for wood for building construction in this region. Europe and Japan are minor but growing producers and consumers of these products. The nonstructural panels are produced throughout the world, and find many applications in furniture, cabinets, and some building construction.

Table 1 World production of wood-based panels and laminated veneer lumber in 2001

Product	*Production (1000 m^3)*
Fiberboard	33,277
Particleboard	60,723
Oriented strand board (OSB)	21,678
Plywood (structural and nonstructural)	55,528
Laminated veneer lumber (LVL)[a]	2,062

[a] Estimated from 2001 North American data and 1999 Europe and Asia data.
Data from FAO (2002) *Forest Products Statistics*. Timber Bulletin no. ECE/TIM/BULL/55/2. Rome: Food and Agricultural Organization. Available online at http://www.fao.org/. UNECE (2002) *Forest Products Annual Market Review 2001–2002*. Timber Bulletin LV ECE/TIM/BULL/2002/3. Rome: Food and Agricultural Organization. Available online at http://www.unece.org/trade/timber/.

Figure 2 Structural wood-based composites used in building construction; OSB floor sheathing, LSL rimboard, I-beams with LVL as flange stock and plywood webs, and LVL floor girder. Photograph courtesy of APA – Engineered Wood Association.

Products and Applications

Panels: Structural Plywood

Structural plywood is produced primarily from softwood species, although some hardwoods are also used. In North America the most commonly used species are southern pine (*Pinus* spp.) and Douglas-fir (*Pseudotsuga menziesii*). These species provide the proper combination of strength, stiffness, and ease of handling. The 2–5-mm thick veneer is produced by peeling logs on a rotary lathe. The veneers are arranged in layers, with the grain perpendicular in adjacent layers, and bonded together using a waterproof adhesive (usually phenol-formaldehyde). The veneer is visually graded, and sometimes machine graded, to eliminate severe defects. The highest-quality veneer is reserved for the highest-quality plywood. Lower-quality veneer can often be used as core plies, or on the backside of the panel.

Structural plywood is used principally in building construction as structural sheathing in floor, wall, and roof systems. Structural plywood has many other uses where strength, stiffness, and dimensional stability are important, such as furniture and cabinet frames, pallet bins, exterior siding, web stock for I-beams (**Figure 2**), and concrete forms. Structural plywood is manufactured in 1.2×2.4 m dimensions. The common thickness range is from 7 to 30 mm depending on the application.

Panels: Nonstructural Plywood

Nonstructural plywood, also called decorative plywood, is produced primarily from hardwood species, although many softwood species are used. In North America, oak (*Quercus* spp.), birch (*Betula* spp.), maple (*Acer* spp.), cherry (*Prunus* spp.), white pine (*Pinus strobus*), and lauan (*Shorea* spp.) are common species used for nonstructural plywood. The face veneer is the highest quality, since its function is decorative. Face veneers are often very thin, generally 0.8 mm and thinner, to provide the most efficient use of the best-quality wood. The back veneer is usually lower quality, although some grades require a good appearance on two sides. The core of nonstructural plywood may be comprised of lower-quality veneer or some other substrate, such as fiberboard, particleboard, or lumber.

Nonstructural plywood has numerous uses in consumer products, where appearance and dimensional stability, and some structural performance is required. Typical uses are furniture, cabinets, store fixtures, decorative paneling, and architectural woodwork. Since the adhesive that is used to manufacture nonstructural plywood is usually urea-formaldehyde, with a low water resistance, these products are limited to interior applications where the potential for moisture exposure is low.

Panels: Particleboard

Particleboard is comprised of wood elements bonded together with an adhesive under heat and pressure. The particles may be generated in a variety of ways starting with logs (rare) or wood residue (typical) from some other wood manufacturing operation. Mechanical devices break down the wood into particles. A clear classification of particleboard is not possible, as modern particleboard manufacturing processes sometimes employ pressure-refined wood fibers in the surface layers. A similar product made from 100% pressure-refined wood fibers is called fiberboard. Virtually any wood species could be used for particleboard, although softwoods and lower-density hardwoods are preferred. Lower-density wood allows for the production of lower-density particleboard without sacrificing strength and stiffness. The most common adhesive used in the manufacture of particleboard is urea-formaldehyde, although some melamine-formaldehyde is sometimes added to improve water resistance. Particleboard is intended for interior applications.

Particleboard is available in a wide variety of dimensions, limited only by the hot-press used in its manufacture. Thickness typically ranges from 12 to 38 mm. The panels are made up to 3.6 m in width and up to 18 m in length. Applications include core stock for furniture and cabinet panels, doors, counter tops, and floor underlayment.

Panels: Fiberboard

Fiberboard may be further classified into insulation board, medium density fiberboard (MDF), and hardboard. The primary difference between these panel types is density and the end-use application. All of these panels are produced from pressure-refined wood fibers. The fibers are individual wood cells or small bundles of cells. Both hardwood and softwood species may be used. Insulation board is a low-density product, less than $30\,\mathrm{lb\,ft^3}$ ($480\,\mathrm{kg\,m^{-3}}$), with very little structural integrity. Its density is less than the density of the wood from which it was produced. MDF is similar to particleboard in its manufacture and end-used applications. MDF offers advantage over particleboard with smoother surfaces, void-free edges, and lower density. Hardboard is a high-density product, over $50\,\mathrm{lb\,ft^3}$ ($800\,\mathrm{kg\,m^{-3}}$). Some hardboard is produced without adhesive, relying instead on lignocellulosic bonding imposed by extreme heat and pressure in the hot-press. Hardboard is typically produced in thickness ranging from 2.5 to 3.2 mm. Individual panels are sometimes bonded together to produce thicker panels. Synthetic or bio-based adhesives are often added to hardboard to improve properties, particularly water resistance.

Insulation board is used for nonstructural wall sheathing where thermal insulation is required. This product has been largely displaced by rigid, synthetic-foam panels. Insulation board is also used for accoustic tiles. MDF is used extensively as core stock in furniture and cabinet panels. It is also used for overlayed and powder-coated millwork. Hardboard is used for exterior siding, cabinets for electrical appliances, flooring, and overlayed decorative paneling.

Panels: Oriented Strand Board

Oriented strand board (OSB) is a structural panel designed for building construction. It is composed of slender wood strands, with the strand length parallel to the grain of the wood. The stranding process requires logs. Many wood species are used. Softwoods, such as the pines, and low-density hardwoods, such as aspen (*Populus* spp.), gum (*Nyssa* spp.), and yellow-poplar (*Liriodendron tulipifera*), are preferred. The strands are oriented and arranged into three layers in the panel. The two outer layers are parallel, and the core layer is either perpendicular to the face layers or not oriented. This cross-lamination concept is similar to plywood. Strength and stiffness is greater in the dimension parallel to the face layer, and the panel has good dimensional stability, with respect to moisture content changes, in both flat-wise directions. Thickness swell has been a problem with some OSB panels. A waterproof adhesive, either phenol-formaldehyde or polymeric methylene diphenyl diisocyanate (pMDI), is used to bond the strands together.

OSB was developed as a direct replacement for the more expensive structural plywood. It is used as structural sheathing for walls, roofs, and floors (**Figure 2**). OSB is also used as web stock in wood composite I-beams, shelving, pallets, and packaging. OSB is manufactured in thickness ranging from 6 to 28 mm. The panels are sold in 1.2×2.4 m dimensions, although the panels are produced in dimensions up to 3.6×18 m.

Structural Composite Lumber: Laminated Veneer Lumber

Laminated veneer lumber (LVL) is produced from veneer and intended for structural framing, where high strength and stiffness are required. Softwoods, such as Douglas-fir and southern pines, are typically used. Some hardwoods are also acceptable. As it is a structural product, only high-quality veneer with high strength and stiffness is acceptable. Unlike plywood, all of the veneer in an LVL billet is aligned in one direction to maximize strength and stiffness in that direction. An advantage of LVL over solid sawn lumber is the dispersion of defects, such as knots and pitch pockets, which greatly reduces the variability of the product. LVL is also more dimensionally stable than solid sawn lumber and it may be produced in large dimensions from small logs.

LVL is used for structural beams (**Figure 2**) and headers in building construction, as well as scaffold planks. Most of today's production is used as flange stock in wood composite I-beams (**Figure 2**). Some LVL is produced specifically for furniture and architectural woodwork, for which some hardwood species are used. LVL is produced in dimensions ranging from 38 to 90 mm thick, up to 1.2 m wide, and 24 m long. The billets are sawn into standard sizes that are compatible with dimension lumber.

Structural Composite Lumber: Parallel Strand Lumber

Parallel strand lumber (PSL) is produced from narrow veneer strips. Currently Douglas-fir, western hemlock (*Tsuga heterophylla*), southern pine, and yellow-poplar are the wood species used for PSL. The process permits veneer with many defects, as these defects will be eliminated or dispersed when the veneer is clipped into the narrow strips. A phenol-formaldehyde adhesive is used to provide excellent water resistance. The mechanical properties are similar to LVL. PSL is produced in large dimensions as a substitute for solid wood timbers.

PSL is intended for structural applications, including beams, columns, and headers. PSL is preferred over LVL for applications that require a large cross-section. When finished properly, PSL has a decorative appearance suitable for exposed timberframe construction.

Structural Composite Lumber: Laminated Strand Lumber

Laminated strand lumber (LSL) is a variation of OSB technology. LSL is produced from long wood strands. The strands are similar to OSB strands in width and thickness, but they are longer. Unlike OSB, all of the strands are oriented in the same direction. This high degree of orientation and long strands produces a structural lumber product with high strength and stiffness. Currently, aspen and yellow-poplar are used to produce LSL, but other low-density species could be used. Unlike OSB, LSL has a uniform density, which better simulates solid wood performance.

LSL is a structural product. It is used for truss cords, rim board in floor systems (**Figure 2**), headers, and columns. Because of its uniform density and good dimensional stability, LSL is also used for furniture and millwork.

Manufacturing Practices

Structural Plywood

All structural plywood is produced from rotary-peeled veneer. The peeler logs are debarked and cut to nominal 1.2 or 2.4 m long peeler blocks. The blocks are conditioned to soften the wood prior to peeling. This is done by soaking the blocks in hot water or spraying them with steam. The blocks are then electronically scanned and positioned in the rotary lathe. Scanning is a rapid and accurate means of maximizing the yield of the highest-quality veneer. The lathe rotates the block against a knife to peel veneer into a continuous sheet, much like paper pulled off a roll (**Figure 3**). The peeling speed is up to 240 m min^{-1}. At the end of peeling, the remaining core, typically 50–100 mm in diameter, is ejected by the lathe operator and saved for other uses.

The continuous sheet of veneer, still wet, is again electronically scanned for defects and then automatically clipped into nominal 1.2×2.4 m sheets, half sheets, or random widths. The veneer is visually

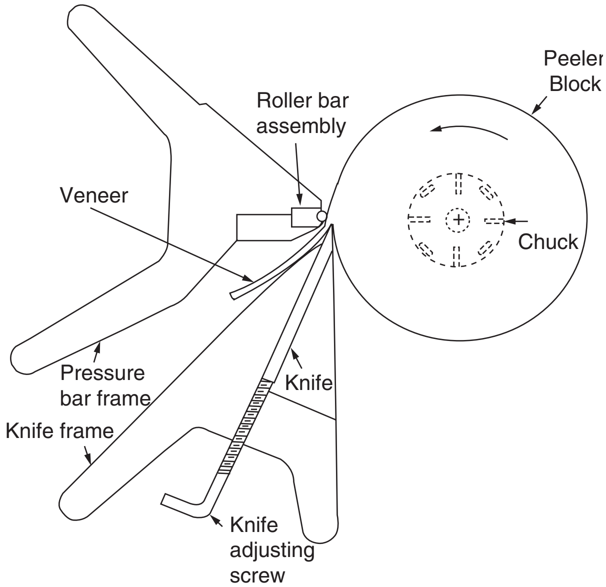


Figure 3 Rotary lathe used to produce veneer for structural plywood and laminated veneer lumber. Detail of peeling veneer from block shown at right. Photograph courtesy of COE Manufacturing.

graded and sorted. All veneer must be dried to the desired moisture content. The target moisture content depends on the adhesive system to be used, but typically is in the range of 5–10%. Electronic moisture detectors are used to identify wet or overdried veneer when it exits the dryer.

State-of-the-art plywood mills assemble full sheets of veneer from the half sheets and random width pieces. A thermoplastic ‘string’ is used to hold the sheets together loosely so that they may be handled by automated equipment. Adhesive is then applied to the dry veneer in precise amounts at the panel layup station. Roll coaters, curtain coaters, or extrusion coaters are used to apply the adhesive to the veneer. Adjacent veneer layers are arranged with the grain perpendicular to one another. The best grade of veneer is used for the face ply, a lower grade for the back ply, and the lowest grade for the core plies. The selection of the veneer grade depends on the desired finished plywood grade. The adhesive is almost always a phenol-formaldehyde formulation, which has a dark red–brown color. This adhesive has very good moisture resistance. Extenders and fillers are added to the resin to control flow and penetration characteristics. Many plywood mills still employ manual labor to assemble the panels at the layup station.

Prior to hot-pressing, the panels are cold-pressed to flatten the veneer and transfer the adhesive from one side of the bondline to the other. The panels are then loaded into a multi-opening heated press. A typical plywood press may process 20–50 panels simultaneously, with one panel per opening. Hot-press conditions are typically 100–200 psi (690–1380 kPa) pressure at 150°C. The time in the press depends on the thickness of the panel. Thicker panels require more time.

After the panels are removed from the hot-press, they are trimmed to the final dimensions, and visually graded. Some mills use ultrasonic detectors to examine each panel for hidden delaminations in the bondline. Some plywood grades are sanded. Secondary processing may include the addition of a tongue and groove on the edges, patches for aesthetic purpose, or overlays for water resistance. Quality assurance testing is routinely performed, and required, for grade stamp approval.

Nonstructural Plywood

There are many similarities between structural plywood and nonstructural plywood manufacturing processes. One major difference is the preparation of the veneer. Rotary peeled veneer is used for core stock and sometimes for face veneer. The fine face veneer is usually produced by slicing. Thin veneer, often less than 1 mm thick, can be produced with a wide variety of grain patterns using any one of a number of slicing techniques. The log is first sawn into a flitch, which is cut to expose the desired grain pattern. Flat, quarter, or rift slicing are common flitch preparations. Prior to slicing, the flitch is conditioned to soften the wood. The flitch is then mounted on a veneer slicer, which moves the flitch in a linear, back and forth motion against a knife (**Figure 4**). With each stroke, a thin veneer, the length and width of the flitch, is removed. The carriage holding the flitch, or knife assembly, is then indexed a distance equal to the thickness of one veneer, and another veneer is cut. Each veneer is stacked in sequence as it is removed from the flitch, and remains together for further processing. This allows the veneer to be matched in panels to achieve interesting grain patterns.

The face veneer is gently dried to a moisture content of 5–10% in a forced-air dryer with restraints to keep the veneer flat. Core and back veneer may be dried more rigorously. The dry veneer is now precision clipped and edge-joined to create large sheets for further processing into plywood.

Nonstructural plywood is typically bonded with urea-formaldehyde adhesive. This is a near-colorless adhesive that produces a strong bond, but is not suitable for high humidity or water exposure. The decorative face veneer may be laid-up over core veneer, or some other substrate, such as particleboard or fiberboard. As with structural plywood, maintaining a balanced construction is important for preventing warp of the panel with subsequent moisture content changes. The remainder of the manufacturing process is similar to structural plywood processing.

Particleboard

Particleboard manufacture typically begins with some mill residue from some other wood processing

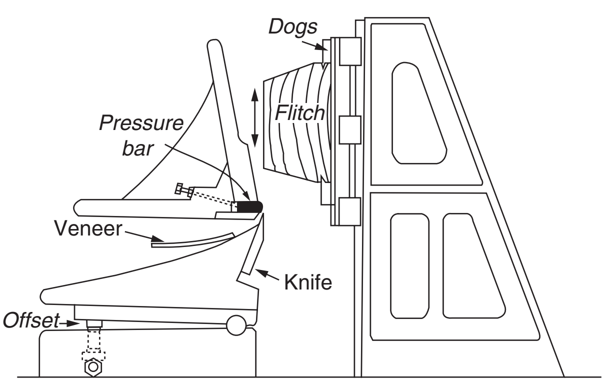


Figure 4 Veneer slicing machine used to produce high-quality face veneer for nonstructural plywood.

operation. Occasionally low-quality logs are used. Some residue, such as sawdust, is so small that no further processing is possible. Larger residue pieces are broken down into more uniform dimensions using various cutting devices, such as chippers, cutter mills, and knife-ring flakers. The desired particle geometry and size depend on the application. Higher strength and stiffness particleboard are achieved using long slender particles. Particleboard with a smooth surface can only be obtained with very small particles. Often fine particles are produced for the face layers of a multilayered particleboard, while the long slender particles are used in the core. Screens are used to separate the particles by size. Oversized particles are processed again, while undersized particles are burned for fuel.

The particles are dried in rotating drum dryers. The particles are tumbled inside the dryer to mix with heated air (200–400°C at the inlet) to achieve the desired particle moisture content, typically 3–6%. Air emissions from wood particle drying systems are a concern. Pollution abatement equipment is used to clean the air stream of particulates, volatile organic compounds, and other potentially hazardous compounds. Wet electrostatic precipitators or thermal oxidizers are commonly used to treat the exhaust air stream.

The dry particles are mixed with adhesive, usually urea-formaldehyde, in an amount of 6–10% based on dry weight. Some phenol-formaldehyde, melamine-formaldehyde, and pMDI are occasionally used. The low-cost urea-formaldehyde is preferred, and is quite suitable for particleboard applications. Wax is also added (1% or less) to impart some temporary resistance to liquid water absorption. Since the particles have a tremendous amount of surface area, and only a small amount of adhesive is added, the adhesive must be atomized and applied as tiny droplets.

The resinated particles are formed into loose mats by a device called a forming machine. Multiple layers are achieved by employing more forming machines. A uniform distribution of particles will provide a uniform density panel. The mats are formed continuously, and either pressed continuously, or the mat is cut and loaded into a multi-opening hot-press.

Continuous hot-presses are becoming more common. In a continuous press two moving metal belts are in direct contact with the mat. These belts run the full length of the press and are synchronized to move the mat slowly through the press. Mechanical pressure in the press creates intimate contact between the particles. Heat is applied to cure the thermosetting adhesive. The pressed panel may be cut to any length. In a multi-opening press the panel size is determined by the press size. Twelve to 16 press openings are typical. Current technology allows mats up to 3.7 m wide to be pressed.

After hot-pressing the raw panels are trimmed, cooled, and cut to size. Sanding is usually performed to achieve accurate thickness and to prepare the surface for bonding of overlay materials.

Fiberboard

The fiberboard manufacturing process begins with wood chips. Occasionally small mill residue may be used. The chips are washed, subjected to pressurized steam, and then fiberized in a device called a disk refiner. The disk refiner uses no knives, but rather two machined disks that rotate in opposing directions to shear the chips into fibers. The wet fibers are then pneumatically transported by steam through a blowline to the next manufacturing step.

Insulation board and wet-process hardboard employ a similar mat forming process to paper manufacture. The wet fiber is diluted to a very low consistency in water and then dispersed on a moving wire screen in a Fourdrinier machine. Water is quickly removed by vacuum suction and the fibers consolidate into a wet mat. Continuous rollers compress the mat and further remove water. Insulation board is then produced by simply drying the mat in an oven. Asphalt is added to insulation board as a binding agent prior to the forming machine. Wet-process hardboard is processed in a heated press. The mat enters the hot-press wet, thus generating a lot of steam when subjected to temperature in excess of 200°C. The mat is pressed on a wire screen to allow the steam to escape, which imparts a screen pattern on the back side of the panel. This hardboard panel is referred to as smooth-one-side (S1S). A variation in hardboard manufacture is to dry the mat prior to hot-pressing. In this case a wire screen is not needed, and the panel is smooth-two-sides (S2S). Hardboard uses little or no adhesive, relying instead on natural lignocellulosic bonding between the fibers. Consequently extreme pressure is needed in the press, resulting in a high-density panel.

Medium density fiberboard (MDF) is a more recent development. The fibers are produced as described above. Adhesive is typically added in the blowline, although separate blenders are sometimes employed. Blowline blending is a simple means of mixing adhesive with the fiber. It consists of a tube into which adhesive is injected and atomized. Turbulence inside the blowline thoroughly mixes the adhesive and fiber. The resinated fiber is then conveyed directly to a tube dryer, where drying to approximately 3–6% moisture content is achieved in a few seconds. This short drying time is not enough to cause the adhesive to cure. Mats are then formed from the dry resinated fibers, hot-pressed, and further processed in a manner similar to particleboard manufacture.

Oriented Strand Board

Oriented strand board (OSB) manufacture is a variation of particleboard manufacture. Certain process steps are modified to account for the long strands and the critical process of orientation. Wood strands are produced from debarked logs on either a disk or ring strander (**Figure 5**). Knives in these devices cut the strands to a precise thickness, width, and length (typically $0.7 \times 19 \times 100$ mm). The strands are dried in rotary dryers. Liquid phenol-formaldehyde or pMDI adhesive is added in a rotating blender using spinning disk atomizers to achieve a fine resin droplet coverage over the surface of the strands. Dry powder phenol-formaldehyde adhesive is sometimes used.

The resinated strands are formed into a three-layer mat. The strands in the face layers are oriented in the same direction, while the core strands are aligned perpendicular to the face, or randomized. Both continuous and multi-opening hot-presses are used by the industry. Secondary processing and testing is similar to that used for structural plywood manufacture.

Laminated Veneer Lumber

Laminated veneer lumber (LVL) manufacture is largely a variation on structural plywood technology. The major differences are in the lay-up of the veneer into billets and the hot-press. LVL has all of the veneer aligned in the same direction. The veneer sheets are overlapped or scarf-jointed to create continuous billets. The billet is then pressed in either a continuous hot-press, or a very long platen press is used. Since LVL is used for long structural members, the platen presses are 20–25 m in length. The pressed billet is then cut to length and ripped to the desired width.

As a critical structural component, LVL uses only the best-quality veneer. To insure adequate strength and stiffness, each sheet of veneer is nondestructively tested, then graded to its apparent modulus of elasticity. The LVL billet is engineered to the desired strength and stiffness by judiciously selecting the proper combination of veneer grades and placing them in the layers best suited for the grade.

Parallel Stand Lumber

The parallel strand lumber manufacturing process requires veneer, so the front end of this process resembles a structural plywood or LVL process. The dry, 3-mm thick veneer is sliced into strands of approximately 19 mm width. Partial sheets of veneer, or veneer with many defects, are well suited for this process because the strands may be random lengths down to a lower limit of about 35 cm. However, since the strands are not substantially compressed in the manufacturing process, the veneer must have acceptable strength and stiffness.

Strands are passed through a double-roll coater to apply a waterproof adhesive (phenol-formaldehyde) to both sides. The strands are then arranged in parallel with a billet-forming machine such that the ends of the strands are randomized in the billet. The unpressed billet is then drawn through a continuous press. The continuous press produces a pressed billet with cross section dimensions of approximately 30×45 cm. Due to the large cross-section, conventional heating is not feasible. Therefore, the continuous press employs a microwave heating section to cure the thermosetting adhesive. The resulting billet is then cross-cut to length and ripped to an appropriate width and thickness.

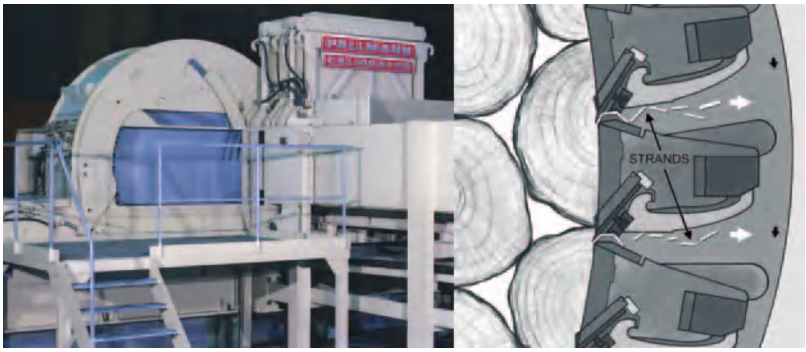


Figure 5 Long-log knife-ring flaker for producing strands for OSB and laminated strand lumber. Cutting action of the knives is shown at right. Photograph courtesy of Pallmann Pulverizers Co., Inc.

Laminated Strand Lumber

Laminated strand lumber manufacturing is a variation of the OSB process. The strands are longer than those found in OSB, and all of the strands are arranged parallel to each other to simulate solid-sawn lumber. The adhesive blending and mat forming are similar to OSB processes. LSL is produced in billets 5–12 cm thick, 2.4 m wide, and 15 m long. Due to its thickness, conventional heating in the press is not practical. An LSL press employs steam injection through the press platens into the mat of strands. The steam greatly accelerates the rate of heat transfer to the core of the mat, thus reducing the time in the press. The steam injection also serves to reduce the gradient in density through the thickness of LVL. Polymeric MDI adhesive is used for the manufacture of LSL due to the steam injection process. This waterproof, thermosetting adhesive requires water to polymerize, while steam interferes with the bond strength development of phenol-formaldehyde adhesives.

Further Reading

APA (1994) *PRP-108 Performance Standards and Policies for Structural Use Panels*. Tacoma, WA: APA – The Engineered Wood Association.

APA (1995) *PS1-95 Construction and Industrial Plywood*. Tacoma, WA: APA – The Engineered Wood Association.

APA (2000) *PRL-501 Performance Standard for APA EWS Laminated Veneer Lumber*. Tacoma, WA: APA – The Engineered Wood Association.

Baldwin RF (1995) *Plywood and Veneer-Based Products: Manufacturing Processes*. San Francisco, CA: Miller Freeman.

CPA (1996) *Particleboard from Start to Finish*. Gaithersburg, MD: Composite Panel Association.

CPA (1998) *MDF from Start to Finish*. Gaithersburg, MD: Composite Panel Association.

Haygreen JG and Bowyer JL (1996) *Forest Products and Wood Science: An Introduction*, 3rd edn. Ames, IA: Iowa State University Press.

HPVA (2000) *ANSI/HPVA HP-1-2000 American National Standard for Hardwood and Decorative Plywood*. Reston, VA: Hardwood Plywood and Veneer Association.

Maloney TM (1993) *Modern Particleboard and Dry-Process Fiberboard Manufacturing*. San Francisco, CA: Miller Freeman.

Sellers T Jr (1985) *Plywood and Adhesive Technology*. New York: Marcel Dekker.

Smulski S (ed.) (1997) *Engineered Wood Products: A Guide to Specifiers, Designers and Users*. Madison, WI: PFS Research Foundation.

Tichy RJ and Wolcott MP (eds) (published annually) *36th International Particleboard/Composite Materials Symposium Proceedings*. Pullman, WA: Washington State University.

US Department of Agriculture (1999) *Wood Handbook: Wood as an Engineering Material*. Gen. Tech. Rep. no. FPL-GTR-113. Madison, WI: US Department of Agriculture Forest Products Laboratory.

Streamflow *see* **Hydrology**: Hydrological Cycle; Impacts of Forest Conversion on Streamflow; Impacts of Forest Management on Streamflow; Impacts of Forest Management on Water Quality; Impacts of Forest Plantations on Streamflow.

SUSTAINABLE FOREST MANAGEMENT

Contents

Overview

H Schanz, Wageningen University, Wageningen, The Netherlands

Introduction

Sustainable forest management (SFM) has become one of the core ideal concepts in the use and conservation of forest resources worldwide. Despite its uncontested appeal, a bewildering variety of interpretations of its meanings does exist, which makes discussions and implementation difficult. Underlying the concept is the ethical principle about how the relation between forests and people should be designed. Dependent on the interpretations, the aspect of continuation in the concept of SFM can include a wide range of different dimensions, including, for example, the maintenance of forest ecological characteristics, the maintenance of yields of forest products and services, as well as the sustenance of human institutions that are forest-dependent. Conflict among these is inherent and reflects other contested values in society. Consequently there cannot be an objective, universally agreed definition of SFM. The various understandings of SFM are outcomes of social or political processes, and are thus context-dependent as well as subject to continuous change. The international forest policy dialogue as well as market-driven certification approaches have provided major stimuli for such processes on national, regional, and local levels. There is widespread agreement that achievement of SFM requires adequate institutionalization as well as a widely shared understanding of the concept.

Bewildering Variety of Meanings

SFM is more and more frequently viewed as an ideal in managing forests worldwide. Numerous declarations have recently been published at national and international levels in which SFM is claimed to be the main objective of all future efforts in forestry. However, despite the long tradition of the term, there exists a virtual wilderness of meanings. The question already rises whether SFM is a mere constraint on forest management or whether it is a goal in itself. Depending on the answer to this question, the terms 'sustainable forest management,' 'forest sustainability,' 'sustainable forests' or 'sustainable development of forests' are interpreted as distinct, different concepts, or as at least partially overlapping synonyms. The discussion of what SFM means precisely has kept the forestry profession busy, probably since the term 'sustainable' was first mentioned explicitly with regard to forest management in 1713 by von Carlowitz in Central Europe. However, despite general agreement on the need to implement SFM, the term means different things to different people. Nevertheless, there is consensus that SFM describes forest conservation practices, including their tools and techniques, that take into account the social, economic, and ecological dimensions of forests in the context of the needs of the present generation and future generations. In this respect SFM forms a strong unifying concept, with no one being conceptually against it.

Why Should Something Be Sustained?

The very core of discussions about the meanings of SFM are formed by the question of why something should be sustained with regard to forests or the relation between forests and people. SFM is thus not a natural characteristic of a forest or a technical issue in forest management planning. Rather, it is an ethical principle about how the relation between forests and people should be designed. History clearly shows that discussions about SFM always peaked in times of perceived or real crisis, such as timber shortages after war in the first half of the twentieth century or massive tropical forest destruction for whatever reason in the late twentieth century (overexploitation, forest fires, conflicting land uses, such as mining, etc.). In that respect also very early efforts such as religious obligations to replant for every tree that fell for whatever reason or to set aside certain forest patches as sacred groves, even though not termed 'sustainable forest management,' must be interpreted similarly. It is thus not a concept with origins limited to European forestry, as is often stated, even though it might have been there that the ethical core was explicitly designed over more than one generation and made an explicit technical science out of it.

What Should Be Sustained?

The second core question in discussions about the meaning of SFM is about the question of what should be sustained. This is well reflected by the etymology of the term 'sustainable,' which is described in dictionaries with synonyms such as continuous, perpetuated, constant, or durable. At first glance SFM therefore seems to show great affinity with concepts such as bag limits in wildlife management, carrying capacity in wilderness and recreation management, and recharge rates in aquifer management. Not surprisingly, discussions on SFM at the beginning of regular forest management often focused on aspects of sustained yield. Sustained yield in this respect was interpreted as constraining the periodic consumption of a renewable forest resource (timber and nontimber) not to exceed its periodic growth. However, the technical constraints for safeguarding continuous supply do not in themselves provide an answer to the question of what should be sustained on the demand side. Despite the voices of a few leaders in the forestry profession at the turn of the twentieth century, it is only more recently that the focus of discussion on SFM has broadened to include values on an ecological, social, and economical dimension similarly. The aspect of continuity in SFM can consequently refer to some quite different things, such as:

- maintenance of forest ecological characteristics, including the production capacity of forest soils, the vegetative renewal capacity, certain forest species and components, as well as biodiversity and natural forest ecological processes
- maintenance of yields of forest products and services
- sustenance of human institutions that are forest-dependent, including community stability, cultural integrity, and labor and income generation.

Reflection of Social Values

Accordingly, more than 14 different categories of definitions of SFM have been identified in literature depending on how the different dimensions are weighted. Even within one single dimension, be it the ecological, economical, or social one, weighting of values can differ greatly, leading to completely different interpretations of SFM. In the ecological dimension, for example, the question of whether ecological processes themselves (implying change and uncertainty) or the existence of individual species at a given time should be sustained has resulted in endless discussions. However, even if agreement about the relative weights of values can be achieved, their operational definition still remains vague and contested, because spatial and time scales often remain unidentified. On a spatial scale, different understandings of SFM are contested, depending on whether the achievement of norms and values is realized on forest stand levels, on district levels, or on regional levels. At a temporal scale a crucial point for discussion and different interpretations for SFM are formed by the way in which social and ecological changes are incorporated in different norms and values. For example, how do we deal with natural fluctuations (e.g., dry years) and disturbances (e.g., storms, forest fires)? The concept of SFM not only comprises three substantive dimensions – ecological, economical, and social – but also temporal and spatial dimensions.

Concept of Conflict

SFM is controversial for good reason: any one definition represents particular values on these five dimensions at others' expense. Inherent in the concept is conflict among the value systems that underlie these differences. SFM is thus a concept reflecting conflict rather than harmony, as it is often misinterpreted. SFM serves as the vehicle by which the underlying norms and values of these standards can be expressed. By supporting a certain understanding of SFM, participants' preferences and values are expressed, but nothing has been harmonized, no value conflicts have been resolved. The only thing that happens is that certain values are discussed so that social bargaining processes, e.g., concerning certification of SFM, may begin.

Thus, the achievement of SFM ultimately depends on the reconciliation of different social perspectives with respect to forest resources in social or political processes. The reasons behind differences in participants' values may be different interests, expertise, or knowledge levels but also different views of how the world works. Reconciliation processes are therefore not easy, and can become very easily corrupt or biased, where there is no right or wrong answer, only more or less appropriate ones.

Whereas in earlier times forest management planning was generally considered a technical issue and responsibility was exclusively dedicated to forest owners or forest professionals, it is increasingly recognized that SFM must integrate narrow private and broader public interests in forest resource utilization through adequate institutional designs of social or political processes. The challenge of SFM is to recognize, accommodate, and respond effectively to diverse and dynamic value perspectives about forest management in society. Achieving SMF is consequently in the first instance a social exercise and only secondarily a technical issue.

Context Dependency

There is widespread agreement between authors that the meaning of SFM is dependent on time and place and that there cannot be an objective, universal definition. What will be sustained, and for whom, is determined through social processes. Still, there are always predominant understandings in certain times and places, reflecting the prevailing social, economic, and political conditions. The understanding of SFM is thus not only context-dependent but also subject to continuous change. The question of which definition will predominate in a certain region and during a certain time period may also be one of political power, and not necessarily only of objective necessities, as is well reflected by the history of the 'sustained yield' principle in Europe and its adaptation when introduced in the USA.

With the age of enlightenment in the eighteenth century, central Europe was ripe for the development of scientific models for the use and conservation of forests, replacing practical and unsystematic approaches which had been predominating in European forestry until then. Based on the idea of continuous production, the aim of achieving, at the earliest practical time, an appropriate balance between growth and harvest was translated into mathematical formulae, which culminated in the ideal model of the 'normal forest.' Whereas initially sustained timber production with special attention to sustaining growing stock was central, the focus switched to sustaining net revenues and aspects of the ground rent when the predominant economic system of mercantilism was replaced by the free-market philosophy. In general, forest management for sustained yield in central Europe in the middle of the nineteenth century had as its objectives the production of annual timber crops of approximately equal size, maintenance of stable industrial communities, furnishing permanent income for forest owners, and purchasing power, and full use of the productive capacity of the forest lands. With the arrival of the first ideas on environmental conservation and the renaissance of a holistic perspective on nature at the turn of the twentieth century, sustained-yield forestry was brought into line with the productive power of the soil and the functioning of the forest as an organic community. With the increasing wealth of society in the twentieth century, when spare time and recreation became more important, the traditional sustained-yield concept gradually shifted to that of SFM for multiple benefits.

When the ideal of the normal forest and sustained-yield regulation necessary to maintain it were introduced from Europe to the USA at the turn of the twentieth century, the ignorance of the context dependencies of the concept gave rise to heavy criticism. The criticisms seemed to have two common elements: (1) perpetual output was perceived as inconsistent with the 'frontier' mentality of a young and still developing American society; and (2) the physical models bore little relation to the economic realities of the predominating liberal capitalism. Consequently, the idea of sustained yield as a production technique designed to ensure a sustained commodity flow over time was broadened to an understanding of SFM, encompassing the continuity of multiple benefit flows and ecological stability while maintaining the potential to respond to evolving demands.

The context dependency of the understanding of SFM is also well illustrated by the rejection of the concept of SFM as being 'reactionary and capitalistic' under communistic sovereignty, as for example in the time of the Soviet Union. Forest resources there were instead interpreted as an important component in the development of a socialistic society, giving space to an alternative interpretation of the concept of extended reproduction.

Formal and Informal Processes

In the beginning of regular forest management, the idea of sustained yield was usually interpreted by the forestry profession and advocated by government and industry. Local communities themselves have not usually promoted sustained yield in such a scientific sense. However, in several cases they have undertaken measures to limit exploitation and protect forests. As the concept has been broadened from sustained yield to SFM, this has changed. The reconciliation of different social values in the respective understanding of SFM now takes place in the form of social processes which encompass socioeconomic impacts and the stakeholder participation. These processes usually began at national or regional level but more frequently became institutionalized at a local level. The character of these processes can be both formal and informal.

The United Nations Conference on Environment and Development (UNCED) in 1992 in Rio de Janeiro provided an important stimulus for discussion about SFM in all types of forest at a global level. Even though the conference did not result in a legally binding instrument on the conservation of forests, its follow-up processes resulted in a clear recognition of the importance of SFM. The issue of SFM was furthermore taken up by several regional political processes, in the follow-up, or parallel, to the United Nations' process, such as the so-called Montreal Process or the Ministerial Conference on the Protection of Forests in Europe – all provided important contributions to the discussions or even binding definitions of SFM for their member parties. These understandings have long departed from the classical understanding of SFM as sustained-yield regulation. The Ministerial Conference on the Protection of Forests in Europe, for example, defines SFM in their Helsinki resolution as 'the stewardship and use of forest lands in a way, and at a rate, that maintains their biodiversity, productivity, regeneration capacity, vitality and their potential to fulfill now and in the future, relevant ecological, economic and social functions, at local, national, and global levels, and that does not cause damage to other ecosystems.'

SFM has also emerged as a consideration in the international trade of forest products. Many consumers, individually and collectively, prefer to buy products obtained from sustainably managed forests and manufactured by environmentally acceptable processes. In response to this demand, several timber certification systems have been established at international as well as regional level, which concur with each other. At a global level, the Forest Stewardship Council (FSC) was founded by environmental nongovernment organizations in cooperation with the timber industry to promote the sustainable management of forests worldwide. By formulating principles, criteria, and indicators for SFM that are differentiated according to different regions of the world, the FSC acts as an accreditation body for certifying organizations, thereby guaranteeing certain minimum standards for SFM. However, given the impossibility of an objective, universally agreed definition of SFM, all certification schemes have also been the subject of conflict.

Another example of how the consumers' call is influencing discussions about SFM is reflected by the ambitious year-2000 objective of the International Tropical Timber Trade Organization (ITTO) which stated that 'ITTO members will progress towards achieving sustainable management of tropical forests and trade in tropical timber from sustainably managed resources by the year 2000.' Even though ITTO's own evaluation showed that only a few countries 'appear to be managing some of their forests sustainably,' it is nevertheless a good example for the many social and political processes which have been started all over the world in search of criteria and indicators for SFM. At the same time, the ITTO example clearly indicates that understanding of SFM needs to be adequately institutionalized, in order to become implemented.

Institutionalization

Experience from all over the world seems to indicate that one of the most important institutional prerequisites for SFM is legislation that establishes appropriate and reliable forms of forest tenure, including various forms of forest ownership and usage rights. There are furthermore clear indications that the political, economic, and ethical setting in which SFM is pursued will determine success or otherwise. As history and practical evidence show, SFM seems not to be feasible unless it benefits from a sound and stable context of consistent developments and converging strategies occurring in related sectors. Implementing SFM thus involves policy action in forestry as well as in other policy fields, with cross-sectoral policy coordination being another crucial institutional device. In many countries the policies of several government ministries have an impact on forest lands.

Significant influential factors for the successful implementation of SFM include financial incentives, a clear sharing of costs and investments, as well as an active, informed civil society.

Symbolic Function

Yet, even if no consensus on criteria and indicators can be achieved, and implementation cannot be adequately institutionalized, the concept of SFM is not without importance for forestry. Critics of SFM have underestimated its emotional and symbolic significance. The bewildering variety of understandings and its multifaceted character is a weakness and a strength at the same time. The concept of SFM can also serve as a platform on which disparate actors can stand together – its ambiguity allows participants with seemingly irreconcilable positions to search for common solutions without appearing to compromise their principles. Furthermore, the informal, personal, and implicit properties of the concept should not be forgotten – its ability to provide a guideline for coping with uncertainty and ignorance in forest management decisions and to serve as an esprit de corps for the forestry profession.

See also: **Mensuration**: Yield Tables, Forecasting, Modeling and Simulation. **Plantation Silviculture**: Multiple-use Silviculture in Temperate Plantation Forestry; Sustainability of Forest Plantations. **Sustainable Forest Management**: Certification.

Further Reading

Aplet GH, Johnson N, Olson JT and Sample VA (eds) (1993) *Defining Sustainable Forestry*. Washington, DC: Covelo.

Clawson M and Sedjo R (1984) History of sustained yield concept and its application to developing countries. In: Steen HK (ed.) *History of Sustained Yield Forestry: A Symposium of the Forestry History Society*, pp. 3–15. Santa Cruz, CA: Forest History Society.

de Montalembert M-R and Schmithüsen F (1993) Policy and legal aspects of sustainable forest management. *Unasylva* 44(175): 3–8.

Lee RG (1982) The classical sustained yield concept: content and philosophical origins. In: LeMaster DC, Baumgartner DM, and Adams D (eds) *Sustained Yield – Proceedings of a Symposium, Spokane, Washington*, pp. 1–10. Washington, DC: Washington State University Cooperative Extension Pullman.

Lee RG (1990) Sustained yield and social order. In: Lee RG, Field DR, and Burch WRJ (eds) *Community and Forestry – Continuities in the Sociology of Natural Resources*, pp. 83–94. Boulder, CA: West View Press.
Romm J (1993) Sustainable forestry, an adaptive social process. In: Aplet GH, Johnson N, Olson JT, and Sample VA (eds) *Defining Sustainable Forestry*, pp. 280–293. Washington, DC: Covelo.
Schanz H (1996) 'Forstliche Nachhaltigkeit' – Sozialwissenschaftliche Analyse der Begriffsinhalte und -funktionen [Sustainable forest management – contents and functions of a central term in a social science perspective]. Dissertation. Schriften des Instituts für Forstökonomie, Band IV. Freiburg, Germany: Universität Freiburg.
Steen HK (ed.) (1984) *History of Sustained Yield Forestry.* IUFRO Symposium Western Forestry Center. Portland, OR: Forest History Society.
Wiersum KF (1995) 200 years of sustainability in forestry: lessons from history. *Journal of Environmental Management* 19(3): 321–329.
Zürcher U (1965) Die Idee der Nachhaltigkeit unter spezieller Berücksichtigung der Gesichtspunkte der Forsteinrichtung [The idea of sustainability in a forest planning perspective]. *Mitteilungen der schweizerischen Anstalt für das forstliche Versuchswesen, Zürich* 41: 87–218.

Certification

S Bass, Department for International Development, London, UK

Introduction

Certification provides a means by which the quality of forest management may be independently assessed to agreed standards. It offers credible evidence that enables the forest manager to obtain benefits, notably access to markets that demand sustainably-produced forest products. Several certification schemes have experienced rapid development and certification is now routine practice. This article reviews the process in general, the key players, and the early achievements of certification in light of its implicit assumptions.

Definitions and Description of Forest Certification Processes

Certification

Certification is the procedure by which a third party provides written assurance that a product, process or service conforms to specified standards, on the basis of an audit conducted to agreed procedures. Certification may be linked with product labeling for market communication purposes. It comprises a variety of mechanical tasks that aim to produce highly objective assessments. However, it tends to have market and political implications, because it results in a judgement of whether a product, process or service is acceptable or not. The International Organization for Standardization (ISO) has set precedents in the various tasks of certification, standardization, and accreditation that are outlined below, and most certification schemes in any sector have chosen to adhere to them. This is partly because ISO standards tend to be recognized by the World Trade Organization (WTO) as not creating unnecessary barriers to trade. Certification of social and environmental performance is already changing the rules of the game for many industries. It has occupied a key role in the 'organic' and 'fair trade' niches of food production for some time; it is emerging in fisheries and tourism; and it is being explored for mining. Certification has had a particularly rapid evolution in the forest sector, where it is becoming routine practice.

Forest Management Certification

Forest management certification is the process by which the performance of on-the-ground forestry operations is assessed against a predetermined set of standards. This is voluntary, at the request of the forest owner or manager. If the forestry operations are found to be in conformance with these standards, a certificate is issued, offering the owner/manager the potential to bring products from the certified forest to the market as certified products. This market potential is realized by a supplementary certification, which assesses the chain of custody of wood (see below). In this sense, forest certification is market driven – aiming to improve forest management through market-based incentives, and to improve market access and share for the products of such management. It addresses the quality of forest management, as opposed to the quality of forest products. In addition, systems for the certification of wood quality exist (see below).

Standards

Standards used in forest certification schemes are of two general types:

- performance standards
- management system standards.

Performance standards look for specified outcomes to be achieved, notably social, environmental, and economic outcomes: these may be expressed as thresholds. In contrast, management system standards look for specified elements in the management system, notably target setting, monitoring, and review, that ensure that performance continuously improves from whatever base. The latter are typified by ISO9000 quality management or ISO14000 environmental management standards. However, all forest certification schemes include some elements of both performance and management standards.

Procedures

Procedures for conducting forest certification can take several months from initial inquiry to issuance of the certificate. At the request of the forest owner or manager, typically the auditor conducts, in the following order:

- an (optional) preassessment or 'scoping' visit
- confirmation of the standard by which the forest will be certified or (if necessary) development of an interim standard
- consultation with stakeholders
- an independent formal audit of the quality of forest management in a specified forest area, under one management regime, against the specified standards, by assessing documents that prescribe and record management, together with checks in the forest and interviews with staff and stakeholders,
- writing the assessment report and, usually, peer review
- a decision to issue a certificate for a period

and/or

- corrective action requests (CARs) – a formal document which details noncompliances identified and remedial measures required within a specified time
- a public summary of the certificate placed on the certifier's website
- regular (annual) audits thereafter to ensure continued compliance and action on CARs, which process maintains the validity of the certificate.

Chain of Custody Certification

Chain of custody certification is a frequent supplement to forest management certification. It verifies the chain of responsibility through which a product passes, e.g., from the forest, through timber processor to manufacturer, to importer, to distributor, to retailer. The result is a certified origin of the forest product concerned.

Forest Product Labeling

Forest product labeling refers to the quality of forest management and the origin of the raw material of which the product is made. It is based on (1) certification of forest management, and (2) verification of the chain of custody. It may be displayed on the physical forest product itself. The same information can also be communicated off-product, i.e., in various promotional materials and communication media. Certification schemes operate strict rules regarding the use of on-product or advertising labels, which are usually trademarked.

Accreditation

Accreditation is the process of recognition – against published criteria of capability, competence, and impartiality – of a body involved in conformity assessment. Accreditation formally recognizes the competence and impartiality of the bodies involved in certification of forest management and the chain of custody, and results in licenses to operate a particular certification scheme. In effect, it 'certifies the certifiers.' With a few exceptions, accreditation is granted by national accreditation bodies, which can be governmental or private. A notable exception is an international body in the case of the Forest Stewardship Council (see below).

Provisions for Specific Circumstances

Acknowledging the specific issues affecting certain product types and producers, certification schemes tend to make provision for:

1. Multiple source chain of custody to enable certification for paper and composite wood products. This may allow processors a mix of certified and uncertified material where this reflects local supplies and so reduces cost. It may also favor mixture with recycled materials.
2. Group certification of smallholders, to allow for several small enterprises to be covered by one certificate, which is held by the group manager. This can reduce certification cost, provided group members are sufficiently similar to create scale economies.
3. Forest manager certification for similar reasons to the above, where a professional manager is responsible for several small areas.
4. Recycled wood certification which accords certified status to reclaimed or recycled wood where chain of custody is known.
5. Ecological zone harmonization of national standards, to ensure that standards covering similar ecological zones, if they were developed separately

by different (national) stakeholders, can be rationalized.

6. Other issues that emerge through reviewing the practice of, and problems faced by, certification schemes. Many schemes operate working groups to identify and respond to such needs.

Thus forest certification is not one single operation, but a mix of mechanical and political functions (**Figure 1**).

The Rationale for and Evolution of Forest Certification

Forest certification has developed in response to the interests and incentives facing many different interest groups. However, its origins lie largely with environmental nongovernmental organizations (NGOs) and the timber retail business. During the 1970s and 1980s, environmental NGOs grew increasingly disillusioned with the failure of government authorities and regulations to improve forest management in tropical regions, with the inadequacy of intergovernmental efforts to tackle deforestation, and with the forest products trade's lack of discrimination in where it sourced its products. By the late 1980s, NGOs had concluded that both the Tropical Forestry Action Plan and the International Tropical Timber Organization (ITTO) had failed to halt asset-stripping approaches to forestry. In Western Europe and North America in particular, NGO campaigns led to the emergence of consumer bans and boycotts against tropical timber, claiming that much of it derived from deforestation. Many retailers could not make counterclaims as they had no idea where their wood came from.

The timber retailers' alarm was exploited constructively by some NGOs (notably the Worldwide Fund for Nature, WWF), who suggested the more attractive possibilities of developing markets for environmentally and socially sound forest products. This brought about one of the first alliances of environmental NGOs and businesses. They developed the idea of a mechanism to allow wood products to be traced back to their forest sources, to verify that the same forest was well managed, and to create market incentives that would make the mechanism viable. Forest owners and managers were then brought into the process. Like the retailers, they were motivated by the prospect that certification would offer a useful marketing tool in the face of consumer boycotts and competition with other materials. They expressed varied expectations ranged from premium prices, to reducing market risks, to maintaining or increasing market share, to product 'green branding' and differentiation to access further markets, to nonmarket motivations such as skills development and being recognized by forest authorities.

Thus the Forest Stewardship Council (FSC) emerged in 1993. (It was not the first forest certification scheme: in 1990 the Rainforest Alliance set up the Smart Wood forest certification program, which provided early lessons for, and is now accredited to, the FSC.) It has now certified forests in all continents, with an almost exponential increase in the area covered. However, numerous other

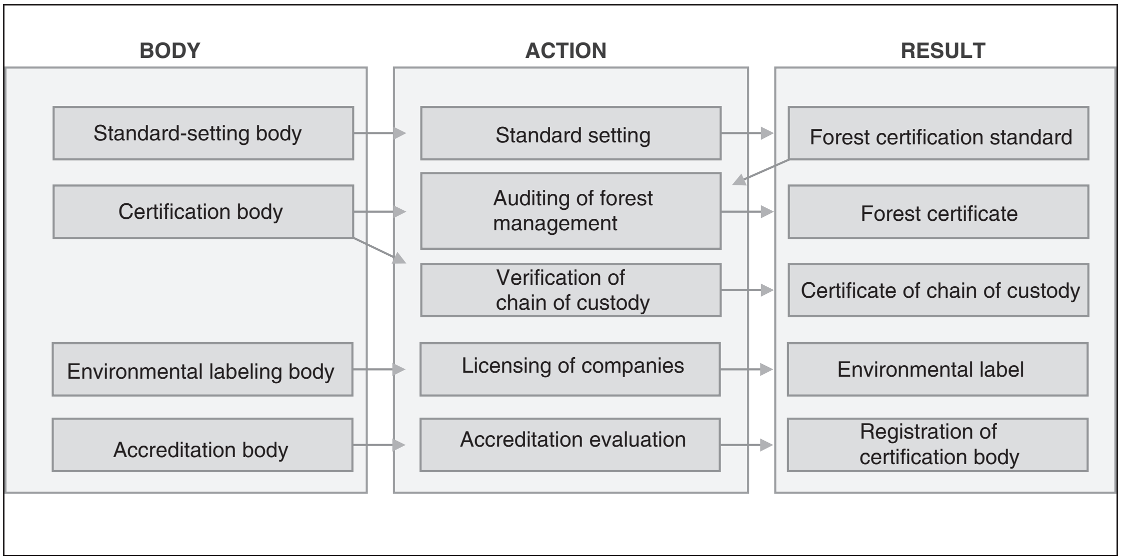


Figure 1 Elements of forest certification. From Bass S and Simula M (1999) Independent certification/verification of forest management. Background paper for WB/WWF Alliance Workshop, 8–9 November 1999, Washington, DC. http://www.worldbank.org/wwf/certwkshp.htm

international and national forest certification schemes have more recently emerged. Many local stakeholders wanted to take charge of the process of developing certification schemes, to ensure they were appropriate to their forest types, enterprise types and governance systems.

Whilst the problems of tropical deforestation were the main drivers of forest certification, certification is now commonplace in temperate and boreal forests as well. This was both in response to NGO and consumer worries about northern forests, and to the interest and opportunism of producers operating in these forests and retailers selling their products. Indeed, to date, more certificates have been awarded by FSC and other schemes to northern forests.

The Forest Stewardship Council

Until the introduction of the Pan-European Forest Certification Framework in 1999 (see below), the FSC was the only fully integrated, international system of forest certification. The FSC's objectives are to promote global standards of forest management, to accredit certifiers that certify forest operations according to such standards, and to encourage buyers to purchase certified products.

The FSC is a membership organization, with decisions made through meetings of a General Assembly, which is divided into three equal chambers: social, environmental, and economic. All three chambers have Northern and Southern subchambers, each with half of the total chamber votes. Governments are not entitled to participate in the FSC's governance, even as observers, although government employees have been very active participants in some FSC national initiatives.

The FSC has a set of ten principles and related criteria (P&C) of forest stewardship, which apply to all tropical, temperate, and boreal forests, both natural forests and plantations, with the tenth Principle being exclusively for plantations (**Table 1**). These P&C serve as a basis for the development of national and regional forest management standards. Certification standards that are consistent with both the P&C and with FSC's process guidelines for standards development are eligible for FSC endorsement. Such standards have been developed by both FSC-organized national working groups and by independent processes, e.g., that of Indonesia. The

Table 1 The Forest Stewardship Council's ten principles of forest stewardship

Principle 1: Compliance with laws and FSC principles
Forest management shall respect all applicable laws of the country in which they occur, and international treaties and agreements to which the country is a signatory, and comply with all FSC Principles and Criteria.
Principle 2: Tenure and use rights and responsibilities
Long-term tenure and use rights to the land and forest resources shall be clearly defined, documented, and legally established.
Principle 3: Indigenous peoples' rights
The legal and customary rights of indigenous peoples to own, use, and manage their lands, territories, and resources shall be recognized and respected.
Principle 4: Community relations and workers' rights
Forest management operations shall maintain or enhance the long-term social and economic well-being of forest workers and local communities.
Principle 5: Benefits from the forest
Forest management operations shall encourage the efficient use of the forest's multiple products and services to ensure economic viability and a wide range of environmental and social benefits.
Principle 6: Environmental impact
Forest management shall conserve biological diversity and its associated values, water resources, soils, and unique and fragile ecosystems and landscapes, and, by so doing, maintain the ecological functions and the integrity of the forest.
Principle 7: Management plan
A management plan – appropriate to the scale and intensity of the operations – shall be written, implemented, and kept up to date. The long-term objectives of management, and the means of achieving them, shall be clearly stated.
Principle 8: Monitoring and assessment
Monitoring shall be conducted – appropriate to the scale and intensity of forest management – to assess the condition of the forest, yields of forest products, chain of custody, management activities and their social and environmental impacts.
Principle 9: Maintenance of high conservation value forests
Management activities in high conservation value forests shall maintain or enhance the attributes which define such forests. Decisions regarding high conservation value forests shall always be considered in the context of a precautionary approach.
Principle 10: Plantations
Plantations shall be planned and managed in accordance with Principles and Criteria 1–9, and Principle 10 and its Criteria. While plantations can provide an array of social and economic benefits, and can contribute to satisfying the world's needs for forest products, they should complement the management of, reduce pressures on, and promote the restoration and conservation of natural forests.

FSC owns a trademark which may be used to label products from certified forests.

The Pan-European Forest Certification Framework

The Pan-European Forest Certification Framework (PEFC) is a voluntary private-sector initiative, designed to promote an internationally credible framework for forest certification schemes and initiatives. Its criteria are consistent with the intergovernmentally agreed Pan-European Criteria and Indicators for Sustainable Forest Management, thereby attracting considerable support from both European and national governments. National certification schemes that meet PEFC requirements can apply for endorsement and the right to use the PEFC trademark for product labeling. In contrast to accreditation by the FSC, PEFC leaves this function to national accreditation bodies. National PEFC governing bodies set standards and operate national schemes, and are represented on the PEFC Council Board.

The initiative was given strong impetus by Austrian, Finnish, French, German, Norwegian and Swedish forest owners, who wished to ensure that small woodland owners are not disadvantaged by certification, and that local conditions are catered for. It was supported by the national forest certification schemes that had been emerging in some of these countries yet which felt themselves to be individually too small to develop an adequate presence. The evolution of PEFC was rapid: it started in August 1998, and was launched in June 1999. Now there are many countries involved, extending into other continents. The rapid development of both country coverage and certified area has entrenched the position of some environmental NGOs; they believe that the ease of achieving PEFC certification, in countries which they perceive to have imperfect forest management, demonstrates that the scheme is not helping to improve forest management and thereby achieves little beyond attempts at market protection.

Regional and National Certification Schemes

At the level of individual countries, the number of certification schemes under development is increasing rapidly. They fall into three main groups:

1. Schemes aligned from the outset with either the FSC or PEFC.
2. Schemes that develop independently but aim for compatibility with the FSC and/or PEFC.
3. Schemes without any links to an umbrella scheme.

Where there is contention over any scheme, it tends to concern:

- the perceived dominance or exclusion of certain parties
- the lack of comparability between specific standards in a given region
- the degree of challenge or 'stretch' represented by the gap between normally applied legal standards and certification standards.

Observations on the Effectiveness of Certification

Forest certification schemes started on the basis of very little experience. Of necessity, they rested on a set of assumptions many of which have never really been made explicit. It is worth reviewing these assumptions in light of a good ten years of experience.

Assumption 1: One Set of Standards Can Apply to All Types of Forest

At the level of their basic principles, certification standards do seem to be applicable to many types of forest. Two observations support this: firstly, most certification schemes have been able to justify, develop, and apply one overarching standard; and secondly, there are considerable similarities in such standards between schemes. In many ways, therefore, certification has coped effectively with a tricky dilemma: how to deal with complexity (in standards and their interpretation) and yet also deliver a simple message to consumers and producers.

Assumption 2: One Set of Standards Can Apply to All Types of Forest Producer

In practice, larger producers find it easier to benefit from certification, as they have better access to information and markets, scale economies, formal management systems on simpler forest types, and an ability to bear risks and costs. The area of certified forest under community or small enterprise management is correspondingly much smaller. Recognizing this lack of uptake, many certification schemes have responded with special schemes for group certification of small growers. However, there are those who question why a small community group occasionally harvesting timber on its own land should be held as accountable as a major corporation harvesting 24 hours a day on leased public land. The fact that standards tend to be focused on performance forestry outcomes, and do not adequately recognize each step achieved in the process of getting there, prejudices against many developing country practices, in particular where there are often many steps to be undertaken. Part of the problem derives also from the next assumption.

Assumption 3: Forest Management Standards Should Be Based on Scientific Principles of Forest Management, with a Strong Emphasis on Records and Clear Business Strategy

Certification is largely document-based, and is predicated on formal means of planning and monitoring. In practice, this assumption has prejudiced against the forestry norms and methods of traditional societies, and against part-time foresters. A national standard which may stretch to some 40 pages is intimidating to people with low literacy levels. Even if it is understood, some current certification standards and procedures cannot recognize good management in some of the complex land use systems of indigenous and community groups. Furthermore, the difficulties faced by certifiers in interpreting social standards in complex social contexts (or at least contexts which will be alien to the certifier) have meant that some inappropriate social CARs have been issued.

Assumption 4: Most Progress in Sustainable Forest Management Will Be Made through Focusing on the Forest Management Unit

It is true that, before certification, 'sustainability' was characterized by too much discussion and too little action. Certification has shifted energies to real forests and real enterprises. Yet some environmental and social services are often realized at the landscape level. Thus the forest unit plays only a partial role, and cannot be responsible for a complete role. Although certification must focus on what the enterprise (or other certified entity) does, it needs to be improved to account for critical sustainability issues at other levels (such as the landscape or the nation), which may not be under the control of that entity but which require its active engagement.

Assumption 5: Voluntary, Market-Based Certification Would Be a Cost-Effective Complement to Traditional Administrative Regulation in Improving Forest Management and Ensuring the Protection of Forest Environments

This assumption is proving to be valid. In some countries, state forest authorities support certification as a 'privatized' form of forest monitoring, and are making incentives available. In countries where regulation and enforcement is weak, certification has ensured that at least some producers are meeting not only legal requirements but also higher standards, and that this is monitored. The presence of evidently good forest management and scrutiny has had useful knock-on benefits locally, notably by improving forest policy debates and provisions.

Assumption 6: By Involving Consumers, Producers, and other Forest Stakeholders in Standards Development, Certification Would Be More Credible than Traditional Regulatory Instruments

In many countries, certification has certainly become as significant as traditional instruments: stakeholders now tend to pay as much attention to developments in certification as they do to developments in national and intergovernmental law. Certification offers broader standards that tend to reflect more stakeholders' needs, improving credibility in many stakeholders' eyes. The key ingredients are: focused participation in defining standards, and verification by third parties using tried-and-tested mechanisms with precedents in other sectors. However, there are some tensions between the values that drive some protagonists of certification and the need for objective scrutiny. This mean that accreditation of certifiers is essential for objectivity but fraught with difficulties. A further problem is the proliferation of certification schemes, which is leading to consumer confusion and a reluctance of firms to be certified at all. Fears of proliferation have prompted considerable efforts by the wood products industry to investigate the potential of mutual recognition or adjustment between schemes.

Assumption 7: By Being Voluntary and Not Involving Government, Certification Would Be Able to Avoid Charges of Trade Discrimination under WTO Rules, and Would Not Be Constrained by any Unprogressive Governmental Approaches to Forestry

In practice, there have been no serious challenges to certification under WTO; forests have been certified in countries where government controls and incentives are weak; and governments have been involved in some schemes. Indeed, the implications of a lack of government involvement in other schemes need serious consideration. This is because of the close relationship of certification standards to regulations, and the fact that some government bodies have direct interests as forest enterprises, as providers of environmental service, and as authorities concerned with the welfare of forest-dependent groups.

Assumption 8: Consumer Demand for Certified Products Will Be Strong Enough to Encourage Producers to Pay the Extra Costs of both Certification and the Necessary Forest Management Improvements

In practice, certified products command only a minority of the forest products market, with most market penetration in Western Europe. The market share of paper and construction timber/panels is particularly small. Consequently, only about 4% of commercial forestry is certified globally (as of 2003). However, all these figures are growing. Certified producers are gaining the benefit of market access, rather than a price premium (although a premium is available in some segments). More probably needs to be done to educate consumers about sustainable forestry and certification if the demand is to rise significantly. In addition, where market benefits have proven elusive, other incentives for certification might also be explored, e.g., access to resources such as land, finance, and insurance.

Assumption 9: Poor Forest Management and Deforestation Would Decline, as the Actors Involved Would Respond to the Incentive Effects of Market-Based Certification

In practice, the high threshold levels of certification standards (and FSC's in particular) have meant that certification has identified currently good practice, rather than improved bad practice. These 'good' producers now meet all current legal requirements, including those that they might normally not bother to meet. Most of them have also tightened management systems, especially for managing environmental impact. However, certification so far is only really inducing competition between excellent producers (just above the certified threshold), and good producers (just below the threshold). There are few incentives to cause the really bad producers to change behavior and be certified. Consequently, the worst forestry problems remain little affected by certification. The need for several thresholds (stepwise or phased approaches) is now being discussed, along with ways to complement certification with instruments to combat illegal logging.

Assumption 10: Certification Can Be a 'Magic Bullet' to Annihilate Multiple Forest Problems

Whilst it is clear that certification is an important innovation, there are many other prerequisites, complements, and alternatives that need to be considered in any given situation. For example, many certified community groups have expressed the opinion that better market information and enterprise management capacity would have been higher priorities than certification – the latter having proven an inefficient means to acquire these assets. Further, policy prerequisites such as recognized forest and trade rights, and state protection of those rights, are necessary for the benefits of certification to be realized. Therefore the challenge is to understand and promote the right 'fit' of certification with other instruments for a given situation.

Conclusion

Because there are few surveys of what forest certification has achieved, the above observations are not definitive. Yet they point to some strengths and limitations that certification schemes, and their stakeholders, should keep under review. Perhaps the limits of the separate evolution of schemes have now been reached: it is important for all schemes to share the lessons and to develop responses together.

It is also important for all major government and multistakeholder initiatives to seriously consider what integral roles there might be for certification. Forest certification is based on concerns of both global and local imperatives for sustainable forest management and reflects the ongoing process of negotiation of the often conflicting ideas of what sustainable forest management is about. Where certification can manage these tensions creatively, it should certainly have an enduring role.

See also: **Genetics and Genetic Resources**: Forest Management for Conservation. **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Operations**: Small-scale Forestry. **Plantation Silviculture**: Sustainability of Forest Plantations. **Social and Collaborative Forestry**: Forest and Tree Tenure and Ownership; Public Participation in Forest Decision Making. **Sustainable Forest Management**: Overview.

Further Reading

Bass S and Simula M (1999) Independent certification/verification of forest management. Background paper for WB/WWF Alliance Workshop, 8–9 November 1999, Washington, DC. http://www.worldbank.org/wwf/certwkshp.htm

Bass S, Thornber K, Markopoulos M, Roberts S, and Grieg-Gran M (2001) Certification's impacts on forests, stakeholders and supply chains. http://www.iied.org

Confederation of European Paper Industries (2002) Comparative matrix of forest certification schemes. http://www.cepi.org

de Camino R and Alfaro M (1998) Certification in Latin America: experience to date, Rural Development Forestry Network paper no. 23c. http://www.odi.org.uk

Eba'a Aryi R and Simula M (2002) *Forest Certification: Pending Challenges for Tropical Timber*, ITTO Technical Series no. 19. Yokohama, Japan: International Tropical Timber Organization.

Elliott C (2000) *Forest Certification: A Policy Perspective*. Bogor, Indonesia: Center for International Forestry Research.

FERN (2001) *Behind the Logo: An Environmental and Social Assessment of Forest Certification Schemes*. Moreton-in-Marsh, UK: FERN.

Higman S, Bass S, Judd N, Mayers J, and Nussbaum R (1999) *The Sustainable Forestry Handbook*. London: Earthscan.

Kanowski P, Sinclair D, Freeman B, and Bass S (2000) *Critical Elements for the Assessment of Forest Management Certification Schemes: Establishing Comparability and Equivalence amongst Schemes*. Canberra, ACT: Department of Agriculture, Fisheries and Forestry-Australia.

Meidengere E, Elliot C, and Oesten G (eds) (2003) Social and political dimensions of forest certification. http://www.forstbuch.de

Proforest (2001) *An Analysis of Current FSC Accreditation, Certification and Standard-Setting Procedures Identifying Elements which Create Constraints for Small Forest Owners*. Oxford: Proforest.

Upton C and Bass S (1995) *The Forest Certification Handbook*. London: Earthscan.

Worldwide Fund for Nature (2001) *The Forest Industry in the 21st Century*. Godalming, UK: WWF Forests for Life Campaign.

Definitions, Good Practices and Certification

M Karki, Medicinal and Aromatic Plants Program in Asia, New Delhi, India

R B S Rawat, National Medicinal Plants Board, New Delhi, India

Introduction

Non-wood forest products (NWFP) are found abundantly in tropical and temperate forests, range, and shrublands throughout the world. However, due to years of unwise use, the availability of certain NWFPs especially medicinal plants in desired quality, quantity, time, and place has become difficult. This raises serious doubts about their availability to meet both the local demand as healthcare products of local poor communities as well as growing demand of national and global phytomedicine industries. The sustainable production, conservation, and use of NWFPs are influenced by a number of factors, including those of a socioeconomic, technical, institutional, and policy nature. Unsustainable harvesting of the raw materials from the wild by untrained and poor collectors, mostly using primitive methods, and the lack of awareness of the real value of the resources are other important factors leading to widescale resource depletion. Rural people in developing countries derive a substantial portion of their income, and food and medicinal products for their basic needs from NWFPs gathered from forests.

This article presents conservation-through-use or sustainable conservation as a good practice to integrate biophysical and socioeconomic tools in the management of NWFP to reduce global poverty and enhance biodiversity conservation. The main premise is that NWFP resources are the natural capital of local people and their wise management can improve livelihoods of the rural people in the developing world who in turn will find incentives to conserve the global environment. However, this new approach to NWFP management needs to be properly and systematically monitored and linked to the prevailing national and global market conditions that permit the conversion of these natural resources into sources of gainful employment and the greater well-being of the local community. Mechanisms need to be developed and broadened to formalize the inclusion of market factors and good social and business behavior in the system of NWFP management. Procedures are needed for inspection of proper collection, cultivation, processing, packaging, marketing, maintaining market-demanded quality and schedules. These procedures should be governed by a certification system, which is scientific in operation and global in its acceptance. Central to this approach is the application of a value or commodity market chain method, which can be monitored by both the producers and consumers. Certification of quality product, good management, and fair trade based on the practices of good collection, cultivation, and management can lead to new and economic opportunities such as niche or green markets, price premiums for good social behavior, and a long-term producer–consumer relationship.

Definition, Scope, and Potential

Background

Non-wood forest products (NWFPs) are the other forest products apart from wood in its broadest sense. According to the Food and Agriculture Organization of the United Nations (FAO), NWFPs consist of goods of biological origin other than wood as well as services derived from forests and allied land uses. NWFPs are also understood as forest produce other than timber (construction wood), which can be harvested on a nondestructive basis from nature. More simply put, NWFPs include all goods of biological origin other than wood in all its forms as well as services derived from forests or similar lands. They include a number of goods such as fodder, fibers, flosses, food and food additives, fertilizer (biomass), medicinal plants and herbal potions, phytochemical and aromatic chemicals, fatty oils, latex, gum resin and other exudates, and different kinds of animal products (honey, wax, lac, silk, etc.). They also include services such as grazing, ecotourism, nature trekking, etc. as well as raw materials for different types of rural and cottage industries.

NWFPs are known by different names such as minor, special, nontraditional, and non-timber forest products. Medicinal and aromatic plants (MAPs) are the most prominent NWFP, which have potentialities to safeguard biodiversity, promote sustainable conservation, and help improve the local and national economies. Long-term and equitable economic development of poor NWFP-dependent communities is possible by promoting better protection of indigenous knowledge and providing direct pecuniary benefits to the local people through wise management of NWFPs. International policy documents such as Convention on Biodiversity (CBD), Trade Related Intellectual Property Rights (TRIPS), and Convention on International Trade in Endangered Species (CITES) provide the international legal platform over which different countries are building up their own system of NWFPS management, development, conservation, and commercialization.

NWFPs and People's Livelihoods

In many developing countries, millions of people residing in and around forests rely on NWFPs for their subsistence. More than half of the employment generated in the forestry sector is through NWFPs. Studies in the Rajasthan state of India have indicated that approximately 5 million indigenous populations sustain themselves through collection, processing, and marketing of NWFPs, which amounts to 50–80% of the total forest revenue in many countries. In the Gujarat state of India, 27% of adults and 72% of children and women collect NTFPs in forest regions, while in the Madhya Pradesh state more than 35% of the forest revenue is from NWFPs. In the NWFP-rich Northeast Himalayas, the contribution of the NWFPs to the local economy is up to 60% (**Table 1**).

Medicinal plants are among the most important NWFPs in poor developing countries. According to the World Health Organization (WHO), 80% of the people in developing countries rely on traditional

Table 1 Contribution of non-wood forest products in the rural economy of the northeast Himalayas (Assam and Meghalaya (ML) case studies)

Product	*NC Hills, Assam*	*Karbianglong, Assam*	*W.K.Hills, ML*	*W.G.Hills, ML*
Percent household involved in extraction of NWFPs				
Bamboo	50–60	45–50	100	100
Subsistence uses	2–3	3–4	0.5	0.7
Commercial uses				
Cane	10–12	12–15	—	—
Subsistence uses	3–4	5–6	0.15	—
Commercial uses				
Others	—	—	45	—
Subsistence uses	—	—	0.3	1
Commercial uses				
Quantity used/sold				
Bamboo				
Subsistence	0.25 t/yr	0.25 t/yr	0.45 t/yr	0.3 t/yr
Commercial	20–30 t/day	35–40 t/day	3–4 t/day	30–40 t/day
Cane				
Subsistence		10–15 kg	5–10 k/yr	—
Commercial	12–15 kg	215 kg/yr	225 kg/yr	—
Others	120–150 kg			
Subsistence			5 kg/yr	70–75 kg/yr
Commercial				
Contribution to household economy				
Bamboo	25–30%	25–30%	15–20%	50–60%
Canes	25–30%	30–35%	15–20%	—
Others	10–15%	15–20%	55–70%	30–35%

natural medicines and 85% of the traditional medicines involve the use of plant extracts. The ancient Indian Classical Ayurvedic texts, *Charaka Samhita*, *Susruth Samhita*, and *Ashtanga Hardaya Samhita*, mention of a large number of medicinal plants for curing different ailments. **Table 2** provides the most commonly used medicinal plants in primary health care. Medicinal plants grow in all kinds of lands throughout the world. A large number of these plants are found in tropical forests and temperate dry slopes, especially in dry and moist deciduous forests and mountainous grasslands. The coastal forests of India, the islands of Borneo and Madagascar, the rainforests of the Amazon and Congo basins, and the entire Hindu Kush, Himalayan and Andean mountain ranges are considered to be the treasure trove of the medicinal plants. Although fewer than 30% of medicinal plants are found in the temperate and dry alpine habitats, they include species of high medicinal value. **Figure 1** gives the distribution of medicinal plants by habits in the Indian subcontinent. One-third each of the medicinal plants are trees and shrubs/climbers and the remaining one-third are herbs/grasses (**Figure 2**). Among the rest of the NWFP species, again more than half are trees. As the demand of several medicinal plants has been increasing at a very fast rate, several species have become threatened or endangered. Threats to wild medicinal plant populations have been classified into seven categories: direct human interference (7.8%), fragmentation (5%), loss of habitat (18.7%), overexploitation (17%), harvest (19.8%), trade (24.6%), and others (7.9%). It may be noted that much of habitat loss and overexploitation are also human-induced.

System of Trade of NWFPs

NWFPs have been traded since the dawn of the exchange and barter system of trade in forest-based goods and services. The intercontinental trade in silk and black pepper dates back several centuries. Today, in most of the developing countries, the national Forest Department leases out the right to collect the NWFPs in designated areas every season or cutting cycle to the highest bidder through a system of auctions or through invitation of bids in a tender system. In this system, basically the state collects rent from the users of the NWFPs. In order to ensure

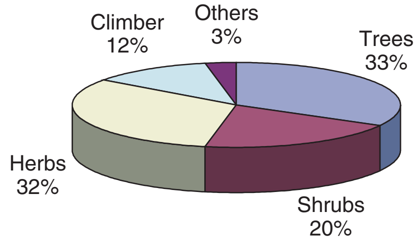


Figure 1 Distribution of medicinal plants by habits, in the Indian subcontinent.

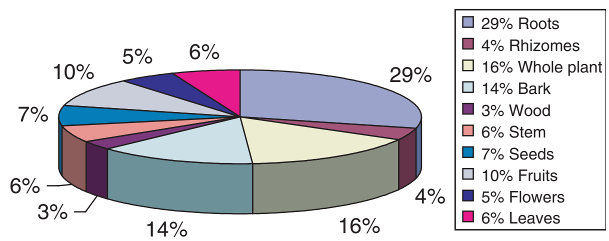


Figure 2 Break down of medicinal plants by their parts utilized, in the Indian subcontinent.

Table 2 Potential NWFP species in the Himalayan Mountains

Local name	*Botanical name*	*Purpose/uses*
Jatamansi	*Nardostachys grandifolora*	Medicine/aromatic oil
Sugandhawal	*Valeriana jatamansi*	Aromatic oils/medicine
Kutki	*Picrorhiza scrophulariflora*	Medicine
Chiraito	*Swertia chiraita*	Medicine/others
Guchichyau	*Morchella conica*	Food/medicine
Timur	*Zanthoxylum armatum*	Food/medicine
Dalchini	*Cinnamomum tamala*	Spice/medicine oil
Hathjadi/Panchaunle	*Dactylorhiza hatagirea*	Food/medicine
Atis	*A. heterophyllum*	Medicine
Pipla	*Piper longum*	Spice/medicine
Padamchal	*Rheum australe*	Medicine
Shikakai	*Acacia rugata*	Medicine
Neem	*Azadirachta indica*	Medicine/biopesticide
Amala	*Phyllanthus emblica*	Food/medicine/vitamin
Barro	*Terminalia bellirica*	Medicine
Haro	*Terminalia chebula*	Medicine
Talispatra	*Taxus wallichinana*	Anti-cancerous medicine
Satawari	*Asparagus racemosus*	Food/medicine

adequate and sustained supplies of NWFPs to local healers and village-based enterprises many countries and states have nationalized the trade in NWFPs. The government fixes minimum prices of select products and marketing is also done by the government on behalf of locals. This system is, however, highly inefficient and is on the decline. In many countries, collection, procurement, and marketing of select items of NWFPs especially medicinal plants, whether nationalized or not, is being undertaken through cooperatives of local peoples called community-based organizations.

Exploitative nature of trade The direction of trade in NWFPs is mostly from developing to developed nations, from rural to urban areas. The significant destinations are countries of the European Union (especially Germany), USA, and Japan. The import policies of these major players are increasingly becoming restrictive and are characterized by preference for standardized, organic, and certified produce. Poor nations who are hoping to conserve biodiversity through improved sales of value-added NWFPs are struggling to find stable markets for their NWFPs. However, there are many factors at their end that create market imperfections, price distortion, and sheer exploitation of collectors and small growers by traders and middlemen. In most of the developing as well as developed countries, there is no systematic national level comprehensive database on production, processing, and marketing-related information on NWFPs. In South Asia, countries like India, Nepal, Bhutan, Sri Lanka, and Pakistan are making some efforts in gathering and disseminating information. A number of sample studies have indicated that approximately 150 NWFPs, including 26 essential oils and a large number of botanicals (ranging between 4000 to 6000), enter national and international markets on a regular basis. The size of the global market for botanicals and homeopathic medicines was more than US$20 billion in 1999 and growing.

Environmental Consequences of NWFP Management

Most of the NWFP species including medicinal plants are used locally and information on supply and demand is often insufficient. It is not known whether the plants are abundant, scarce, or under extinction threat or not; if under cultivation then whether the techniques used are proper or not; what gaps exist in market linkages, and whether the species are endangered or threatened. If they are scarce, what conservation measures would be appropriate is also not clearly known. Undoubtedly, the conservation approach needs considerable policy support, which in most countries is weak. Generally, product samples are not screened for quality, ineffective marketing methods are applied, packaging is of poor standard, and the products have a very limited shelf-life. The situation calls for effective regulatory frameworks both to control infringements of conservation laws and also to provide incentives to local people to use best practices. These are the reasons why NWFPs certification has a big role to play, as it can promote good sourcing, good field collection, good manufacturing, and good laboratory practices in the management of NWFP species.

NWFP Certification

Increasing global awareness of sustainable forest management and liberalized economic development along with the universal acceptance that market forces and consumer preferences dictate the quality of forestry products including NWFPs is necessitating a shift in the management paradigm that ensures the sustainable use of NWFP resources. There is also a need to ensure consumer acceptance and the creation of social and environmental accountability in the trading of natural forest produce. Certification of forests NWFPs is emerging as a widely accepted and effective instrument for possible solutions to these problems.

Evolution of Certification Concepts and Practices

Certification is a process by which the performance of on-the-ground production and handling operations is assessed against a set of predetermined set of standards and guidelines. Certification is a relatively new concept in marketing, which has been initiated to implement the provisions of WTO and other international agreements. In order to encourage sustainable forest management, the majority of timber-exporting countries have, on their own, initiated certification of their forest products. It has since become not only an important tool for conservation of rich forest flora and fauna, but also a promotional label to market forest products from sustainably managed forests. Developing countries, by using this tool wisely, can find their own niche in global NWFP markets and can thereby ensure a greater flow of benefits to the local communities through production of certified forestry products. Certification can create economic incentives to achieve and maintain high standards of forest and NWFP management worldwide.

Rationale for Certification

The certification process commenced with a strong focus on the goal of improving forest management standards, and in particular contributing strongly to reducing the rate of deforestation and degradation of the world's forests, with the initial focus heavily oriented to tropical forests. The aim has been to use market forces to encourage and enable improved management of the forests. Those promoting this new tool hope that buyers, especially in Western countries, will show a preference for certified products, which in turn will either encourage producers to improve their forest management in order to tap this demand, or force them to do so under the threat of losing markets if they do not. The focus has, however, changed considerably as the realities of what it might or might not be able to achieve have become recognized. It has also changed to reflect the interests of many different groups that have become involved with this process one way or another – environmentalists, forest managers, governments, industry, traders, retailers, certifying companies, consultants, investment firms, aid agencies, etc. As a market instrument, certification has both strengths and weaknesses, which vary with the specific circumstances of the producing country, the type of ownership of the NWFP resources, the social and institutional environment and, last but certainly not least, the markets served. A point that should be noted is that sustainable forest management is possible without certification, but the reverse is not.

Objectives of NWFP Certification

The basic objective of certification is to provide proof that all quality control criteria and standard specifications set for a particular production and marketing system have been complied with. The aim is to either increase market share, or at least avoid loss due to boycotts or restrictions such as are increasingly common in some parts of Europe and the USA. The idea is to discourage unethical and unsustainable commercialization of forest products, especially in NWFPs, which is rampant in trade with developing countries. The specifications encompass technical (raw materials, manufacturing process, etc.) as well as legal and financial compliance (environment laws, labor laws, taxes, etc.). The objective of NWFP certification should be to provide solutions towards a responsible trade of NWFPs following the principles of sustainable forest management. Its aim should be to fulfill the following objectives and criteria:

- control and ensure sustainable forest resource management techniques
- have a depth of science with a global scope and be carried out by an active and democratic organization
- manage NWFP resources economically and sustainably
- create a transparent and traceable system that addresses public concerns on environmental values
- manage resources holistically and equitably
- balance the need to extract resources from the environment with maintaining integrity of the ecosystem
- improve livelihood opportunities for local communities, especially women and marginalized groups.

Types of Certification

Basically there are three types of certification that are relevant to NWFPs:

1. Management certification as prescribed by organizations such as the Forest Stewardship Council.
2. Organic certification which complies with standards called as a set of 'Basic Standards for Organic Production and Processing' set by the International Federation of Organic Agriculture Movements (IFOAM). These have to be largely adopted with regional and local specifications throughout the world. IFOAM Basic Standards are also now recognized by the International Standards Organizations (ISO) as universal guidelines.
3. Fair Trade certification which ensures that the trade in NWFPs is done ethically and that proper mechanism of benefits flowing to the collectors and growers is in place.

Potential Advantages of NWFP Certification

Certification has an excellent potential to yield a variety of benefits reflected in the economic, environmental, and social spectrum.

Ecological benefits

- Maintenance and enhancement of forest resource productivity
- Improvement in conservation of biodiversity and its associated benefits such as the hydrological cycle of the area, forest ecosystems, soil fertility due to use of organic substances, and, subsequently, an increase in agricultural production
- Maintenance of ecological functions and integrity of forest ecosystems and their resultant benefits as NWFPs comprise a large and diverse floral vegetation.

Economic benefits

- Increased returns to the producers compared to uncertified forest produce, as certified NWFPs often are high-value low-volume products.

- Greater consumer preferences for certified products provide wider and larger market accessibility and competitive advantages.

Social benefits

- Development and improvement of the company's or producer's public image and workers' satisfaction.
- Improvement in the condition of workers, indigenous communities, and local people through participation of stakeholders in the development of NWFP-based forest/farm management standards.

Other advantages

- Increased market share or at least protection from the loss of the existing market share against the substitutes, such as forest and synthetic products.
- Market premium from selling 'green' products and greater market insurance.
- Long-term supply security because of the sustainability of the resource base, especially forests.
- Establish a basis for comparing different management practices and setting common standards, thus improving the image with a range of interest groups.

Possible disadvantages

- Initial high cost, both financial and managerial, due to initial investment.
- Reduced (short-term) revenue due to reduced output volumes.
- Loss of some control to other groups (e.g., to those developing the certification standards; those less close to the resource).
- Lack of consumer awareness making it hard to achieve an accelerated market penetration.

Components of Certification

Certification of either forest management or organic farms or fairly trading business comprises several activities, each of which has its own rules and guidelines: The main components are:

- certification
- standardization
- accreditation
- logo use (labeling).

Certification Certification is a potential market instrument that can contribute towards improving forest management and at the same time provide an assurance that a product or service is in conformity with certain specified standards. There are two main components of certification: (1) certifying the standards of NWFP-based forest management, and (2) certifying the products from these forests. The first involves an investigation of all the aspects relating to NWFP management including social, economic, and environmental conditions and assessment of how the management of these is being addressed. The process may then include the second component, that of product certification and the associated labeling.

Currently, a wide range of actions is under way concerning certification of NWFPs worldwide. The shift of emphasis from timber and timber products to NWFPs is a recent development. However, attention has mostly included pulp and paper and tea products. First, since a large number of NWFP species collected and transported are straight from the forests, it has been extremely difficult to trace the source of origin of the produce. It is still harder to find out whether or not the harvesting was done in an environmentally sound manner and that the produce available is not responsible for any damage done at the social, economic, or environmental levels. These gaps indicate that there is an urgent need for developing a certification process specifically targeted to the needs of NWFPs. Second, the present trend in management and trade does not lay any emphasis on the process of harvesting of NWFPs either from forested or agricultural lands. The primary forest produce gatherers go to the forests and harvest forest produce without giving much consideration to sustainable harvesting levels and techniques. They have little regard and information regarding the regeneration and health of the forests. Thus, there is a need to check the process of harvesting as well as building capacity of the forest produce collectors and farmers, at the same time as developing the framework for promoting certification of NWFPs including medicinal plants. Recently, several organizations especially the US-based Rainforest Alliance have started certifying NWFPs such as Brazil nuts, maple syrup, and chicle. However, there is considerable variation in what is being certified and some misunderstanding as to what certification of a NWFP actually means. A common assumption is that certification of a NWFP is a guarantee that it has been collected and/or produced in a sustainable way. This may not, in fact, be the case. There are three different certification approaches for NWFPs.

Certificate of origin This is used for a variety of products, including food and medicinal items. It guarantees only that a given product comes from a certain region or area – not necessarily that it has a certain standard of quality. An example is the Denomination of Controlled Origin (DOC) label used for wines, cheeses, and other products by many countries. Certain high-value edible NWFPs, such as truffles and morel mushrooms, are increasingly being certified through such documentation of origin systems.

Product quality standards Organic certification is being used for an increasing number of products, from food to textiles. It certifies that the full production sequence of a product (from the farm up to processing) has respected the criteria set by the competent authority for organic production and chain-of-custody protocols. The quality parameters are set by buyers or their organizations and may differ from market to market.

Social certification This involves documentation of certain social aspects of production, assuring that the labor conditions for production are acceptable, for example, or that the benefits are equitably distributed to those involved in production. Social-based certification schemes have existed for a long time for agricultural and manufacturing products (e.g., for soccer balls certified to have been produced without child labor).

Need for Generic Guidelines for NWFP Certification

As social and cultural issues are important in NWFP certification, there is a need to develop guidelines specifically covering this aspect. The solutions suggested need to be field-tested to determine the relative strengths and weaknesses during the implementation period in the following areas: (1) wider applications, (2) adequacy of plant indicators and verifiers, and (3) suitable species-specific indicators and verifiers. Field tests should be carried out at multiple locations to gather enough data to adequately assess and monitor sustainable NWFP management. In developing specific guidelines, there is a need to interact with a wide range of groups working on sustainable forest management and certification of products including workers engaged in fair trade and organic production and certification as well as the broader community practicing ecologically sustainable forest management. NWFPs do not appear to be adequately covered by any existing certification program, but most programs can make significant contributions to the process by which standards are developed and tested in the field. The work requires wider consultation and multi-stakeholder collaborations at all times. Certifiable NWFP management processes need to ensure long-term ecological viability of NWFP populations. NWFP harvesting and management can have lower impacts on forest ecosystems than timber harvesting, but care must be taken that species are not over-harvested, and appropriate protection must be provided for vulnerable species in residual stands. Assessments of the field conditions need to be completed prior to the commencement of production and collection activities based on the scale, type, and intensity of management operations.

Performance Indicators and Verifiers

NWFP species, in general, are no more or less susceptible to exploitation than trees. However, parameters to determine (1) the impact of harvest intensity and frequency, (2) the differential response to disturbances including invasion, (3) different regeneration and growth characteristics of different species, and (4) the degree to which the plant depends on animals for pollination and dispersal may need to be defined. Geographic and climatic variations, such as elevation, aspects, and moisture, may also influence production and desirable levels of harvest. Therefore there is a need to divide the broad category of NWFPs into classes, which are based upon the product or plant part harvested, in order to define the performance indicators and verifiers. The following classes of NWFPs has been suggested by the Rainforest Alliance:

- exudates
- vegetative structures: apical bud, bark, root, leaves
- reproductive propagules, fruit, seed.

The purpose is to achieve more effective field assessments by providing information necessary to define sustainability. Species-specific performance indicators, verifiers, and other guidance documents will be required for globally traded NWFPs. These indicators and verifiers can be based upon the general principle that the management plan, implementation activities, and monitoring need to ensure sustainable yield, ecological balance, and good soil/watershed health. Training, capacity building, and empowerment of the stakeholders, accompanied by the provision of information dissemination, are highly desirable activities to provide appropriate benefits to the various stakeholders involved in this sector.

Good Collection, Sourcing, and Manufacturing Practices

WHO has recognized the need to protect medicinal plants by promoting their sustainable use through a system of nondestructive harvesting and cultivation. In order to achieve this through the member countries, a series of good practices such as good agricultural and field collection practices (GAFCP) and good manufacturing practices (GMP) has been proposed. The purpose of GAFCP and GMP is to provide guidelines and set standards regarding the general strategies, basic methods, and simple rules of the game for both small- and large-scale field collections, harvesting, and postharvest handling of fresh NWFPs such as medicinal plant materials. Under these good practices rules, collection practices should ensure the long-term survival of wild populations and their associated habitats. Management plans for field collection should 'provide a rationale for setting harvest levels and describe the implementation of harvest practices that are suitable to each medicinal plant species and plant part used (root, leaves, fruits, etc.). Field collection of medicinal plants raises a number of complex environmental, technical, and social issues that vary widely from region to region and species to species. In many parts of the world, collection of medicinal plants is a cultural practice dating back many centuries, and which has been well recognized and documented as having a strong scientific basis as the practices were refined through years of trials and testing. It is acknowledged that these issues (some of which are outlined below) cannot be fully covered by the guidelines for good practices alone.

- The population density and geographic distribution of species must be identified and a harmony created between level of extraction and resource base to be maintained.
- Essential biological, social, and commercial information must be obtained and targets disseminated to the collectors, growers, processors, and local traders.
- Research on the morphology and variability of the plant must be undertaken in order to develop a 'search image' for the species and maintain authenticity of the plants.
- Training of personnel should be conducted on site or prior to departure so as to ensure quality maintenance across the chain of operations.
- Collection practices should ensure the long-term survival of wild populations and their associated habitats based on the biophysical requirement of each ecosystem and species.
- Medicinal plant parts should be collected during the appropriate season or time period to ensure both sustained yield and species survival.
- Mechanical instruments must be clean and kept in proper condition and operated correctly to ensure quality of the processed products.
- During collection, the crew should be trained to detect and remove nonmedicinal parts, foreign matter, and damaged/decomposed medicinal plants from the lot.
- The collected raw medicinal plant materials should not come into direct contact with soil, and in case of roots, the attached soil should be washed off properly.
- After collecting and harvesting, the raw medicinal plant parts may be subjected to appropriate preliminary processing. The collected raw medicinal plant material should be protected from pests, rodents, and other animals and stored in proper sanitary conditions.
- Species that are designated as rare or scarce should not be collected from the wild. Collection of the oldest and youngest members of the population should be avoided to maintain ecological balance.
- Medicinal plants should not be collected in areas where pesticides or other possible contaminants are used or found.
- Only ecologically sound and nondestructive means of collection should be employed and collectors must be trained in such methods.
- Different plant species or plant materials should be packed and transferred in separate containers. Cross-contamination should be avoided at all times.
- Cultivation, collection, and harvesting of medicinal plants must be carried out respecting the laws of the land. The provision of national and international conventions such as the Convention on Biological Diversity (CBD) must be respected.
- Agreements on the return of immediate and/or long-term benefits and compensation for the use of sourced medicinal plant materials must be discussed and agreed to in writing prior to collection or cultivation.
- Medicinal plants that are protected by national and international laws such as Control of International Trade in Endangered Species (CITES) must not be collected illegally, and legal procedures must be followed.
- When medicinal plant materials are used from threatened/endangered/protected medicinal plant species through cultivation, the medical plant materials obtained should be given appropriate documentation to certify the source of origin according to national and international legislation, to demonstrate that no plants were collected from the wild population.

Constraints and Issues in Implementing Good Practices

There are a host of issues and constraints that need to be resolved to successfully implement good practices and certification of good practices, quality products, and fair trade. Among them policy and institutional issues are the most important.

NWFP policy issues Critical review of the existing NWFP policies, legal framework, and institutional environment accompanied by justified revisions considering the above-mentioned issues are the most urgent tasks for achieving sustainable management of NWFP resources in developing countries. The policy and regulatory constraints are mainly of four types.

Regulatory policy issues The regulatory policies are related to harvesting/collection, transport, and processing of NWFPs. Unsustainable harvesting of NWFPs from the wild is a serious issue which is also related to the principles and mechanism of appraising, monitoring, enforcing, and sanctioning rule-breakers in the sustainable management and harvesting of NWFPs. Various types of permits have been designed to implement regulatory policies, although no systematic and detailed inventory of NWFPs has so far been undertaken. The transaction cost of these instruments such as issuing permits, monitoring sustainable harvesting, enforcement of rules, etc. is a serious financial and economic issue. Moreover, the provision of these permits has encouraged rent-seeking behavior among various stakeholders.

Fiscal policy Fiscal policies are related to the imposition of various types of taxes and subsidies that affect various agents involved in the collection, processing, and export of NWFPs. Revenue collection mechanisms such as royalties, and export and other informal taxes are included in this category. Some of the community forestry projects are now providing materials such as seeds and seedlings, and some block grants to promote the cultivation of NWFPs. Major fiscal policy constraints in the development of NWFP subsector are: (1) the system of royalty fixation and collection is irrational and (2) different forms of informal taxes are levied by various organizations which create various forms of disincentives.

Institutional and policy issues The instruments and organizations using the rules and regulations to regulate NWFP trade and use comprise the institutions and organizations relevant to the NWFP policies. The revenue collection mechanisms used by the government are fundamental for the sustainable NWFP management, local addition, and generation of employment for the poor. Coordination and cooperation among the NWFP stakeholders are the major policy issues having impacts on the conservation and sustainable use of the NWFP resources. The major institutional constraints in the development of the NWFP subsector remain the lack of coordination among different stakeholders for policy coordination and project implementation.

Marketing and trade issues Many agents and institutions are involved in the collection, trade processing, and marketing of NWFPs. Marketing information on, and knowledge of, NWFPs is very weak among collectors, traders, and government officials. Similarly, the capital market is imperfect in rural areas. This has led to high interest rates being paid by NWFP collectors in the remote areas of the Himalayas. Input and output markets need to be made more effective and efficient for the growth of NWFPs.

A major issue in the marketing and trade of NWFPs is the lack of a system of transparent and accessible information collection, dissemination, and use by the collectors and growers so as to increase their bargaining power in negotiating the price of the NWFP. The nationalization or ban of collection and sales of many NWFP species has restricted the free and assured supply to the market resulting in a limited number of buyers who operate in monopsonic/monopolistic conditions.

General Opportunities in Implementing Good Management Practices

A large number of MAP species that are currently harvested from the wild are also possible to be regenerated *in situ* and cultivated *ex situ* by training and organizing traditional collectors and farmers. Different types of micro-enterprises, producer companies, and services agencies can be set up to produce quality raw materials, to insure that rural livelihoods are supported. Relevant factors for this type of development include:

- Existence of a high level of market demand, accessibility, and scope for reaching international, regional, national, and local markets with organic and certified products.
- Possibilities for augmenting raw material supplies through domestication, *ex situ* cultivation, and sustainable harvesting (many countries have large areas under forests, shrublands, and rangelands).
- Access to postharvest and processing technology, availability of skilled labor, infrastructure, and capital (e.g., the savings-to-loan ratio is quite low in South Asia and government budgets are not spent properly).

- Potential for decentralized production, processing, and marketing, and thereby downstreaming of the benefits to the local people as the supply chain of the quality MAP products link rural to urban areas.
- Economic viability of raw material collection, cultivation, primary processing, and marketing as the investment is low and returns are assured or have less risk.
- Availability of reliable markets for quality products, e.g., a buy-back guarantee to the collectors within the country and region.
- Possibility for creating MAP-based small and micro enterprises as well as organizing a viable enterprise support service, in the private sector, in order to provide credits, extension services, technical advice, plant management training, and market information on reliable terms and conditions.

Discussion

Sustainable and equitable commercialization of NWFPs holds a great promise in promoting economic growth and social equity in poverty-stricken but biodiversity-rich developing countries. The existing system of extraction and trade is exploitative, inequitable, and unsustainable. A certifiable system backed by implementation of good production, processing, and marketing practices using the commodity chain model is felt to be an answer, that can lead to better market access, product assessment, product development, and certification. Lessons learned from different parts of the world can provide us with in-depth knowledge of the diversity, complexity, and potentials of NWFPs in improving livelihoods and conserving biodiversity.

However, this article further suggests an approach of improved management practices and regulatory frameworks to contain NWFP resource misuse and environmental degradation. Training and capacity-building of local people are necessary prerequisites for implementing good management practices that can lead to income generation and local biodiversity conservation. When communities are provided with technical, financial, managerial, marketing, and training support, they will have better incentives to conserve the NWFP diversity of their forests. As community groups move from being only suppliers of raw materials to being processors and market players of those raw materials, they become aware of the greater values of the resources that can be realized by them, and thereby promote the conservation of those resources to assure a sustainable supply for their commercial operation. This in essence is the foundation for the institutionalization of good practices and of acquiring national and international certification.

See also: **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest; Forest Biodiversity Prospecting; Medicinal and Aromatic Plants: Ethnobotany and Conservation Status; Medicinal Plants and Human Health; Tribal Medicine and Medicinal Plants. **Non-wood Products**: Resins, Latex and Palm Oil; Rubber Trees; Seasonal Greenery. **Silviculture**: Bamboos and their Role in Ecosystem Rehabilitation; Managing for Tropical Non-timber Forest Products.

Further Reading

Chamberlain J, Bush R, and Hammett AL (1998) Non-timber forest products: the OTHER forest products. *Forest Products Journal* 48: 11–19.

FAO (1995a) *Report of the International Expert Consultation on Non-Wood Forest Products, Yogyakarta, Indonesia*. FAO Technical Paper no. 3. Rome: Food and Agriculture Organization.

FAO (1995b) *Non-Wood Forest Products for Rural Income and Sustainable Forestry*. FAO Technical Paper no. 7. Rome: Food and Agriculture Organization.

FSC (1998) *Principles and Criteria for Forest Management*. London: Forest Stewardship Council.

GOI, Planning Commission (2000) *Report of the Task Force on Conservation and Sustainable Use of Medicinal Plants; Government of India*. New Delhi, India: Planning Commission, Yojana Bhawan.

IFOAM (2003) *Small Holder Group Certification: Compilation of Results*. IFOAM Compilation no. 03-03. Tholey-Theley, Germany: International Federation of Organic Agriculture Movements.

IIRR (2000) *Workshop on Shifting Cultivation for Sustainability and Resource Conservation in Asia*, August 14–27 2000, Manila, Philippines.

Karki M (2000a) Commercialization of natural resources for sustainable livelihoods: the case of forest products; In: *Growth, Poverty Alleviation and Sustainable Management in the Mountain Areas of South Asia*. pp. 293–320. Feldafing, Germany: German Foundation for International Development.

Karki M (2000b) Development of biopartnership for sustainable management of medicinal and aromatic plants in South Asia. In: *Proceedings of 21st IUFRO Congress*, August 6–12 2000, Kuala Lumpur, pp. 51–60.

Karki M (2001) Institutional and socioeconomic factors and enabling policies for non-timber forest products-based development in northeast India. In: *Pre-identification Workshop for NTFP-led Development in Northeast India*, February 22–23 2001, Rome, pp. 43–57(1–14).

Karki M (2002) Certification and marketing strategies for sustainable commercialization of medicinal and aromatic plants in Chhattisgarh. In: *Proceedings of National Research Seminar on Herbal Conservation, Cultivation, Marketing and Utilization with special emphasis on Chhattisgarh*, December 13–14 2001, Raipur, India, pp. 15–17.

Karki M (2003) Certification and marketing strategies for sustainable commercialization of medicinal and aromatic plants in South Asia. In: *Proceedings of IUFRO All Division 5 Forest Products Conference*, March 11–15 2003, Rotorua, New Zealand.

Karki M, Tiwari BK, Badoni AK, and Bhattarai NK (2003) Creating livelihoods and enhancing biodiversity-rich production systems based on medicinal and aromatic plants: preliminary lessons from South Asia. In: *Proceedings of 3rd World Congress on Medicinal and Aromatic Plants for Human Welfare*, February 3–7 2003, Chiang Mai, Thailand.

Kinhal GA (2003) Regulatory framework for harvest and trade in wild species of medicinal plants: principles, design and challenges. In: *Proceedings of the Workshop on Certification of Non-Wood Forest Produce Including Medicinal, Aromatic and Dye Plants*, pp. 10–12. 9 April, 2003, Raipur. Raipur, Chattisgarh, India: Chattisgarh Forest Department.

Pierce A and Laird SA (2003) Sustainable botanicals: in search of comprehensive standards for non-timber forest products in the botanicals trade. *International Forestry Review*.

Planning Commission, Government of India (2000) *Report of the Task Force on Conservation and Sustainable Use of Medicinal Plants*. New Delhi: Planning Commission, Government of India.

Rainforest Alliance (1988) *The Conservation Agriculture Program, Certification Criteria, 1998*. New York: Rainforest Alliance.

WHO (2002a) *WHO Traditional Medicine Strategy 2002–2005*. Geneva, Switzerland: World Health Organization.

WHO (2002b) *WHO Guidelines of Good Agricultural and Field Collection Practices (GACP) for Medicinal Plants* (Draft). Geneva, Switzerland: World Health Organization.

Causes of Deforestation and Forest Fragmentation

J Ghazoul and J Evans, Imperial College London, Ascot, UK

Introduction

At the close of the twentieth century there remained an estimated 1700 million ha of tropical forests and 1600 million ha of temperate forests worldwide. These figures represent about 60% of the original forest cover that is estimated to have existed some 8000 years ago. Much of this loss can be directly attributed to human impacts over the last three millennia, with increased clearance in recent centuries, and even more recently in tropical regions. Forests provide important resources and a multitude of natural services and their recent rapid destruction is causing increasing concern due to environmental, social, and economic problems across the globe. However, developing solutions is proving to be a highly complex task due to the variety of causes of deforestation and conflicting stakeholder interests.

Deforestation is the complete or almost complete removal of tree cover and conversion of the land to other uses. Technically, deforestation may be defined as the semipermanent depletion of tree crown cover to less than 10%. In this respect a distinction needs to be made between deforestation and forest degradation, which is the significant damage to forest ecosystems but without the total elimination of forest cover.

This article begins by describing current deforestation trends. The present causes of deforestation in recent years are discussed, followed by the consequences of deforestation for a variety of environmental parameters. Solutions to the deforestation problem are presented, and potential future trends are described with a brief discussion of the impact of projected climate change.

Historical Deforestation and Land Clearance

At the advent of agriculture some 8000 years ago forests are thought to have covered approximately 40% of the world's land area, or about 6000 million ha. Up to 1500 AD the spread of agriculture across the globe resulted in the clearance of many forests, particularly those on the most accessible and fertile land. However, in the last 200 years deforestation rates have increased greatly. Between 1850 and 1980, 15% of the world's forests and woodlands were cleared. The world forest area has now shrunk to 3500 million ha as a consequence of human exploitation, most of which occurred in the latter half of the twentieth century.

Contemporary Deforestation

Deforestation and land clearance in the twentieth century increased greatly, with the highest rates of clearance occurring since 1960. Most current deforestation occurs in the tropical regions, while in temperate countries there has been a net increase of forest cover by 0.1% due to reforestation and regeneration policies. In Canada the area of land under tree cover increased by 1.4 million hectares to 417.6 million ha in the late 1980s. The Food and Agriculture Organization (FAO) has estimated annual rates of forest clearance in developing countries at 15.5 million ha for the period 1980–1990, and 12.3 million ha for 1990–2000. Thus, the total area of forest cleared during this 20-year period is approximately 280 million ha.

The causes of deforestation vary among regions. In Africa FAO reports that the major direct cause of deforestation is clearance by farmers driven by increasing population pressures. In Latin America settlement and infrastructure projects in forested areas result in clearance of land for cattle ranching and permanent agriculture, often combined with financial incentives such as subsidies and favorable tax policies. In Asia intensive timber harvesting and shifting cultivation as well as the expansion of large-scale agricultural projects and plantation crops such as oil palm and rubber and, to a lesser extent, transmigration projects, all contribute to deforestation. Forest land is often not suitable for sustainable agricultural development and, as soils become exhausted, new areas of forest have to be cleared. For example, 80% of the Amazon basin is ill-suited to sedentary farming. Desertification through unsustainable agricultural development has contributed to much deforestation in drier regions of Africa and Asia.

Most deforestation is concentrated in relatively few tropical countries. Fifty percent of global deforestation occurs in 10 developing countries (**Table 1**). Brazil is typical of tropical countries in that deforestation rates were low until the 1970s. Since then extensive spread of agriculture and ranching, encouraged by government subsidies, and clearance by landless farmers, has resulted in very rapid deforestation. Large-scale development and industrial projects such as mining and hydroelectric plants have contributed to these high deforestation rates in the tropics. Thus deforestation is largely a tropical issue (**Table 2**). As a large proportion of the world's biodiversity is found within tropical forests, tropical deforestation impacts also have very great relevance to global biodiversity.

In temperate countries there is no overall deforestation in terms of net area but a small increase in forest cover owing to policies of afforestation. However, this statement disguises a steady and continuing transition from natural forest formations to managed and plantation forests. In this sense there is some clearance of natural forest in temperate regions with the consequent loss of biodiversity. This trend is likely to decrease as conservation priorities assert themselves, except in eastern Europe and Russia where the importance of forest resources as an accessible and tradeable commodity takes priority. Nevertheless, in Europe as a whole there is very little natural forest undisturbed by human intervention, the forest of Bialowiezca in Poland being one of the few extensive examples of reasonably extant forest not dissimilar to the ancient 'wild wood.'

Causes of Deforestation

There is no single cause of deforestation but rather it is the result of the interaction of social, economic, political, and cultural forces with the environment. Several underlying socioeconomic causes create conditions that favor forest clearance by readily identifiable direct causes.

Underlying Causes of Deforestation

The underlying causes of deforestation are the factors that give rise to conditions in which forest clearance becomes a rational or necessary behavior. They may be local or national socioeconomic or political forces, or they may be external global forces such as the state of the global market economy. They are generally beyond the control of an individual but strongly influence the decisions individuals make regarding the management and use of forests and forest resources.

Table 1 'Top 10' deforesting countries in terms of annual rate of forest loss (1995)

Country	*Ranking*	*Annual loss (hectares)*
Brazil	1	2 550 000
Indonesia	2	1 080 000
Congo	3	740 000
Bolivia	4	580 000
Mexico	5	510 000
Venezuela	6	500 000
Malaysia	7	400 000
Myanmar	8	390 000
Sudan	9	350 000
Thailand	10	330 000

Reproduced with permission from FAO (1999) *State of the World's Forests 1999*. Rome, Italy: Food and Agriculture Organization of the United Nations.

Table 2 The rate of annual forest loss (1995) expressed as a percentage of forest area in 10 important deforesting countries and regions

Country	*Ranking*	*Annual loss (%)*
Philippines	1	– 3.5
Sierra Leone	2	– 3.0
Pakistan	3	– 2.9
Thailand	4	– 2.6
Paraguay	5	– 2.6
Central America	6	– 2.1
Caribbean Islands	7	– 1.7
Cambodia	8	– 1.6
Ecuador	9	– 1.6
Myanmar	10	– 1.6

Reproduced with permission from FAO (1999) *State of the World's Forests 1999*. Rome, Italy: Food and Agriculture Organization of the United Nations.

Population growth and poverty Population growth is one of the most publicized but misleading underlying factors for tropical deforestation. Increasing populations place pressure on forests and the resources they supply. The rural poor have very few economic options and are often forced to seek short-term solutions to their economic problems. These solutions include clearing forested land to grow subsistence crops. Opportunities for improving livelihoods by other means are limited due to low political priority, the lack of rural capital, low capacity of subsistence farming to generate income, and the lack of infrastructure and education.

Development policies and tax incentives Debt repayments constitute a large proportion of the national budget of many tropical countries, and structural adjustment programs introduced as a result often favor the maximization of foreign exchange through direct and unsustainable exploitation of forest capital, and by conversion of forests to agriculture for export crops. Large-scale extensive agricultural development, frequently at the expense of small farmers as well as forest cover, is further encouraged through the provision of state subsidies for agriculture and livestock expansion, reduction in income and corporate taxes, and tax breaks on imports of equipment for new industries. Expansion of agricultural crops for export or to satisfy national demands destroys forest directly, but it also causes the displacement of subsistence farmers who are forced to relocate and clear new and often marginal lands elsewhere.

The privatization of public resources, advocated by the World Bank and some bilateral donor agencies, favors management strategies that maximize the short-term economic gain for the new owners, while nonmonetary forest services, such as soil conservation and watershed protection, are not valued highly in a market-driven environment. Government incentives and subsidies have allowed some otherwise uneconomical industries to prosper at the expense of forest cover, while development projects often fail to account fully for the value of forest capital lost.

A failure to understand the real value of forests' goods and services results in the establishment of poor policies. The institutional weakness of the national forest department or corruption within the government can lead to policy decisions that favor private interests at the expense of the benefits to society as a whole. In recent years there has been an improvement in the reformulation of forest policies of several tropical countries. Subsidies that promote cattle ranching have been withdrawn in Brazil, while Costa Rica is now beginning to account for the destruction of forest capital in its national economic accounts.

Tenurial policies Much agricultural land in the tropics is owned by large landowners or corporations and improved agricultural production is obtained using chemical fertilizers and pesticides which, together with mechanization of labor, is most efficient on large-scale agricultural systems. This favors large farmers who have the capital to invest in such innovations and the land area to benefit from economies of scale. Small farmers who may not have legal title to their land are frequently displaced or forced to sell their land through mounting debts. These farmers often move to the forest frontier to clear a new plot of land, and it is usually politically easier for governments to ignore deforestation than to deal with the difficult issues of land redistribution or job creation.

Legal ownership of land has a great effect on the attitude people have to the land. Without legal land title there is little incentive to invest in increasing land productivity. It becomes economically logical to pursue short-term gain and to move on to clear new forest land once productivity declines. As most tropical forest lands are owned by the state, clearance is often illegal and governments are unwilling to grant legal title to small farmers for land acquired in this way. Lack of land ownership excludes farmers from obtaining credit to purchase seed or fertilizers and pesticides and discourages any long-term investment. In many Pacific-rim countries customary land ownership prevails. Precise boundaries are frequently unsurveyed and local communities and groups know only from tradition what is their land. Wholesale allocation of logging rights can be conveyed either by the local people themselves with relatively little outside control or, conversely, imposed from outside by governments that fail to account for local people's interests. In either case the land tenure system is a weak instrument in preventing unplanned deforestation and land clearance.

Market demands As populations grow and become more affluent the demand for forest products rises, particularly for industrial timber and pulpwood for making paper. However, while it can be readily demonstrated that some countries have significant forest product exports (**Table 3**), the extent to which international markets contribute to deforestation varies greatly from country to country. In the top 10 deforesting countries it is the national demand for forest products that accounts for most industrial deforestation. Furthermore, there is not a strong link

Table 3 The importance of exports to the forest-based economies of the top 10 deforesting countries in 1996

Country	*Timber products*[a]			*Paper and paperboard*[b]			*Charcoal and fuelwood*			*Total*
	Production	*Export*	*%*	*Production*	*Export*	*%*	*Production*	*Export*	*%*	*(%)*
Brazil	107 360	5019	4.7	12 110	3396	28.0	135 652	63	0.05	3.3
Indonesia	64 711	9414	14.5	7021	2342	33.4	153 540	1039	0.7	5.7
Congo, DR	3554	227	6.4	3	0	0	45 142	0	0	0.5
Bolivia	1070	150	14.0	2	0	0	1419	0	0	6.0
Mexico	9063	557	6.1	3558	328	9.2	16 731	136	0.8	3.5
Venezuela	1790	52	2.9	900	50	5.6	918	0	0	2.8
Malaysia	50 923	16 143	31.7	777	41	5.3	10 035	186	1.9	26.5
Myanmar	3399	689	20.3	24	0	0	20 612	53	0.3	3.1
Sudan	2321	0	0	3	0	0	14 600	0	0	0
Thailand	3636	614	16.9	2744	335	12.2	36 894	53	0.1	2.3

All values in thousand m^3.
[a] Includes industrial roundwood, sawnwood, and wood-based panels.
[b] Includes pulp for paper.
Reproduced with permission from FAO (1999) *State of the World's Forests 1999*. Rome, Italy: Food and Agriculture Organization of the United Nations.

between rising international demand for forest products generally and deforestation. This is, first, because almost all pulp and paper comes from temperate forests or specially established tropical plantations, since paper manufactured from mixed tropical forest is generally expensive and has poor quality owing to the lack of wood uniformity. Second, much of the world's industrial-grade timber is softwood, i.e., coniferous, and tropical forests are overwhelmingly broad-leaved hardwoods. Supplies of industrial lumber in tropical countries increasingly come from tropical conifer plantations, notably of pines and cypress. Clearance of forest for agricultural production also appears to be driven by growing national demand for agricultural crops (over and above those for crops). All of the important deforesting countries listed in **Table 1**, except for Thailand, remain net importers of rice or maize and for many of these countries self-sufficiency in agricultural production has been a primary development goal that has led to policies that encourage conversion of forests to fields. Over the past decade, for example, the domestic demand for palm oil in Indonesia has led to the widespread establishment of plantations even though palm oil exports have remained at between 6% and 8% of the total production. Similarly, rising production of beef in Central and South America to feed a growing domestic market has resulted in extensive deforestation by ranchers, farmers, and land speculators.

Deforestation due to agricultural and livestock production is therefore largely due to the growth in the domestic markets and only partially attributable to markets in the developed world. Although the importance of export markets should not be underestimated, national market forces appear to be more important than international trade in determining the rates and extent of tropical deforestation. Consequently, it is likely that international trade offers only limited scope for reducing deforestation rates in most tropical countries.

Undervaluation of forests and forest products Where logging has preceded wholesale land clearance, it is often because the value placed on the timber is no more than the cost of extraction and marketing. The value does not reflect cost of replacement nor cost of growing beyond what is often a nominal payment of royalty to the owner. If timber were valued to reflect its true cost of replacement, then growing trees to produce timber would become economically worthwhile and hence potentially a sustainable option. While it is not worthwhile, deforestation, especially in the tropics, is likely to continue because clearance and conversion are perceived as more profitable. However, undervaluation has a further dimension. The non-timber benefits and services trees and forests provide are often far more important than their timber products. Environmental benefits of soil protection, shelter, microclimate amelioration, and contribution to regional and global hydrological and carbon cycles all confer great benefits which are rarely quantified and hardly ever incorporated in economic assessments. Only when massive downstream flooding is traced back to wanton deforestation in the catchment are such connections made.

A major underlying cause of deforestation is this widespread failure to value sufficiently both forest products and the many environmental benefits forests bring. Regrettably, it is largely because simple and widely accepted approaches to such valuations in economic terms do not exist. For example, stumpage, the charges that governments demand from loggers for state-owned timber, often undervalues the resource, which encourages waste and makes other land uses more economically attractive.

Weak government institutions While almost all countries have explicit forest laws and policies designed to conserve forest, two features of forest conditions in tropical countries exacerbate the risk of deforestation. First, extensive forests are likely to be remote from towns and cities and hence far from the rule of law. It is easy for illegal logging and clearance to continue unseen and unchecked. Second, forest services are frequently the 'Cinderella' organization of government, being viewed as inferior to agriculture and even wildlife and tourism. Few resources are attracted and poorly paid staff often have difficulty both in ensuring that sustainable management practices are implemented and in imposing their authority on perhaps large private-sector interests. Quite apart from the risk of corruption that these circumstances afford, many staff, once trained, simply dislike the remoteness of forest management and supervision and prefer the white-collar work of the city office.

Direct Causes of Deforestation

Shifting cultivation The contribution of small-scale shifting agriculture to tropical deforestation remains unresolved due to the widely variable agricultural practices that are encompassed by this term. Some types of small-scale agriculture undoubtedly cause deforestation, but the inherent stability and long-term viability of many shifting cultivation systems are unlikely to result in long-term forest clearance. The least destructive form of shifting cultivation is where land cultivated for 2–3 years is then left for a long fallow period. This long fallow shifting cultivation only occurs under conditions of very low human population density.

Expanding populations, land scarcity, and government policies have also created shifted cultivators who now form the typical slash-and-burn farmers of recent decades. Unlike the traditional farmers who have practiced shifting cultivation for decades, these shifted agriculturists have been forced by circumstances or government policy to cultivate habitats that are unfamiliar to them. Government resettlement and transmigration schemes such as those in Indonesia attract migrants for whom forest cultivation is an unfamiliar means of generating a livelihood and income. Similarly, in the Amazon, migrant cultivators are attracted to the forest frontier where they clear and cultivate land for a few years. This land quickly becomes exhausted due to unsuitable soils or farming techniques and the land is sold to cattle ranchers while the 'farmers' move on to clear more land.

Commercial agriculture Large-scale commercial agriculture is most frequently practiced by large corporations or state enterprises. These large operations can dispossess local landowners and farmers of the best and most fertile agricultural land, indirectly leading to deforestation in areas to which the farmers relocate. The establishment of oil palm plantations in valleys of Honduras in the 1970s displaced thousands of farmers who were forced to clear forests from steep slopes to establish new farms.

Commercial agriculture often leads to direct conversion of large tracts of forest to plantation estates and rice fields. This has been particularly prevalent in Indonesia and other regions of Southeast Asia where oil palm, coconut, or rubber plantations have been established on cleared forest land. In Indonesia oil palm plantations have increased from about 4 million ha in 1980 to 5.8 million ha in 1995. Land clearance for agricultural development is often subsidized by governments and, because the owners of the agribusiness companies are politically well appointed, there is little interest in forest protection. Areas for conversion are frequently burnt as this is the least extensive method of clearance, and natural events such as the 1997–1998 El Niño are used as an opportunity to do so.

Cattle ranching and livestock grazing Intensive clearing of forest land in South and Central America has arisen from expansion of cattle ranching which was economically attractive due to low risk, little labor, well-established markets, and the availability of government subsidies. Cattle ranching expanded initially in response to the opening of large markets in North America, but has been sustained by the growing domestic markets for beef. Ranchers cleared forest land either by purchasing it directly and employing labor, or by purchasing land from slash-and-burn farmers and converted this land to grasslands. The shifting cultivators would move deeper into the forest to repeat the cycle. The area of pasture in Central America is estimated to have increased from 3.9 million ha in 1955 to 13.4 million ha in 1995 and has been largely at the expense of the area's tropical forests. Thus, deforestation in Latin America due to ranching is also associated with slash-and-burn agriculture and land speculation.

Livestock grazing causes deforestation in Africa wherever herds exceed the carrying capacity of the area. Such pressure is acute in the drier tropics such as the Sahel region of Africa and in the Middle East where large flocks of sheep and goats are maintained.

The history of deforestation around the Mediterranean is linked to grazing regimes, especially by goats, but past simplistic assumptions have given way to the recognition that climatic, sociological, and agrarian factors have also contributed to forest clearance.

Infrastructural development Through the 1970s and early 1980s, development of the Amazon, which is illustrative of similar strategies throughout the tropics, was actively encouraged by the Brazilian government through the building of roads, tax incentives and subsidies, massive resettlement, and large-scale development programs. The Trans-Amazonian highway opened up millions of square kilometers of inaccessible forest to colonization and allowed further expansion of the cattle industry. Such roads improve access to poorly developed areas and therefore tend to increase the adjacent land value for nonforest uses and encourage land speculation and deforestation. Recent slowing of deforestation is due to Brazil's economic recession and has been aided by changes in government policies on tax incentives and subsidies, and increased enforcement of environmental regulations. Logging roads in Asia also facilitate deforestation by allowing access to farmers and illegal loggers who follow and deforest an area that is otherwise merely degraded through selective logging.

Plantations Much forest has been cleared for commercial plantation crops such as rubber, oil palm, and the beverage crops of cocoa, coffee, and tea. Huge areas of dipterocarp forest in peninsular Malaysia have been converted to oil palm or rubber plantations and, while such perennial woody crops offer some soil protection, the loss in biodiversity is enormous. Indeed, it can be argued that the great bulk of the world's tropical plantation crops, about 26.5 million ha, are on former forest land.

A key principle of good forest stewardship is that forest plantations for timber production are only located on already cut-over, abandoned, or waste land and in this way can actually help deflect pressure away from natural forest. However, the subject is not quite as simple since many forests have enjoyed enrichment by planting or have arisen through tree-planting operations, such as many 'natural' forests in France, Germany, and elsewhere.

Fuelwood collection and charcoal production Fuelwood accounts for over 50% of global wood use and for some 80% of all wood use in developing countries. Dependence on fuelwood is expected to decrease gradually with the introduction of electricity, kerosene, and propane, but heavy dependence on fuelwood by the rural poor is expected to continue well into the twenty-first century. Fuelwood collection as an agent of deforestation is particularly marked around urban centers and villages where continuous collection results in the gradual degradation and eventual deforestation of accessible areas. This is critical in the dry tropics along with domestic use of wood for other uses such as construction and fencing material.

Logging The most optimistic independent estimates of the amount of sustainably managed productive forest in the tropics are no more than 2% of the productive forest area. Most tropical logging consists of short-term exploitation of timber products with little concern for the future potential of the forest. This is largely due to insecurity of tenure and short concession periods. Although the intensity of logging in the tropics is usually low, removal of only 10% of the timber trees can result in damage to 55% or more of the remaining trees. Nevertheless, logging operations in the tropics usually result in degradation of the forest rather than its complete elimination. Deforestation does occur along logging roads, where forest is cleared for several meters either side, allowing the sun to dry the road surface. Poorly designed roads can result in severe erosion and landslides as well as facilitating movement into the area by illegal loggers and slash-and-burn cultivators, who often cause much greater damage than the initial logging operations. Logging continues to be one of the most important causes of forest degradation but not deforestation, although intensive logging in Southeast Asia has resulted in the conversion of thousands of hectares of forest to alang-alang (*Imperata cylindrica*) grassland that excludes almost all other vegetation.

Following industrial extraction of timber farmers, agribusinesses, ranchers, fuelwood collectors, and illegal loggers move in along logging roads to clear the land for other uses. Management plans and government policies oblige industrial foresters to prevent encroachment of this sort, but these rules are poorly enforced due to lack of will or staff.

The length of concessions is very often short, sometimes less than 10 years, and very rarely more than the rotation of the crop. In the absence of a long-term commitment the logging company has little incentive to invest in long-term forest management. Concessions are also granted for timber only with little regard for the other resources provided by the forest and the impact of the logging on local people.

Fire Serious losses in forest cover in Southeast Asia and South America have been reported as a result of forest fires in 1997 and 1998. The causes of these fires are new large-scale commercial agricultural projects (including plantations) and shifting cultivation. The fires were exacerbated by the dry coarse woody debris left after logging operations and the very dry climatic conditions caused by the El Niño phenomenon. The area of forest consumed by fires in 1997–1998 has not been accurately documented but estimates vary from 170 000 ha to over 2 million ha. Extensive fires in tropical moist forests have been previously associated with El Niño phenomenon, as in 1982, but the underlying causes are clearance of forest to establish plantations of oil palm, pulp wood, and rice and, in South America, cattle pastures and shifting cultivation.

Alternatives for Sustainable Development

Protection and Management of the Remaining Forests

Protected-area systems Protected-area systems are needed to conserve habitat and biodiversity from encroachment and poaching. The majority of countries fall well short of placing 12% of their land surface within a protected area system as endorsed by the United Nations Conference on the Environment and Development (UNCED). To be effective, protected areas need to be sufficiently large to conserve all the biodiversity they contain and to include a broad range of naturally occurring forest types and all stages of natural succession. To be successful, protected-area systems need to be supported by adequate funding and legislation and managed by strong institutional departments. However, forest protection must be developed with the cooperation of the local communities that use forest resources, as alienation of them has led to failure or inadequate protection.

Joint forest management New approaches to managing forest resources involve partnerships between local communities and local or national governments. These partnerships provide for sensitive management that acknowledges the needs of all stakeholders by providing a wide variety of benefits in a sustainable manner. Forest management decisions are made at a local level and are informed by state-supported science and developmental technologies. Providing local stakeholders with access to and benefits from forest resources and empowering them with the management of these resources encourages sustainable development and investment in forests.

Sustainable timber harvest procedures Timber harvest practices that minimize damage to forests are well known but rarely implemented due to the perceived high cost. Indeed, over a short time scale, reduced impact logging procedures are more costly, but over the longer term they are cheaper due to increased efficiency of extraction (by eliminating extraction of low-value trees and damage to high-value timber) and reduced damage to the remaining forest stand. National standards for logging operations, where they exist, are often flouted and enforcement is weak.

To encourage sustainable timber production, most timber-producing countries have adopted criteria and indicator systems for sustainable forest management. These systems provide tools for assessing the state of forests which can be used to promote and inform sustainable forest management. Their development has been hampered by the complexities of definition of sustainable forest management and how to interpret the information generated. However, intergovernmental processes and market-led certification schemes seek to encourage wise and sustainable forest management.

Socioeconomic and Agricultural Development

Improving the productivity of subsistence agriculture and ranching Greater productivity from and improved use of existing agricultural land, through intensification of agroforestry, will lessen the pressure for clearance of new forested lands and will promote private investment into currently occupied land which in turn encourages sustainable use. State-supported investment in deforested marginal lands, fair credit schemes, and educational development are all needed to provide extension services to improve the efficiency of land use.

An estimated 200 million ha of degraded lands exist in upland watersheds of tropical countries as a result of deforestation. Restoration of these lands through tree planting or for agricultural production will further alleviate the pressure on forest lands from agricultural expansion. Multiple-use species provide both benefits directly and additionally serve to renew a watershed's ability to regulate groundwater and reduce soil erosion (**Table 4**).

Tree plantations Tree and forest plantations are not substitutes for natural forest but, appropriately sited, they can alleviate deforestation pressures. Plantations on already degraded land can be an excellent source of industrial-grade timber, pulpwood for paper-making, and fuel–solid firewood and charcoal. Thus they provide an alternative source of such products. In the tropics and subtropics there are estimated to be about 70 million ha of industrial plantations, of which probably 55 million ha are reasonably well stocked. This area is slowly increasing, is often more productive than temperate

Table 4 Soil erosion rates

	Rate (t ha^{-1} $year^{-1}$)
Undisturbed natural forest	Negligible
Cut-over forest with litter and organic matter intact	1–5
Cut-over forest with litter and organic matter removed	30–100
Forest plantations with litter and undergrowth	0.5–3
Forest plantations with no undergrowth and litter removed	up to 100
Undisturbed or lightly grazed grassland	2–10
Cultivated arable land (depending on slope, terracing, and soil type)	20–400

Reproduced with permission from Evans J (1992) *Plantation Forestry in the Tropics*. Oxford, UK: Oxford University Press.

plantations, and represents a major new wood resource. Taking the world as a whole, nearly half of all industrial timber is likely to be sourced from plantations by about 2020.

Profitable plantations risk undermining the perceived value of natural forest and may accelerate conversion of these to plantations. If the primary cause behind deforestation is the conversion of land for agricultural development it is unlikely that plantations will reduce deforestation. However, tree plantations do offer an opportunity to reduce the pressure on natural forests if the latter are exploited primarily for wood products.

Policy and Institutional Reform

Forest valuation and the reformation of government policies and institutions National policies need to promote the necessary framework that encourages sustainable forest use before community-level projects can have an effect. However, undervaluation of forests by governments and people undermines forestry institutions nationally and internationally, making it difficult to enact the necessary changes. The lack of forest-user taxes and low stumpage fees discourage sustainable management of forests by undervaluing the resource. Subsidies to competing land uses should be removed and effective natural resource accounting should be established to reflect true forest values. Opportunity costs and externalities associated with conversion need to be factored into assessments of forest values. Thus, the value of the ecosystem services as well as alternative income-generating businesses, such as tourism, should be considered. Furthermore, forest land value can be greatly increased by more efficient use of a greater range of forest resources, and by improved marketing of them. The absence of clear policy guidelines and trends in forests and forest resources lead to a confusion of strategies among national and international organizations. Strengthening of these institutions and developing mutually agreed frameworks that provide for more effective policy development and monitoring is needed if deforestation is to be arrested.

Provide education Educating the public as well as political and economic decision-makers about environmental and socioeconomic issues related to forests is crucial if policies promoting forest preservation through sustainable use are to be heeded. Education must be based on thorough and demonstrable arguments about the economic, social, environmental, and biological benefits of using forests wisely, and the costs associated with deforestation.

Conclusion

Deforestation is largely a tropical issue. The quality of data on deforestation rates has been improving but remains poor and a source of contention and debate. The causes of deforestation are complex and multifaceted, though socioeconomic factors and trade are foremost. Deforestation impacts on the environment through loss of biodiversity and disruption of ecosystem processes, as well as the economy by affecting ecosystem services and inefficient squandering of resources. Perhaps the most tragic consequence is the loss of traditional beliefs and customs and the displacement of forest-dependent communities. Solving the problem of deforestation requires a suite of strategies that include establishing an effective and global protected area network to preserve forest biodiversity, and the genuine implementation of good practice guidelines. Ultimately, a reformulation of policy and a change in the attitudes of decision-makers are needed to ensure that forests are correctly valued economically, socially, and biologically.

Acknowledgement

This contribution is adapted with permission from Ghazoul J and Evans J (2001) Deforestation and land clearing. In: *The Encyclopedia of Biodiversity*, Levin SA (ed.) Academic Press.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation. **Environment**: Environmental Impacts. **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Landscape and Planning**: Perceptions of Nature by Indigenous Communities. **Plantation Silviculture**: Forest Plantations. **Silviculture**: Managing for Tropical Non-timber Forest Products. **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

Brown K and Pearce D (1994) *The Causes of Tropical Deforestation*. Vancouver, Canada: University of British Columbia Press.

Brown D and Schreckenberg K (1998) *Shifting Cultivators as Agents of Deforestation: Assessing the Evidence*. Natural Resources Perspective Number no. 29. London: Overseas Development Institute.

Bryant D, Nielsen D, and Tangley L (1997) *The Last Frontier Forests: Ecosystems and Economies on the Edge*. Washington, DC: World Resources Institute.

Byron N and Shepherd G (1998) *Indonesia and the 1997–98 El Niño: Fire Problems and Long Term Solutions*. Natural Resource Perspective Number 28. London: Overseas Development Institute.

Downton MW (1995) Measuring tropical deforestation: development of the methods. *Environmental Conservation* 22: 229–240.

Evans J (1992) *Plantation Forestry in the Tropics*. Oxford, UK: Oxford University Press.

FAO (2001) *State of the World's Forests 1999*. Rome: Food and Agriculture Organization of the United Nations.

Fisher BS and de Fegely R (1999) *A Study on the Global Outlook for Plantations*. Technical Paper for the Intergovernmental Forum on Forests. Canberra, Australia: Commonwealth of Australia.

Myers N (1989) *Deforestation Rates in Tropical Forests and their Climatic Implications*. London: Friends of the Earth.

Rowe R, Sharma NP, and Browder J (1992) Deforestation: problems, causes and concerns. In: Sharma NP (ed.) *Managing the World's Forests: Looking for Balance between Conservation and Development*, pp. 33–45. Iowa: Kendall/Hunt.

WCFSD (1999) *Our Forests, Our Future*. World Commission on Forests and Sustainable Development. Cambridge, UK: Cambridge University Press.

T

TEMPERATE AND MEDITERRANEAN FORESTS

Contents

Northern Coniferous Forests

C D B Hawkins, University of Northern British Columbia, Prince George, BC, Canada

Introduction

The northern coniferous forest or temperate needleleaf forest is restricted, essentially, to western North America. It also occurs in small elevational bands on mountain ranges of Europe, Asia, eastern North America, Mexico, Mesoamerica, and the coastal plains of the southeastern United States. The northern coniferous forest is conventionally a synonym for the boreal forest. Depending on the authority, the northern coniferous forest can be considered a southern offshoot of the boreal forest on the Rocky, Coast, Cascade, Appalachian, Alps, Carpathians, Urals, and Himalaya mountain ranges, as well as mountains in northern China, Korea, and Japan, or it can be restricted to montane coniferous forest. Pinaceae (pines, spruces, firs, and larches) are the major northern coniferous forest family and account for its economic importance. There are also mixed coniferous–deciduous stands in the western North American northern coniferous forest with trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Compared to the boreal forest, the northern coniferous forest is warmer and more productive: mature trees $\geq$25 m compared to $\leq$23 m. This article focuses on western North America because compared to other areas of the world, there are still large areas of natural northern coniferous forest.

Generally mountains become wetter, colder, and windier with increasing elevation. This results in distinct zones or bands of vegetation. A given vegetation zone tends to be found at higher elevations on drier sites compared to wetter, on south aspects compared to north, and at southern latitudes compared to northern. Low to mid elevation northern coniferous forests are rich in species diversity while the upper northern coniferous forest is less complex. The upper northern coniferous forest and lower subalpine have similar species composition and they are transitional to one another.

Distribution

Western North America

The northern coniferous forest includes the central plateaux of British Columbia and isolated Intermountain, mountain ranges between the Cascade–Sierra ranges as well as the Rocky Mountains. In the Rocky Mountains, it extends from the southern Yukon to south central New Mexico. Some consider it to include the Madrean (Mexican) section of the Rocky Mountains and the Coastal, Cascade, and Sierra Nevada ranges while others consider the Madrean and Sierra Nevada to be part of the southern coniferous forest. The Sierra Nevada is excluded from the northern coniferous forest as: (1) true coniferous forests are relatively rare in the northern hemisphere south of 40° N latitude; and (2) giant sequoias (*Sequoiadendron giganteum*) are present in the Sierra Nevada, which some authors consider to be members of the subtropical mountain system.

Rocky Mountains The Rocky Mountain (19–65° N latitude) northern coniferous forest has a subalpine forest above, characterized by subalpine fir (*Abies lasiocarpa*), white or Engelmann spruce (*Picea glauca*, *P. engelmannii*), and depending on latitude other conifer species. Species diversity increases moving south from the boreal forest.

In the Boreal Rocky Mountains (53–65° N latitude), the northern coniferous forest is above the boreal forest dominated by aspen, balsam fir (*Abies balsamea*), white spruce, and jackpine (*Pinus banksiana*), with black spruce (*Picea mariana*) and tamarack (*Larix laricina*) in wetter areas (**Figure 1**). The northern coniferous forest is not complex having both boreal and subalpine species plus lodgepole pine (*Pinus contorta* var. *latifolia*). White spruce dominates at low and mid elevations. Common broadleaf trees are birch hybrids (*Betula* spp.), aspen, and balsam poplar (*Populus balsamifera*). The northern limit is marked by the absence of lodgepole pine and subalpine fir. The southern boundary is the transition between the Peace and Fraser River drainages. This roughly corresponds to Engelmann spruce and Douglas-fir's (*Pseudotsuga menziesii* var. *glauca*) northern distribution limit.

The Central Rocky Mountain (45–53° N latitude) northern coniferous forest is a rich productive forest rising to 1800 m in elevation above Rocky Mountain (western) juniper–ponderosa pine (*Juniperus scopulorum–Pinus ponderosa*) woodlands from 800 to 1500 m. It is dominated by cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), and Douglas-fir on the western slopes. Western white pine (*P. monticola*) and western larch (*Larix occidentalis*) are common on mesic and drier sites as are white–Engelmann (interior) spruce hybrids on wetter ecosystems (**Figure 2**). This is the most productive complex of the northern coniferous forest with site indices at 100 years (SI_{100}) of 40 m for spruce and 38 m for white pine and Douglas-fir. The eastern slopes are less diverse and not as productive. Aspen and paper birch are the dominant broadleaf species and are usually found in seral mixed species stands. The subalpine forest, in addition to *Abies* and *Picea*, has whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), mountain hemlock (*Tsuga mertensiana*), and subalpine larch (*Larix lyallii*). The Central sector is defined by the distribution of whitebark pine.

Ponderosa pine parklands in the Southern Rocky Mountains (33–45° N latitude) are below two northern coniferous forest zones. The lower is a Douglas-fir forest with white fir (*Abies concolor*) and Colorado blue spruce (*Picea pungens*) and the upper is a lodgepole pine forest. Aspen is the primary broadleaf species. The subalpine, in addition to spruce and fir, has bristlecone pine (*Pinus aristata*).

The Madrean (19–35° N latitude) northern coniferous forest has complex topography and flora. About half of the world's pine species occur in Mexico. Fir forests (*Abies concolor*, *A. religiosa*, and *A. guatemalensis*) with codominant *Pinus*, *Quercus*, *Pseudotsuga*, and *Cupressus* species usually occur below *Pinus hartwegii* forests. Douglas-fir associated with *P. flexilis* and *Abies concolor* occurs below the fir-dominated forests. A ponderosa pine parkland is

Figure 1 Boreal Rocky Mountain northern coniferous forest rising above the boreal forest at 59° N.

Figure 2 Central Rocky Mountain northern coniferous forest at 54° N; mixed wood stands dominate recent cutovers.

below the Douglas-fir forest and above a mixed pine–oak (*P. edulis*, *P. cembroides–Quercus arizonica*, *Q. gambelii*) chaparral in southern regions and a pinyon–juniper (*P. edulis–Juniperus* spp.) pygmy conifer woodland in northern regions.

Plateau The Nechako and Fraser Plateaux comprise much of central British Columbia. The western portions are in the rainshadow of the Coast Mountains and are less productive than more easterly portions (**Figure 3**). Rain shadow areas are dominated by lodgepole pine with interior spruce occurring on rich, moist soils. The primary species, moving east away from the rainshadow, are interior spruce and subalpine fir with Douglas-fir occurring on drier sites. Lodgepole pine is a seral species on much of the plateau but it may be the climax species of the rainshadow region.

Intermountain From 37° to 45° N latitude, between the Rocky Mountains and the Cascade–Sierra complex are mountain chains, isolated like islands, in an otherwise very arid, high elevation environment. Above a pinyon–juniper woodland from 1500 to 2500 m is the northern coniferous forest. A white fir montane forest with lodgepole pine, ponderosa pine, and Douglas-fir on mesic sites characterizes the region. The subalpine is dominated by limber pine, subalpine fir, and the intermountain bristlecone pine (*Pinus longaeva*). On very arid ranges, the subalpine is absent and pinyon pine covers the slope.

Mesoamerica Low mountain pine forests of Guatemala, Belize, Honduras, and Nicaragua are usually stands of *Pinus oocarpa* although *P. caribaea* may be present. *Pinus hartwegii* and *Juniperus standleyi* are the major species of high mountain humid forests in northern Mesoamerica. *Abies guatemalensis* and *A. religiosa* continue southwards from Mexico and dominate the high mountain, perhumid forests of northern Mesoamerica.

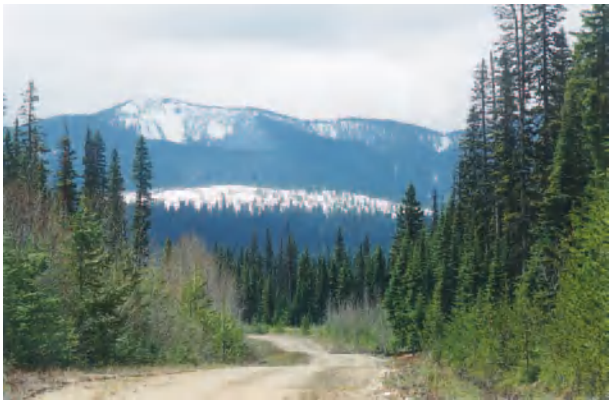


Figure 3 Northern coniferous forest on the rolling eastern Fraser Plateau; interior spruce and subalpine fir dominate on mesic and wetter sites.

Coast and Cascade Mountains In the Coast and Cascade Ranges (43–49.5° N latitude), the northern coniferous forest starts immediately above the temperate coniferous forest. Along the western slope of the Cascades and in the Coast Range, the northern coniferous forest has a lower amabilis fir (*A. amabilis*) zone and an upper mountain hemlock zone. These forests are nearly as productive as those of the Central Rocky Mountains. The northern coniferous forest consists of a ponderosa pine forest often with Douglas-fir, and a mesic *Abies* or mountain hemlock forest above 1500 m, but below the subalpine on the eastern Cascade slopes.

Other Northern Coniferous Forests

Appalachians Above the elevational limit of the deciduous forest along the Appalachian chain are dense, even-aged, red spruce (*Picea rubens*) stands. *Abies* increases in abundance with elevation (*A. balsamea* in the north, *A. fraseri* in the south). Pure subalpine stands can form if the mountain has sufficient elevation. In mixed spruce–fir stands, fir is shorter-lived and faster-growing than spruce. The Appalachian northern coniferous forest has been severely impacted by acid rain, woolly aphid, and unknown mortality agents over the past 25 years.

Southeastern USA Pre-European settlement pine forests were old and open, and contained a two-layered canopy and diverse groundcover. Upland pine forest of the southeastern USA can be classified into three general communities: northern pine barrens, xeric sand communities, and mesic pine communities. Pine–oak forests (*Pinus serotina–Quercus stellata*, *Q. marilandica*) of the northern pine barrens are confined to Delaware Bay. Longleaf pine (*P. palustris*) dominates the xeric, well-drained coarse sands of the southern coastal plain. Historically fire return intervals of 3–6 years maintained the open nature and facilitated reproduction of this forest. Mesic pine communities are generally dominated by an even-aged, closed canopy of longleaf, loblolly (*P. taeda*), pond (*P. serotina*), and/or slash (*P. elliottii*) pine. Species composition depends on site quality and disturbance frequency. Today's pine forest is young, dense, dominated by loblolly pine with a substantial hardwood component, has little or no groundcover, and accounts for nearly 60% of the USA's wood production.

Europe The northern coniferous forest is a significant component of mountain forests in France, Germany, and Switzerland. Generally it is found above a beech–conifer (*Fagus sylvatica*–conifer) mixed wood, and is typified by a spruce–fir (*Abies alba*–*Picea abies*) forest below a pine–larch (*Pinus cembra*, *P. nigra*, *P. sylvestris*–*Larix decidua*) forest. In the Carpathian Mountains, a spruce northern coniferous forest lies above a broadleaf forest and below a mixed beech–fir forest. The northern coniferous forest of the Ural Mountains is a spruce–fir (*Picea obovata*–*Abies sibirica*) forest below a spruce–fir–Siberian stone pine (*Pinus sibirica*) forest.

Asian subcontinent The northern coniferous forest in northern and northwest Pakistan is diverse. It contains deodar (*Cedrus deodara*), kail (*Pinus wallichiana*), spruce (*Picea smithiana*), and silver fir (*Abies pindrow*), with chir (*Pinus longifolia*) at lower elevations and on hot southerly aspects. A subalpine spruce–fir forest again lies above the northern coniferous forest. The northern coniferous forest of the Himalayas continues eastward from Pakistan to Sikkim at high elevations: 1500–3300 m in the west, 2750–3350 m in Sikkim. Pencil juniper (*Juniperus macropoda*) and pine (*Pinus gerardiana*) are found throughout Kashmir while in moister valleys there are deodar and silver fir. In Nepal or the central Himalayas, northern coniferous forest species include silver fir, *Picea smithiana*, cedar, hemlock (*Tsuga dumosa*), and kail. Kail, *Picea spinulosa*, *Juniperus wallichiana*, hemlock, and *Larix griffithii* are the northern coniferous forest species at the eastern end of the Himalayas.

East Asia In China, the northern coniferous forest is a spruce–fir (*Picea brachytyla*–*Abies fabri*) forest with hemlock (*Tsuga chinensis*). Eastward to Korea, the northern coniferous forest is north of 40° N latitude. Species include *Picea jezoensis*, *Abies nephrolepis*, *Larix koreanna*, *Picea koyamae*, *Pinus koraiensis*, and *A. holophylla*. The northern coniferous forest decreases in elevation moving north along the Japanese island chain. The forest is fir–spruce (*A. homolepis*–*Picea jezoensis*) with a yew (*Taxus cuspidata*) component.

History of the Northern Coniferous Forest in Western North America and Europe

Expansion of high montane and mixed coniferous forest at high latitudes and high elevations began 35 to 11 million years before present (BP). This coincided with a significant drop in North American temperature. Cooling continued from 10 to 2 million years BP concomitant with a retreat in hardwood forests from mid and high latitudes and a continental expansion of coniferous forest. The present day Boreal and Central Rocky Mountain northern coniferous forest regions were covered with ice when the Cordilleran and Laurentide ice sheets joined at the last glacial maximum (LGM) about 18 000 years BP. The LGM defined present North American distributions of plant communities. Glacial refugia existed in the Queen Charlotte Islands, the exposed Coastal Plain, and areas to the south of the ice sheet (e.g., Clearwater River drainage in Idaho). The ice sheets separated and retreated from 13 500 to 11 000 years BP. This resulted in a corridor, the Rocky Mountain Trench, for northern coniferous forest species migration from refugia. It is predicted that with climate change the northern coniferous forest will expand into boreal and subalpine forests in coming centuries.

Much of northern Europe was covered by large ice sheets at the LGM, about 22 000 to 14 000 years BP. Forests and woodlands were nonexistent except for isolated pockets of woody vegetation in southern European mountains. Birch and conifers (open woodland) were present in European Russia 13 000 years BP. Open woodland returned to much of Europe by 12 000 years BP. Open woodland retreated during the younger Dryas and forest returned to much of Europe by 9000 to 8000 years BP. A warm period persisted from 7000 to 5000 years BP and forests spread northward. Present-day northern coniferous forest was established about 4500 years BP.

Environment

Climate

Climate is the most important determinant of natural terrestrial ecosystems. In western North America, the northern coniferous forest has a continental climate with a moderating maritime influence. Similar to the boreal forest, winters are cold and summers are short: growing degree days average about 90 in the north to more than 120 in the south. Mean annual temperature ranges from 0.5°C in the north and at high elevations to 9°C in the south. The average temperature drops below 0°C for approximately 4 months (range 1–5) of the year, and rises above 10°C for 2–5 months. Generally, frost can occur in any month. Precipitation varies by locality; it is least in valleys and increases with slope position. It ranges from 300 to 1650 mm, of which 25–50% falls as snow.

Soils

Over time, soils develop as a function of parent material, climate, biota, and topography. Generally northern coniferous forest soils are young. In the Central Rocky Mountains, mesic soils are humo–feric podzols and brunisolic or orthic gray luvisols. Podzolic soils are typical of the northern coniferous forest but given the complex topography and variety of parent materials, many soil types can develop. Podzols are well drained and are leached of clay and organic matter. The lack of calcium in these soils makes them susceptible to erosion and weathering. Brunisolic soils result from slow weathering and/or restricted development due to long winters and low temperatures in cold climates and lack of soil moisture in dry climates. Brunisols are found primarily in forested areas such as lodgepole pine forests. Luvisolic soils are characterized by a horizon of clay in the subsoil resulting from leaching which may restrict root penetration. Luvisols form under forest cover having either high rainfall or low temperature. The northern coniferous forest organic soil layer arises through slow humification of forest litter low in nutrients and high in resins, waxes, and lignins. Climate warming may promote a change in soil type due to increased respiration and accelerated loss of organic matter.

Disturbance

Historically, fire has been the most important and conspicuous disturbance agent of the Rocky Mountains. European settlement and fire suppression reduced fire frequency in the northern coniferous forest in the twentieth century. Consequences include altered species composition, increased insect and pathogen epidemics, and enhanced probability of catastrophic fires due to increased fuel loading. The fire cycle or fire return interval lengthens with increased elevation. Fire intensity decreases with increased fire frequency: low-intensity fires every 5–12 years in ponderosa pine woodlands versus stand-replacing fires every 100 years in lodgepole pine forests to every 200–400 years in higher elevation forests.

Insect and pathogen outbreaks are also primary northern coniferous forest disturbance agents. The spruce beetle (*Dendroctonus rufipennis*) killed virtually all spruce in northwestern Colorado during the 1940s. The mountain pine beetle (*D. ponderosae*) infested 2 million ha in the western USA from 1979 to 1983. On the Fraser and Nechako plateaux in British Columbia, in excess of 5 million ha of the northern coniferous forest were infested with mountain pine beetle in the spring of 2003. Many have attributed serious pest outbreaks in the northern coniferous forest to the success of wildfire control programs and climate change. Fungal pathogens such as *Armillaria*, *Phellinus*, and *Tomentosis* can also be significant disturbance agents.

There are other northern coniferous forest disturbance agents. Wind destroys patches of old, high-elevation stands with increased bole rot. Avalanches can be significant disturbance events on a local scale. In some areas, indiscriminate grazing by native and domestic ungulates can impact regenerating vegetation or lead to forest degradation.

Global Warming

Past changes in climate were natural processes that probably drove species extinction as well as speciation. The current concern surrounding climate change is relevant because (1) the rate of change appears to be greater than most previous changes, (2) ecosystems are often more fragmented, except perhaps in the boreal forest, resulting in barriers to species migration, and (3) most ecosystems serve multiple needs and loss – damage to forests will have significant environmental, economic, and social impacts.

Warming is expected to be more significant at higher latitudes. To accommodate changing climate patterns, species will shift to more northern latitudes and higher elevations. This will alter the northern coniferous forest distribution. In addition to increased temperature and precipitation, frequency of extreme weather events will increase.

Temperature is hypothesized to increase by 1° to 4.5°C within the present century. With a temperature change of 3°C, species would have to move about 250 km in latitude or 500 m in elevation to maintain the same temperature. Tree species have variable rates of migration, 1 to 45 km per century. Predicted temperature shifts requiring migrations of over 100 km per century are beyond the dispersal abilities of coniferous species. If species cannot migrate, they will: (1) exist at current locations with reduced productivity and presence, (2) adapt slowly to changing conditions, or (3) become extinct. Where there are obligate community relationships, e.g., deer and forest type, deer will only be able to migrate at the same speed as the tree species unless an alternate forest type is found. This could lead to local extinctions.

Forest Dynamics, Management, and Utilization

Stand Dynamics

Stand development following disturbance is a function of local elevation, moisture gradients, and soil. Mesic stands in the northern coniferous forest exhibit developmental stages widely encountered in boreal and montane conifer forests. The first stage or establishment stage is characterized by little competition and significant seedling establishment and growth. The second, stem exclusion stage is typified by competition among trees resulting in mortality and increased tree size. Little, if any, recruitment occurs. The third, understory reinitiation stage results when gaps occur in the canopy allowing new regeneration. The fourth, equilibrium or old-growth stage is when, simplistically, tree mortality is balanced by tree recruitment. Due to frequent disturbances, stands rarely reach the equilibrium stage in the northern coniferous forest; a noted exception is the Central Rocky Mountain's hemlock–cedar-dominated forests.

Where competition is minimal and seed supply is abundant, establishment occurs in 10 years. However, establishment is typically prolonged, 40–70 years, particularly on severe or very good sites where herbs can overtop seedlings. At higher elevations, tree establishment is slower and results in multiple age classes. Consequently the stem exclusion stage is bypassed, and tree mortality and recruitment of the third stage follow stand establishment. At lower elevations where fires are not detrimental to the canopy trees, seedling regeneration occurs in waves assisted by a good seed year, favorable weather, and no fire. Stand dynamics can also vary along environmental gradients: on a mesic north-facing slope an even-aged Douglas-fir stand will develop while on the adjacent south-facing slope an uneven-aged, open Douglas-fir stand will establish with understory lodgepole pine.

Productivity

In the Rocky Mountain northern coniferous forest, biomass peaks early in stem exclusion, declines as mortality increases and then increases as recruitment proceeds. Species diversity tends to track resource availability, dropping dramatically at the start of stem exclusion and staying low until understory reinitiating. The northern coniferous forest is a moderate carbon store compared to temperate rainforest and boreal forests. The northern coniferous forest produces 6–18 tonnes ha^{-1} $year^{-1}$ compared to 4–12 tonnes ha^{-1} $year^{-1}$ on upland boreal sites and 15–25 tonnes ha^{-1} $year^{-1}$ in the temperate rainforest.

Nontimber forest products and environmental services can be classified as being market or nonmarket regulated. Market products and services include grazing, medicinal plants, edible products (mushrooms, wild rice), decorative products, trapping, and outfitting. Nonmarket items include traditional first nation's uses, hunting, fishing, birdwatching, and ecotourism. In order to provide timber, nontimber forest products, and environmental services, northern coniferous forest seral stage diversity must be maintained.

Environmental Services

The northern coniferous forest provides many important values or services in addition to fiber production for subsistence and industrial uses. Watershed quality and water production is a function of a healthy, intact forest cover. Forest cover regulates snow storage and snowmelting rates by snow interception, shading, and wind amelioration. Peak flow and soil erosion are reduced by intact forest cover. Erosion is further reduced when groundcover vegetation is present. Maintenance of northern coniferous forest forested slopes helps regulate stream temperature and stabilize steep slopes.

Wildlife species diversity is a function of the complexity of tree species and associated understory vegetation. Wildlife is directly linked to seral stages of the northern coniferous forest (or any plant community). As wildlife species have different preferences for different plant species, they have different life or stand developmental stage (seral) needs. Time of year (season) may also result in different habitat needs for a species. Maintenance of riparian areas is crucial for fish survival and mature forest habitat is critical to some species' survival. Therefore, it is important to have seral stage (structural) diversity, including standing and fallen dead wood, to maintain northern coniferous forest species diversity.

Forests in the northern coniferous forest are increasingly managed to provide leisure and recreational services. They include hiking, photography, birdwatching, hunting, and fishing. This places leisure and recreational management in conflict with traditional forest product management. In addition to parks and wilderness areas for recreational services, managing for northern coniferous forest seral stage diversity will provide ongoing recreational opportunities.

Management and Utilization

Industrial activity in the northern coniferous forest varies by locale. About half of the world's pulp comes from the northern coniferous forest. In Canada, there is significant harvesting activity as the northern coniferous forest is second in productivity only to the northern temperate coastal forest. In the western USA, logging activities have fallen during the 1990s due to a focus on forest services rather than forest products: 57 million m^3 were cut on US National Forests in 1986 and 23 million m^3 were cut in 1996. The northern coniferous forest is part of the industrial forest of Europe while on the Asian subcontinent it provides fuel and subsistence for local peoples as well as industrial wood.

Depending on northern coniferous forest locale, even- or uneven-aged management may be utilized.

Silvicultural system selection dictates harvesting systems and equipment (if any). Steep slopes in much of the northern coniferous forest also influence equipment selection. In general, cable systems are required on steeper ground while ground-based systems can be used if slopes do not exceed 30–50%. Soils of the northern coniferous forest are young and often thin, which influences equipment selection. The risk of soil degradation is generally greater with ground-based systems. Harvesting is highly mechanized on large-scale western North American operations whereas in Eastern and Central Europe, power saws and small tractors are used in small-scale forestry operations. In Asia, past forestry practices have significantly compromised the productivity of the northern coniferous forest due to flooding and erosion. Small-scale fuelwood collection and mechanized harvesting are both practiced in the Asian northern coniferous forest.

Significance

The northern coniferous forest provides a significant proportion of the world's industrial forest products as well as nontimber forest products and environmental services. It helps to maintain the social fabric of indigenous peoples and preserve aboriginal culture. The northern coniferous forest also provides services such as watershed integrity, habitat, and recreational and leisure opportunities. Compared to boreal and subalpine forest, the northern coniferous forest is diverse and productive. A challenge for northern coniferous forest managers, worldwide, is to maintain structural and species diversity without compromising the potential of the northern coniferous forest to provide its products and environmental services.

See also: **Operations**: Forest Operations Management. **Temperate and Mediterranean Forests**: Southern Coniferous Forests; Subalpine and Boreal Forests; Temperate Broadleaved Deciduous Forest. **Temperate Ecosystems**: Pines; Spruces, Firs and Larches

Further Reading

Barbour MG and Christensen NL (1993) Vegetation of North America north of Mexico. In: Flora of North America Editorial Committee (ed.) *Flora of North America, Introduction*, Vol. 1, pp. 97–129. New York: Oxford University Press.

Christensen NL (2000) Vegetation of the southeastern coastal plain. In: Barbour MG and Billings WD (eds) *North American Terrestrial Vegetation*, 2nd edn, pp. 396–448. New York: Cambridge University Press.

Delcourt PA and Delcourt HR (1993) Paleoclimate, paleovegetation, and paleofloras of North America north of Mexico during the Late Quaternary. In: Flora of North America Editorial Committee (ed.) *Flora of North America, Introduction*, Vol. 1, pp. 71–94. New York: Oxford University Press.

Farjon A (1998) *World Checklist and Bibliography of Conifers*. Kew, UK: Royal Botanic Garden.

Haden-Guest S, Wright JK, and Tecloff EM (eds) (1956) A World Geography of Forest Resources. New York: Ronald Press.

Hartshorn GS (2000) Tropical and subtropical vegetation of Mesoamerica. In: Barbour MG and Billings WD (eds) *North American Terrestrial Vegetation*, 2nd edn, pp. 623–659. New York: Cambridge University Press.

Meidinger D and Pojar J (1991) *Ecosystems of British Columbia*. Victoria, Canada: Province of British Columbia.

Oliver CD and Larson BC (1996) *Forest Stand Dynamics*, updated edn. New York: John Wiley.

Peet RK (2000) Forests and meadows of the Rocky Mountains. In: Barbour MG and Billings WD (eds) *North American Terrestrial Vegetation*, 2nd edn, pp. 75–121. New York: Cambridge University Press.

Veláquez A, Toledo VM, and Luna I (2000) Mexican temperate vegetation. In: Barbour MG and Billings WD (eds) *North American Terrestrial Vegetation*, 2nd edn, pp. 573–592. New York: Cambridge University Press.

Southern Coniferous Forests

I R Smith, University of Queensland, St Lucia, Australia

Introduction

When referring to coniferous forests, an image comes to mind of the great boreal forests of the northern hemisphere or carefully managed and regular pine plantations. The native conifer forests of the southern hemisphere rarely conform to this image. In fact, except in a few cases, the term 'coniferous forest' is a misnomer and most of the associations described in this section might more properly be called 'forests with a coniferous element.' Most of the southern hemisphere conifers are of exclusively southern hemisphere families or, in the case of those families which are represented in both hemispheres, are of genera which are represented only in the southern hemisphere. In a total of 67 conifer genera and 557 species worldwide, 31 genera and some 200 species are largely southern and 160 species are totally southern. Of those genera that are found in both hemispheres only one 'northern' genus is found in the southern hemisphere while 12 'southern' species extend into the northern hemisphere mainly into closely adjacent areas such as Malesia, the Philippines and northern South America. The Pinaceae, which dominate northern forests, are not represented in the southern hemisphere except in extensive plantations or as naturalized exotics.

Conifer forests in the northern hemisphere tend to dominate in more extreme climates where the ability of conifers to compete with angiosperms is enhanced. Thus, they are most abundant at high altitude, high latitude, and in other cold, high rainfall areas. These areas are more extensive in the north, with the great high latitude land-dominated boreal region having no southern analog since the break-up of Gondwana.

The other factor that has a bearing on the differences between the northern and southern conifer forests is the relatively greater oceanic effects on the climate of the southern hemisphere. Annual seasonal effects are less extreme than in the large continental masses of the north, but conversely there are greater, and less regular, year to year climatic changes under the influence of such phenomena as the El Niño Southern Oscillation.

The southern conifers tend to occupy similar niches to their northern cousins, but the geographic extent of the niches is much smaller and as a result, many species of southern conifer have small geographical ranges. There is fossil evidence that southern conifer diversity was much higher at times in the past.

There are close analogs in both conifer genera and forest types across the southern lands as a result of their common Gondwanan heritage. Fossil records indicate that Antarctica once shared a similar coniferous flora. South Africa, which has only a limited conifer flora, is the exception to this and there are puzzling aspects to both its present-day and fossil coniferous flora.

Little study has been carried out on the ecological associates of the southern conifers, especially fungal associations. The Araucariaceae, Podocarpaceae and *Callitris* spp. (Cupressaceae) in Australia have vesicular–arbuscular mycorrhizae (VAM). *Wollemia nobilis* (Araucariaceae) also has ecto-endomycorrhiza. VAM mycorrhizae have been associated with Araucariaceae and Podocarpaceae since the Jurassic.

There is a range of particular insects associated with the Araucariaceae, including weevils, chrysomelid leaf beetles, and scolytid bark beetles. The first two araucarian beetle groups have been associated since the early Jurassic while the bark beetles colonized them at the end of the Cretaceous.

As with the northern conifers, many of the southern conifers are very desirable timber species and were heavily exploited (and overexploited) for timber. As will be discussed later, several species have been plantation grown and natural stands have been managed for silviculture. In addition *Araucaria araucana* and *A. angustifolia* in South America and *A. bidwillii* in Australia were valued for their edible nuts and played an important part in indigenous culture in two continents.

Coniferous Forest Types in the Southern Hemisphere

To cover the diversity of those forests containing southern conifers in a brief treatment such as this is best done using a simple classification drawing on the similarity between southern forests. The following classification is introduced:

1. Tropical and subtropical rainforests with coniferous elements, with or without coniferous emergents.
2. Warm temperate rainforest with coniferous emergents.
3. Temperate rainforests containing conifers.
4. Arid zone coniferous forests and woodlands.
5. Heathland and shrubland with coniferous emergents/components.
6. Alpine and subalpine shrubland and forest with conifers.

Some clarification is required for these terms. Tropical and subtropical rainforests are complex forests with multiple layers and characterized by large numbers of lianas and epiphytes. The complexity and leaf sizes generally reduce from tropics to subtropics and with increasing altitude and/or soil fertility. Warm temperate rainforests are found only in Australia and are much simpler rainforests (often dominated by older Gondwanan elements) on less fertile soils. The cool temperate rainforests are the classic fern/southern beech/conifer forests of southern Australia, Chile and Argentina, and New Zealand.

Often these forests can overlap. On the central coast of New South Wales the three types are found at the same latitude but separated by soil/moisture/altitude gradients.

In using such a classification, there is a range of species with specialist niches, which will be omitted, e.g., *Microstrobos fitzgeraldii* with a specialized niche in the spray zone of waterfalls in the Blue Mountains of New South Wales, Australia. There are also likely to be oversimplifications and omissions in dealing with such a complex subject in such a brief treatment. For instance the monkey-puzzle (*Araucaria araucana*) in Chile and Argentina exists in forest types (3), (4), (5), and (6) but is only dealt with below in (5). Further reading will be necessary to elaborate such a complex subject.

1. Tropical and Subtropical Rainforests with Coniferous Elements, with or without Coniferous Emergents

Forests of this type are represented in Australia, New Caledonia and other Pacific Islands, New Guinea, and South America. With *Agathis* spp. as an emergent they also extend into Malesia. It is important to note that while conifers are emergent they are not the only emergents as in many parts of the forest large angiosperms such as *Ficus* spp. are also important. While the lower forest layers are normally dominated by angiosperms, conifers especially Podocarpaceae and Cupressaceae can also form an important part of both the canopy and understory.

The most developed of these types of forest are found in New Caledonia, especially on the 'Grand Terre' or Main Island. New Caledonia has a total of 43 conifer species of which 26 are found in rainforest associations. The high diversity of conifers and the survival of many primitive angiosperms on New Caledonia is attributed to the dominance (but not exclusivity) of ultramafic soils on the island which acted as a barrier to many modern species. However, the ultramafics are an intrusion that postdates the Gondwanan geology of New Caledonia so the conifers have radiated since the ultramafics were put in place. The ultramafics may have been a barrier to the movement of some angiosperm groups on to these areas (e.g., Poaceae does not occur on New Caledonian ultramafics), so making radiation and survival more likely. Where this forest occurs there is often a gradient from a lowland rainforest to an evergreen cloud forest. Overall 14 species of Araucariaceae, 11 species of Podocarpeaceae, two Cupressaceae and a single species of Taxaceae occupy niches in these forests. The araucarians (*Araucaria* and *Agathis* species) plus *Retrophyllum comptonii* and *Dacrydium araucarioides* form both the canopy and emergent layers (however, these latter two form an emergent layer only on 'cuirasse' boulder fields that are largely unvegetated), and *Austrotaxus spicatus*, *Libocedrus austrocaledonica*, and the majority of the Podocarpaceae are found in the understory. Angiosperms such as *Metrosideros* (Mytraceae) and *Quintinia* (Saxifragaceae), and primitive groups such as Winteraceae are also found in the understory and canopy. Most species have strong Gondwanan associations. In some areas unusual, almost pure tree layer stands occur, such as *Agathis montana* on several mountain tops and *Neocallitropsis* in some wetlands in the south of the main island, and *Araucaria columnaris* in a pure narrow band on calcareous rocks on the seashore on the main island, the Isle of Pines, and the Loyalty Islands.

Through the Pacific Islands between New Guinea and Fiji similar associations of conifers occur. These rainforests are often more complex and diverse than New Caledonia, but the number of conifer species is lower, with one coniferous emergent (*Agathis macrophylla*) and from one to seven species of podocarps. The isolated South Pacific island Norfolk Island has one emergent araucarian, Norfolk Island pine (*Araucaria heterophylla*) which now dominates foreshore ornamental plantings in warmer parts of the world.

New Guinea has variants of the same structure but once again with high diversity with four species of Araucariaceae, 29 species of Podocarpeaceae, and two Cupresseaceae. As with New Caledonia, the araucarians tend to be emergent with the other conifers mixed with angiosperms in the canopy and understory. The podocarps are rare at low altitude (mostly *Podocarpus*, some *Falcatifolium*, etc.) but increase with altitude and may dominate mid and upper altitude forests (mostly *Dacrycarpus* and *Dacrydium*). The Araucariaceae have a patchy distribution in the forests. There is little information on the ecology of *Agathis macrophylla* and the threatened *A. spathulata*, but more is known of the biology of hoop pine (*Araucaria cunninghamii* var. *papuana*) and klinki pine (*A. hunsteinii*). Both are mast seeders and occur in lower to mid montane forests with overlapping ranges. They can form mixed stands but normally either one or the other is found with klinki most common from 700 to 1000 m above sea level and hoop more common above 1000 m. In these forests the tall emergent *Araucaria* spp. appear to exhibit additive basal area, where the presence of emergents does not tend to subtract from the total basal area of the remainder of the stand. This phenomenon has also been reported from the temperate kauri forests of New Zealand.

In Australia, this type of forest extends from Cape York in Queensland to south of Sydney but only one podocarp species is present in the southern part of the range, south of Coffs Harbour. North of Coffs Harbour, on the New South Wales north coast, emergent Araucariaceae become a feature and other conifer species gradually increase. Overall there are five Araucariaceae, six Podocarpaceae, and one Cupresseaceae (*Callitris macleayana*) present in these forests. Araucarian emergents are most commonly found in drier types of rainforest or on poorer substrates. The most common is *Araucaria cunninghamii*, which has a discontinuous distribution from Dorrigo (near Coffs Harbour) to Cape York. *Araucaria bidwillii* has a restricted distribution (which appears to be an interglacial refugium) north and west of Brisbane and in two relict areas north and south of Cairns. *Agathis robusta* is found in a small area in South Queensland and the wet tropics while *A. atropurpurea* and *A. microstachya* are confined to scattered areas of the wet tropics. The forests containing Araucariaceae are normally known as Araucarian vine forests (in several variants). Extensive plantations of *Araucaria cunninghamii* have been planted in Queensland as well as a small area of *A. bidwillii*.

In tropical and subtropical South America two Araucariaceae and up to seven podocarps occur in tropical montane forests. The podocarps follow a similar pattern to Australia as part of a generally angiosperm dominated forest, with seven species in Peru declining to one in northeast Argentina. In southeast Brazil and northeast Argentina they form part of the canopy under the emergent Parana pine (*Araucaria angustifolia*) in an association known as Araucarian moist forest, which in the past formed extensive stands. It is interesting to note the structural similarities of many of these forests in different continents (**Figures 1** and **2**). Extensive plantations of *A. angustifolia* have been established in Brazil, as well as *A. araucana* in Andes of Chile and Argentina, from wet forests including *Nothofagus* at high altitude, to dry open forests on the Argentinean side.

Figure 1 *Araucaria angustifolia* forest, Brazil. Courtesy of Rudi Seitz.

In South Africa, three of the four podocarp species may be considered to be part of a subtropical evergreen forest, although the forest is not strictly analogous to any of the other southern conifer forests in this group and has structural similarity to some of the simpler subtropical rainforest types of Australia.

Status In Australia and New Caledonia these forests, while heavily cleared and logged in the past, are generally well protected although some minor clearing on private land still occurs. In South America and New Guinea clearing for agriculture and illegal or poorly controlled logging remains a continuing threat.

2. Warm Temperate Rainforest with Coniferous Emergents

This is one of the most restricted types and is found only in Australia from Victoria to the Queensland on poorer soils derived from rhyolite, trachyte, and metasediments in the northern part and on the more fertile eutrophic rocks in southern cooler regions. It requires rainfall over 1300 mm per year. It is characterized by a two-strata layer with a more limited range of species than the above type, with stranglers, palms, woody vines, and buttressing rare or absent. The tree trunks tend to be slender and uniform in appearance. Tree and ground ferns are frequent, and epiphytes can be common but are not generally abundant in the numbers or species present. Angiosperms are such species as coachwood (*Ceratopetalum apetalum*), sassafras (*Doryphora sassafras*), and scentless rosewood (*Synoum glandulosum*). Hoop pine (*Araucaria cunninghamii*) is found in some patches north of Dorrigo, but its main claim to fame is that it is in this association that Wollemi pine (*Wollemia nobilis*), representing a third araucarian genus (previously only known from fossils) was found in 1994, with a tiny distribution in two stands in deep sandstone gorges just north of Sydney.

Status Most of this type is found in protected areas, but smaller patches embedded in sclerophyll forest may be vulnerable to wildfire. *Wollemia nobilis* has adapted to wildfire by strong coppicing mechanisms. The main threat to *W. nobilis* is considered to be introduction of pathogens by illegal visitors to the site.

3. Temperate Rainforests Containing Conifers

These forests are the dominant vegetation of the wetter coastal and montane areas of Chile and Argentina, New Zealand, and Tasmania. In only a

Figure 2 *Araucaria bidwillii* forest, Bunya Mountains, Queensland, Australia.

few parts of this forest type are conifers as dominant as they are in the equivalent forest types of the North American Pacific coast, but there are also few areas where conifers are not part of this forest.

The conifer families present are Araucariaceae, Cupressaceae, Podocarpaceae, and, in Tasmania only, Taxodiaceae (although Taxodiaceae is now generally included in the Cupressaceae). The most common angiosperms associated with such species are old Gondwanan families such as the family Winteraceae and species of *Nothofagus*, *Metrosideros*, *Quintinia*, *Weinmannia*, etc.

Conifer dominated forests of alerce (*Fitzroya cupressoides*) and *Pilgerodendron uviferum* once dominated the wet soils of the valley between the Chilean coastal ranges and the Andes but were cleared by early Spanish settlers restricting this forest type to less conifer dominated montane forests, although *P. uviferum* is still present in large stands in the Chiloe archipelago.

Conifer dominated forests are also present on the west coast of New Zealand's South Island, on wet river terraces. These forests are dominated by the podocarps *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *P. taxifolia*, *Dacrycarpus dacryioides*, and *Manoao colensoi*. These forests are associated with the angiosperms *Metrosideros*, *Knightia*, *Quintinia*, and *Weinmannia*. There is a great variation in the dominance of conifers in other areas of New Zealand. *Nothofagus* species tend to dominate the forests closer to the treeline but *Libocedrus* is a major component sometimes dominating stands. Other conifers also occur in these beech forests. There appears to be a long-term dynamic interaction between *Nothofagus* and conifers depending on large- and small-scale disturbance. Indeed disturbance is a major factor in most forests with a high conifer component. In Westland, the river terrace forest probably results from periodic flooding, while in the central North Island the large podocarp stands appear to have been associated with the enormous Taupo eruption that occurred about 1800 years ago. There is evidence that over time the podocarps decline until angiosperms dominate the canopy, but podocarps remain as emergents and enough survive to maintain a population until the next catastrophic disturbance.

In New Zealand's northland, the kauri (*Agathis australis*) is added to the forest mix to form some of New Zealand's most famous forests with some existing kauris up to 50 m tall and up to 4.5 m in diameter. While not tall by world standards, this tree has little taper until the crown so the kauri appears as a solid block of timber. There is evidence that the kauri as a component of mixed angiosperm coniferous forests has expanded and retreated with long-term climatic variation.

In Tasmania, conifers are a less dominant feature of the forests but podocarps such as celery top pine (*Phyllocladus aspeniifolius*) and King Billy pine

(*Athrotaxis selaginoides*) occur in rainforests dominated by *Nothofagus* and sassafras (*Atherosperma moschatum*). Probably one of the main reasons for the nondominance of conifers is the dynamic, fire-mediated relationship between rainforest and wet tall eucalypt forest. The other important rainforest species, a podocarp, Huon pine (*Lagarstrobos franklinii*), is virtually confined to riparian forests of the south and southwest with the exception of a few stands away from the river systems.

Status In Chile, this forest is not secure particularly in the northern part of the forested region. Although a reasonable percentage is in protected areas, not all forest types are represented. Much clearing occurred during early European settlement especially in the valley between the coastal range and the Andes. A variety of pressures still exists including clearing, selective legal and illegal logging affecting forest structure and replacement by exotic plantations. In New Zealand much of the original forest was cleared for agriculture, grazing, and exotic plantation. Much remains in mountainous areas and in the Westland area of the South Island. Remnant areas in the North Island are now generally secure. In Tasmania, large areas are preserved in the World Heritage area, but in large areas where eucalypt is logged the cyclical progression to rainforest has been halted by silviculture practice.

4. Arid Zone Coniferous Forests and Woodlands

The *Callitris* forests and woodlands of Australia, and the drier forests of cipré (*Austrocedrus chilensis*) in Chile and Argentina form an unusual and distinctive coniferous forest type and one where the forest ecology is most sensitive to human interference. The almost extinct drier mountain forests of Clanwilliam cedar (*Widdringtonia cedarbergensis*) and *W. schwartzii* with an asteraceous understory of the South African Cape region also fit into this group. In dense stands of these species, fire has an extreme behavior with high rate of spread, crown fire, and spotting. Even in more open woodland with these species, fire can be intense due to dry grass and shrub understory. The Pilliga Scrub in New South Wales, one of the largest cypress forests, has been referred to as 'big fire country' with up to 100 000 ha of a total of 500 000 ha being burnt in one fire.

The forests have contrasting post-European fire histories. The cipré forests originally covered a vast area of the drier foothills and lower slope area of the Andes in Chile and Argentina. It is a long-lived species which existed in an environment of infrequent catastrophic disturbance (e.g., volcanic activity) and requires a time period of over a 100 years to regenerate. With more frequent fires since European settlement a large area of its former range has been converted to shrubland. Fire and overexploitation have also reduced the South African cedar forests (*Juniperus* extends in to southern hemisphere in Africa, but is northern in relationship) to small remnants, although there is now a strong conservation push to preserve and extend these.

The *Callitris* forests have had a more complex history. The most common forest consists of *Callitris glaucophylla* as a codominant with a number of *Eucalyptus*, *Angophora* and *Casuarina* species. This forest type extends from southern Queensland into northern Victoria. Other species such as *Callitris priessii* and *C. endlicheri* also form similar, but more geographically restricted forests. *Callitris intratropica* forms small stands in savanna vegetation in northern Australia and several species also form similar associations in sandy soils of some coastal areas. Early records and analysis of stumps indicates that under Aboriginal land management practices the *C. glaucophylla* forest was more an open woodland with a grassy understory (**Figure 3**).

Cessation of Aboriginal burning following European settlement combined with a series of good seasons resulted in a dense but fire-prone forest dominated by cypress. This forest has since been modified and diminished by a variety of factors.

Most important has been clearing for grazing and agriculture, with large areas cleared particularly since 1945. Grazing by rabbits and severe drought has also impacted on populations with some populations not recovering from extreme droughts. Although wildfire often stimulates 'wheatfield' regeneration, overfrequent fire can cause loss of this ecosystem. A large number of forests can no longer be considered natural (however that may be defined in this complex system), as they are silviculturally manipulated production forests.

Status The Australian *Callitris* forests, although under pressure, can be regarded as secure due to their large area and management as a timber resource.

The cedar forests of South Africa and the cipré forests of South America are threatened. The following are listed by the IUCN (World Conservation Union) as threats to the cipré forests. They could be repeated almost exactly for *Widdringtonia* in southern Africa:

- Habitat loss/degradation – agriculture – livestock (ongoing);
- Habitat loss/degradation – land management of non-agricultural areas (ongoing);
- Habitat loss/degradation – extraction – wood – clear-cutting (ongoing);

Figure 3 *Callitris glaucophylla* woodland in New South Wales, circa 1910. Reproduced with permission from Baker RT and Smith HG (1910) *A Research on the Pines of Australia*, Technical Education Series no. 16. Sydney, Australia: New South Wales Department of Education, Technical Education Branch, Government Printer.

- Habitat loss/degradation – infrastructure development – human settlement (ongoing);
- Habitat loss/degradation – fires (ongoing);
- Invasive alien species (directly affecting the species) – pathogens/parasites (ongoing)
- Changes in native species dynamics – predators.

5. Heathland and Shrubland with Coniferous Emergents/Components

These are interesting associations and are found in four widely dispersed forms: *Araucaria araucana* in southern South America, *Widdringtonia* in 'fynbos' heathland in South Africa, 'maquis' with araucarian emergents in New Caledonia, and 'kwongan' (heathlands) with *Actinostrobus* species in southwest Australia.

As previously discussed the *Araucaria araucana* forests in drier high altitude sites could be regarded as part of a number of associations, but it has been included here as fire interactions form a common component of these associations. *Araucaria araucana* has a range of fire adaptations including basal epicormic buds, protected terminal buds and thick bark. The trees grow over a shrub canopy made up primarily of *Nothofagus* species (the structure differs at lower altitudes and higher moisture areas and can vary in height). Some of these higher altitude stands of *A. araucana* in many ways appear to provide a structural analog to high-latitude southern hemisphere Cretaceous forests.

In New Caledonia, araucarians exist in most forest types, but the most interesting are emergent araucarians of a number of species up to 7–8 m high overtopping a shrub layer to 2.5 m on ultrabasic substrates. Other conifers may also occur in the shrub to small tree layer (*Dacrydium*, *Podocarpus*, *Neocallitropsis*).

In the Cape Province of South Africa *Widdringtonia* spp. are small tree emergents above a heath layer of Proteaceae, Restionaceae, and ericoid shrubs. All species are to some degree fire dependent, seeding after fire from retained cones. *Widdringtonia whytei* has fire resistant bark, and *W. cupressoides* resprouts after fire from underground tubers, an unusual habit in conifers. All species have suffered badly under a regime of overfrequent fires.

Interestingly, a similar habit is found in southwest Western Australia in kwongan where one of the two *Actinostrobus* species is also a resprouter. In nearby tall eucalypt forests (and extending on to adjacent heaths) is the only fire-adapted podocarp, *Podocarpus drouynianus*, which resprouts after fire.

Status The *A. araucana* forests are protected but still vulnerable to the wide range of human impacts including illegal logging. In New Caledonia, the maquis areas are not suitable for agriculture, but are subject to human-induced wildfires. In South Africa the communities containing *Widdringtonia* are badly affected by wildfire, alien species invasion, and overexploitation of *Widdringtonia* for timber. However, active conservation activities are targeting preservation of all the species but particularly *W. cedarbergensis*. In Western Australia the kwongan has been affected by overclearing, overfrequent fire, and infection by the exotic root fungus *Phytophthora cinnamomi*.

6. Alpine and Subalpine Shrubland and Forest with Conifers

In South America, South Africa, New Guinea, and New Zealand there is a range of montane and subalpine forest types that are typical of these areas. Generally these tend to be part of an altitudinal gradation, e.g., afromontane forest contains *Widdringtonia* species that are also common at lower altitudes and *Librocedrus* in New Zealand also forms a distinctive subalpine forest type.

Only in Australia has a distinctive alpine conifer flora developed (or persisted). Two Tasmanian podocarps, *Microcachrys tetragona* and *Microstrobos niphophilus*, occur as shrubs above the eucalypt treeline. A Tasmanian Cupresseaceae, *Diselma archeri*, although most common as a shrub in the alpine and subalpine zone, also extends below the treeline. *Podocarpus lawrencei* occurs as a pioneer shrub on alpine scree slopes in Tasmania, New South Wales, and Victoria but is also found as a small tree below the treeline. In Tasmania, King Billy pine (*Athrotaxis selaginoides*) can exist as a low twisted 'krummholz' tree in subalpine shrubland. The second true species, *A. cupressoides* (pencil pine) occurs at higher altitudes than *A. selaginoides*, although there is overlap between the two. It has more compact foliage and does not grow to such a large tree.

Status The Australian alpine zone is very small and fragile by world standards and is vulnerable to climate change. Warmer temperatures could effectively eliminate Australian alpine areas or reduce them to tiny remnants. Wildfires can invade alpine and subalpine areas and recovery is slow. Human-induced changes could prevent recovery after climate change cycles.

Conclusion

The conifers of the southern hemisphere are a distinctive group occurring in a large range of forms and occupying a large range of ecological niches from tropical rainforest to alpine shrublands and semi-arid woodlands. They have a distinctive place in the paleobotanical history of conifers and have been used (and have great potential) for silvicultural and horticultural use. In the past they have been little studied but this is beginning to change and further study is likely to lead to both a greater understanding of the group and a greater utilization of their unique characteristics.

See also: **Biodiversity**: Endangered Species of Trees. **Entomology**: Bark Beetles. **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest. **Temperate Ecosystems**: Fagaceae; Pines. **Tree Breeding, Practices**: Southern Pine Breeding and Genetic Resources. **Tree Physiology**: Mycorrhizae. **Tropical Ecosystems**: Southern Hemisphere Conifers; Tropical Pine Ecosystems and Genetic Resources.

Further Reading

Bieleski R (ed.) (in press) *Proceedings of the International Araucariaciae Symposium*, (2003) Auckland. Auckland, Australia: International Dendrology Society.

Bowman DM (2000) *Australian Rainforests: Islands of Green in a Land of Fire*. Cambridge: Cambridge University Press.

Dargavel J, Hart D, and Libbis B (2001) *Perfumed Pineries: Environmental History of Australia's* Callitris *Forests*. Canberra, ACT: Australian National University.

Enright NJ and Hill RS (eds) (1995) *Ecology of the Southern Conifers*. Melbourne Victoria: Melbourne University Press.

Enright NJ, Ogden J, and Rigg LS (1999) Dynamics of forests with Araucariaceae in the Western Pacific. *Journal of Vegetation Science* 10: 792–804.

Haebich A (2002) *On the Bunya Trail*, Queensland Review Special Edition vol. 9.2. Brisbane, Queensland: University of Queensland Press.

Hill RS (ed.) (1994) *History of the Australian Vegetation: Cretaceous to Recent*, p. Cambridge. UK: Cambridge University Press.

Hill RS and Brodribb TJ (1999) Southern conifers in time and space. *Australian Journal of Botany* 47: 639–696.

Hueck K (1966) *Die Wälder Südamerikas*. Stuttgart, Germany: Gustav Fischer Verlag.

Klein RM (1960) O aspecto dinâmico do pinheiro Brasileiro. *Sellowia* 12: 17–44.

Lowry PP (1996) Diversity, endemism, and extinction in the flora of New Caledonia: a review. In: Peng CI and Lowry PP (eds) *Rare, Threatened, and Endangered Floras of the Pacific Rim*, pp. 181–206. Taipei: Institute of Botany, Academica Sinica.

Neira E, Verscheure H, and Revenga C (2002) *Chile's Frontier Forests: Conserving a Global Treasure*. Washington, DC: World Research Institute.
Reitz R and Klein RM (1966) *Araucariaceae*. Flora Ilustrada Catarinense.
Specht RL, Dettman ME, and Jarzen DM (1992) Community associations and structures in the late Cretaceous vegetation of southeast Australia and Antarctica. *Paleogeography, Paleoentology, Paleoecology* 94: 283–309.
Stockey RA (1994) Mesozoic Araucariaceae: morphology and systematic relationships. *Journal of Plant Research* 155(6): 806–815.
Taylor TN and Taylor EL (1990) *Antarctic Palaeobiology: Its Role in the Reconstruction of Gondwana*. New York: Springer-Verlag.
Worldwide Fund for Nature (2003a) *South Malawi Montane Forest Grassland Mosaic*: *Ecoregion Profile*. Stellensboch, South Africa: Worldwide Fund for Nature.
Worldwide Fund for Nature (2003b) *Drakensberg Montane Grasslands, Woodlands and Forests*: *Ecoregion Profile*. Stellensboch, South Africa: Worldwide Fund for Nature.

Subalpine and Boreal Forests

N A Balliet and C D B Hawkins, University of Northern British Columbia, Prince George, BC, Canada

Introduction

Many biogeographers consider boreal and subalpine forests as one biome, others separate them because, although boreal and subalpine forests share many similar attributes with respect to climate, vegetation, and soil, there are significant differences between the two. In this article the two will be treated separately.

Subalpine forests are high-elevation forests that occur in mountainous regions around the world. Coniferous subalpine forests, however, are largely limited to the northern hemisphere. These forests are found immediately above the northern coniferous forest in the European Alps, the mountains of east-central Europe, the Urals, the Himalayas, the mountains of northeast China, and the Appalachians, the Sierra Nevada, Cascade and Coastal Ranges and the Rocky Mountains of North America.

The majority of subalpine forests are dominated by *Picea*, *Abies*, *Pinus*, and *Larix* species; however, some variation does occur among regions (see **Table 1** for common names of these species). Subalpine forests of the European Alps are characterized by *Picea–Abies* forests at lower elevations and *Larix–Pinus* forests at higher elevations. The mountainous regions of Romania, Yugoslavia, and Bulgaria are characterized by *Abies*, *Larix*, *Picea*, and *Pinus* species, whereas the Urals are dominated by *Abies*, *Picea*, and *Pinus* species. The subalpine forests of the Himalayas are characterized by *Abies* and *Picea* at lower elevations and *Juniperus*, *Larix*, *Pinus*, and *Taxus* species at higher elevations, whereas the mountainous regions of northeast China support *Picea–Abies* species at elevations between 2500 m and 3500 m.

Table 1 Some species commonly occurring in subalpine and boreal forests, with their common names

Species	*Common name*
Abies balsamea	Balsam fir
Abies lasiocarpa	Subalpine fir
Abies sibirica	Siberian fir
Betula papyrifera	Paper birch
Juniperus spp.	Juniper spp.
Larix dahurica	Dahurian larch
Larix laricina	Tamarack
Larix lyallii	Subalpine larch
Larix sibirica	Siberian larch
Picea abies	Norway spruce
Picea engelmannii	Engelmann spruce
Picea glauca	White spruce
Picea mariana	Black spruce
Pinus albicaulis	Whitebark pine
Pinus aristata	Bristlecone pine
Pinus banksiana	Jack pine
Pinus contorta	Lodgepole pine
Pinus flexilis	Limber pine
Pinus sibirica	Siberian pine
Pinus sylvestris	Scots pine
Populus balsamifera	Balsam poplar
Populus tremuloides	Trembling aspen
Salix spp.	Willow spp.
Taxus spp.	Yew spp.
Thuja plicata	Western red cedar
Tsuga heterophylla	Western hemlock
Tsuga mertensiana	Mountain hemlock

Due to distinct differences in species, climate, and soils, the subalpine forests of the Sierra Nevada and Cascade and Coastal Ranges in North America will be excluded from this description (*see* **Temperate and Mediterranean Forests**: Southern Coniferous Forests; Temperate Broadleaved Deciduous Forest). Additionally, because the Appalachians are often considered temperate and because subalpine forests are only found on the highest peaks, these forests will be covered elsewhere (*see* **Temperate and Mediterranean Forests**: Temperate Broadleaved Deciduous Forest).

In western North America, subalpine forests occur along the entire length of the Rocky Mountains. These subalpine forests will be the focus of this article, where, owing to their similarities with the boreal forest, they are often referred to as mountain, taiga, or boreal forests.

The boreal forest (separate from the subalpine forest) is commonly referred to as taiga (a Russian term), or northern coniferous forest. Although it is restricted to the northern hemisphere, it forms nearly a continuous belt of coniferous trees across portions of North America and Eurasia. In Canada, it extends from coast to coast. It is bordered by the northern coniferous forest, temperate forest, or prairie to the south and tundra to the north. In Eurasia, it extends across Norway, Sweden, Finland, Russia, and Siberia, where it is bordered by tundra to the north and steppe or northern temperate forest to the south.

The boreal forest is characterized by a mosaic of coniferous genera including *Abies*, *Larix*, *Picea*, and *Pinus*, and broadleaf genera including *Betula*, *Populus*, and *Salix*. These genera occur as both pure and mixed stands across the landscape.

Subalpine Forests

While the following description focuses on subalpine forests of the Rocky Mountains, many of the characteristics are common to subalpine forests around the world.

Distribution

In Western North America, subalpine forests are found along the Rocky Mountains from as far south as Mexico to north of the Arctic Circle. The subalpine forests of the Rocky Mountains can be divided into four regional groups: Boreal, Central, Southern, and Mexican. The most northerly section, the Boreal Rocky Mountain forest (**Figure 1**), extends from Alaska south to the Peace River in Northern British Columbia. The Central Rocky Mountain forest extend south from the Peace River to Wyoming. The Southern Rocky Mountain forest extend south from Wyoming to New Mexico. The most southerly group, the Mexican Rocky Mountain forest (also sometimes called the Madrean Rocky Mountain forest), extend south from New Mexico into southern Mexico and even into the mountains of Guatemala. Most consider the Mexican or Madrean Rocky Mountain forest to be part of the southern coniferous forest, however (*see* **Temperate and Mediterranean Forests**: Southern Coniferous Forests).

Postglacial Development

Currently there is very little information on the postglacial development of subalpine forests. Although pollen cores taken from lakes reveal that pioneer species such as *Betula*, *Juniperus*, *Populus*, and *Salix* were followed after glaciation by coniferous species such as *Abies*, *Larix*, *Picea*, and *Pinus*, it is unknown whether the present forest is a recent development or has been in existence for some time. It is believed the subalpine forest reached its modern state between 6000 and 5000 years ago.

With the retreat of glaciers, *Betula* and *Picea* spp. migrated west and northwest across Canada from refugia south and southeast of the continental ice sheet. *Larix* and *Populus* spp. may have followed the

Figure 1 Subalpine forests of the Boreal Rocky Mountains.

same migration pattern. In the west, *Pinus* spp. migrated from refugia south of the ice up the Rocky Mountain Trench as the Cordilleran and Laurentide ice sheets separated. Today, the Rocky Mountain subalpine forest occurs in the steep mountainous terrain of western North America above the northern coniferous forest.

Climate

The subalpine forest is characterized by a short growing season (less than 90 growing degree days); winters are generally long with heavy snow, while summers are short, dry, and cool. The climate varies somewhat with elevation and slope position (i.e., windward versus leeward slopes); temperatures drop while precipitation, solar radiation, wind, and snow depth and duration increase with increasing elevation. As such, the subalpine forest is often divided into two subzones: the lower subalpine area (1200–1800 m elevation), which is defined by a closed forest and a relatively favorable climate, and the upper subalpine area (1800–2300 m), which is characterized by open parkland or woodland and a harsher climate. These zones are found at lower elevations in the north and at higher elevations in the south.

Soil

Subalpine forests are most frequently associated with luvisols, brunisols, and regosols. Luvisols are characterized by an accumulation of clay; conversely, brunisols and regosols are poorly developed soils. Soils of the subalpine forest are typically shallow and generally poor in nutrients. They can also be acidic, and erosion is common due to frost heaving and steep slopes.

Vegetation

Rocky Mountain subalpine forests consist mainly of conifers with a few hardy deciduous species. These forests are often viewed as a southern extension of the boreal forest, particularly in the most northerly zone, the Boreal Rocky Mountain Forest, where it is often difficult to separate the boreal forest from the subalpine forest and the northern coniferous forest. Although vegetation varies somewhat with elevation, slope position, and soil, particularly from north to south and east to west, the Rocky Mountain coniferous forests are remarkably similar in species composition and stand structure along their entire length.

The lower subalpine area is typified by a closed forest of productive *Picea engelmannii* (south of 54° N), *P. glauca* (north of 54° N), *Abies lasiocarpa*, *Pinus contorta*, and *Populus tremuloides*, whereas the upper subalpine area is typified by shorter, open grown *Abies lasiocarpa*, *Picea engelmannii*, and *P. glauca*. *Picea* and *Abies* species tend to dominate the mature forests, whereas *Pinus contorta* dominates in the drier parts of the zone where fire disturbance has occurred. At the timberline, harsh climatic conditions affect tree growth. These trees grow in clumps and are often stunted, flagged or krummholz. In the Northern Rockies, the treeline is dominated by *Larix lyallii*, whereas in the Central Rockies *P. albicaulis* and *Pinus flexilis* dominate. This area is dominated by *P. aristata* in the Southern Rockies.

Ecosystem Dynamics

Subalpine forests are disturbance driven, with a mean disturbance return interval of 150 to 350 years. Although fire is the most important form of natural disturbance in these forests, wind, insects, disease, ungulate browsing, avalanches, landslides, extreme weather, and volcanism also play a role.

Successional patterns vary from north to south along the Rocky Mountains. In the Boreal Rocky Mountain Forest, *Betula papyrifera*, *P. balsamifera*, and *Populus tremuloides* are successional following fire disturbance. *Abies* spp and *Picea glauca*. follow. The Central Rocky Mountain Forest is somewhat more variable. In general, *Pinus contorta*, *Populus tremuloides*, and *P. balsamifera* are successional following fire, whereas, *Picea engelmannii* dominates older forests, although *Abies lasiocarpa*, *Betula papyrifera*, *Larix* spp., and *P. mariana*, and are also present. *Picea engelmannii* appears on the south eastern slopes of the Central Rocky Mountain forest, while *Larix lyallii*, *Pinus albicaulis*, and *P. flexilis* appear near the timberline. On the southwestern slopes of the Central Rocky Mountain Forest, *Abies* spp., *Tsuga heterophylla*, and *Thuja plicata* are associated with *Larix lyallii*, *Picea* spp., *Pinus albicaulis*, and *Tsuga mertensiana* appear at higher elevations. The subalpine forests of the Southern Rocky Mountain forest are dominated by *Abies lasiocarpa* and *Picea engelmannii*.

Damaging Agents

Insects and disease Many species of insect and disease impact trees in the subalpine forest. Although insects such as spruce budworm (*Choristoneura* spp.), bark beetles (*Dendroctonus* spp.) and white pine weevil (*Pissodes strobi*), are the major pests to conifers of the subalpine forest, diseases such as mistletoe (*Arceuthobium* spp.), western gall rust (*Endocronartium harkenssii*), and broom rusts are also present.

Fire and wind Fires in the subalpine forest are infrequent but tend to be stand destroying, making them an important part of the successional pattern in these forests. Shallow soils are common in the subalpine forest, which make for a poor rooting medium leaving trees susceptible to windthrow.

Avalanche paths Avalanche paths are common in the subalpine forest. Recurrent slides leave many of these paths devoid of trees and dense with shrubs and herbaceous species.

Climate change Global climate change may have serious implications for subalpine forests. Although temperatures are not expected to rise higher than they have historically, the rate of change appears to be much faster than it has been in the past. Global warming of 1.0–4.5°C over the next 100 years is anticipated. It is likely that changes in precipitation patterns and carbon dioxide levels will also accompany changes in temperature. All of these changes may result in latitudinal or, to a limited extent, elevational shift in species ranges. Differences in dispersal ability may also result in changes in plant communities and competition between 'exotic' species, which could result in extinction for some species. Extinction may also occur because species cannot adapt or move fast enough under the changing conditions.

Forest management Forests in the lower subalpine area are highly productive. *Abies lasiocarpa*, *Picea glauca*, *P. engelmannii*, and *Pinus contorta* are the largest and most productive species in the subalpine forest. As such, these species are a highly valuable resource where timber harvesting is the major economic activity. These large, nature forests, however, are also highly valuable caribou habitat. In recent years, efforts have been made through alternative silviculture systems such as variable retention, shelterwoods, or group selection, to protect the structural and functional integrity of caribou habitat in these high elevation forests.

Boreal Forests

Distribution

The boreal forest (**Figure 2**) forms a circumpolar forest belt in the northern hemisphere and as such it is one of the world's largest forested areas, and a major carbon reservoir.

Postglacial Development

The majority of the area covered by the boreal forest today was once completely covered by ice. As the ice sheets melted, the land was slowly invaded by herbaceous plants and shrubs, followed by conifers. Although the distribution of boreal species was

Figure 2 The boreal forest in northeastern British Columbia.

largely a response to climate and soil, species dispersal rates and locations of refugia played a large role following glaciation. In North America, refugia existed south, west, and east of the ice. Species migration in the boreal region was similar to that of the subalpine region, with *Picea*, *Betula*, *Populus*, and *Larix* spp. migrating west and northwest across Canada and *Pinus* spp. migrating north up the Rocky Mountain Trench as the Cordilleran and Laurentide ice sheets separated. Due to the lingering ice sheets, the boreal forest in eastern Canada is believed to be younger than the boreal forest in western Canada.

Climate

The climate of the boreal forest varies somewhat between coastal and continental regions. In continental regions, winters are long, cold, and dry, while summers are short, moderately warm, and moist, whereas in coastal regions, such as eastern Canada and Scandinavia, the climate tends to be warmer and moister. In general, however, an average of 100–900 mm of precipitation falls annually and the mean annual temperature does not rise above $-0.5°C$.

Terrain and Soil

The terrain of the boreal forest is diverse. Rolling uplands are interspersed with lakes of varying sizes, bogs, and wetland communities. Bogs or peatlands are thick deposits of peat and organic soils often saturated with water that cover vast areas of the boreal forest. Bedrock outcrops, eskers, and moraines are also common.

Boreal forests are most frequently associated with podzols (spodosols). These soils are characterized by an accumulation of organic matter as well as iron and aluminum deposits. They are acidic and have low nutrient status. Other soil types commonly found in the boreal include luvisols and organics. Luvisols are defined by an accumulation of clay, whereas organic soils are composed largely of organic matter and tend to be poorly drained. Pockets of continuous and discontinuous permafrost exist throughout the boreal forest, chilling the soil above and slowing decomposition. Permafrost also forms an impenetrable layer, retarding drainage.

Vegetation

Coniferous trees dominate the boreal forest; however, hardy deciduous species such as *Betula papyrifera*, *Populus balsamifera*, and *P. tremuloides* are also common. Shrub willow (*Salix* spp.) is also very common on the wetter areas. In western North America, *Picea glauca*, *P. mariana*, *Larix laricina*, *P. banksiana*, *P. contorta*, *A. lasiocarpa*, and *A. balsamea* dominate the boreal forest, whereas, in eastern North America, *A. balsamea* forms the climax species. In Scandinavia and western Russia, *Picea abies* and *Pinus sylvestris* dominate, whereas *Abies sibirica*, *L. dahurica*, *Larix sibirica*, and *Pinus sibirica* dominate in Siberia.

The boreal forest is often divided into three latitudinal zones: closed forest, lichen woodland, and forest–tundra. The closed forest at lower latitudes is characterized by continuous northern coniferous forest with *Betula* and *Populus* spp. intermixed. Maximum tree height in these forests is about 23 m. The trees of the lichen woodland at mid latitudes are shorter and more open than those of the closed forest; however, they are not as scattered as the trees of the forest–tundra. The treeline is often found at the northern limit of the forest–tundra zone and is analogous to the treeline above subalpine forests. Temperature appears to regulate the northern and southern bounds of the boreal forest: respectively, the boundaries correspond roughly to 13°C and 18°C July mean temperatures.

The mosaic of forest communities found in the boreal forest is largely due to a response to climate, topography, the presence or absence of permafrost, soils, fire activity, as well as the reproductive capacity, vigor, and distribution of boreal tree species.

Productivity Productivity of the boreal forest is limited by low atmospheric temperatures, the presence of permafrost and low soil temperatures, thick organic layers with slow rates of decomposition, and poorly drained acidic soils with low nutrient availability. This is why it is one of the major carbon reservoirs on earth. Consequently, productivity of the boreal forest varies widely with latitude, proximity to the coast, topography, and seral stage. In general, however, productivity differs greatly from the lowlands to the uplands. The most productive sites are the lowland floodplains. These sites are dominated by *Populus balsamifera*. In contrast, *Picea mariana* sites are the least productive.

Ecosystem Dynamics

The boreal forest is disturbance driven with a mean disturbance return interval of 50–200 years in North America and 50–270 years in Sweden. Although fire is the main disturbance factor, insect outbreaks and windthrow also play a key role. These frequent and diverse disturbance regimes in conjunction with a varied environment are thought to contribute to the diversity of forest types and the range in stand productivity typical of the boreal forest.

Most boreal species have evolved with fire and have adapted their growth and reproductive strategies accordingly. These diverse responses have led to a variety of successional pathways, and a diverse landscape.

Many boreal species have adapted an even-aged growth strategy. For instance, *Pinus banksiana* and *P. contorta* have adapted to poor dry sites, whereas *Picea mariana* has adapted to poor wet sites. In both cases, the extreme environmental conditions under which these species grow and reproduce leaves them relatively free of interspecific competition.

Boreal species also vary widely in their shade tolerance, longevity, and regeneration strategies. For example, *Betula papyrifera*, *Populus balsamifera*, and *P. tremuloides* are early successional species, regenerating quickly following disturbance. As a result, however, these species are short-lived and shade-intolerant. Conversely, *Picea glauca* and *Abies* spp. are long-lived and shade-tolerant, making them keystone species in late successional and climax boreal forest types.

Indigenous Use

The indigenous people of Canada's boreal forest region have been harvesting a wide variety of natural products from the forest, to maintain their culture, for thousands of years. These products were used for a wide variety of purposes including (but not limited to) medicine, food (e.g., berries, roots, bark, small and large mammals), shelter, baskets, and clothing.

Damaging Agents

Insects and disease Insects and disease, are important components of forest ecosystem dynamics in the boreal forest. For boreal conifer species, the major pests include spruce budworm (*Choristoneura* spp.), bark beetles (*Dendroctonus* spp.), and Siberian silkworm (*Dendrolimus sibericus*), all of which can cause widespread damage. For instance, the spruce budworm has been an extensive and extended problem in northeastern British Columbia as well as in eastern Canada. White pine weevil (*Pissodes strobi*), mistletoe (*Arceuthobium* spp.), western gall rust (*Endocronartium harkenssii*), and broom rusts are also present; however, these are minor pests compared to those mentioned above.

Fire and wind Fire is an important aspect of ecosystem dynamics in the boreal forest. Fires destroy mature and overmature forests which are then replaced by new forests. Although stand-destroying fires are frequent, they tend to be small. Due to shallow rooting, boreal trees tend to be susceptible to windthrow, which opens up small gaps allowing species to regenerate in the openings.

Pollution and climate change The boreal forests of eastern North America and Europe have been severely impacted by acid deposition (i.e., acid rain). Acid rain acidifies the soil which makes it toxic to plant roots, leaving the trees more susceptible to damage from insects and disease.

As discussed for subalpine forests, global climate change may also have serious implications for boreal forests. Change may result in a northward latitudinal shift in species ranges. However, in some areas, barriers such as urban areas may limit migration. The increase in temperature could enhance soil respiration and accelerate carbon emissions from the vast stored pool of the boreal forest.

Changes in temperature and precipitation will also have an impact on disturbance mechanisms such as insects, drought, and fire, influencing their occurrence, timing, frequency, duration, extent, and intensity. For example, extended periods of drought may result in fires burning more frequently, over larger areas, and at higher intensity, further reducing carbon storage in the boreal forest.

Industrial activities Historically, boreal forests have played an important role in the economic development of northern countries. Resource extraction (e.g., trapping and forestry activities) began in the nineteenth century in Scandinavia and the twentieth century in Canada. Today, the boreal forests of North America and Europe continue to be an important region for the production of minerals, petroleum, hydroelectricity, and timber. The Siberian boreal forest is currently undergoing rapid development.

Although the majority of the boreal forest is suitable for sustainable resource extraction, industrial activities can result in the destruction of permafrost and the surrounding landscape. In Scandinavia, for example, large-scale forestry operations have transformed virtually all forested land into intensively managed secondary forests.

This emphasis on large-scale industrial resource extraction has resulted in conflicts between traditional resource users and industrial users world wide. The Temagami region of Ontario, for example, has been in dispute since the mid nineteenth century. The Teme-Augama Anishnabai people seek land claim settlements, the government seeks to establish industrial logging and mining operations in the area, and environmental groups seek to protect old-growth forests.

Subalpine and Boreal Forests: A Comparison

There are some distinct differences between subalpine and boreal forests even though in many ways they are similar. Subalpine and boreal forests both occur in the northern hemisphere, but subalpine forests are restricted to high elevation mountainous regions, while boreal forests occur at northerly latitudes. Subalpine and boreal forests likely shared similar postglacial development patterns. As the ice sheets retracted, species migrated northward and upward with continued warming and species migration from southern refugia; the northern coniferous forest established below the subalpine forest. Subalpine and boreal forests both have short growing seasons due to long winters. As the boreal is a cold biome, organic matter decays slowly and it is a major carbon sink along with the coastal temperate forest.

Subalpine forests are characterized by dry summers and snowy winters, whereas boreal forests are characterized by warm moist summers and cold dry winters. Subalpine forests occur in mountainous terrain, where soils tend to be shallow and low in nutrients. Boreal forests occur in rolling terrain with many lakes, bogs, and wetlands interspersed. Soils are also low in nutrients and permafrost can be continuous or discontinuous. This too contributes to the slow decay processes in the boreal forest. Both subalpine and boreal forests are dominated by coniferous trees with some hardy deciduous species. *Abies* and *Picea* species dominate the subalpine forest with *Pinus* species occupying the higher elevations near timberline and drier microsites. The boreal forest is characterized by a mosaic of *Abies*, *Betula*, *Larix*, *Picea*, *Pinus*, and *Populus* species. Subalpine forests become more open with increasing elevation as boreal forests do with increasing latitude. Both subalpine and boreal forests are disturbance driven, largely by fire which occurs at intervals of 150–350 years in subalpine forests and at slightly shorter intervals of 50–270 years in boreal forests. Insects, diseases, and wind also play a role in the ecosystem dynamics of both forests. Climate change is also a concern for both forest types. Changes in temperature, precipitation, and carbon dioxide levels may lead to shifts in species ranges, either latitudinally or elevationally.

Both forests are valued for their timber resources, while the boreal forest region is also valued for minerals, petroleum, and hydroelectricity, as well as for indigenous peoples' needs. Consequently, environmental groups are increasingly interested in protecting the boreal forest from such industrial activity as well as implementing actions to minimize the effects of global warming. Loss of the boreal forest could have serious global consequences, including impacts on the economy, the atmosphere, and the water supply.

See also: **Ecology**: Natural Disturbance in Forest Environments. **Environment**: Impacts of Elevated CO_2 and Climate Change. **Temperate and Mediterranean Forests**: Northern Coniferous Forests. **Temperate and Mediterranean Forests**: Southern Coniferous Forests; Temperate Broadleaved Deciduous Forest. **Temperate Ecosystems**: Alders, Birches and Willows; Pines; Spruces, Firs and Larches.

Further Reading

Billings WD (1990) The mountain forests of North America and their environments. In: Osmond CB, Pitelka LF, and Hidy GM (eds) *Plant Biology of the Basin and Range*, pp. 17–86. New York: Springer-Verlag.

Bonnan GB (1992) Processes in boreal forests. In: Shugart HH, Leemans R, and Bonan GB (eds) *A Systems Analysis of the Global Boreal Forest*, pp. 9–12. New York: Cambridge University Press.

Brown S (1990) Structure and dynamics of basin forested wetlands in North America. In: *Ecosystems of the World*, vol. 15, *Forested Wetlands*, pp. 171–199. New York: Elsevier.

Critchfield WB (1985) The late Quaternary history of lodgepole and jack pines. *Canadian Journal of Forest Research* 15: 749–768.

Elliott-Fisk DL (2000) The taiga and boreal forest. In: Barbour MG and Billings WD (eds) *North American Terrestrial Vegetation*, 2nd edn, pp. 41–73. New York: Cambridge University Press.

Gawthrop D (1999) *Vanishing Halo*. Vancouver, Canada: Greystone Books.

Henry JD (2002) *Canada's Boreal Forest*. Washington, DC: Smithsonian Institution Press.

Larsen JA (1980) *The Boreal Ecosystem*. New York: Academic Press.

MacDonald GM (1987) Postglacial development of the subalpine–boreal transition forest of western Canada. *Journal of Ecology* 75: 303–320.

Peet RK (2000) Forests and meadows of the Rocky Mountains. In: Barbour MG and Billings WD (eds) *North American Terrestrial Vegetation*, 2nd edn, pp. 75–121. New York: Cambridge University Press.

Pielou EC (1988) *The World of Northern Evergreens*. Ithaca, NY: Cornell University Press.

Pielou EC (1991) *After the Ice Age*. Chicago, IL: University of Chicago Press.

Pojar J (1996) Environment and biogeography of the western boreal forest. *Forestry Chronicle* 72(1): 51–57.

Temperate Broadleaved Deciduous Forest

P S Savill, University of Oxford, Oxford, UK

Introduction

Deciduous temperate forests (sometimes called summer-green forests) are dominated by broadleaved trees which lose their leaves during winter. They constitute the main potential natural vegetation over much of temperate Europe, eastern Asia, and northeastern North America, and also appear in some climatically comparable, but much smaller, regions in the southern hemisphere. Owing to the deciduous habit of the main dominants and the characteristic dying-down of many of the associated plants as the trees come into leaf, these forests look entirely different in spring, summer, autumn, and winter. The deciduous habit is a strategy to deal with the lack of sunlight and cold temperatures in winter.

The regions potentially occupied by temperate broadleaved deciduous forest are among the most densely populated on earth and much of the original forest has been cleared. Only patches remain, few of which approach a truly natural condition, but many retain a seminatural character. Most of the earliest civilizations emerged in places with Mediterranean climates, and this led to early large-scale destruction of their forests. By the Middle Ages, the most important forest left in Europe was the broadleaved deciduous one. However, clearance of this was already widespread and more was lost or altered over the ensuing centuries. The fertile former forest ground was ideal for agricultural use as arable or pasture land. In some cases, the depredations of domestic animals were sufficient to prevent trees from regenerating and transformed these forests to grasslands.

Distribution

Temperate broadleaved deciduous forests occur in three major zones. In western and central Europe they extend across Poland and central Russia, down the mountain chains of southern Europe and into Asia minor; eastern Asia, including eastern China, Korea and Japan; and eastern North America. There is a smaller zone in South America (**Figure 1**).

1. In western and central Europe the temperate deciduous forests occur from the Atlantic coast, northwards to almost 60° N, eastwards to the Ural mountains of central Russia and down into the Caucasus and Elburz mountains of northern Iran, and southwards at higher altitudes in central Spain, southern Italy, and Greece. The tree and shrub composition is relatively poor to the north, with many species having failed to return after past glaciations. In many parts of Europe (e.g., the

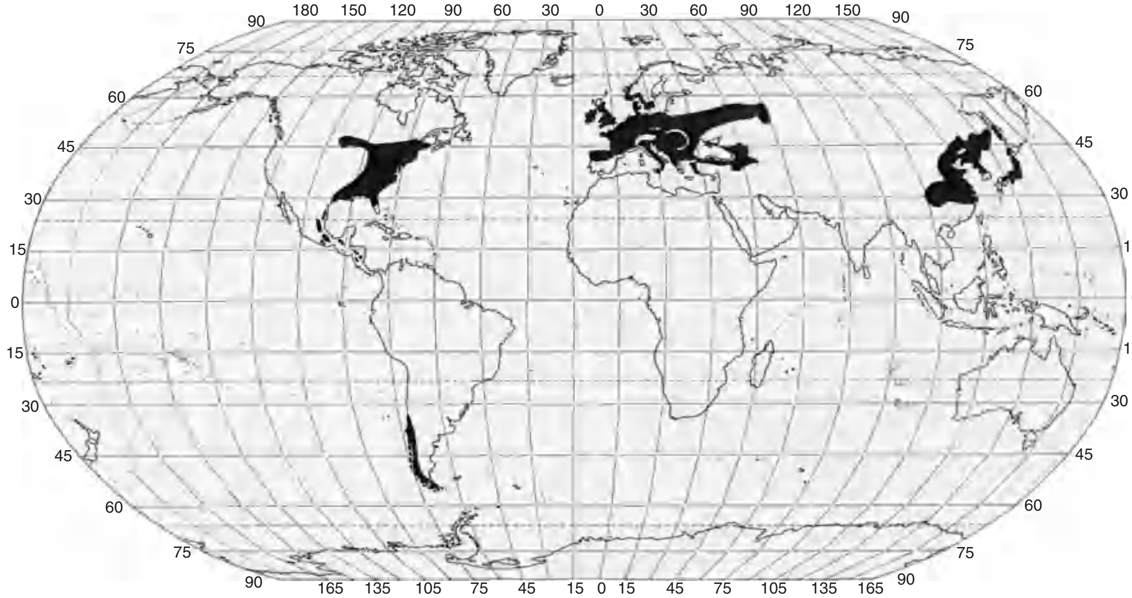


Figure 1 Distribution of temperate deciduous forests. Reproduced with permission from Röhrig E and Ulrich B (eds) (1991) *Ecosystems of the World*, vol. 7, *Temperate Deciduous Forests*. London: Elsevier.

UK and Ireland), no truly natural woodland at all has survived. As elsewhere, prehistoric people cleared the majority of the original natural forests.

2. In northern Japan and adjacent parts of eastern continental Asia, the forests lie mostly between 30° and 50° N, extending to 125° E in the northwest, and 115° E in the southwest. In China intensive agriculture has caused this region to be largely cleared of natural vegetation for at least 4000 years.
3. In eastern North America, the forests lie in a belt from the coast, northwards to between around 35–48° N, and to the Great Lakes, and west to beyond the Mississippi. Almost all the forests of eastern North America are second growth, the original forest having been cleared by early settlers, but they contain a great diversity of flora and fauna. This is especially true of the Appalachian plateau of eastern Kentucky and Tennessee which was never glaciated, and western North Carolina and Virginia. The Great Smoky mountains have been designated a world biosphere reserve to help protect the rich assortment of species.
4. In the southern hemisphere, there is a small area of temperate deciduous forest in Chile and southwestern Argentina between 35° and 55° S, and in Tasmania. The majority of southern deciduous forests are located in Chile where they extend from higher altitudes on the Coastal and Andean mountain ranges of central–southern Chile to temperate cold-humid climates in Patagonia and Tierra del Fuego. Since colonial times the forests of central–southern Chile have been under intense pressure for transformation to agricultural and pasture uses and, more recently, for the establishment of fast-growing exotic forest plantations.

Figure 2 Beech (*Fagus crenata*) in Ishikawa Prefecture, Japan, in autumn. The dark-green evergreen trees are *Cryptomeria japonica* and *Pinus parviflora*. Courtesy of Koso Saito.

Figure 3 Beech (*Fagus sylvatica*) woodland in winter in Belgium. The trees are leafless, and no green ground vegetation can be seen. Even in summer it is sparse in this type of woodland where the trees cast a very heavy shade.

Climate and Seasonal Changes in the Forest

Most temperate deciduous forests have mild, damp climates, with average temperatures in the coldest months of between 18° and −30°C. Monthly average temperatures in the warmest months are greater than 10°C, but seldom exceed 22°C. Precipitation is reasonably well distributed throughout the year, totaling 750–1500 mm or more. The growing season is about 6 months or a little longer, and never less than 4 months.

No other ecosystem is characterized by such marked seasonal changes as the temperate deciduous forest. It has four distinct seasons, spring, summer, autumn, and winter (**Figures 2–5**). In the autumn (late August to early October) the leaves change

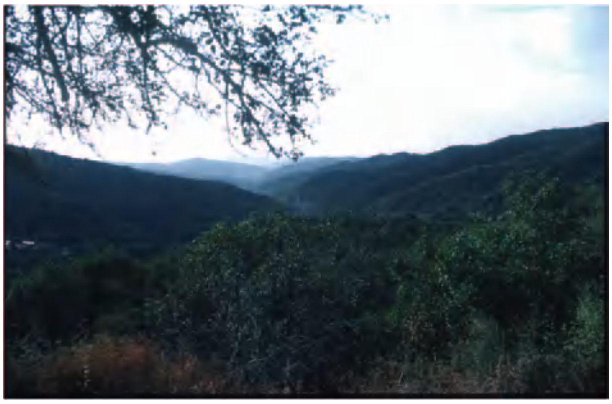


Figure 4 Walnut (*Juglans regia*) forest in summer in Kyrgyzstan. All the canopy trees in this picture are walnuts. The lower shrub/small tree stratum consists of fruit trees, including apples (the ancestors of many cultivated apples), plums and *Crataegus* species. Courtesy of Gabriel Hemery.

Figure 5 Spring in oak (*Quercus robur*) woodland in southern England. Spectacular displays of bluebells (*Hyacinthoides non-scripta*) are characteristic of many of these woods.

color and fall off the trees. During the winter months nearly all the trees are leafless; only a few species (e.g., holly – *Ilex aquifolium*) retain their foliage.

In spring, the ground vegetation becomes active first, including many herbs with perennial bulbs, tubers, or corms. They exhibit a distinct seasonality, taking advantage of the brief period of maximum light to flower very early in spring, before the leaves of the trees expand and cut most of it off. They flower and fruit rapidly and die down soon afterwards, as in the case of the lesser celandine (*Ranunculus ficaria*), and bluebell (*Hyacinthoides non-scripta*). Other species such as yellow archangel (*Lamiastrum galeobdolon*) appear somewhat later while the trees' leaves are expanding. Activity in the ground vegetation is followed by the shrubs, and then the trees. Buds burst and the leaves expand quickly, as soon as temperatures become suitable. In Europe and North America, bud burst progresses from the south to the north and from the more maritime to the more continental regions. The foliage is fully developed early in the season, so little photosynthetic time is lost. Flowering of trees also tends to be completed early, giving ample time for the development and ripening of the fruit. In a few species, the flowers open before the leaves expand (e.g., *Corylus* and *Populus*), allowing freer access for the wind and insects for pollination. Most trees flower at the time the leaves begin to expand in spring; very few (like *Tilia*) flower in summer. Spring also sees many insects, and in America a few mammals emerge from hibernation; many birds breed in deciduous woodlands, and later various summer-migrant birds arrive.

During summer the leaves of the trees are fully grown and form a dense canopy that keeps the forest interior shady but cooler and more humid than in the open. Various shade-bearing lower plants are adapted to tolerate the low level of light, and make use of occasional sun flecks (e.g., wood sorrel (*Oxalis acetosella*)). Insect life is abundant, with plant leaves, nectar, and sap providing rich supplies of food – in turn, these provide food for resident and migrant birds and mammals.

Autumn can be the most visually striking season of all in some regions, offering brilliant displays of leaves: reds of maples, yellows of birches, and oranges of various other species. The change in color, triggered by shortening day length, is caused by the cessation of chlorophyll synthesis (the green pigment in leaves), and breakdown of existing chlorophyll. This unmasks the other colored pigments in the leaves which are phenolic compounds that are present all the time. They have two functions: (1) being unpalatable and relatively indigestible, they provide leaves with a partial means of resistance to attacks by damaging fungi and leaf-eating insects; and (2) they act as filters to ultraviolet light and prevent damage to the leaves from it. The main pigments are anthocyanin, which gives the glowing reddish colors (bluish purple to scarlet), depending on the acidity of the cell sap, and carotene and xanthophyll, which give the orange and yellow colors.

The actual colors particular trees assume depend upon the mixture of the particular pigments in the leaves. The variety of colors both between and within species is due to the slightly varying strategies trees adopt to provide protection from potential predators and fungi. Some species are dependable in producing good colors almost every year; others are spectacular quite irregularly. Some species change to only one color (e.g., birches and some maples turn yellow; *Acer palmatum* red). Others show every tint from purple to yellow (e.g., cherry).

Autumn is also the time when most trees and shrubs produce fruit. Some species, especially oaks, have 'mast' years. These occur periodically in, say, one year in 4 or 5 when vast numbers of acorns are produced. This glut of food is conserved by squirrels, woodpeckers, and jays by burial in the soil or in holes in trees.

Winter is a period of dormancy for many species of trees and also ground vegetation, insects, and some mammals. Some species of birds migrate instead.

Why be Deciduous?

In comparison with the evergreen leaves of conifers, deciduous leaves are very efficient users of solar energy. They have higher photosynthetic rates per unit dry weight of leaf than the perennial evergreen leaves found on many conifers (about 10–14 mg $CO_2\,g^{-1}\,h^{-1}$ compared to 4–6 mg $CO_2\,g^{-1}\,h^{-1}$ in conifers). They are also much less expensively constructed in terms of content of assimilated carbon so that a proportionally larger part of the carbon gain by the tree, due to photosynthesis, is available for the growth of the nonphotosynthetic stems, roots, and fruits. A deciduous habit is very effective at making trees competitive if the growing season is at least 4 months in duration, where the climate is relatively humid, and where soil water and nutrients are readily available. In such environments the trees can produce sufficient photosynthate for at least the year's maintenance, growth, and reproduction, and they are competitive with evergreens. Shedding thin deciduous leaves in winter and the protection of meristems from water loss represents a considerable energy saving compared to maintaining a mass of thick evergreen leaves over winter. However, when the growing season becomes unduly restricted by winter cold or a long dry season, and on soils with low mineral resources, evergreen leaves can be an advantage.

This is because they are retained for several years. The evergreen habit enables leaves that are already on the tree to contribute to photosynthetic gain as soon as environmental conditions are suitable, even if the new leaves flush relatively late. They can also store nutrients in excess of current requirements for later use. The disadvantage of being evergreen is that the carbon input, or cost of constructing the leaves, is much higher than for deciduous leaves. It takes several years for a substantial leaf biomass to accumulate. The high structural cost provides protection against heat, cold, desiccation, and possibly predation and can be justified if the leaves serve for long periods but the trees have to accumulate leaf biomass over several years before fast rates of growth are achieved. Some evergreen trees are more competitive than deciduous ones in temperate deciduous climates where soils have few mineral resources and are drought-prone. Thus pines are often found on sandy soils in these regions. For example, *Pinus rigida* is the dominant pine in the New Jersey Pine Barrens, and Scots pine (*P. sylvestris*) is found on the heathlands in much of western Europe. Evergreens also predominate in boreal climates and can be very productive in climates with prolonged droughts such as in tropical monsoon and Mediterranean regions.

Because of leaf retention, there is often a much greater leaf biomass, or leaf area index (LAI), in evergreen forests. (LAI indicates the area of leaves per unit area of ground, and is indicated in units of square meters of leaf per square meter of ground.) For example, the LAIs in deciduous forests are typically between 4 and 7 whereas among evergreen conifers they can range up to 20.

Soil

Brown forest soils (alfisols, in the American soil taxonomy) develop under temperate broadleaved deciduous forests. These are among the most fertile, most easily worked, and most easily cleared of the temperate zone soils. Many have been under continuous cultivation since Neolithic times. Some of the world's major agricultural regions are found in the temperate deciduous forest zone, which is why there are so few of the original deciduous forests left. Part of the reason for their fertility is that most soils in the temperate deciduous forest zones are relatively young, having started to develop (in North America and Europe) after the last glaciation, about 12 000 years ago. They are therefore relatively rich in nutrient elements compared with, for example, most tropical rainforest soils, which are much older.

The leaves of deciduous broadleaved trees retain the major nutrient bases when they drop in the autumn. Thus the litter under this forest is not as acidic as under evergreen trees and aluminum and iron are not mobilized from the A horizon. The autumn leaf fall provides an abundant and rich organic matter which begins to decay rapidly in spring just as the growing season begins. The organic content gives both the A and B horizons a brown color.

Ultisols replace alfisols in the southeastern USA, where the older soils of unglaciated regions have been weathered to a much greater degree and are more completely leached than the younger soils to the north. Distinctive red or yellow subsoils have developed under the warmer climate. Ultisols are generally less fertile than alfisols.

Productivity

The productivity of temperate deciduous forests tends to be higher in the southern part of its range (in the northern hemisphere), and generally at lower elevations. However, since climate and light levels are broadly similar, net productivity is controlled primarily by local variations in nutrient and moisture regimes, as well as the inherent capacities of the various species to grow.

Productivity of the trees in stable temperate deciduous forests is usually quoted as around 10–12 dry $t\,ha^{-1}\,year^{-1}$. Young stands on productive sites can achieve as much as 25 $t\,ha^{-1}\,year^{-1}$. The average usable production of wood is usually considered to be about 40% of net primary production, giving levels of 4–5 dry $t\,ha^{-1}\,year^{-1}$. Total above-ground biomass in mature forests is 150–400 $t\,ha^{-1}$. In addition, in unmanaged forests, there may be about 20% of this volume lying as dead wood on the forest floor.

Strata

Most temperate deciduous forests have closed canopies, but open stands occur as well, particularly where the climate is dry and/or large grazing animals are abundant. Trees usually form only a single main stratum, story, or layer, though there may be an understory of shrubs, medium-sized trees, and saplings below.

These forests are among the most intensively managed in the world, so often they comprise only a single layer of developing overstory trees. Although natural temperate deciduous forests are more structured, they still tend to be far less luxuriant than moist tropical forests. Typically they consist of:

1. An overstory tree stratum, 20–35 m high, dominated regionally by various combinations of a rather limited number of genera.
2. A moderately developed subcanopy, mixed with but below the overstory and containing dying light-demanding trees and suppressed shade-tolerant trees; the latter can include younger specimens of the tall trees, but also medium-sized species such as (in Virginia, northeast USA) the Allegheny serviceberry (*Amelanchier arborea* var. *laevis*) and (in western Europe) the wild service tree (*Sorbus torminalis*) or field maple (*Acer campestre*).
3. An understory or shrub layer, including shrubs, smaller species of trees, and/or saplings of the taller trees. Species usually limited to this layer include (in Europe) hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*), and holly (*Ilex aquifolium*). This stratum is most noticeable when the tree stratum is not well developed; when it is, the development of shrubs and regeneration beneath it is scanty and may be missing altogether.
4. A low-growing herb layer of perennial forbs that flower in early spring; and sometimes, a ground layer mainly of mosses; lichens and mosses also grow on the trunks of trees.

The tree stratum occasionally consists of pure or nearly pure stands, with only slight differences in age (e.g., *Fagus sylvatica* in Europe). Mixed-species stands that are more or less even-aged and composed predominantly of late successional species (e.g., *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia* and *Tilia americana*) are common in northeastern North America. More mixed-age forests occur, for example, in the oak-dominated forests of Europe, with hornbeam (*Carpinus betulus*) and other species as an understory. Truly all-aged forests are found where a strongly continental climate or very moist or very dry soils prevent the dominance of any species with a high degree of shade tolerance.

Climbers such as ivy (*Hedera helix*), honeysuckle (*Lonicera periclymenum*) in Europe, and wild grape (*Vitis* spp.), poison ivy (*Rhus* spp.), and Virginia creeper (*Parthenocissus quinquefolia*) in North America climb the trees to flower and fruit high in the forest canopy. However, they are relatively few in number.

Tree Flora

Many tree genera are common to all three of the northern hemisphere temperate deciduous forest zones. Included among them are *Acer* (maple), *Castanea* (chestnut), *Fagus* (beech), *Juglans* (walnut), *Quercus* (oak), *Tilia* (basswood or lime), and *Ulmus* (elm). Different species of the genera occur on each continent. In South America, *Nothofagus* is a common genus (**Figure 6**).

In other respects, the climatic changes and successive glaciations during the Pleistocene, which gave rise to repeated migrations of the flora, have

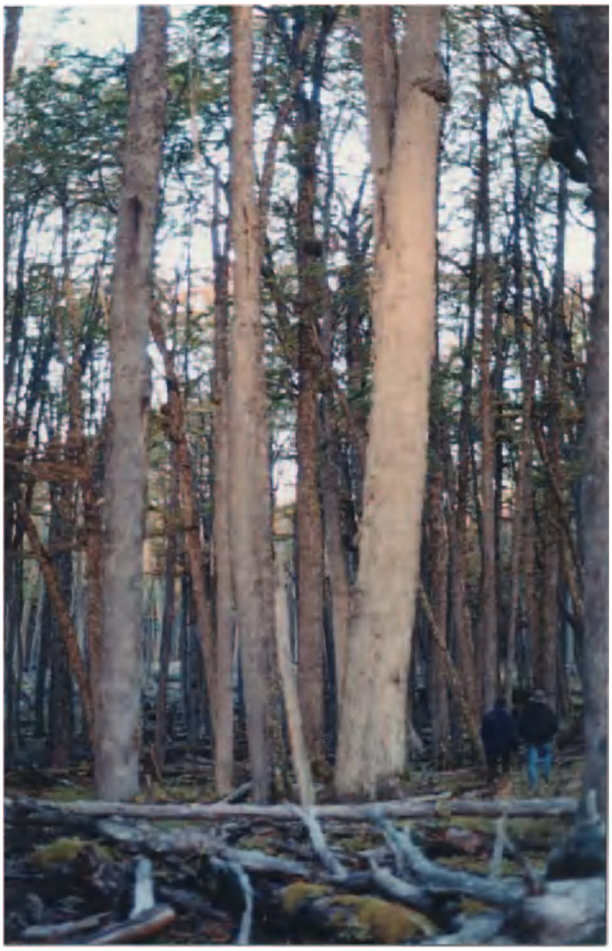


Figure 6 Dense and apparently undisturbed *Nothofagus pumilio* forest in autumn, Tierra del Fuego, Chile. Courtesy of Franz-E Arnold.

resulted in substantial differences in the floras of deciduous forests. In North America and eastern Asia migrations were relatively unaffected by the large north–south mountain ranges (e.g., the Rocky Mountains and Appalachians), whereas the east–west ranges in Europe reduced the opportunities for plants to retreat to warmer regions and recolonize during interglacial periods. As a result, there are far fewer genera and species in Europe compared with eastern Asia and North America and, because of this, the relatively few European species tend to be more dominant due to the lack of competitors.

Although they naturally intergrade, as well as vary in detail, a number of main types of deciduous temperate forests are usually recognized:

- Western and central European oakwoods tend to be relatively open and light. The dominant species are the pedunculate and sessile oaks (*Quercus robur* and *Q. petraea*). Associated trees that are more or less common according to the nature of the soil include ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*), birch (*Betula pendula* and *B. pubescens*), elm (*Ulmus glabra, U. procera, U. carpinifolia*), lime (*Tilia cordata, T. platyphyllos*), cherry (*Prunus avium*), alder (*Alnus glutinosa*), and aspen (*Populus tremula*). Small trees and large shrubs include hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*), field maple (*Acer campestre*), crab apple (*Malus sylvestris*), and three species of *Sorbus* (rowan, wild service tree, and whitebeam). There are also two evergreens, yew (*Taxus baccata*) and holly (*Ilex aquifolium*).
- The more luxuriant forests of eastern North America, eastern Asia, and southeastern Europe/Asia minor differ in species composition but are similar in appearance. The principal species usually include various oaks (*Quercus* spp.), beeches (*Fagus* spp.), birches (*Betula* spp.), hickories (*Carya* spp.), walnuts (*Juglans* spp.), maples (*Acer* spp.), limes (*Tilia* spp.), elms (*Ulmus* spp.), ash (*Fraxinus* spp.), tulip trees (*Liriodendron* spp.), sweet chestnuts (*Castanea* spp.), and hornbeams (*Carpinus* spp.). The lower stories are normally more luxuriant and varied than in the western and central European forests. In the colder eastern and more northern parts of North America, conifers such as *Pinus strobus* begin to appear with the deciduous trees.
- Beech forests which, especially in Europe, with the very shade-tolerant *Fagus sylvatica* form almost uniform, closed canopies and cast such dense shade that few shrubs or herbs can grow. Similar types, though on a smaller scale, are found with *F. orientalis* in Turkey and other parts of its range, and with *F. crenata* in Japan. In the higher mountains of central and southern Europe, the conifers *Abies alba* and *Picea abies* become admixed.
- Southern beech, especially *Nothofagus nervosa* (syn. *N. procera*) and *N. obliqua*, usually with associated evergreens such as *Laureliopsis philippiana, Laurelia sempervirens*, and *Persea lingua*. Numerous ferns and bryophytes are features of these forests.
- The damper deciduous woodlands, especially those on marshy ground, are dominated by alders (*Alnus* spp.), willows (*Salix* spp.), poplars (*Populus* spp.) and birches (*Betula* spp.). The understories may be dense, and climbers and epiphytes numerous.

See also: **Forest Ecosystems**: Fagaceae (Oaks, Beeches, Hickories and Nothofagus); Juglandaceae (The Walnut Family: Walnuts, Hickories, Pecans). **Plant Diversity in Forests**. **Genetics of Oaks**.

Further Reading

Ford Robertson FC (ed.) (1971) *Terminology of Forest Science, Technology, Practice and Products*. Washington, DC: Society of American Foresters.
Helms JA (ed.) (1988) *The Dictionary of Forestry*. Bethesda, MD: Society of American Foresters; and Wallingford, UK: CABI Publishing.
Packham JR, Harding DJL, Hilton GM, and Stuttard RA (1992) *Functional Ecology of Woodlands and Forests*. London: Chapman & Hall.
Peterken GF (1996) *Natural Woodland: Ecology and Conservation in Northern Temperate Regions*. Cambridge, UK: Cambridge University Press.
Polunin N (1960) *Introduction to Plant Geography and Some Related Sciences*. London: Longman.
Röhrig E and Ulrich B (eds) (1991) *Ecosystems of the World*, vol. 7, *Temperate Deciduous Forests*. London: Elsevier.
Walter H (1979) *Vegetation of the Earth and Ecological Systems of the Geo-Biosphere*. New York: Springer-Verlag.

Mediterranean Forest Ecosystems

B Fady, Institut National de la Recherche Agronomique, Avignon, France
F Médail, Université d'Aix–Marseille III, Aix-en-Provence, France

Introduction

Occupying only 2% of the world's surface area, the Mediterranean biome contains nearly 20% of the earth's total plant diversity, making the five regions of the world under a Mediterranean climate (the Mediterranean Basin, California, the South African Cape Province, south and southwestern Australia, and parts of central Chile) a very significant biodiversity hot spot, second only to tropical regions (**Figure 1**). Strong biogeographical, environmental and human-made constraints have shaped this structural and functional diversity. The most typical characteristics of Mediterranean forests, compared to temperate or boreal forests, are their spatial and temporal complexity and heterogeneity, not only in terms of the physical factors (geography, geology, geomorphology, pedology, and bioclimate) that prevail where they grow, but also in terms of their biological components and attributes: functional dynamics at local and landscape levels, floristic and faunistic composition, richness and biogeographic origins.

Mediterranean forests represent 1.8% of world forest area. In this article, we will focus our attention on forests of the largest Mediterranean region of the world, the Mediterranean basin, where historical and paleogeographical episodes, long-term human influence, and current geographical and climatic contrasts have created both high species and ecosystemic diversity and heterogeneity. A short comparative overview of all world Mediterranean forests will also be presented.

Definition of Mediterranean Forests

The Mediterranean Climate: A Strong Driver for Forest Type Diversity

The Mediterranean region *sensu stricto* is usually defined by its climate, which in turn is responsible for its flora. It stretches between the northern latitudes of

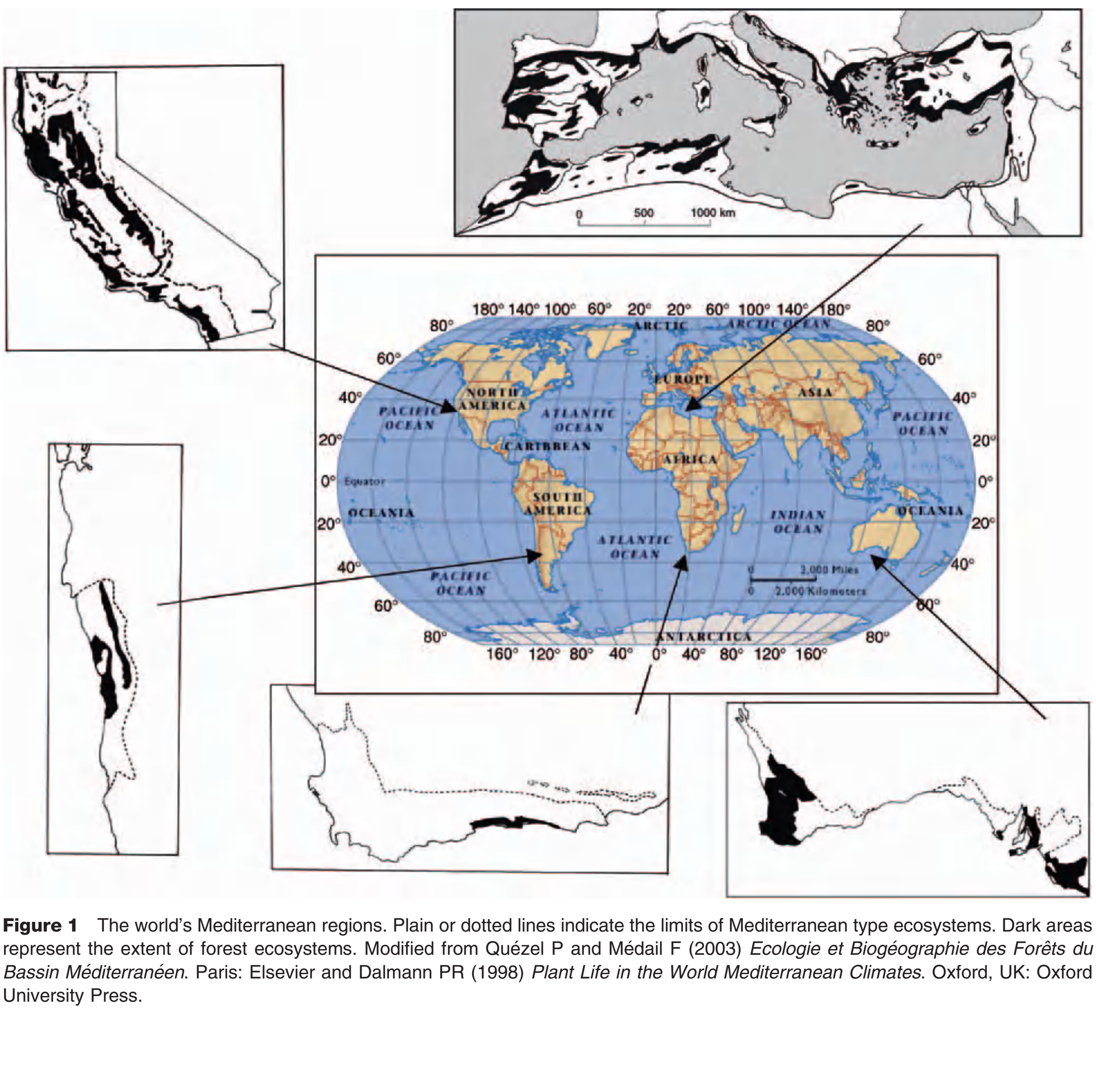


Figure 1 The world's Mediterranean regions. Plain or dotted lines indicate the limits of Mediterranean type ecosystems. Dark areas represent the extent of forest ecosystems. Modified from Quézel P and Médail F (2003) *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen*. Paris: Elsevier and Dalmann PR (1998) *Plant Life in the World Mediterranean Climates*. Oxford, UK: Oxford University Press.

25° and 45° over approximately 2 300 000 km^2. The originality of the Mediterranean climate, which is transitional between temperate and dry tropical climates, lies in the existence of a combined dry and hot summer period of variable length, which imposes a strong water stress on the vegetation during its growing season.

Mean minimum temperatures of the coldest month (m) are often used to define climatic subdivisions (**Table 1**). These values are correlated with elevation and to a lesser extent with increased latitude and continentality. In most places, m is between 0 and +3°C although extremes can reach +8 to +9°C in desert margins and −8 to −10°C on the highest mountains. This large-scale potential gradient is often locally modified by rainfall, soil type, and millennia-long human impact which has durably affected ecological equilibrium. The distribution of Mediterranean forest species is also shaped by irregular events such as late spring below freezing temperatures and absolute minimum temperatures. For example, the extremely cold winters of 1956 and 1985 contributed to determine the distribution of the olive tree (*Olea europaea*), Aleppo pine (*Pinus halepensis*), and holm oak (*Quercus ilex*) in the northern Mediterranean.

Rainfall is extremely variable among the Mediterranean regions, with mean annual values ranging from 100 to 2000 mm. The lowest values are found at desert margins especially in North Africa and the Near East. Below 100 mm per year is the borderline between the Mediterranean and the desert climates. Rainfalls higher than 1500 mm are mostly found on coastal mountain ranges. Rainfall plays an essential role in the organization of Mediterranean forests and can be used to define six different bioclimatic types (**Table 2**). Rainfall can also be extremely variable from year to year, which increases vegetation water stress, especially south of the Mediterranean.

Main Characteristics and Functional Definition

In the Mediterranean region, both open and closed canopy tree populations are considered to be forests. Closed canopy forests are similar in structure to temperate forests, such as those most common in Europe, where the undergrowth is limited and contains mostly shade-tolerant herbaceous species. Open canopy forests have few trees and their undergrowth is limited to a few or no forest-type herbaceous species. For ecological and functional reasons (see 'Current vegetation types' below), all Mediterranean ecosystems of more than 0.5 ha, where tree density is over 10% and tree height can reach over 5 m, are considered to be forests by the Food and Agriculture Organization (FAO) of the United Nations.

Mediterranean forests are less productive than the average world forests. The most productive ones are located in southern Europe, which contains more than 80% of total Mediterranean tree standing volume (**Table 3**).

Most comparative ecological and ecophysiological studies have shown that plant communities in the five Mediterranean regions of the world demonstrate similar strategies to resist climatic and edaphic stress as well as natural and human disturbances, such as wild fires. Sclerophylly (evergreen leaves coated with a thick cuticule) is one such common and widespread strategy. Other strategies include resprouting after disturbance, disturbance-dependent seed production and germination, complex root systems, cellular tolerance to low water potentials or high secondary compound production (e.g., terpenes).

Table 1 Vegetation levels showing the correspondence between temperature variants and dominant (and frequent) woody types of the Mediterranean basin

Vegetation level	*Temperature variant*	m *(°C)*	*T (°C)*	*Dominant woody species*
Infra-Mediterranean	Very hot	> +7°C	> +17°C	*Argania*, *Acacia gummifera*
Thermo-Mediterranean	Hot	+3 to +7°C	> +17°C	*Olea*, *Ceratonia*, *Pinus halepensis* and *P. brutia*, *Tetraclinis* (*Quercus*)
Meso-Mediterranean	Temperate	0 to +3°C	+13 to +17°C	Sclerophyll *Quercus*, *Pinus halepensis* and *P. brutia*
Supra-Mediterranean	Cool	−3 to 0°C	+8 to +13°C	Deciduous *Quercus*, *Ostrya*, *Carpinus orientalis* (*Pinus brutia*)
Mountain-Mediterranean	Cold	−7 to −3°C	+4 to +8°C	*Pinus nigra*, *Cedrus*, *Abies*, *Fagus*, *Juniperus*
Oro-Mediterranean	Very cold	< −7°C	< +4°C	*Juniperus*, prostrate spiny xerophytes

m, mean minimum temperatures of the coldest month; T, mean annual temperature.
Data from Quézel P and Médail F (2003) *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen*. Paris: Elsevier.

Table 2 Types of bioclimates and their theoretical correspondence with the main vegetation types of the Mediterranean basin

Bioclimate	*Mean annual rainfall (for m = 0°C)*	*Number of months without rainfall*	*Main vegetation type*
Per-arid	<100 mm	11 to 12	Saharan
Arid	100 to 400 mm	7 to 10	Steppe and pre-steppe *(Juniperus turbinata*, *Pinus halepensis*, *Pistacia atlantica)*
Semi-arid	400 to 600 mm	5 to 7	Pre-forest *(Pinus halepensis*, *P. brutia*, *Juniperus* spp., *Quercus)*
Subhumid	600 to 800 mm	3 to 5	Forest (mostly sclerophyll *Quercus*, *Pinus halepensis*, *P. brutia*, *P. pinaster*, *P. pinea*, *P. nigra*, *Cedrus)*
Humid	800 to 1000 mm	1 to 3	Forest (mostly deciduous *Quercus*, *Pinus brutia*, *P. pinaster*, *P. nigra*, *Cedrus*, *Abies*, *Fagus)*
Perhumid	>1000 mm	less than 1	Forest (deciduous *Quercus*, *Cedrus, Abies, Fagus)*

m, mean minimum temperatures of the coldest month.
Data from Quézel P and Médail F (2003) *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen*. Paris: Elsevier.

Table 3 Distribution of forest volume and surface area among the three ecoregions of the Mediterranean basin

Region	*Mean biomass volume ($m^3\,ha^{-1}$)*	*Surface area, in 2000 ($ha \times 10^6$)*	*Forest area in the major forested countries of each region (%)*
Middle East	66	11	Turkey (90%)
North Africa	35	6.1	Morocco (50%) Algeria (35%)
Southern Europe	100	30	Spain (30%) Italy (25%) Greece (10%)

Data from Food and Agriculture Organization.

Forest Paleoecology: Current Biodiversity Explained by History

Pre-Pleistocene History: The Mixing of Floras of Different Origins

The current flora of the Mediterranean region arises from several biogeographic origins. Its coniferous flora diversified during the Cretaceous. Its angiosperm flora diversified during the early Tertiary, when the Mediterranean region was situated at the crossroads between Laurasia and the remains of Gondwana. Thus it includes tropical elements, mostly of African and Asian lineages, as well as extratropical elements, of autochthonous and northern lineages. This complex geological-scale paleogeography is one of the reasons that the Mediterranean has such a high plant biodiversity and woody species endemism. Two different lineage groups can be described for angiosperms:

1. A **pre-Pliocene group**, consisting of mostly sclerophyll taxa which resprout from stumps after disturbance (fire, clearance) and are often found in the most complex stages of ecosystem dynamics (e.g., *Arbutus unedo, Olea* spp., *Quercus* spp.).
2. A **post-Pliocene group**, including nonsclerophyll taxa which are obligate seeders after disturbance and are mostly found in the less advanced stages of ecosystem dynamics (e.g., *Cistus* spp., *Lavandula* spp.). These taxa successfully diversified and competed with taxa of the pre-Pliocene group due to their short life cycle, high seed production, and ecological plasticity towards the highly fluctuating Mediterranean bioclimatic cycles.

Strategies considered as typically Mediterranean could thus have emerged at the end of the Tertiary under a tropical climatic regime well before the advent of the Mediterranean climate, at the beginning of the Quaternary. Similarity between Mediterranean woody plants could be due more to phylogenetic inertia than to common adaptive strategies. The ability of Mediterranean woody species to resprout after fire, for example, does not originate from an adaptation to recurrent fires, but rather from an older adaptation to herbivory.

From Glacial Refugia to Current Distribution: Holocene Recolonization Pathways around the Mediterranean

In the more recent past, Mediterranean glacial refugia have played a key role in shaping the current genetic diversity of woody species and the spatial distribution of the main forest ecosystems around the Mediterranean and in Europe. Refugia are territories somewhat sheltered from the climatic disturbance of the most recent ice age (Würm) where plants survived the effects of the last glacial maximum (about 20 000 years ago). They contributed to the forest recolonization process that started approximately 13 000 years ago and lasted throughout the Holocene. They are responsible for the high floristic diversity of Mediterranean forests (compared to that of temperate European forests). Glacial refugium distribution estimated using paleoecological and phylogeographical data matches that of current high floristic richness and high endemism and rare woody species hot spots around the Mediterranean.

The main regions where temperate and thermophilous forest species survived around the Mediterranean are the Iberian, Italian, and Balkan peninsulas, the Black Sea region, some areas in North Africa, and the largest Mediterranean islands. Territories that link these primary refugia, such as the south of France and the borders of the Adriatic Sea (Slovenia and Croatia), possibly acted as secondary refugia. These refugia were characterized by high species richness. Once climatic conditions became truly favorable, the expansion of a highly diversified deciduous forest could happen rapidly over large territories, such as in the Pindos mountains in northwestern Greece where over 20 deciduous woody species could already be found in the early Preboreal (about 10 000 years ago). Some tree genera such as *Pinus*, *Quercus*, and *Corylus* seem to have been present in all southern European refugia, although others had a clear geographic distribution, e.g., *Abies alba, Fagus sylvatica* and *Carpinus* in the Italian and Balkan refugia (possibly in Spain as well), and *Tilia* and *Ulmus* in the eastern Mediterranean (**Figure 2**).

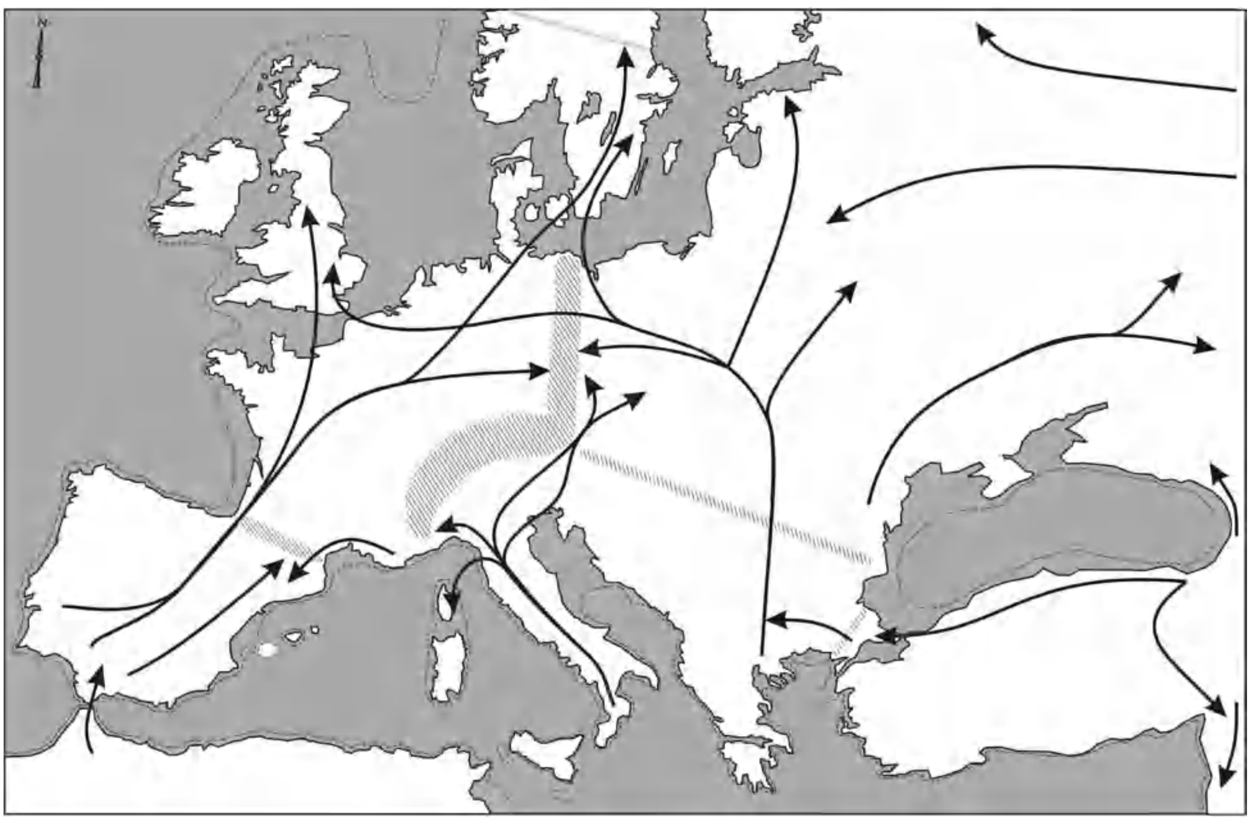


Figure 2 Main Holocene recolonization routes from glacial refugia in Europe. Dotted lines indicate the extent of land masses during Late Glacial maximum. Large shaded areas represent main hybrid zones and smaller ones represent secondary hybrid zones. Reproduced with permission from Quézel P and Médail F (2003) *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen*. Paris: Elsevier.

Current Vegetation Types

Structural and Regional Typology

The current diversity of Mediterranean forest structures can be organized into three major structural types based on bioclimatic and/or human impact criteria.

True forest vegetation types These are made of metastable equilibrium vegetation structures. Shade-tolerant plant species growing on evolved soils are dominant (**Figure 3**). These true forests constitute what were previously considered to be 'climax' forests; they are in fact the potential structures at the end of a dynamic ecological cycle that can be achieved where soil and climate conditions are favorable and where the impact of humans is not too strong.

Preforest types These can be divided into two categories. Under perhumid, humid, and subhumid bioclimates, they consist of vegetation structures that have undergone severe human impact, although their soil is still relatively well preserved (**Figure 4**). They are transitory structures from true forests to more open systems. Under semi-arid bioclimatic conditions, or under particularly stressful conditions (e.g., ultramafic substrates) in any bioclimate, preforests are composed of shrub-dominated vegetation structures with scattered trees (matorrals) under equilibrium (or close to equilibrium) at the human timescale. Conifer species play an important role in these structures.

Presteppic forest types Very frequent in southern and eastern Mediterranean, these consist of open-vegetation structures dominated by nonforest plant species under scattered trees. Nonforest species are steppe-type perennial species that can eventually be replaced by ruderal annual species when grazing occurs. Soils are usually poor and topsoil is frequently missing. Presteppes are most frequent under warm and hot temperature variants of arid (and sometimes semi-arid) bioclimates. They gradually merge into steppes under hotter and drier conditions. On mountains, presteppes are a transitional vegetation structure from forests (or preforests) to high elevation steppes dominated by low and scattered cushionlike spiny xerophytes.

These three main structural forest types are found in the four major geographical subdivisions of the Mediterranean basin (**Table 4**).

Current Evolution: Sclerophyllous Trees Replaced by Deciduous Trees

Traditional agriculture and grazing have been decreasing since the mid-twentieth century on low to medium elevation mountain ranges in the northern Mediterranean. This has led to a dramatic increase in forest cover and a change in forest composition. Concurrently, atmospheric CO_2 has been increasing because of industrial activity, thus increasing the productivity of many Mediterranean trees such as *Quercus ilex* and *Q. pubescens*.

One of the results of these changes is the physiognomical convergence of Mediterranean and non-Mediterranean forests when dominated by the same deciduous tree species (*Quercus*, *Fagus*, *Acer*, *Sorbus*). Areas where woody sclerophyll plants and heliophyllous conifers (*Pinus halepensis*, *P. sylvestris*) used to be the dominant species are now colonized by these deciduous trees, along with some mesophilic conifers (*Abies*, *Taxus*) and laurophyllous trees (*Ilex aquifolium*, *Laurus nobilis*). Deciduous *Quercus* around the Mediterranean and in California, and *Nothofagus* in Chile, currently play an extremely

Figure 3 Example of a true forest vegetation type: the Mediterranean *Fagus–Abies* mixed forest of Mont Ventoux, southeastern France.

Figure 4 Example of a true preforest vegetation type: cattle grazing in the Algerian Aures *Cedrus atlantica* forest.

Table 4 Main forest types of the four major geographical subdivisions of the Mediterranean basin, arranged according to vegetation level (see Table 1). Species names for each community refer to the dominant woody species

Vegetation level	*Northwestern Mediterranean communities*	*Southwestern Mediterranean communities*	*Northeastern Mediterranean communities*	*Southeastern Mediterranean communities*
Infra-Mediterranean		*Argania spinosa* and *Acacia gummifera*		
		Acacia raddiana		
Thermo-Mediterranean	*Olea europaea*, *Ceratonia* and *Chamaerops*	*Olea europaea*, *Ceratonia* and *Chamaerops*	*Olea europaea* and *Ceratonia*	*Olea europaea* and *Ceratonia*
	Quercus ilex and *Q. suber*	*Q. ilex* subsp. *rotundifolia*, *Q. suber*	*Quercus ilex*	*Quercus ilex*
	Pinus halepensis, *P. pinaster*, *P. pinea*	*Pinus halepensis* and *P. pinaster*	*Pinus halepensis*, *P. brutia*, *P. pinea*	*Pinus halepensis or P. brutia*
	Juniperus turbinata, *J. phoenicea*	*Juniperus turbinata, J. phoenicea*	*Cupressus sempervirens*	*Cupressus sempervirens*
	Quercus coccifera	*Quercus fruticosa*	*Quercus coccifera* subsp. *calliprinos*	*Quercus infectoria* and *Q. coccifera* subsp. *calliprinos*
		Pistacia atlantica	Formations with *Quercus ithaburensis* and *Q. pubescens*	*Quercus pubescens*, *Q. ithaburensis*
		Tetraclinis articulata, *Cupressus atlantica*		
Meso-Mediterranean	*Quercus ilex*, *Q. suber*	*Olea europaea*, *Ceratonia* and *Chamaerops*	*Quercus ilex*	*Quercus ilex*
	Quercus pubescens	*Quercus ilex* subsp. *Rotundifolia*, *Q. suber*	*Quercus coccifera* subsp. *calliprinos*	*Quercus coccifera* subsp. *calliprinos*
	Quercus coccifera	*Quercus canariensis*	*Quercus ithaburensis*	*Quercus ithaburensis*
	Quercus petraea subsp. *broteroi*	*Pistacia atlantica*	*Q. brachyphylla*, *Q. pubescens*	*Quercus infectoria*, *Q. cerris* subsp. *pseudocerris*
	Pinus halepensis	*Tetraclinis articulata*	*Pinus halepensis, P. brutia*	*Pinus brutia*, *P. halepensis, P. pinea*
	Quercus canariensis, *Q. pyrenaica*		*Cupressus sempervirens*	*Cupressus sempervirens*
				Cedrus brevifolia and *Quercus alnifolia* (Cyprus)
Supra-Mediterranean	*Quercus pubescens*, *Q. cerris*, *Q.petraea*	*Quercus canariensis*, *Q. faginea*, *Q. afares*	*Quercus frainetto* and *Q. cerris*	*Quercus frainetto* and *Q. cerris*
	Quercus faginea	*Quercus ilex* subsp. *rotundifolia*, *Q. suber*	*Quercus pubescens*, *Q. ithaburensis*	*Quercus infectoria*
	Abies alba, A. pinsapo	*Cedrus atlantica* and *Abies marocana*	*Abies cephalonica*	*Pinus brutia*
	Quercus robur, Q. petraea and *Q. pyrenaica*		*Cupressus sempervirens*	*Pinus nigra* subsp. *pallasiana*
	Ostrya carpinifolia and *Carpinus betulus*		*Ostrya carpinifolia* and *Carpinus orientalis*	*Carpinus orientalis* and *Ostrya carpinifolia*
	Pinus sylvestris		*Quercus petraea* and *Castanea sativa*	*Cupressus sempervirens*
	Castanea sativa		*Quercus pubescens* subsp. *anatolica*	*Quercus macranthera* subsp. *syspirensis*
Mountain-Mediterranean	*Pinus sylvestris*	*Pinus nigra* subsp. *mauretanica*	*Pinus nigra* subsp. *pallasiana*	*Pinus nigra* subsp. *pallasiana*
	Pinus nigra (subsp. *salzmannii* or *laricio)*	*Cedrus atlantica*	*Pinus heldreichii*	*Cedrus libani*
	Abies alba or A. pinsapo	*Abies marocana or A. numidica*	*Abies cephalonica, A. borisii-regis*	*Abies cilicica*
	Juniperus thurifera subsp. *thurifera*	*Juniperus thurifera* subsp. *africana*	*Abies nordamanniana, Abies bornmuelleriana* and *Juniperus excelsa*	*Juniperus foetidissima* and *J. excelsa*
	Fagus sylvatica subsp. *sylvatica*	*Quercus ilex* subsp. *rotundifolia*	*Fagus sylvatica sensu lato*	*Fagus sylvatica* subsp. *orientalis*
	Pinus uncinata and *P. mugo*		*Quercus petraea*	*Quercus petraea*
				Quercus brantii, *Q. ithaburensis* subsp. *look*
Oro-Mediterranean	*Juniperus thurifera* subsp. *Thurifera*	*Juniperus thurifera* subsp. *africana*	*Juniperus excelsa*	*Juniperus excelsa*
		Quercus ilex subsp. *rotundifolia*		

important role in the forest recruitment dynamics of previously traditionally cultivated or grazed lands. In forests least affected by humans, structures are shifting towards old-growth forest types where vertebrate seed dispersal plays a crucial role, and floristic and faunistic compositions are shifting towards medio-European or Euro-Asian dominated assemblages. Using sclerophylly to define Mediterranean forests is thus now an oversimplification.

Human Impact

Although human impact may have been already significant when people lived as hunter–gatherers, for example in increasing seed dispersal though seasonal migrations, it became truly significant for Mediterranean forests with the advent of domestication, about 10 000 years ago in the Near East. Because of an ever-increasing need for arable land for crop cultivation and grazing, the area of forest declined over the centuries, first sporadically around the main human settlements during the Atlantic period (about 4700 to 4500 years ago), then systematically during the Bronze Age and throughout Antiquity. Wood was then also used on a large scale for shipbuilding, carpentry, and many areas of human social life. Although it often slowed down during the Middle Ages as demographic pressure lessened, deforestation re-increased during the Renaissance. By the end of the nineteenth century, after the Industrial Revolution, the Mediterranean forest had lost three-fourths of its initial postglacial area. The consequences of this millennia-long impact have affected both vegetation structures and biodiversity.

Vegetation Structures

In areas where agricultural and grazing effects are the strongest, i.e., North Africa and most semi-arid and arid Eastern Mediterranean zones, forest ecosystems are no longer resilient, and a degradation cycle (often irreversible) starts as soil structure and water, nutrient, and carbon cycles are also affected, with often spectacular and dramatic effects (e.g. floods, landslides).

Four levels of increasing severity on forest structures can be described:

1. Transformation of forests and preforests into matorrals with scattered trees (‘matorralization’).
2. Transformation of woody matorrals dominated by resprouters into secondary, lower, matorrals mainly composed by seeders (‘dematorralization’).
3. In semi-arid bioclimates, replacement of matorrals by steppes dominated by non-woody perrenial species or low chamaephytes (‘steppization’).
4. Invasion of forest ecosystems by annual, often ruderal, or low-palatability species (‘therophytization’).

Biodiversity

Human impact on forest ecosystems can significantly modify all natural processes that regulate biodiversity at population, species, and ecosystem levels. Three categories of human impacts can be recognized, from strongest to probably least consequential.

Habitat destruction and fragmentation Traditionally the longest standing impact on forests over time, in relation to human settlements, habitat destruction has been driven by agriculture and grazing, wars and industrial activities, and carried out with tools such as wildfires and clear-cutting. It has led to the disappearance of ecosystems and species, as well as isolation of those that have remained. The main impacts on genetic processes for isolated populations are (1) reduction of long-distance gene flow, (2) increase of genetic drift and of consanguineous mating, leading to (3) loss of adaptive potential and eventually, (4) disappearance when the number of reproducing individuals is too small or when deleterious genes have accumulated.

Species introduction Exotic forest genetic resources have often been transported by humans throughout historical times because they were a potential food supply (e.g., *Pinus pinea, Olea europapaea*), had landscape or religious value (*Cupressus sempervirens*), or were able to stop degradation processes and yield more wood than the local resource (e.g., in France, *Pinus nigra* subsp. *nigra* and *Cedrus atlantica* during the nineteeth century). More recently, with the advent of tree breeding, selected varieties have been planted extensively. Introduction of new taxa has led to the creation of completely new ecosystems, thus increasing biodiversity locally. However, phytosanitary risks are high in these artificial forests as they usually lack a complete biologically functional structure. Risks of hybridization are high when the exotic resource is genetically close to the local resource (e.g., subspecies of *Pinus nigra*), with potential reduction of fitness for the local resource.

Forestry practice Forests have been managed since the Middle Ages in Europe. Loss of biodiversity cannot be positively linked to forestry practice, except in the case of seed transfer over regions with very different ecological requirements (e.g., in southern France, Aleppo pines imported from Sicily died from frost during the winters of 1984 and 1985). However, recent studies indicate that reforestation reduces genetic diversity because of plant material selection in the nursery. When a stand is prepared for natural regeneration, a significant part of the sexually mature trees is removed, and thus part of the genetic diversity is eliminated from the original population, which may disturb mating systems, increase consanguineous mating and genetic drift, and impact the selective value of the future stand. Due to their long life cycle (long juvenile and long sexual maturity phases) and overlapping generations, trees may be able to compensate efficiently for these genetic impacts in their long-term adaptation.

Different Recent Human Impacts around the Mediterranean Basin

Although human impact was broadly similar during the Holocene, it diverged sharply among the different Mediterranean ecogeographic regions during the twentieth century.

In the northern Mediterranean, after the Industrial Revolution, the least productive agricultural and grazed lands were abandoned and became progressively colonized by expansionist (mostly conifer) species. Open lands have progressively changed into non human-impacted (except for some large-scale wildfires) preforest and forest structures. The FAO reported an annual increase of 0.3–0.9% in forest cover in the 1990s. There is a growing concern over loss of human-made biodiversity because of the disappearance of open grass and shrub ecosystems. Although habitat destruction remains a concern, especially along the coast because of urban extension, the main risks for forest genetic resources come from forest management, with the introduction of species and improved varieties and seed transfer, and their corollaries, hybridization and gene flow from cultivated to wild compartments.

In the southern Mediterranean, the use of forest resources is generally not sustained, although the FAO reported positive forest cover increase (from 0.2% to 1.4%) in the 1990s. Habitat destruction for agriculture, grazing, fuel wood, construction, etc. remains the major type of human impact. In North Africa, forest area per capita is less than 0.1 ha although it is 0.2–0.4 ha in the northern Mediterranean. In the past 30 years, forest product use has dramatically increased due to human demography. Illegal cuttings, forest clearing, overgrazing, and fuelwood exploitation are rapidly destroying forests and their associated biological resources. Low socioeconomic standards of rural populations are thus also a significant cause of habitat destruction.

In the eastern Mediterranean, the trend is somewhat similar to that of North Africa. Habitat destruction remains a high risk in countries where forest cover is already very limited and forest resources not sustained (e.g., Syria, Lebanon). In other countries, forest cover has grown tremendously (+4.9% in Israel) or steadily (+0.2% in Turkey) in the 1990s because of active reforestation and conservation programs.

Conservation of Mediterranean Forest Biodiversity: An International Effort

The need to conserve forests and their biodiversity has been internationally recognized since the United Nations Conference on Environment and Development (UNCED) in Rio during 1992. Conservation of biodiversity needs to be undertaken at three complementary levels:

- genes, where evolution can occur
- species and populations, where reproduction and gene flow can occur
- ecosystems (habitats), where organisms are sustained.

Ecosystems are usually preserved separately from genes. Species and populations can be a means to sustain gene diversity and future adaptation (forestry approach to conservation) or the primary target to protect through diversified and functional habitats (ecological approach to conservation).

Forest genes and populations Many forest conservation and sustainable management strategies designed globally can apply to the Mediterranean. Such is the case of the *in situ* and *ex situ* conservation networks advocated by the European Forest Genetic Resource Conservation Program (EUFORGEN), although they are still rare around the Mediterranean. *In situ* networks concern species of high ecological, patrimonial, and/or economic value that are not threatened with short-term extinction in their natural environment (e.g., *Pinus brutia* in Turkey, *Abies alba* in France). They are designed to make genetic evolution possible under current ecological constraints. *Ex situ* networks generally concern rare and endangered forest species. They are made of collections of selected or remaining genotypes conserved outside their normal ecological conditions. One current sustainable management strategy is the control of the origin and commerce of forest reproductive material (in Europe, see European Union directives 66/404/CEE and 71/161/CEE), which must come from certified seed stands and seed orchards and whose transfer from one ecological zone to another is under strict control. Other initiatives, sponsored by the FAO and the UN Environmental Program, have produced sets of indicators and guidelines for replacing yield-oriented forest management practice by the sustainable management of forest resources in Mediterranean countries.

Forest species and ecosystems (habitats) Species and ecological diversity are typically conserved and managed in natural parks and reserves. Many of such structures exist around the Mediterranean. However, out of 425 Man and Biosphere Reserves worldwide, only 32 shelter significant Mediterranean forest areas. Eastern Mediterranean forests are notably underprotected. Particularly, conservation of potential and old-growth sclerophyll and deciduous Mediterranean forests remains extremely limited as less than 2% have been included in natural parks or reserves. Old-growth Mediterranean forests contain many typical species that are rare because linked to large, nonfragmented, and undisturbed forest areas. Some of these species are functionally primordial, e.g., those related to organic matter decomposition. Because Mediterranean biodiversity arises from a high spatial and temporal heterogeneity, natural parks and reserves designed for Mediterranean forests must be large enough to include disturbance cycles (open and closed canopy structures, large vertebrate populations, fires, etc.) which can guarantee the maintenance of this typical biodiversity. They must also be large enough to include a complex mosaic of functionally diversified ecological structures, at equilibrium. Such requirements have guided the European Natura 2000 (European Union habitats directive 92/43/CEE) initiative for habitat conservation and the international efforts of the World Parks Congresses sponsored by the World Conservation Union (IUCN). Ideally, these guidelines should be included into forest practice, thus linking gene and ecosystem-oriented approaches to sustainable resource management.

A Global Comparative Assessment of the World Mediterranean-Type Forests

Species richness and diversity, which are the most frequently used parameters to describe and assess biodiversity, are scale-dependent. Three main types of spatial scales are generally recognized (**Table 5**). This partitioning of biodiversity makes it possible to compare ecosystem types. At the local scale (less than 0.1 ha), Mediterranean biodiversity is two times lower than that of tropical regions. Mean local (alpha) floristic diversity of the world Mediterranean forests is between 10 species m^{-2} and 25 to 110 species 1000 m^{-2}. At this spatial scale, woody plant communities of the Mediterranean basin are both very heterogeneous and also among the richest types, ahead of the alpha diversity found in the western Cape Province. However, habitat (beta) and regional (epsilon) scale diversities are much higher in the western Cape Province than around the Mediterranean, although they concern mainly matorral type (fynbos) vegetation.

From a biogeographic and ecological point of view, several forest types of the Mediterranean basin are relatively similar to those of the California Floristic Province, due to a pre-Atlantic ocean land connection which lasted until the Eocene (Madro-Tethysian flora) and explain the existence of some common tree genera (*Pinus*, *Quercus*, *Arbutus*, *Cupressus*, *Juniperus*). At low and medium altitudes, physiognomical similarities exist for sclerophyll oak forests. The existence of thermophilous coniferous at the thermo- and meso-Mediterranean (*Pinus halepensis*, *P. brutia*, *P. pinaster*) and thermo- and meso-Californian (*Pinus attenuata*, *P. sabiniana*, *Cupressus macrocarpa*) levels, but also of several mesophilous coniferous (*Abies*, *Pinus*) at higher altitude constitutes another key feature. A recent survey indicates that the Mediterranean region harbors a higher tree richness (290 indigenous trees with 201 endemics) than the California Floristic Province (173 trees with 77 endemics), although its area is seven times larger.

Northern hemisphere Mediterranean forests show a higher structural and species diversity than those of the southern hemisphere, because the latter cover less extensive areas and, as in South Africa, may be completely outside the range of Mediterranean bioclimate. The Southern Cape forests are very patchy and scarce, mainly made up of plants of a cool and humid Afromontane origin, with warm subtropical elements; sclerophyll trees and conifers (*Afrocarpus*, *Podocarpus*) predominate. Forests of Mediterranean Chile are more diverse due to the strong latitudinal gradient and the increase in rainfall from north to south; semi-arid *Acacia caven* and *Prosopis chilensis* forests in the north are succeeded by subtropical broadleaved and sclerophyll forests in the central region, and by deciduous *Nothofagus* forests farther south. Together with species-rich sclerophyll matorrals (kwongan and mallee), the woodlands of Mediterranean Australia are dominated by *Eucalyptus*, *Acacia*, and *Casuarina* on relatively fertile soils where mean annual rainfall exceeds 400 mm.

Outlook for the Future

The originality of the Mediterranean biome is dependent upon the interaction of complex ecological factors. However these ecosystems are fragile and global warming will undoubtedly soon be a major source of disturbance. Research and long-term monitoring of biodiversity and ecosystem functioning

Table 5 Main patterns of forest biodiversity in the five Mediterranean regions of the world in relation to spatial scale, species composition and level of disturbance

Major biodiversity drivers	*Mediterranean Basin (2 300 000 km^2)*	*California Floristic Province (324 000 km^2)*	*Mediterranean Chile (140 000 km^2)*	*South and southwestern Australia (112 000 km^2)*	*Western Cape Region (90 000 km^2)*
Patterns of plant diversity					
Local within habitat (alpha diversity)	Medium to very high	Low to medium	Medium	Low to high	Medium to high
Differentiation among habitats (beta diversity)	Medium	Medium	Low to medium ?	High	Medium to high
Regional (epsilon diversity)	Medium	Medium	Low	High	High
Total plant species richness	~30 000	~4450	~2540	~8000	~9000
Major forest trees					
Sclerophyll	*Arbutus unedo*, *A. andrachne*, *Olea europaea*, *Ceratonia siliqua*, *Erica arborea*, *Phillyrea latifolia*, *Quercus ilex*, *Q. suber, Q. coccifera*	*Arbutus menziesii*, *Heteromeles arbutifolia*, *Lithocarpus densiflora*, *Quercus agrifolia*, *Q. chrysolepis*, *Q. wislizenii*, *Umbellularia californica*	*Colliguaja odorifera*, *Cryptocarya alba*, *Drimys winteri*, *Jubaea chilensis*, *Kageneckia angustifolia*, *Lithraea caustica*, *Peumus boldus*, *Maytenus boaria*, *Nothofagus dombeyii*, *Quillaja saponaria*	*Eucalyptus* spp. (*E. marginata*, *E. diversi-sicolor*, *E. incrassata*, *E. oleosa*, *E. wandoo*, *E. camaldulensis*, *E. calophylla*, *E. baxteri*), *Melaleuca* spp., *Acacia* spp., *Leptospermum* spp., *Banksia* spp.	*Maytenus* spp., *Olea capensis*, *Ocotea bullata*, *Virgilia divaricata*, *V. oroboides*, *Ilex mitis*, *Cunonia capensis*, *Pittosporum viridiflorum*, *Platylophus trifoliatus*, *Pterocelastrus rostratus*, *Schefflera jumbellifera*, *Sideroxylon inerme*
Broadleaved and semibroadleaved	*Castanea sativa*, *Fagus sylvatica*, *Carpinus orientalis*, *Fraxinus ornus*, *Ostrya carpinifolia*, *Platanus orientalis*, *Quercus pubescens*, *Q. canariensis*, *Q. afares*, *Q. ithaburensis*, *Q. pyrenaica*, *Q. frainetto*	*Aesculus californica*, *Quercus lobata*, *Q. douglasii*, *Q. engelmannii*, *Q. kelloggii*, *Q. garryana*	*Acacia caven*, *Nothofagus obliqua*		*Celtis africana*, *Ficus sur*, *Calodendron capense*
Coniferous and Casuarina (coniferous-like leaves)[a]	*Abies alba*, *A. borisii-regis*, *A. cephalonica*, *A. cilicica*, *Cedrus atlantica*, *C. libani*, *Cupressus sempervirens*, *Juniperus excelsa*, *J. thurifera*, *J. turbinata*, *Pinus brutia*, *P. halepensis*, *P. nigra*, *P. pinaster*, *P. pinea*, *P. sylvestris*, *Tetraclinis articulata*	*Abies bracteata*, *A. concolor*, *A. magnifica*, *Calocedrus decurrens*, *Cupressus macrocarpa*, *Pinus attenuata*, *P. contorta*, *P. coulteri*, *P. edulis*, *P. juarezensis*, *P. jeffreyi*, *P. lambertiana*, *P. monophylla*, *P. torreyana*, *Pseudotsuga menziesii*, *P. macrocarpa*, *Sequoia sempervirens*, *Sequoiadendron giganteum*	*Araucaria araucana*, *Austrocedrus chilensis*, *Fitzroya cupressoides*	*Casuarina* spp. (e.g., *C. pusilla*, *C. muellerana*)	*Afrocarpus falcatus*, *Podocarpus latifolius*, *P. elongatus*, *Widdringtonia cedarbergensis*
Impact of forest fires	Strong impact of anthropogenic fires; natural fires very rare	Predominance and high frequency of natural fires	Rarity of natural fires; anthropogenic fires uncommon	Frequent natural and anthropogenic fires	Frequent natural and anthropogenic fires
Other disturbances	Destruction and fragmentation, overgrazing, clear-cutting	Destruction and fragmentation, biological invasions	Destruction and fragmentation, overgrazing	Destruction and fragmentation, biological invasions	Destruction and fragmentation, afforestation, biological invasions

[a] Total plant richness refers to angiosperms, gymnosperms, and pteridophytes.

at a cross-continental Mediterranean scale must be combined with public awareness strategies and international policy-making, not only to understand but also to protect Mediterranean ecosystems effectively and use them efficiently, now and in the future.

See also: **Biodiversity**: Biodiversity in Forests; Endangered Species of Trees; Plant Diversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife. **Environment**: Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Forest Management for Conservation; Population, Conservation and Ecological Genetics. **Landscape and Planning**: Landscape Ecology, the Concepts. **Silviculture**: Forest Dynamics. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Temperate and Mediterranean Forests**: Southern Coniferous Forests. **Temperate Ecosystems**: Fagaceae; Pines; Spruces, Firs and Larches. **Tropical Ecosystems**: Acacias; Eucalypts.

Further Reading

Arroyo MTK, Zedler PH, and Fox MD (eds) (1995) *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia*. New York: Springer-Verlag.

Dalmann PR (1998) *Plant Life in the World's Mediterranean climates*. Oxford: Oxford University Press.

Davis GW and Richardson DM (eds) (1995) *Biodiversity and Ecosystem Function in Mediterranean-Type Ecosystems*. New York: Springer-Verlag.

Di Castri F and Mooney HA (eds) (1973) *Mediterranean-type ecosystems*. New York: Springer-Verlag.

FAO (2001). *State of the World's Forests 2001*. Rome: Food and Agriculture Organization of the United Nations.

Johnston VR (1994) *California Forests and Woodlands: A Natural History*. Berkeley, CA: California University Press.

Moreno JM and Oechel WC (eds) (1994) *The Role of Fire in Mediterranean-type Ecosystems*. New York: Springer-Verlag.

Oldeman RAA (1990) *Forests: Elements of Sylvology*. Berlin: Springer-Verlag.

Quézel P and Médail F (2003) *Ecologie et Biogéographie des Forêts du Bassin Méditerranéen*. Paris: Elsevier.

Teissier du Cros E (ed.) (2001) *Forest Genetic Resources Management and Conservation: France as a Case Study*. Paris: Ministry of Agriculture and Fisheries, Bureau of Genetic Resources, Commission of Forest Genetic Resources, INRA DIC.

TEMPERATE ECOSYSTEMS

Contents

Alders, Birches and Willows

S Harris, University of Oxford, Oxford, UK

Early botanists considered the alders (*Alnus*), birches (*Betula*), and willows (*Salix*) part of a large, closely related group of catkin-producing, woody species, known as the Amentiferae. This group was presumed to have a single origin, and also included the walnuts, oaks, figs, and elms. We now know, based on detailed morphological and molecular analyses, that many of these families are not closely related and that superficial resemblance based on catkins is due to convergence. In addition to sharing catkins, alders, birches, and willows are ecologically similar since they are important pioneer species of the northern temperate region. Furthermore, they have a diverse array of similar uses, especially gunpowder production.

Alnus and *Betula* comprise the monophyletic subfamily Betuloideae of the family Betulaceae, whilst the other four members (*Carpinus*, *Corylus*, *Ostrya*, and *Ostryopsis*) comprise subfamily Coryloideae. Traditionally, *Salix* and the genus *Populus* have comprised the family Salicaceae. However, using molecular data it has been proposed that the family Salicaceae should also encompass other genera, most notably the acyanogenic genera of the Flacourtiaceae.

The biology and ecology of alders, birches, and willows are briefly described and then the diverse uses of these important trees and shrubs are presented.

Alnus

The genus *Alnus* comprises approximately 25 species of small to large trees or shrubs of the temperate and boreal zones of the northern hemisphere and Central America to the high elevations of South America, although the genus is poorly understood in Central America and China. Members of the genus are often associated with wet sites, swamps, and stream margins, and their ability to fix nitrogen means *Alnus* species are important early successional species. For example, *A. viridis* is an important pioneer, whilst others are important components of mature forest (e.g., *A. rubra* in the floodplain forests of the North American Pacific North-west). Alders, as with other Betulaceae, have male and female flowers separated into different catkins. Alders are wind-pollinated, producing large amounts of pollen. Pollen release occurs before (subgenus *Alnus*) or at the same time (subgenus *Alnobetula*) as the new leaves unfold or in late summer (subgenus *Clethropsis*), just after the new catkins mature. The woody alder infructesences produce small, abundant, winged fruits that are carried primarily by wind but also by water. In some species (e.g., *A. serrulata*), the wings are reduced to ridges, and the fruits are dispersed primarily by water. *Alnus* species form a polyploid group ($2n = 14-56$; $2x-8x$). Fossil material attributable to the genera *Alnus* and *Betula* appears earlier in the fossil record than other Betulaceae, whilst *Alnus* fossils are known from as early as the Miocene. Furthermore, analyses of chloroplast DNA and pollen data have enabled the postglacial history of *A. glutinosa* to be reconstructed and glacial refugia to be identified.

The genus is divided into four subgenera: *Alnus*, *Alnobetula*, *Clethropsis*, and *Cremastogyne* (**Table 1**), although these have also been recognized as separate genera. *Alnus* nomenclature is complicated by morphological variation and hybridization. For example, in subgenus *Alnobetula*, numerous subspecies are described in the circumpolar species *A. viridis*. Alder hybrids form readily when species grow together; for example, in North America, *A. incana* subsp. *rugosa* hybridizes with *A. serrulata*, leading to extensive hybrid swarms that complicate the differentiation of the taxa. However, most species are either geographically or ecologically differentiated.

Seed is an effective way of raising alder, although many species can be vegetatively propagated. Large areas of alder growth may give the impression of extensive clonal population growth. However, allozyme studies indicate that populations of *A. incana* subsp. *rugosa* and *A. viridis* subsp. *crispa* are the result of sexual reproduction. Furthermore, inbreeding is very low and gene flow is high. For best growth, alders (e.g., *A. glutinosa*, *A. rubra*, *A. cordata*) must be symbiotically associated with the nitrogen-fixing actinomycete *Frankia*, which leads to formation of root nodules. Few pests and diseases appear to affect alders, although scale insects can be a problem in *A. serrulata* in North America. However, in recent years in the UK, natural populations of *A. glutinosa* have been lethally affected by the fungal pathogen *Phytophthora cambivora*. In North America, *Fomes ignarius* is the most significant fungal pathogen of

Table 1 Characteristics of the main grouping within the genus *Alnus*

	Subgenus Alnus	*Subgenus* Alnobetula	*Subgenus* Clethropsis	*Subgenus* Cremastogyne
Distribution	Temperate and boreal northern hemisphere, Central and South America	Temperate and boreal northern hemisphere	Eastern North America, eastern Asia	South-central Asia
Habit	Small trees to medium-sized shrubs	Small trees to shrubs	Small trees	Small to medium-sized trees
Fruits	Wingless or narrow wings	Two large lateral membranaceous wings	Wingless	Broad hyaline wings
Infructesence	Short pedunculate	Long pedunculate	Short pedunculate	Long pedunculate
Catkins	Catkins racemose, develop during growing season before anthesis and exposed during winter	Catkins racemose, develop during growing season before anthesis and only male exposed during winter	Catkins solitary or racemose clusters	Catkins solitary
Flowering	Spring	Spring	Fall	Spring
Buds	Stipitate, two-scaled	Subsessile, several imbricate scales	Naked	Stipitate, two-scaled
Examples	*A. incana A. serrulata*	*A. viridis A. sieboldiana*	*A. maritima A. nepalensis*	*A. cremastogyne*

trees older than 40 years, whilst *Taphrina* species may affect female catkins.

Betula

The genus *Betula* comprises approximately 35 species of small to large trees or shrubs of the temperate and boreal zones of the northern hemisphere. The genus occupies a wide range of habitats, including peat lands, stream banks, lake shores, damp woods, ruderal habitats (including road and rail margins), and alpine and tundra sites. In addition, the genus reaches the northern limit of tree growth. Birches are wind-pollinated, producing large amounts of pollen, and the achenes are wind-dispersed. The female catkins appear with the new growth, whilst anthesis occurs as the leaves unfold. However, ovule fertilization occurs much later than pollination. *Betula* species form a polyploid group ($2n = 28$–112; $2x$–$8x$), whilst some hybrids are aneuploid. Fossil material attributable to the genus *Betula* has been found in deposits from the Upper Cretaceous and appears to have been highly diversified by the Middle Eocene.

The genus is divided into four series, Albae, Costatae, Acuminatae and Humiles (**Table 2**), although some species (e.g., *B. utilis*, *B. nigra*) are difficult to place in these series. *Betula* nomenclature is complex due to the patterns of morphological variation, the wide ecogeographic range of some species (e.g., *B. pubescens*) and the existence of hybridization and introgression within and between the series. In northern Europe, there has been considerable discussion as to whether *B. pendula* and *B. pubescens* are separate species or intraspecific variants. In many cases across their ranges, the two species are readily distinguished. However, morphological intermediates do occur, although these are rarely sterile, triploid hybrids, as might be expected (*B. pendula* ($2n = 2x = 28$), *B. pubescens* ($2n = (4x) = 56$)), which suggests that there is a complex interaction between the morphological and cytogenetic variation. Areas where introgression is important include Kamchatka (e.g., *B. platyphylla* introgresses with *B. ermanii*) and north-east North America (e.g., *B. populifera* introgresses with *B. cordifolia*), whilst in northern Europe *B. pubescens* hybridizes with *B. nana*.

Series Albae and Costatae contain the most important forestry species. Seed is an effective way of raising birch although, when seed is collected from natural or cultivated specimens, the possibility that it may be of hybrid origin must be considered. Birch seed is orthodox, and if dried and stored in cool conditions it will remain viable for many years. Many *Betula* species can be vegetatively propagated from soft or semiripe side shoots, whilst grafting is important if particular genotypes are to be maintained. In the case of grafting, the scion and rootstock should come from the same series of the genus, although in practice *B. pendula* is very commonly used.

The leaves of birches are often rich in resins, whilst the barks, particularly of white-barked birches, are rich in phenolics. Furthermore, the bark of series Albae species contains granules of the triterpenoid betulin, which makes the bark waterproof. These compounds are thought to be important antifeedants, especially effective against browsing mammals, in the winter months. Many insect species feed

Table 2 Characteristics of the main grouping within the genus *Betula*

	Series Albae	*Series Costatae*	*Series Acuminatae*	*Series Humiles*
Distribution	Circumpolar	North America, Transcaucasia, temperate Far East	Japan, Sino-Himalayas	Circumpolar
Habit	Small to medium-sized trees	Large trees	Medium-sized trees	Shrubs
Leaves	Thin, weakly veined with long petiole	Strongly and deeply veined, most with single-toothed margin	Strongly and deeply veined, double-toothed margin	Small, rounded, with few veins
Stem	Bark white (due to betulin), peeling in sheets	Bark dark, most lack betulin	Bark dark, most lack betulin	Bark dark, lack betulin
Catkins	Pendulous, long, fragile, and break up readily in the fall	Upright, short (even globose), persistent, often until early spring	Pendulous, long	Upright, male catkins borne laterally
Ecology	Pioneer species. Fast-growing, relatively short-lived, requiring high light intensity. Not adversely affected by wind exposure	Mixed mesophytic forests. Shade-tolerant, wind-shy	Mesophytic forests	Montane and alpine regions. Peat lands, bogs, tundra
Examples	*B. papyrifera B. populifolia*	*B. alleghaniensis B. lenta*	*B. maximowicziana*	*B. nana B. glandulosa*

on birch, of which one of the most economically important in North America is the bronze birch borer (*Agrilus anxius*), although others include the gypsy moth (*Lymantria dispar*), tent caterpillars, leaf miners, and scale insects. Fungal diseases may also be significant, especially the heartwood rots, caused by *Fomes* and *Poria* species, e.g., *F. ignarius*, and nectria canker (*Nectria galligena*).

Salix

The genus *Salix* comprises approximately 400 species of dwarf or procumbent shrubs to large trees and is found in most parts of the world, particularly the temperate and boreal regions, although there are tropical and subtropical species (e.g., *S. humboldtiana*). One species *S. mucronata*, crosses the equator in Kenya. The genus is very diverse, but poorly known, in western China. Willows occupy a wide range of habitats and climatic zones; the majority of species are pioneers and shade-intolerant (e.g., *S. repens*). Most willows are scrub, marginal, or riverine species, although some are forest-dominants; the association of willows with water is reflected in the origin of the generic name (derived from Celtic, meaning 'near water'). Willows become increasingly important on upland and northward from the boreal forest into the arctic, where they are the most important woody species (e.g., vegetation succession on glacial moraines). In such habitats, willows tend to have underground branches and act as herbaceous perennials. *Salix* species are almost all dioecious, having separate male and female plants, and produce catkins in the spring. Willows, except subgenus *Chosenia*, are usually insect-pollinated (Hymenoptera and Lepidoptera), and the seeds have tufts of hair that aid in wind dispersal. *Salix* species form a polyploid group ($2n = 38$–224; base numbers 11, 12, 19), although aneuploidy appears to be common in some species and hybrids. Fossil material attributable to the genus *Salix* has been found in deposits from as early as the Miocene.

The genus is conveniently divided into four subgenera: *Salix*, *Caprisalix*, *Chamaetia*, and *Chosenia* (**Table 3**); subgenus *Chosenia* is sometimes regarded as a distinct genus. However, the intrageneric division of *Salix* is controversial and numerous alternative schemes have been published. Subgenus *Salix* species are commonly called the true willows, whilst the members of subgenus *Caprisalix* are the sallows and osiers. The accurate identification of *Salix* species is difficult since it is often necessary to have mature flowers and leaves, structures that are usually not available at the same time. *Salix* nomenclature is complex due to the patterns of morphological variation and hybridization, although most species of subgenus *Salix* do not hybridize with those of the other two sections. Most hybrids are fertile, hence it is possible for individual plants to have complex hybrid parentages, e.g., artificial hybrids have been created involving up to 14 *Salix* species, whilst hybrids of three or more species are frequently found in the UK. This means that in areas where there are numerous interfertile species it may be difficult to establish accurately the identity of individual trees. Furthermore, many hybrids are clones of a single sex, e.g., *S.* × *calodendron* is known only from female plants. Furthermore, natural hybridization is complicated by the separation of the sexes and interspecific differences in flowering periods.

Subgenera *Salix* and *Caprisalix* contain the most important forestry species, although subgenus *Chamaetia* contains some of the most important high-latitude species. In natural populations, *Salix* produces large amounts of easily germinated, very short-lived seed, whilst some species form extensive clonal stands (e.g., *S. repens*, *S. herbacea*). In

Table 3 Characteristics of the main grouping within the genus *Salix*

	Subgenus Salix	*Subgenus* Caprisalix	*Subgenus* Chamaetia	*Subgenus* Chosenia
Distribution	Temperate and boreal, plus few tropical and subtropical Old and New World	Temperate and boreal, plus few tropical and subtropical Old and New World	Temperate and boreal	North-East Asia
Habit	Medium-sized trees, large shrubs	Small trees, shrubs	Dwarf, creeping shrubs	Large trees
Floral nectaries	2 + nectaries in male flowers, 1–2 nectaries in female flowers	1 nectary	Nectaries fused	Absent
Male flowers	3–10(12) stamens	2 stamens	(1–)2 stamens	Five stamens
Catkins	Erect; stalked on leafy shoots	Erect; sessile or subsessile, precocious	Erect; on leafy shoots	Pendulous
Pollination	Insect	Insect	Insect	Wind
Examples	*S. alba S. babylonica*	*S. caprea S. viminalis*	*S. herbacea S. polaris*	*S. arbutifolia*

cultivation, *Salix* species are readily propagated from seed, although more generally they are vegetatively propagated from hardwood cuttings; some species, e.g., *S. caprea*, are difficult to root from cuttings. Vegetative reproduction has the advantage that particular cultivars can be maintained, and it is essential for the propagation of male clones. The economic importance of the genus has led to the selection of many local *Salix* genotypes, all of which are maintained through clonal propagation. For established lowland species, coppicing and pollarding are effective forms of management for wood products, although large amounts of organic material must be available in the soil.

Willows are the hosts of many insect species. Willows are prone to fungal diseases (e.g., *Melampsora* leaf rusts and *Armillaria*), and the planting of single areas with single clones may make disease control difficult. The bacterium *Erwinia salicis* is an important threat to the production of high-quality cricket bats from *S. alba*.

Utilization

Timber

Betula species (e.g., *B. alleghaniensis*, *B. lenta*, *B. pubescens*) are important hardwoods for the production of veneers and plywoods. *Alnus* species produce soft, fine-grained woods used for pilings, beams, and shipbuilding (e.g., *A. acuminata*, *A. jorullensis*). The wood of larger *Salix* species is used for building purposes, whilst female clones of *S. alba* var. *caerulea* are the sole source of wood for cricket bats. *Alnus*, *Betula* and *Salix* species are important pulpwood sources.

Wood Products

Salix is an important raw material of rural crafts (e.g., hurdles, coracles, baskets) in both the New and Old Worlds. Basketry is an example where particular species produce different qualities of products, e.g., *S. triandra* (rods), *S. purpurea* (thin withies for fine basketry), and *S. viminalis* (withies for basketry). Furthermore, male and female clones produce different qualities of rods and withies. Birch bark (e.g., *B. papyrifera*) is used for canoe and roof construction. Furthermore, birch bark has been used as writing material, e.g., the oldest (*c.* 1800 years old) known Buddhist manuscripts. Birch branches have also been used for brush construction and administering corporal punishment (the name *Betula* is derived from the Latin 'to beat'). *Betula* and *Salix* species are used as short-rotation biomass crops.

Fuelwood

Alnus, *Betula*, and *Salix* species are important fuelwood sources, e.g., *Salix* woodchips in Sweden. All three genera have been widely used for charcoal production and are important in gunpowder manufacture.

Medicines, Food, Chemicals

Alder, birch, and willow have limited food value, although *Salix* species are important pollen and nectar sources for bees early in the year. In the northern Appalachians, *B. lenta* sap is tapped in spring and fermented to produce birch beer, tea is made by infusing birch bark and twigs, and birch bark (rich in oil and starch) is a famine food. Medicinally, salicin has been extracted for centuries from willow bark and used as a febrifuge and analgesic, although this has been superseded by salicylic acid (aspirin), and wintergreen (methyl salicylate) is extracted from *B. lenta* and *B. alleghaniensis*. The astringent properties of alder bark are used for the treatment of burns and infections, whilst the triterpenes betulin and lupeol, extracted from bark and wood of *A. rubra*, have some *in vitro* antitumor activity. Birch and alder pollens are important sources of hayfever allergens, whilst birch sap may cause contact dermatitis. Distillation of *B. pendula* bark and wood is used to produce pyroligneous oil for the preparation of leather, and *B. pubescens* and *B. pendula* leaves produce a green dye.

Habitat Amelioration

Salix species are often planted along riverbanks, subject to extensive flooding, to minimize soil erosion, whilst others (*S. purpurea*, *S. interior*) are used for estuarine land reclamation. *Salix* species are also important as windbreaks and for the treatment of wastewater. *Betula* species are used as heavy-metal bioindicators (e.g., *B. populifolia* for lead in Wisconsin, USA), whilst alder leaves accumulate gold.

Ornamentals

Alnus and white-barked *Betula* species have wide-ranging horticultural uses. Many *Salix* species and selected cultivars (particularly males) are grown (e.g., for stem color), whilst weeping (e.g., *S. babylonica*) types are popular in riverine situations.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Reproductive Ecology of Forest Trees. **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species; Genecology and Adaptation of Forest

Trees; Genetic Systems of Forest Trees; Population, Conservation and Ecological Genetics. **Temperate and Mediterranean Forests**: Subalpine and Boreal Forests; Temperate Broadleaved Deciduous Forest. **Tree Physiology**: Physiology of Sexual Reproduction in Trees.

Further Reading

Argus GW (1973) *The genus Salix in Alaska and the Yukon*. Ottawa: National Museums of Canada.

Chase MW, Zmarzty S, Lledo MD, *et al.* (2002) When in doubt, put it in Flacourtiaceae: a molecular phylogenetic analysis based on plastid *rbc*L DNA sequences. *Kew Bulletin* 57: 141–181.

Chen ZD, Manchester SR, and Sun HY (1999) Phylogeny and evolution of the Betulaceae as inferred from DNA sequences, morphology, and paleobotany. *American Journal of Botany* 86: 1168–1181.

Furlow JJ (1990) The genera of the Betulaceae in the Southeastern United States. *Journal of the Arnold Arboretum* 71: 1–67.

Hibbs DE, DeBell DS, and Tarrant RF (1994) *The Biology and Management of Red Alder*. Corvallis, OR: Oregon State University Press.

Newsholme C (1992) *Willows. The Genus Salix*. Portland, OR: Timber Press.

Savill PS (1991) *The Silviculture of Trees used in British Forestry*. Wallingford, UK: CAB International.

Fagaceae

R Rogers, University of Wisconsin–Stevens Point, Stevens Point, WI, USA

Introduction

The following sections characterize members of the beech family (Fagaceae) in relation to their taxonomy, distribution, ecology, and silviculture. Also included is information about their botanical importance as well as their significance in meeting human needs.

The beech family contains some of the world's most important trees to human culture. Uses are myriad and include such things as woven baskets, toys, storage containers, ship timbers, and food sources. However, members of the beech family are generally acknowledged as most important sources of hardwood timber (oak (*Quercus*), beech (*Fagus*), and chestnut (*Castanea*)), chestnut, and cork and tannins from the oaks (**Figure 1**).

Figure 1 Cork oak (*Quercus suber*) plantation in Portugal showing tree trunks whose bark has been stripped for cork. Photograph courtesy of Heinrich Speicker, Institut für Waldwachstum, Albert-Ludwigs-Universität Freiburg, Freiburg, Germany.

Taxonomy

The beech family contains from six to nine genera (*Fagus*, *Nothofagus*, *Lithocarpus*, *Castanopsis*, *Colombobalanus*, *Castanea*, *Chrysolepis*, *Quercus*, and *Trigonobalanus*) and includes between 600 and 900 species, although numerous classification issues exist which accounts for the variation in the number of genera (**Table 1**). Perhaps the best-known members of the beech family are the oaks which are recognized by their distinctive fruit, the acorn (**Figure 2**). The genera of Fagaceae as we know them probably became established about 60 million years ago during the late Cretaceous period in geologic history following migration from areas centered in tropical mountains.

Characteristics that unite members of the family include leaves with a single blade that are either persistent or deciduous and which often remain on the tree after withering and dying. Leaflike appendages (stipules) are present at the base of a relatively short leaf stem (petiole). Leaves are arranged in an alternate pattern on the stem. Veins of the leaves are featherlike and have branches that are laterally connected to a central stem.

Male and female flowers are found within the same tree. Female flowers are wind pollinated. Male flowers are pendulous spikelike structures while female flowers are on short spikes with few flowers or may be grouped in clusters near the base of the male flowers. Although female flowers may contain one or two ovules, only one develops to maturity.

The fruit is distinctive and consists of a nut that is surrounded by an outer somewhat firm yet elastic coat that is partially or completely enclosed by a cluster of bracts (**Figure 3**). The nut contains only one seed which lacks food reserves associated with the embryo but which has large, fleshy primary

Table 1 Distribution of the beech family (Fagacaeae)

Genus	*Number of species*	*Range*
Beech (Fagus)	10	Northern hemisphere
Oak (Quercus)	400	Northern hemisphere; red oak group (Lobatae) restricted to North America
Southern beech (Nothofagus)	40	Australia, Chile, Argentina, New Zealand, New Guinea, and New Caledonia
Chestnut (Castanea)	10	Southern Europe, northern Africa, southwestern and eastern Asia, and eastern United States
Chinkapin (Castanopsis)	150	North America, China, India, and Malayan archipelago
Tanoak Lithocarpus	100–200	North America (1 species), Asia
Chinquapin (Chrysolepis)	2	Western United States
Colombobalanus	1	Columbia, South America
Trigonobalanus	2	China, Malaysia

Figure 2 Acorns of northern red oak (*Quercus rubra*).

Figure 3 Fruit of tanoak (*Lithocarpus densiflorus*).

leaves that it uses for its initial nourishment upon germination. The fruit matures in one or two seasons. A botanic comparison of the well known genera is given in **Table 2**.

Beech (*Fagus*)

There are 10 species of beeches all of which are found in the northern hemisphere. One species is found in North America, one is European, one is found in the Caucasus Mountains on the border between Europe and Asia, and the rest are found within the temperate regions of eastern Asia. Although the beech genus is relatively small, the European beech has been used extensively for ornamental purposes and many horticultural varieties exist which display a vast array of morphological characteristics such as coloration and form (**Figure 4**).

Oak (*Quercus*)

Worldwide there are about 400 species of oaks, and they are taxonomically divided into three groups: (1) the red oak group (*Quercus* section *Lobatae*), (2) the white oak group (*Quercus* section *Quercus*), and (3) the intermediate group (*Quercus* section *Protobalanus*). All three groups include tree and shrub species. The red oaks and white oaks include evergreen and deciduous species, whereas the intermediate oaks are all evergreen. The red oaks are found only in the western hemisphere where their north–south range extends from Canada to Colombia. In contrast, the white oaks are widely distributed across the northern hemisphere. The intermediate group comprises only five species, all of which occur within southwestern USA and northwestern Mexico. Many of the world's oaks occur in regions with arid climates, including Mexico, North Africa, and Eurasia, where they are often limited in stature to shrubs and small trees. About 80% of oaks occur below 35° N latitude and fewer than 2% (six or seven species) reach 50° N.

The most reliable distinction between the white oaks and red oaks is the inner surface of the acorn shell. In the white oaks it is hairless or nearly so, whereas in the red oaks it is conspicuously hairy or velvety. In the intermediate group, this characteristic is not consistent among species. The

Table 2 Summary of characteristics of the more common genera in the beech family

Genus	*Leaves*	*Flowers*	*Fruit*
Beech (*Fagus*)	Deciduous	Male are in heads, female are in short spikes with two to four flowers	A triangular nut occurring in twos enclosed by a bur covered by weak unbranched spines; matures in one season
Chestnut (*Castanea*)	Deciduous	Male, female, or both borne on erect many-flowered apetalous spikes	A rounded nut occurring singly or in twos or threes covered by a bur having sharp, rigid, branched spines; matures in one season
Chinkapin (*Castanopsis*)	Persistent	Similar to chestnut	The same as chestnut but takes 2 years to mature
Tanoak (*Lithocarpus*)	Persistent	Similar to chestnut	An acorn which matures in 2 years
Oak (*Quercus*)	Deciduous or persistent	Male are borne in many-flowered apetalous spikes; female are borne in several-flowered spikes	An acorn which matures in 1 or 2 years
Southern beech (*Nothofagus*)	Deciduous or persistent which are small, oval, and have finely toothed edges	Male are bell-shaped of varying numbers; female are generally few in number and borne on stalks	Similar to beech
Chinquapin (*Chrysolepis*)	Persistent	Chestnutlike spikes of creamy-white; male flowers are borne in the leaf axils; female flowers usually occur in a cluster at the base of male spikes	Spine-covered bur which encloses from one to three nuts

Figure 4 Leaves of copper beech (*Fagus sylvatica* '*Purpurea*'). Photograph courtesy of Heinrich Speicker, Institut für Waldwachstum, Albert-Ludwigs-Universität Freiburg, Freiburg, Germany.

Figure 5 Leaves of white oak (*Quercus alba*). Note absence of bristles at the ends of the leaf lobes.

leaves of the white oaks are usually rounded and without bristle tips (**Figure 5**), whereas the leaf lobes of the red oaks are usually pointed and often bristle-tipped (**Figure 6**). To many botanists and others, the most important difference between the white oaks and red oaks is the length of the acorn maturation period. Acorns of species in the white oak group require one season to mature whereas species in the intermediate and most of the red oak group require two seasons. The white oaks and intermediate oaks are characterized by the presence of tyloses (occlusions) in the latewood vessels (water-conducting cells) of the xylem whereas tyloses are usually absent in the red oaks. These vessel-plugging materials confer greater decay resistance to the wood of the white and intermediate oaks than the red oaks. Other morphological features that differentiate the three groups and species within them are presented in various taxonomic treatments.

Figure 6 Leaves of northern pin oak (*Quercus ellipsoidalis*) showing bristle-tipped leaves.

Of the more than 250 oak species occurring in the western hemisphere, the largest number occur in Mexico and Central America. About 10 species occur in Canada while 90 species of oaks are native to the continental USA. Oak hybrids are not uncommon where species ranges overlap as evidenced by the more than 80 hybrids recognized in the USA alone.

The oaks are distinguished from other members of the beech family (e.g., the beeches and chestnuts) by their fruit, the acorn. With one exception, all plants that produce acorns are oaks. The exception is the genus *Lithocarpus*, which includes the tanoak of Oregon and California. Although represented by only one North American species, *Lithocarpus* is represented by 100 to 200 species in Asia. Some taxonomists think *Lithocarpus* may be an evolutionary link between the chestnut and the oak.

Southern Beech (*Nothofagus*)

Southern beech or *Nothofagus* is a genus of some 40 species that only occur in the temperate regions of the southern hemisphere. The name *Nothofagus* means 'false beech'; however, *Notofagus* meaning 'southern beech' might have been more appropriate and in fact the original intent of the nomenclature. Some plant historians have suggested that the original name was mis-spelled by inserting the *h*. Nine species of *Nothofagus* occur in South America while three occur in Australia. The importance of their timber is second only to that of the eucalypts.

Besides Australia, Chile, and Argentina, *Nothofagus* is also represented in New Zealand, New Guinea, and New Caledonia. Paleobotanists believe the current distribution of *Nothofagus* species resulted from the continental drift that occurred following the break-up of the Great Southern land. Forests of *Nothofagus* were noted as early as the mid-nineteenth century by the botanist Sir Joseph Hooker who accompanied James Ross on exploratory trips to the Southern Ocean between 1839 and 1843.

Chestnut (*Castanea*)

Castanea is the generic name for the chestnuts whose alternate name is chinkapin, not to be confused with *Castanopsis* and *Chrysolepis*, genera whose species are also commonly referred to as chinkapins or chinquapins. *Castanea* is a relatively small genus consisting of 10 species distributed across southern Europe, northern Africa, southwestern and eastern Asia, and the eastern United States. Prior to the 1930s in the eastern USA, the American chestnut (*Castanea dentata*) was prized for its high-quality, durable wood and sweet fruit but it is now relegated to a shrubby form because of its susceptibility to a pathogenic organism, the chestnut blight (*Endothia parasitica*). The blight eventually kills the stem but the root system is resistant to infection and results in sprout growth which is in turn killed back in a never-ending cycle.

Chinkapin (*Castanopsis*)

Most botanists agree that the taxonomy of *Castanopsis* is poorly understood. Only two of about 150 species of *Castanopsis* are found in North America whereas the rest are found in the forests of China, India, and the Malayan archipelago. These two are distinct from their Asian relatives, and systematists have created a new genus for them called *Chrysolepis*. The American species have a flower structure that is intermediate between *Castanopsis* and *Lithocarpus* suggesting a more primitive form within the family Fagaceae. The new scientific names for the American species, with the older names in parentheses, are *Chrysolepis chrysophylla* (Dougl.) Hjelmqvist (*Castanopsis chrysophylla* (Dougl.) A. DC.) for giant chinkapin and *Chrysolepis sempervirens* (Kell.) Hjelmqvist (*Castanopsis sempervirens* Dudl.) for evergreen chinkapin.

Ecology

Beech (*Fagus*)

Approximately 12% of all species in Fagaceae appear in the 2003 IUCN *Red List of Threatened Plants*.

Beech is found mixed with other temperate deciduous species and requires a site with a well-drained soil with good moisture holding capacity; it is more particular in that regard than many of the species it associates with. However, it does not tolerate soils that experience either prolonged flooding or dry periods. Beeches are extremely tolerant of shade and can persist under the shade of other species for decades.

European beech (*Fagus sylvatica*) is a dominant species in the broadleaved forests of Europe located principally in the foothills of mountainous areas. It was once more extensive in its distribution and composition than nowadays because of forest exploitation practices of past centuries which resulted in reforesting former broadleaved forests with faster growing species such as Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Efforts are under way to increase the proportion of broadleaved forests in Europe and in Germany in particular in order to return to the 'more natural' forest conditions of former times. Sessile oak (*Quercus petraea*), English oak (*Q. robur*), and European hornbeam (*Carpinus betulus*) are frequent associates.

Similarly, the American species, American beech (*F. grandifolia*) enjoys a wide range covering all of the eastern part of the USA on mesic sites and is associated with a large number of trees in a number of forest types. Like its European cousin, it has a distinctive smooth light-gray bark that remains so until maturity. Some of its principal associates include sugar maple (*Acer saccharum*), red maple (*A. rubrum*), yellow birch (*Betula alleghaniensis*), American basswood (*Tilia americana*), black cherry (*Prunus serotina*), eastern white pine (*Pinus strobus*), and red spruce (*Picea rubra*), as well as several hickories and numerous oaks and, in the southern part of its range, southern magnolia (*Magnolia grandiflora*). Beech is an important component of 20 forest cover types in eastern US forests and is one of the dominant species in three types; sugar maple–beech–yellow birch, red spruce–sugar maple–beech, and beech–sugar maple. It is found in lesser amounts in 17 other types.

American beech reproduces by seed which germinates on mineral soils but is best on forest soils containing humus. It is prevalent on podzolic soils. The largest species are found on alluvial bottom lands of Ohio and the lower Mississippi River valleys, and along the western slopes of the southern Appalachian Mountains. American beech also reproduces by root sprouts which can develop into desirable trees. Root systems are generally shallow compared to species with which it associates. Beech are long-lived trees only being exceeded by white oak (*Q. alba*) and sugar maple. Crown spread typically is wide compared to its associates. However, they can prune themselves well provided that stand density is not too low.

Southern Beech (*Nothofagus*)

The temperate regions of the southern hemisphere do not have direct counterparts of the northern temperate broadleaf deciduous forest. Instead the humid subtropical climate regions have a mixed (broadleaf and needleleaf) evergreen forest whose biogeographic interest stems from the occurrence of Gondwanan relicts: *Araucaria* pines (South America and Australia), *Podocarpus* pines (South America, Africa, and Australia), and the evergreen southern beech *Nothofagus* (South America, Australia, and New Zealand).

In general, southern beeches are slow-growing trees found in temperate rainforests of the southern hemisphere whose origins are believed to have been derived from a time when there was a single primordial landmass in the southern hemisphere called Gondwana. Continental drift is presumed to be the reason for the widespread occurrence of the genus across the southern hemisphere in essentially similar habitats in such places as South America, Australia, New Zealand, New Caledonia, and Papua New Guinea. Trees of some species can be quite large and may reach a height of 30 m or more with diameter at 1.3 m above the ground (diameter at breast height, dbh) of 1 m and occasionally up to 2 m. The strong similarity of form and the persistence of these trees in comparable habitats across southern hemisphere landmasses supports other evidence that these trees have survived largely unchanged since continental separation. In fact, fossil *Nothofagus* leaves have even been found on the Antarctic continent. Interestingly, other plant and animal species exclusively associated with southern beech forests also have close relatives associated with the comparable trees all across the southern landmasses. Beech orange fungus and the Peloridiidae bugs are good examples.

The extent of southern beech forests has been reduced in certain places. Southern beech forests in Australia were once far more widespread, when the climate was wetter and fire was less frequent.

The subantarctic forests of evergreen southern beech in Patagonia are threatened with extinction. They occupy a 60-km wide strip along the base of the Andes and extend, in pockets, 1500 km from the Province of Neuquén south to Tierra del Fuego. Two indigenous species – the lenga (*Nothofagus dombeyi*) and ñire (*N. procera*) trees – dominate the forest, which serves as home to pumas, guanacos, southern river otters, geese, Andean condors, and huemul deer. Logging and forest clearing have been extensive in the region's northerly latitudes, and now threaten the southern forests of lenga and ñire. However, the boundaries of Perito Moreno National Park in Patagonia are being expanded through land donated by the Patagonian Land Trust in an effort to preserve these forests of evergreen southern beech.

The American Chinquapins (*Chrysolepis*)

The uniqueness of the two species of the American genus *Chrysolepis* in relation to the species within *Castanopsis* level does not translate to differences between the American species. The ranges of the shrub form of giant chinkapin and of evergreen chinkapin overlap from northern coastal California into the Cascade Range of Oregon. The two species probably hybridize where they co-exist. An apparently continuous intergradation of characters can be found in the Cascades in southern Oregon and in the Siskiyou Mountains.

The two growth forms of giant chinkapin are probably not the result of plastic phenotypic response to site conditions, although they may be in portions of the species range. In the northern Coast Ranges of California, the tree form occupies relatively moist conditions; the shrub form grows on dry, sterile ridgetops in chapparal communities. In the central part of the Cascades of Oregon, the pattern is reversed – the tree form is found primarily in relatively open and dry ridgetop forest communities, and the shrub form is spread through the more mesic forest stands. Only the shrub form is found at high elevations in the Cascade Range.

This variation is due to the probable existence of at least three ecotypes of giant chinkapin: (1) a dry-site chaparral shrub ecotype of southwestern Oregon and northwestern California which probably matches the taxonomic category of *Castanopsis chrysophylla* var. *minor*; (2) a high-elevation ecotype adapted to heavy snowpack, cool temperatures, and short growing seasons found along the Oregon Cascades and in eastern Oregon; and (3) a tree form that occurs in forest stands at lower elevations. The latter ecotype seems well adapted to dry, relatively infertile sites but can and does do well in more mesic conditions that have a history of disturbance by fire.

Oaks (*Quercus*)

It is an understatement to say that oaks are found on a wide variety of sites, soil conditions and landforms throughout its range in the northern hemisphere. It is worth noting that one species (*Quercus humboldtii*) crosses the equator and is found in Ecuador.

Located between 5900 and 8600 feet (1800 and 2600 meters) above sea level, the Cachalú Biological Reserve in Colombia features one of the last remnants of pristine oak forests of this species. The 2000-acre (800-hectare) reserve is in northern Colombia in the Eastern Cordillera Montane Forest and is part of a 'globally outstanding' ecoregion. Oak prefers high altitudes, 1000–2600 m above sea level, with annual precipitation of 1500–2500 mm and temperatures of 16–24°C. Ecologically very plastic, it can be found both in moderately fertile and deep soils and in degraded, almost barren soils. Nevertheless, it grows better on shallow soils with a thick layer of humus, and relatively loose soils with good drainage and a pH between 5.8 and 7.0. It is intolerant of shade and will dominate competing species.

The oaks are widely distributed throughout the temperate regions of the northern hemisphere. Generalizing about the ecological relations of the genus is dangerous at best given the enormous number of species and their genetic, morphological, and life history diversity. The reader is directed to local or regional guides to the various species.

The oaks of the Mediterranean region of southern Europe and northern Africa typically are shrubby or low-growing trees that are adapted to dry growing conditions. They typically are found in savanna like environments and may co-exist with various agricultural crops. The world's cork supply comes chiefly from cork oak growing in Portugal, Spain, and north Africa.

Conversely, oaks can be found on extremely dry sites to those inundated by flood waters and span the shade tolerance spectrum from intolerant to moderately tolerant. Oaks have been known to reproduce by seed and by sprouting from stumps, seedlings, and rhizomes. Regeneration strategies are largely species-site dependent and the anomalies in regeneration strategy among the oaks emphasize the difficulty of generalizing their regeneration ecology across species and habitats. Different oaks have solved their regeneration problems in different ways and some are more flexible than others in reaching a successful establishment. Each species, environment, physiology, and genetics determine its ability to regenerate successfully.

Oaks are one of the most, if not the most, important hardwood species of the USA. The genus is represented throughout the USA except for the Great Plains area to the west of the Mississippi and east of the Rocky Mountains. The greatest variety of oaks occurs in the eastern deciduous forest most of which is classified as the oak-hickory forest region. Of the 145 forest cover types defined by the Society of American Foresters in the USA 31 contain oak in the name or are included as part of a species list defining a name. Of these, 23 oak types are found east of the Mississippi River. In addition, many of the non-oak types have oak as a common associate.

Although oaks are relatively intolerant of shade, species vary considerably in this regard. In some habitats, oaks are vulnerable to replacement by more tolerant species such as maples and beeches. Compared to other competitors, oak seedlings grow more slowly during the years following establishment. When young oaks are overtopped and heavily shaded few survive for very long. However, oaks tend to be relatively drought tolerant and often survive on sites that limit the establishment and development of associated species with less drought tolerance. On droughty sites oak stems and shoots often die back but have a remarkable capacity to sprout from the roots when growing conditions become favorable again. These sprouts often have the capacity to outgrow competitors. Oaks tend to accumulate on these dry sites and may eventually dominate the overstory vegetation.

Most forest ecologists class oaks as a genus whose species for the most part become established following disturbances to the forest overstory. These disturbances may be natural such as fire and windstorm, extensive or intensive, or may result from harvesting activities. Much of the current oak forest in the USA is the result of early forest exploitation and fires used to clear land for agriculture during settlement times. Oak opportunistically occupied sites in the Appalachian Mountains following the destruction of the American chestnut (*C. dentata*) by the chestnut blight in the 1930s.

Silviculture

Beech (*Fagus*)

Beech is classed as very tolerant of shade and hence possesses the ability to regenerate beneath tree canopies. However, on very poor soils or in very cold climates, beech may be less tolerant. This suggests silvicultural systems that retain an overstory component such as individual tree selection or group selection methods of harvesting. Beech prune themselves in well-stocked stands but open-grown trees tend to have wide crowns and lower limbs close to the ground. Often other species are purposely introduced into beech stands to increase stand density and act as 'trainers' in order to promote self-pruning. For example, European hornbeam is used to 'train' European beech in order to promote straight stems and encourage early self-pruning of lower branches. Beech responds readily to thinnings even at late ages and rapidly expands its crown following thinning. Thus beech is capable of producing high volume increment even to relatively old ages (130–150 years). When grown for high-quality wood the silvicultural target is to grow beech to 60 cm dbh in 110–140 years at a density of 80–110 trees per hectare. Thinnings are restricted to these 'crop trees' to keep their crowns in a free-to-grow condition. This sometimes means that thinnings must be from above (i.e., removing some dominant trees).

Southern Beech (*Nothofagus*)

Clear-felling has been the common way of harvesting southern beech in New Zealand and other areas across its distribution in the southern hemisphere. However, research is ongoing in New Zealand to find out if group selection (an uneven-aged silvicultural method) could be used to sustain southern beech forests. The group selection method is a modification of the single-tree selection method whereby openings larger than the crowns of the largest trees are made in the forest canopy. Typical openings range from 0.1 to 0.25 hectare. In large part, this method requires adequate advance regeneration to successfully regenerate the stand.

Oak (*Quercus*)

As a genus, oak has a wide ecological amplitude, that is it has a wide range of habitat conditions that individual species can tolerate. Therefore making silvicultural generalizations is difficult at best and an interested reader is best advised to seek regional or local information about the oak species and the location in which it is found.

Having said that, the potential exists for applying both even-aged and uneven-aged silvicultural methods to stands dominated by oak. In order for uneven-aged silvicultural methods to succeed there must be a sustained, periodic recruitment of oak reproduction into the overstory. This is a necessary prerequiste to create and maintain a negative exponential diameter distribution, a stand structure characteristic of uneven-aged stands. Although it may be possible, through thinning, to create the requisite diameter distribution without adequate regeneration, it cannot be sustained. Any event, natural or otherwise, that interrupts this process, will disrupt the recruitment of stems into succeeding size classes. The single-tree selection method is one way of creating this type of stand structure. From outward appearances, the single-tree selection method may seem to represent the most 'natural' of the silvicultural systems. The naturalness of the method nevertheless may be deceptive because there must be silvicultural control of the rate of natural reproduction, stand structure, and density. For all but the most shade-tolerant species, greater silvicultural control is obtained through single-tree selection than any other silvicultural method. Applying this method to the relatively shade-intolerant oaks with their erratic seed production cycles, seedling establishment, and other regeneration uncertainties is problematic. However, despite these problems, there is evidence that the method is suited to some oak forests.

Stands that are managed using even-aged silvicultural methods are regenerated naturally at the end of their rotation by one of three techniques: (1) clear-cutting, (2) shelterwood, or (3) seed tree. Although all three methods can be used to regenerate the spectrum of shade tolerant to shade intolerant oaks, they are most suited to the intolerant to mid-tolerant species. If clear-cutting is contemplated one should consider the suitability of the ecosystem for meeting oak reproduction requirements, the likelihood of regeneration success, and economic, social, and ecological implications. Clear-cutting is successful if oak regeneration of sufficient size is present in the stand before it is harvested.

The shelterwood method is employed principally to create conditions suitable for the establishment and development of tree reproduction. Typically, there is a preparatory cut to facilitate crown expansion and seed production, an establishment cut to prepare a seedbed, and a removal cut to release the newly established regeneration. There are several variants of this system in the way the cuts are carried out and how long trees are retained. The key to using shelterwood successfully to establish and maintain oak stands is in manipulating stand density in order to control light and competition on the forest floor. This may entail controlling the understory vegetation in addition to manipulating the overstory.

The seed tree method leaves 20 or fewer seed trees per hectare. Although applied successfully in certain locations, the seed tree method generally provides too little regeneration too late. However, it could be useful in providing mast for wildlife and may have a greater visual appeal than a clear-cut.

Tree diameter growth is sensitive to stand density. If the goal of a forest management program is to produce large diameter trees in the shortest time possible, then stand density needs to be reduced as early as 15 years for some species to provide the maximum amount of growing space needed by the average tree. However, this approach may not be economically feasible. Thinning only around a smaller number of 'crop' trees ensuring that they have sufficient growing space may be a more cost effective solution.

Special situations require special considerations. The leaves of Mongolian oak (*Q. mongolica*) furnish food for the silk worm in northeastern China. The silviculture of these stands aims to create large crowns with nutritious leaves and to manage the density of silkworms that feed on the leaves. In the cork oak forests of Portugal and Spain, silvicululral techniques focus on the timing, method, and intensity of stripping bark from the trees.

Chinkapin, Chinquapin

Chinquapins are vigorous sprouters and most trees originate as root crown sprouts. Mature trees tend to have straight boles and narrow crowns. They exist singly or in small groves. Natural regeneration is usually sparse or lacking. The best evidence suggests that the greatest success in regenerating chinquapin is achieved by covering seed in partially shaded, moist conditions.

Utilization

A small market exists for chinkapin wood for furniture and cabinet stock and decorative veneer. However, it is difficult to dry without the wood checking (splits and cracks). Southern beech is noted for its high-quality timber that is used for fine woodwork. The genus is second only to the eucalypts in wood production in the southern hemisphere. Beech is excellent for turning and steam bending. It wears well, is easily treated with preservatives, and is used for flooring, furniture, veneer, and containers. The nut is eaten by people and is an important source of food for wildlife. European beech has many horticultural varieties used in cultivated landscapes. Similar uses can be described for oak. Other well-known uses of oak include staves for barrels used for whiskey and wine, and cork for wine and other stoppers. The wood of tanoak (*Lithocarpus*) is hard, strong, and fine-grained but is mostly used for pulp and firewood. Tannin is extracted from tanoak bark (as well as oak) and used for tanning leather.

See also: **Non-wood Products**: Cork Oak. **Silviculture**: Coppice Silviculture Practiced in Temperate Regions; Natural Stand Regeneration; Silvicultural Systems; Unevenaged Silviculture. **Temperate and Mediterranean Forests**: Mediterranean Forest Ecosystems; Southern Coniferous Forests; Temperate Broadleaved Deciduous Forest. **Tree Breeding, Practices**: Genetics of Oaks. **Tropical Forests**: Tropical Montane Forests.

Further Reading

Burns RM and Honkala BH (tech. coords.) (1990) *Silvics of North America*, vol. 2, *Hardwoods*. Agriculture Handbook no. 654. Washington, DC: US Department of Agriculture Forest Service.

Eyre FH (ed.) (1980) *Forest Cover Types of the United States and Canada*. Washington, DC: Society of American Foresters.

Faculty of Forestry, University of Zagreb (1996) *Pedunculate Oak in Croatia*. Zagreb, Croatia: Vinkovci. (In Croatian with English summaries and articles.)
Johnson PS, Shifley SR, and Rogers R (2002) *The Ecology and Silviculture of Oaks*. Wallingford, UK: CAB International.
Royal Botanic Gardens, Kew (2002) *Electronic Plant Information Centre*. Available online at http://www.kew.org/epic/
Spiecker H, Mielikainen K, Kohl M, and Skovsgaard J (eds.) (1996) *Growth Trends in European Forests*. European Forest Institute Research Report no. 5. Berlin, Germany: Springer-Verlag.
van den Berg AKJ, Matos AP, Ferreira A, *et al.* (1979–2001) *Investigacao em Sobreiro e Cortica*. Lisbon, Portugal: Centro de Estudos Florestais, Instituto Superior de Agronomia, Tapada da Ajuda. (CD Rom.) Available online at http://www.isa.utl.pt/def/cef/
Watson L and Dallwitz MJ (1992) *The Families of Flowering Plants: Descriptions, Illustrations, Identification, and Information Retrieval*. Available online at http://biodiversity.uno.edu/delta/

Juglandaceae

R Rogers, University of Wisconsin–Stevens Point, Stevens Point, WI, USA

Introduction

The following sections characterize members of the walnut family (Juglandaceae) in relation to their taxonomy, distribution, ecology, and silviculture. Also included is information about their botanical importance as well as their significance in meeting human needs.

The walnut family contains tree species that produce some of the world's finest high-quality hardwood that is used to manufacture cabinets and fine furniture (walnut). Moreover, there are species in this family that are important sources of edible nuts (walnut and pecan). Members of the family are found in the north temperate and subtropical regions of the world, extending to India, Indochina, Malaysia, and Andean South America. The family is not present in Africa and Australia.

The walnut family originated during the Eocene epoch of the Tertiary period of geologic time about 65 to 55 million years ago. The climate of Eocene times was subtropical and moist throughout North America and Europe. Palm trees and alligators were found as far north as the Dakotas in the USA, while at high northern latitudes in Greenland and Siberia, moist temperate zone forests were dominated by giant redwoods and deciduous trees such as beech, chestnut, and elm, while cycads, magnolias, and fig trees flourished in Alaska. The walnut family reached its greatest extent in numbers and distribution at that time after which it has steadily declined.

Taxonomy

The most recent taxonomic information indicates that the walnut family (Juglandaceae) comprises eight genera (*Alfaroa*, *Carya*, *Cyclocarya*, *Engelhardtia*, *Juglans*, *Oreomunnea*, *Platycarya*, and *Pterocarya*) with about 50 species (**Table 1**). However, some taxonomists report as few as seven genera (*Cyclocarya* omitted) and as many as nine genera (*Annamocarya* added) that include 60 species.

Members of the walnut family are mostly trees (often resinous), but a few are shrubs. All family members have more or less aromatic leaves which are mostly deciduous and consist of individual leaflets arranged like a feather with a central axis and lateral branches (pinnate) or arranged similar to pinnately compound leaves but leaflets are arranged groups of three (ternate). The leaves of the majority of the species are spirally arranged on twigs but they are oppositely arranged in two genera, *Alfaroa* and *Oreomunnea*. Superposed buds are common (bud found above lateral bud).

Male and female flowers are usually found on the same tree although occasionally sexes are found on separate trees. Flowers are wind pollinated and are mostly in the form of catkins.

Fruit is a nut encased within a husk (drupe-like) or a disk-winged nutlet. A drupe is usually a one-seeded fleshy fruit with the outer layer (husk) fleshy and the inner layer bony. Husks may split to release

Table 1 Distribution of the genera of the walnut family (Juglandaceae)

Genus	*Number of species*	*Range*
Juglans	20	North, Central, South America; Europe, and Asia
Carya	16	North America (13) and Asia (3)
Platycarya	1	China, Japan, Korea, and Vietnam
Englehardia	7	Southern and southeastern Asia, and northern India
Cyclocarya	1	China
Pterocarya	6	Eastern and southwestern Asia
Alfaroa	5	Central and South America
Oreomunnea	3	Mexico, Central and South America

the nut or may remain whole. The botanic characteristics of some of the more common genera are shown in **Table 2**.

There are about 20 species of walnut (*Juglans*) which are found mainly in the temperate and subtropical areas of the northern hemisphere. These species are distributed in North, Central, and South America, Eastern Europe, and Asia. Six species are native to the USA while three are native to Asia. The best-known is eastern black walnut (*Juglans nigra*), a native of eastern North America, for its use in the manufacture of fine furniture. The eastern European species, English or Persian walnut (*J. regia*), is important in the production of nuts for human consumption.

At one time, prior to glaciation, Europe, Asia, and North America were home to many species of hickories (*Carya*); however, many of them were driven to extinction by the advance of the glaciers, especially in Europe. Today about 16 species remain. Three are native to Asia while the rest are found in North America. One species is restricted to Mexico.

The hickories are subdivided into two groups: the true hickories and the pecan hickories. The true hickories are distinguished from the pecan hickories by differences in leaves, fruit husks, and bud scales. True hickories usually have seven or fewer leaflets per leaf while pecan hickories have more than seven leaflets. Fruit husks are unwinged (although they may have ribs) in the true hickories while the husks are broadly winged at the sutures in the pecan hickories. The buds of true hickories consist of more than six overlapping scales while the pecan hickories have buds that consists of from four to six scales that are valvate (non-overlapping).

The genus *Platycarya* consists of only one species (*P. strobilacea*) found in China, Japan, Korea, and Vietnam. There are about seven species in the genus *Engelhardtia* widely distributed in southern and southeastern Asia and northern India. There is one species in the genus (*Cyclocarya*, *C. paliurus*) and it is found in China. The genus *Pterocarya* has six species distributed across eastern and southwestern Asia. Five species are listed for the genus *Alfaroa* located primarily in Central America. The members of this genus are unusual in the walnut family because the leaves are arranged oppositely on the stem. This leaf arrangement is also the case for the genus *Oreomunnea* which contains three species distributed through Mexico and Central America.

Ecology

Walnut (*Juglans*)

Black walnut (*J. nigra*) typically grows as scattered individual trees or in small groups throughout the central and eastern parts of the USA (**Figure 1**). Black walnut grows best on good sites in sheltered areas on well-drained bottomland sites in the Appalachians and the Midwest. Black walnut is sensitive to soil conditions and develops best on deep, well-drained, nearly neutral soils that are generally moist and fertile. Walnut grows best on sandy loam, loam, or silt loams. Walnut is common on limestone soils and grows especially well on deep loams, windblown soils, and fertile water deposited soils.

Black walnut grows in many of the mixed mesophytic forests but is seldom abundant. Usually it is found scattered among other trees and pure stands are rare, small, and usually located on the forest edge. An antagonism between black walnut and other plants growing within the root zone has been documented and attributed to juglone, a toxic substance found in the leaves, bark, nut husks, and roots of walnut trees. Some species are immune but others are not such as paper birch (*Betula papyrifera*), red pine (*Pinus resinos*), eastern white pine (*P. strobus*), Scotch pine (*P. sylvestris*), and apple (*Malus pumila*). Tomato (*Lycopersicon esculenta*) plants are especially susceptible. Root system is deep and wide-spreading and black walnut is smoderately tolerant of flooding. However, it is intolerant of

Table 2 Summary of characteristics of the more common genera in the walnut family

Genus	*Leaves*	*Twigs*	*Fruit*
Juglans (walnut)	Deciduous, odd-pinnate, alternate	Pith chambered	Nut encased in husk which may or may not split
Carya (hickory)	Deciduous, odd-pinnate, alternate	Pith solid	Nut surrounded by husk most split on maturity
Platycarya	Deciduous, odd-pinnate, alternate	Pith solid	Small flattened narrowly two-winged nutlet
Engelhardia	Deciduous, semievergreen or evergreen, even-pinnate, alternate	Pith solid	Three-winged nutlet
Cyclocarya	Deciduous, odd-pinnate, alternate	Pith chambered	Disk-winged nutlet
Pterocarya	Deciduous, odd or even pinnate, alternate	Pith chambered	Two-winged nutlet
Alfaroa	Opposite	Pith solid	Nut enclosed in husk
Oreomunnea	Opposite	Pith solid	Three-winged nutlet

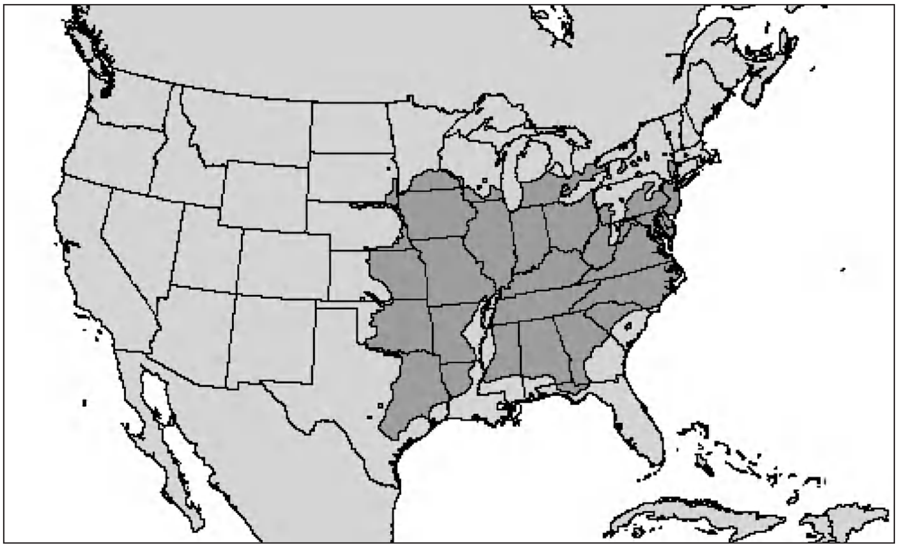


Figure 1 Range of black walnut (*Juglans nigra*). Adapted from Little EL, Jr (2003) *Digital Representations of Tree Species Range Maps. Atlas of United States Trees*. http://climchange.cr.usgs.gov/data/atlas/little/.

shade and in mixed species forests it must be in dominant or codominant canopy position if it is to survive.

Black walnut contains great genetic variation for growth and survival. More than 400 black walnut cultivars have been named and released over the last 100 years. However, hybridization is not common among species of walnuts. In fact, crossing between black walnut and butternut (*J. cinerea*) is difficult or impossible.

Ranging from cool temperate steppe to wet through subtropical thorn to moist forest life zones, English Walnut (*J. regia*) is reported to tolerate annual precipitation of 310–1470 mm, annual temperature of 7.0–21.1°C, and pH of 4.5–8.2. It thrives on rich, sandy loam, well-drained, slightly acid or neutral soils. English walnut responds well to cultivation and fertilization. In areas where hardiness is a problem, trees should not be forced into excessive vegetative growth and minimum temperature should not go below −29°C. If growth begins early in spring crop and foliage may be damaged by late frosts. When fully dormant, trees can withstand temperatures from −24°C to −27°C without serious damage.

Most true hickories are found on medium to dry sites and are often found in association with oaks (*Quercus* spp.). In fact, the largest forest region in the USA is situated in the eastern USA and is named the Oak–Hickory Forest because of the close association between the two genera. Most hickories are classed as moderately tolerant of shade and are considered to be relatively slow growing compared to its associates. There are exceptions however. Shellbark hickory (*Carya laciniosa*) is very shade tolerant, exceeded only by sugar maple and beech.

The pecan hickories, on the other hand, are found on moist but well-drained ridge bottoms in river bottoms with other bottomland hardwoods. The exception is bitternut hickory (*C. cordiformis*) which is found on a wide variety of sites including dry, gravelly uplands. Pecan (*C. illinoinensis*) is the largest of the hickories and attains a height of 35–40 m and a diameter (at breast height, dbh) of 60–120 cm or more.

The other six genera are typically found in semitropical forests characterized by mixed species forests in relatively high rainfall areas on mountain slopes and in valleys. Some, like *Oreomunnea*, are found in cloud forests. Cloud forests are usually found in humid areas 1000 m above sea level. In such forests, trees usually reach more than 20 m. Here the mean annual temperature varies from 12°C to 23°C and the annual mean precipitation is always higher than 1000 mm and sometimes exceeds 3000 mm. In many cases the forests are enshrouded in semipermanent mist, giving rise to the term cloud forest. Cloud forests harbor many species that can be found in the rain forests, but are typically rich in epiphytes, parasitic plants, bromeliads, vines, etc.

Silviculture

Walnuts are generally a minor tree species in most landscapes and as a consequence not cultured in a natural setting. If an individual tree is encountered in a forest stand its growing space requirements are assessed and the individual is released from competition as required. Release is necessary in high-density stands because stem diameter growth of walnut is extremely sensitive to the degree of crowding in a stand. Trees have been mechanically pruned to increase stem quality. Research and experience has shown that with proper thinning and pruning it is possible to produce 40 cm saw logs in 30–35 years and veneer logs (50 cm) in 40–50 years. Given a silvicultural objective of veneer logs, the recommended stocking and spacing for an average stand diameter of 50 cm dbh should be 62 trees per hectare at a spacing of 13 m between trees.

Pecans should be grown on sites that have well-drained, deep soils (1.2–2 m) with moderate soil moisture holding capacity. Pecan trees are native to river valley soils and have a relatively high water requirement. They do best on sandy loam soils but also can be grown on heavier soils such as clay loams if the soils are well drained. In areas where the soil is lighter and relatively dry, irrigation is required. When pecan trees are fully mature, approximately 20 years after planting, tree spacing should be approximately 20–25 m between rows and also between trees within rows, or 15–22 trees per hectare.

Utilization

English walnut (*Juglans regia*) is native to the region in Eurasia extending from the Near East through to the Himalayas and on to Western China. This single species is known by various names: Persian, French, Turkish, Italian, Circassian, and Carpathian walnut. Walnuts must have been harvested from earliest times but the earliest records of growing of orchards of walnut trees go back to classical Greek and Roman times. Besides the nuts, trees are also a source of high-quality wood used for furniture and gun-stocks. Growing of walnuts in Europe began in the 1500s; but by the 1600s walnut was replaced by mahogany as the wood most favored for furniture. They are now grown worldwide and the largest production is from California. Black walnut and other walnuts are used in much the same way as European walnut.

Hickories produce heavy, strong, shock-resistant wood with a high fuel value. These characteristics make hickory suitable for handles used in axes, hammers, and other striking instruments. Pecan is not only valuable as a fine furniture wood but the nut is prized for food. Species in the *Engelhardtia* and *Pterocarya* also produce fine cabinet woods.

See also: **Temperate and Mediterranean Forests**: Temperate Broadleaved Deciduous Forest. **Temperate Ecosystems**: Fagaceae. **Tropical Forests**: Tropical Montane Forests.

Further Reading

Burns RM and Honkala BH (tech. coords.) (1990) *Silvics of North America*, vol. 2, *Hardwoods*. Agriculture Handbook no. 654. Washington, DC: US Department of Agriculture Forest Service.

Eyre FH (ed.) (1980) *Forest Cover Types of the United States and Canada*. Washington, DC: Society of American Foresters.

Royal Botanic Gardens (2002) *Plant Information Centre*. Available online at http://www.kew.org/epic/

VanSambeek JW (ed.) (1997) *Knowledge for the Future of Black Walnut*: Proceedings of the 5th Black Walnut Symposium, July 28–31 1996, Springfield, MO. Gen. Tech. Rep. no. NC-191. St Paul, MN: US Department of Agriculture Forest Service, North Central Forest Experiment Station.

Watson L and Dallwitz MJ (1992) *The Families of Flowering Plants: Descriptions, Illustrations, Identification, and Information Retrieval*. Available online at http://biodiversity.uno.edu/delta/

Pines

P W Rundel, University of California, Los Angeles, CA, USA
D M Richardson, University of Cape Town, Cape Town, South Africa

Introduction

Pines clearly form the most ecologically and economically significant tree group in the world. The genus *Pinus* contains 110 species (**Table 1**), comprising more than half the species in the Pinaceae and almost 20% of all gymnosperm species. Ecologically, pines also influence the structure and function of many forest ecosystems. They affect biogeochemical processes, hydrological and fire regimes, and provide food and create habitats for animals. Pines are important, and very often dominant, components of the vegetation over large parts of the northern hemisphere (**Figure 1**). Economically, pines play a major role as sources of timber, pulp, resin, nuts, and other products. Pines have also been cultivated in many parts of the world, both within and well outside their natural range, and they form the foundation of exotic forestry enterprises in many southern hemisphere countries. Moreover, pines have featured in ancient myths and rituals throughout human history, and have been celebrated in visual art, prose, poetry, and music.

Pines are found in a remarkably wide range of environments, from above the arctic circle where winters are very cold and growing seasons are short, to the tropics where frost never occurs and growth continues through the year. Pines are the dominant trees over large parts of the boreal forest, or taiga, which covers about 12 million km^2 of the northern hemisphere. In temperate latitudes of the northern hemisphere they occur abundantly in high mountains, in Mediterranean-climate regions, and mixed with junipers over extensive semi-arid woodlands. Some pine species form virtually monospecific forests over very large areas whereas others form mixed forests with other conifers (notably spruce and fir species) and broadleaved trees (notably oak, poplar, birch, and alder species), or form subtropical savannas or open woodlands. In temperate regions, and even more so in the tropics, pines are usually associated with acidic, nutrient-poor soils. Pines possess a range of specialized mechanisms that enable them to thrive (and usually attain dominance) in these harsh environments. That pines are not restricted to such sites is clearly shown by their ability to spread into more productive sites, both within and outside their natural ranges, following disturbance that reduces the competitive superiority of vigorous angiosperms. The disturbance regime is thus an important determinant of pine distribution and abundance in the landscape. Fire is the driving force in succession in nearly all pine habitats.

The Origin and Evolution of Pines

The expansion of angiosperms and the concurrent decline of gymnosperms in the late Mesozoic had a significant impact on the phytogeographic history of the earth. The earliest-known angiosperms arose in the Early Cretaceous (130–90 million years ago), and there are now between 250 000 and 300 000 extant species. The first gymnosperms arose in the Middle Devonian (365 million years ago), much earlier than the angiosperms, but the group never achieved a high diversity of species. Evidence from fossilized cones shows that ancestors of the Pinaceae had evolved by the mid-Jurassic, and that pines themselves had evolved by the Early Cretaceous. Most of the other modern genera of the pine family appeared only in the Early Tertiary or later.

By the end of the Mesozoic (65 million years ago), pines had diversified into two major groups, or subgenera (**Table 2**); the subgenus *Pinus* (diploxylon or hard pines, with two fibrovascular bundles in each needle) and subgenus *Strobus* (haploxylon or soft pines, with one fibrovascular bundle in each needle). At this stage, pines had migrated throughout the middle latitudes of the supercontinent Laurasia. However, as major environmental changes occurred in the Early Cretaceous (between 130 and 90 million years ago), the diversification and rapid spread of angiosperms throughout middle latitudes pushed most conifers to small, cool or dry refugia in polar latitudes and scattered upland refugia at middle latitudes.

Intensive mountain-building events in the Tertiary created the environmental heterogeneity that drove the radiation of pine taxa in secondary centers of diversification, notably Mexico and northeastern Asia. Angiosperms that were best adapted at that time to tropical and subtropical conditions declined dramatically throughout middle latitudes following climatic deterioration at the end of the Eocene, allowing pines to expand their ranges.

Like the Eocene, the Pleistocene was also characterized by profound environmental changes that influenced the evolution of pines. However, whereas events in the Eocene completely reshuffled elements of the genus, Pleistocene changes caused pine species and populations to shift first toward the equator, then poleward (and to lower, then higher elevations), following the cycle of glacial and interglacial periods. Such migrations had important influences on the genetic diversity of pines. In some areas, such as the Pacific Northwest of North America, pine distributions were not so much split into distinct ranges by glaciations, as fragmented into small, semidisjunct populations. Such migrations served to promote intraspecific diversity while not necessarily promoting speciation. Although geographic conditions prevented pines from migrating south of the Sahara Desert, Nicaragua in Central America, or Java and Sumatra in Asia, the success of planted pines in the southern hemisphere shows that large parts of this hemisphere are highly suitable for pine growth.

Many significant changes in the abundance and geographic ranges of pines have occurred since the end of the last glacial period as pines rapidly expanded their ranges into deglaciated regions of North American and Europe. Wood rat middens preserved over the past 40 000 years at many sites in the Great Basin and other parts of the southwestern United States show a replacement of pinyon–juniper woodland by desert scrub in the Great Basin with warming at the end of Pleistocene.

Why Are Pines so Successful?

It is in the role of aggressive postdisturbance colonizers that pines are most clearly differentiated

Table 1 List of *Pinus* taxa, with common names, selected morphological features, and biogeographic region and habitat; figures relate to conditions regularly observed in the field (figures in brackets indicate exceptional dimensions)

Pinus *taxon*	*Common name*	*Needle number*	*Needle length (cm)*	*Needle longevity (years)*	*Cone length (cm)*	*Height (m)*	*Biogeographic region*	*Habitat*
P. albicaulis	Whitebark pine	5	3–7	5–8	4–8	5–10(30)	Western North America	Subalpine
P. aristata	Colorado or Rocky Mountain bristlecone pine	5	3–4	10–20	5–6(11)	5–15(30)	Rocky Mts, North America	Subalpine
P. armandii	Chinese white, Armand('s), or David's pine	5	8–15(18)	2–3	8–14	20–30	West and central China, Taiwan	Temperate montane
P. attenuata	Knobcone pine	3	9–15	4–5	8–15	10–20	Baja California, California, southwest Oregon	Mediterranean coastal
P. ayacahuite	Mexican white pine	5	8–15(22)	3	25–45	35–50	Mexico, Central America, Arizona, New Mexico	Tropical montane
P. balfouriana	Foxtail pine	5	(1.5)3–4	10–30	6–9(12)	10–22	California	Subalpine
P. banksiana	Jack pine	2	2–5	2–4	3–3.5	10–18(20)	Canada, northern USA	Boreal forest
P. bhutanica	Bhutan white pine	5	12–28	2–3	12–20	25	Himalayas	Temperate montane
P. brutia	Eastern Mediterranean or Calabrian pine	2	8–15	?	6–9	10–25	Eastern Mediterranean Basin	Mediterranean coastal
P. bungeana	Lacebark pine	3	6–8	3–4	5–6	15(30)	Central and north China	Temperate montane
P. canariensis	Canary Island pine	3	20–30	2–3	10–20(25)	30	Canary Islands	Mediterranean
P. caribaea	Caribbean pine	(2)3(4–5)	15–25	2	5–12	20–30	Caribbean area, Central America	Tropical/savanna
P. cembra	Swiss stone or Arolla pine	5	7–9	3–12	4–10	8–20(25)	Central Europe	Subalpine
P. cembroides	Mexican pinyon	(2)3(4)	2–6(7)	3–4	1–3.5	5–10(15)	Northwest Mexico, southwest USA	Arid/montane
P. chiapensis	Chiapas white pine	5	10–12	?	7–16	40	South-central to south Mexico, Guatemala	Tropical
P. clausa	Sand pine	2	6–9	2–3	3(4–8)	6(10)	Southeastern USA	Subtropical
P. contorta	Lodgepole pine	2	2–8	3–8	2–6	3–46(50)	Western USA	Temperate montane/subalpine
P. c. subsp. *bolanderi*	Bolander pine	2	2–5	?	?	6–15	California	Temperate
P. c. subsp. *contorta*	Shore or beach pine	2	2–7	?	2–5	3–10(16)	Coastal north California to British Columbia	Temperate
P. c. subsp. *latifolia*	(Rocky Mountain) lodgepole pine	2	(4)5–8	5–18	?	40–46	Rocky Mts, North America	Temperate montane
P. c. subsp. *murrayana*	Sierra (Nevada) lodgepole pine	2	(5–8)	?	2–5	15–40(50)	Sierra Nevada to Baja California	Temperate montane/subalpine
P. cooperi	Cooper pine	5(6–8)	8–10	?	6–10	30–35	Western Mexico	Tropical montane
P. coulteri	Coulter or bigcone pine	3	16–30	3–4	20–35	15–25	California, Baja California	Mediterranean coastal
P. cubensis	Cuban pine	3	10–14	?	4.5	?	Cuba	Tropical/savanna

P. culminicola	Potosí pinyon	(3–4)5(6)	5–6	?	3–5	1–5	Northeast Mexico	Tropical
P. dabeshenensis	Dabie Shan white pine	5	5–14	?	11–14	20–30	Eastern China	Temperate
P. dalatensis	Dalat or Vietnamese white pine	5	4–10	?	5–10	?	Vietnam	Tropical
P. densata	Sikang or Gaoshan pine	2(3)	8–14	3	4–6	30	China	Temperate montane
P. densiflora	Japanese red pine	2	(6)9–12	2–3	3–5	20–30 (36)	Japan, Korea, China	Temperate
P. devoniana	Michoacán pine	5	20–35	?	20–30	20–30	Mexico, Guatemala	Tropical
P. discolor	Border pinyon	3	2–6	?	2–3	5–10	Southwest USA, central and northwest Mexico	Arid/montane
P. donnell-smithii	Donnell Smith pine	5–6(7–8)	5–22	?	10–13	25	Guatemala	Tropical/subalpine
P. douglasiana	Douglas pine	5	20–35	?	7–10	20–35	West Mexico	Tropical
P. durangensis	Durango pine	6(7–8)	12–20	?	7–10	30–40	Northern and central Mexico	Tropical
P. echinata	Shortleaf pine	2	7–11	3–5	4–7	15–30(35)	Southeastern USA	Subtropical
P. edulis	Colorado pinyon	2	2–4	4–6	3–6	5–15	Western USA	Arid
P. elliottii	Slash pine	2–3	15(–30)	2	8–18	25–30	Southeastern USA	Subtropical
P. engelmannii	Apache pine	(2)3(4–5)	25–35	?	(10)–15	25(– 30)	West Mexico, Arizona, New Mexico	Temperate/montane
P. fenzeliana	Fenzel pine	5	4–18	?	6–10	13–50	South China to central Vietnam	Temperate
P. flexilis	Limber or Rocky Mountain white pine	5	3–8	5–6	7–15	7–15 (24?)	Western North America	Subalpine
P. gerardiana	Chilgoza or Gerard's pine	3	6–10	?	12–20	10–20(25)	Punjab, Afghanistan, Pakistan	Temperate montane
P. glabra	Spruce pine	2	(4)6–8	2–3	4–9	22–35	Southeastern USA	Temperate
P. greggii	Gregg's pine	3	8–15	2–3	8–14	10 – 15(25)	East Mexico	Tropical
P. halepensis	Aleppo pine	2(3)	6–12(15)	2	5–12	10–20(25)	Mediterranean Basin	Mediterranean coastal
P. hartwegii	Hartweg pine	3	8–16	?	8–14	20–30	Mexico, Guatemala	Tropical/subalpine
P. heldreichii	Heldreich whitebark or Bosnian pine	2	6–10	2–3(6?)	7–8	20(30)	Balkan peninsula, Greece	Temperate montane/subalpine
P. herrerai	Herrera pine	3	10(10–25)	?	2–3(4)	20–25(35)	West Mexico	Tropical
P. hwangshanensis	Hwangshan (Huangshan) pine	2	5–9	?	4–6	25	Central and eastern China	Temperate
P. jaliscana	Jalisco pine	4–5	12–16	?	4–8	20–30	West Mexico	Tropical
P. jeffreyi	Jeffrey pine	3	12–15(23)	4–6	15–30	25–50(60)	California, Baja California	Temperate montane
P. johannis	Zacatecas pinyon (pine)	3	3–5	?	3–4	2–4	Northeast Mexico	Arid/montane
P. kesiya	Khasi or Khasya pine	3	12–20(22)	2	5–7(10)	20–35(45)	Southeast Asia	Tropical
P. koraiensis	Korean stone pine	5	(6)8–13	2	9–20	20–35	Korea, Japan, northeast China, Siberia	Temperate montane
P. krempfii	Krempf pine	2	3–7	?	7–9	12–30	Vietnam	Tropical
P. lambertiana	Sugar pine	5	(5)8–10	2–4	25–50(60)	75	Baja California, California, Oregon	Temperate montane
P. lawsonii	Lawson's pine	3–5	15–20	?	6–8	25–30	South Mexico	Tropical

continued

Table 1 Continued

Pinus *taxon*	*Common name*	*Needle number*	*Needle length (cm)*	*Needle longevity (years)*	*Cone length (cm)*	*Height (m)*	*Biogeographic region*	*Habitat*
P. leiophylla	Smooth-leaved or Chihauhuan pine	5	5–9(15)	2	4–6.5(8)	20–25(30)	Mexico, Arizona, North Mexico	Temperate montane
P. longaeva	Western, Great Basin, or Intermountain bristlecone pine	5	1.5–3	10–33(45)	6–9.5	16	Western USA	Subalpine
P. luchuensis	Luchu pine	2	15–20	?	<5	<20	Japan, Ryukyu (Luchu) Islands	Temperate
P. lumholtzii	Lumholtz pine	3	(15)20–30	?	4–5(7)	10–20	Central Mexico	Tropical
P. massoniana	Masson, or Chinese red pine	2	15–20	?	5–6	8–25(30)	Central and eastern China, Taiwan	Temperate montane
P. maximartinezii	Martínez or Maxi pinyon	5	7–11	?	15–23	6–10	South Mexico	Arid/montane
P. maximinoi	Maximino pine	5	15–28	?	5–8	20–35	Mexico, Central America	Tropical
P. merkusii	Merkus or Tenasserim pine	2	17–25	1.5–2	5–9	20–30	Southeast Asia	Tropical/savanna
P. montezumae	Montezuma or roughbranched pine	(3–4)5(6–8)	15–25	3	(6)12–15	20–30(35)	Mexico, Guatemala	Tropical
P. monophylla	Singleleaf pinyon	1(2)	3–6	4–12	5–8	5–10	Southwestern USA to northern Baja California	Arid
P. monticola	Western white pine	5	(4)7–13	3–4	14–25(30)	50–55(70)	Western North America	Temperate montane
P. morrisonicola	Taiwan white pine	5	4–10	?	7–11	25(30)	Taiwan	Temperate
P. mugo	Dwarf mountain pine	2	3–8	5+	3–5(6)	2–6	Europe	Subalpine
P. muricata	Bishop pine	2	7–15	2–3	4–9	10–15(25)	California, Baja California	Mediterranean coastal
P. nelsonii	Nelson pinyon (pine)	3	5–10	?	7–12	5–10	Northeast Mexico	Arid
P. nigra	European black or Austrian pine	2	8–16	4(8)	3–10	20–40	Europe, Mediterranean Basin	Temperate
P. nubicola	Perry's pine	5–6(7–8)	25–43	?	10–15	25–30	South Mexico, Central America	Tropical
P. occidentalis	Hispaniolan pine	(3)4–5	11–18	?	5–7(8)	18	Caribbean Islands	Tropical montane/savanna
P. oocarpa	Eggcone pine	(3–4)5	20–25	?	6–10	15–30	Mexico and Central America	Tropical
P. palustris	Longleaf pine	3(5?)	20–45	2	15–25	25–30	Southeastern USA	Subtropical
P. parviflora	Japanese white pine	5	5–8	3–4	5–10	20–30	Japan	Subalpine
P. patula	Mexican weeping pine	3(4–5)	15–25(30)	3–4	7–10	30–35	East Mexico	Tropical
P. peuce	Macedonian or Balkan (white) pine	5	6–12	?	8–15	20–30	Balkan Peninsula	Temperate montane
P. pinaster	Maritime or cluster pine	2	(10)15–20(25)	3	10–22	20–35(40)	Western Mediterranean Basin	Mediterranean coastal
P. pinceana	Weeping or Pince pinyon	3	6–8(14)	?	5–10	4–10	Northeast Mexico	Arid/montane

P. pinea	Mediterranean stone, Italian stone, or umbrella pine	2	(8)12–15(20)	2–3	10–15	15–30	Mediterranean Basin	Mediterranean coastal
P. ponderosa	Ponderosa or western yellow pine	(2)3(4–5)	17–25	4–6	5–15	10–50(72)	Western USA	Temperate montane
P. praetermissa	Styles's pine	5	8–16	?	3–5	15	West Mexico	Tropical
P. pringelei	Pringle's pine	3(4–5)	15–25	?	5–8	15–30	South Mexico	Tropical
P. pseudostrobus	False Weymouth pine	5(6–8)	20–25	?	8–15	30–40	Mexico, Guatemala	Tropical
P. pumila	Dwarf stone pine	5	4–6	5	3–5(6)	1–4	East Asia	Boreal forest, subalpine
P. pungens	Table Mountain pine	2	5–7(9)	3	6–10	15–20	Northeastern USA	Temperate
P. quadrifolia	Parry pinyon	4–5	1.5–5	?	3.5–6	5–15	South California Baja California	Arid/montane
P. remota	Texas or paper-shell pinyon	2	3–5	?	2.5–3.5	3–8	Texas, northeast Mexico	Arid
P. resinosa	Red pine	2	12–18	4–5	3.5–6	20–30(40)	Northeastern USA, Canada	Temperate
P. rigida	Pitch pine	(2)3	5–10(12)	2–3	3–4(5–10)	10–25(30)	Northeastern USA	Temperate
P. roxburghii	Chir pine	3	20–30	1–3	10–15(20)	40–50 +	Himalayas	Temperate montane
P. rzedowskii	Rzedowski pinyon	(3)4(5)	6–10	?	10–15	15–30	Southwest Mexico	Tropical
P. sabiniana	Foothill or digger pine	3	15–25(30)	3–4	15–25	15–25	California	Mediterranean coastal
P. serotina	Pond pine	3	15–20	2–3	5–8	20	Southeastern USA	Temperate
P. sibirica	Siberian stone pine	5	(5)10–13	?	6–12	20–35	Central Asia	Boreal forest
P. squamata	Qiaojia pine	5	9–17	?	9	?	Southwest China	Subtropical montane
P. strobus	Eastern white pine	5	6–10(12)	2–3	8–20	25–30(40)	Northeastern USA and Canada	Temperate
P. sylvestris	Scots pine	2	3–7	2–8	3–6	30(35)	Europe, central Asia	Boreal forest, temperate, subalpine
P. tabuliformis	Chinese red pine	2–3	10–12(13–17)	?	4–9	25(30)	North and west central China	Temperate montane
P. taeda	Loblolly pine	3	12–22	3–4	6–12(15)	20–30	Southeastern USA	Temperate
P. taiwanensis	Taiwan red or Formosa pine	2	8–12	?	4–8	20–25(35)	Taiwan	Tropical montane
P. tecunumanii	Tecun Umán pine	4–5	14–21	?	4–7	50	Central America	Tropical
P. teocote	Twisted-leaved or Aztec pine	(2)3(4–5)	8–15	3	4–7	8–25(30)	Mexico, Guatemala	Tropical
P. thunbergii	Japanese black pine	2	7–12	3–4	4–6	30–40	Japan, Korea	Temperate
P. torreyana	Torrey pine	5	15–30	3–4	10–15	5–10(15)	California	Mediterranean coastal
P. tropicalis	Tropical pine	2(3)	15–30	?	?	?	Cuba	Tropical/savanna
P. uncinata	Swiss mountain pine	2	(3)5–6	5 +	4–6	10–20	Europe	Temperate montane
P. virginiana	Virginia or scrub pine	2	4–8	3–4	3–7	8–15(30)	Eastern USA	Temperate
P. wallichiana	Himalayan blue pine	5	11–18(20)	3–4	20–30	50 +	Himalayas	Temperate montane
P. wangii	Wang pine	5	2.5–6	?	4.5–9	20	Southwest China	Temperate
P. washoensis	Washoe pine	3	10–15	4–6	7–10	35(70)	Sierra Nevada	Temperate montane
P. yunnanensis	Yunnan (white) pine	2–3	15–20(30)	?	3–7(10)	15–30	China	Temperate montane

Adapted from Richardson D (ed.) (1998) *Ecology and Biogeography of* Pinus. Cambridge, UK: Cambridge University Press.

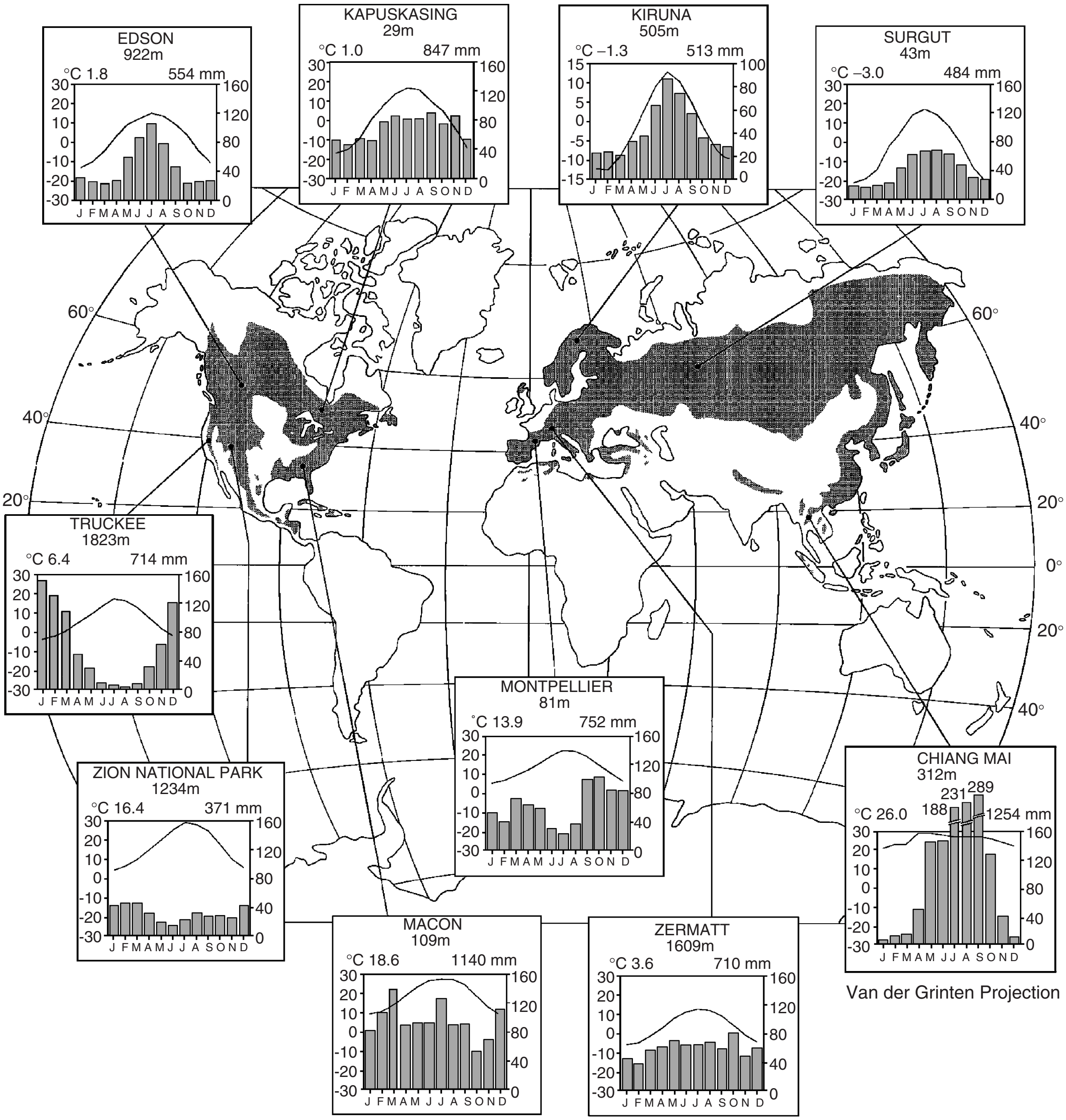


Figure 1 The worldwide distribution of the genus *Pinus* with examples of the varied climate regimes in which pines occur. Reproduced with permission of Cambridge University Press from Richardson D (ed.) (1998) *Ecology and Biogeography* of Pinus. Cambridge, UK: Cambridge University Press.

from firs, spruces, other conifers, and from angiosperm trees. An idealized 'pine prototype' would conform with the following profile: a light-demanding, fast-growing tree that regenerates as even-aged cohorts following landscape-scale disturbance, and retains its position in the landscape by exploiting aspects of its regeneration biology. This is an oversimplification, however, when one considers the wide range of habitats in which pines occur, and the range of life history syndromes evident in the genus.

Among the factors that have contributed to the ecological success of pines are their abundant output of seeds from an early age, their effective mechanisms for long-distance seed dispersal, their ability to colonize nutrient-poor and disturbed sites, and their mating system that permits inbreeding and selfing in isolated trees and confers resilience at

Table 2 Systematic relationships within the genus *Pinus*. Subgeneric categories are based on data in Richardson (1998) and personal communications from Aaron Liston (Oregon State University)

Genus *Pinus*
  Subgenus *Pinus*
    Section *Pinus*
      Subsection *Pinus* (Eurasia, North Africa, northeastern North America, Cuba):
        P. densata, *P. densiflora*, *P. hwangshanensis*, *P. kesiya*, *P. luchuensis*, *P. massoniana*, *P. merkusii*, *P. mugo*, *P. nigra*, *P. resinosa*, *P. sylvestris*, *P. tabuliformis*, *P. taiwanensis*, *P. thunbergii*, *P. tropicalis*, *P. uncinata*, *P. yunnanensis*
      Subsection *Pinaster* (Canary Islands, southern Europe, North Africa, West Asia, Himalayas):
        P. brutia, *P. canariensis*, *P. halepensis*, *P. heldreichii*, *P. pinaster*, *P. pinea*, *P. roxburghii*
    Section *Trifolius*
      Subsection *Contortae* (North America):
        P. banksiana, *P. clausa*, *P. contorta*, *P. virginiana*
      Subsection *Australes* (Eastern USA, Caribbean, Central America):
        P. caribaea, *P. cubensis*, *P. echinata*, *P. elliotii*, *P. glabra*, *P. occidentalis*, *P. palustris*, *P. pungens*, *P. rigida*, *P. serotina*, *P. taeda*
      Subsection *Ponderosae* (Western North America to Central America):
        P. cooperi, *P. coulteri*, *P. devoniana*, *P. donnell-smithii*, *P. douglasiana*, *P. durangensis*, *P. engelmannii*, *P. hartwegii*, *P. jeffreyi*, *P. maximinoi*, *P. montezumae*, *P. nubicola*, *P. ponderosa*, *P. psudostrobus*, *P. sabiniana*, *P. torreyana*, *P. washoensis*
      Subsection *Attenuatae* (Western USA, adjacent to Mexico):
        P. attenuata, *P. muricata*, *P. radiata*
      Subsection Oocarpae (Mexico, Central America):
        P. greggii, *P. herrerae*, *P. jaliscana*, *P. lawsonii*, *P. oocarpa*, *P. patula*, *P. praetermissa*, *P. pringlei*, *P. tecunumanii*, *P. teocote*
      Subsection *Leiophyllae* (Mexico and southwestern USA):
        P. leiophylla, *P. lumholtzii*
  Subgenus *Strobus*
    Section *Parrya*
      Subsection *Balfourianae* (Western USA):
        P. aristata, *P. balfouriana*, *P. longaeva*
      Subsection *Cembroides* (Southwestern USA, Mexico):
        P. cembroides, *P. culminicola*, *P. discolor*, *P. edulis*, *P. johannis*, *P. maximartinezii*, *P. monophylla*, *P. pinceana*, *P. quadrifolia*, *P. remota*, *P. rzedowskii*
      Subsection *Nelsoniae* (Mexico):
        P. nelsonii
    Section *Strobus*
      Subsection *Gerardianae* (East Asia, Himalayas):
        P. bungeana, *P. gerardiana*, *P. squamata*
      Subsection *Kremfianae*
        P. krempfii
      Subsection *Quinquefolius* (North and central America, southeast Europe, Asia):
        P. albicaulis, *P. armandii*, *P. ayachuite*, *P. bhutanica*, *P. cembra*, *P. chiapensis*, *P. dabeshanensis*, *P. dalatensis*, *P. fenzeliana*, *P. flexilis*, *P. koraiensis*, *P. lambertiana*, *P. monticola*, *P. morrisonicola*, *P. parviflora*, *P. peuce*, *P. pumila*, *P. sibirica*, *P. strobus*, *P. wallichiana*, *P. wangii*

the population level under a wide range of disturbance regimes.

Morphological Traits of Pines

Pines, like many other conifers, typically have a main trunk which can grow to a large size. The largest species of pines in the world are found in California and the Pacific Northwest of the USA. Growth conditions in these regions favor immense size in many conifer genera, including *Abies*, *Picea*, *Pseudotsuga*, *Thuja*, *Tsuga*, *Sequoia*, and *Sequoiadendron*. The largest species of pine in both height and girth is *Pinus lambertiana* which reaches over 75 m in height and more than 5 m in diameter in the Sierra Nevada of California. Three other pines from the western USA, *P. jeffreyi*, *P. monticola*, and *P. ponderosa*, all reach heights of 60 m or more.

Pines can, however, be quite short in stature in more extreme habitats. The pinyon pines usually attain heights of no more than 5–10 m when mature. Timberline pines also may be low growing, particularly when they occur as multistemmed krummholz shrubs at the upper limits of tree distribution. Most of these timberline species have the genetic potential for taller growth, and may reach 10–20 m in height under more favorable conditions.

Many pines are very long-lived, and the two bristlecone pines, *Pinus aristata* and *P. longaeva*, are the oldest living organisms in the world, with the latter reaching documented ages of nearly 5000 years. *Pinus albicaulis*, *P. balfouriana*, and *P. flexilis* may live for more than 2000 years, while others such as *P. jeffreyi*, *P. monticola*, and *P. ponderosa* can reach ages beyond 1000 years. All of these are montane or timberline species from western North America.

Because of their great ages, pines have played a fundamental role in the development of the modern science of dendrochronology, beginning with the pioneering work of Andrew Douglas in the American Southwest. Douglas developed the concept of cross-dating to compare and extend tree ring measures over broad regional areas to identify year-to-year variation in climate. It was this research that led to the establishment of the Laboratory of Tree Ring Research at the University of Arizona in 1906. Collaborative work with anthropologists soon led to what were then revolutionary approaches to dating the construction of Indian dwellings in Chaco Canyon and Mesa Verde in the Southwest. These studies allowed the earliest measurement and linkages of floating chronologies to develop long-term records over more than 2000 years, and had profound impacts in the field of anthropology.

The field of dendrochronology has expanded greatly in scope and depth in recent decades. Chronologies of living *P. longaeva* tied to floating records in logs show promise of developing a 10 000-year record across the Holocene. Tree ring chronologies are also proving to be valuable records of alteration of typical forest growth regimes resulting from fires and from atmospheric pollution or other causes.

Although all pines share the defining morphological trait of possessing pine needles, there is a wide variation in the size and manner of needle display. Needles are arranged in bundles (generally termed fascicles or needle clusters), with the number of needles per fascicle being a reasonably constant and species-specific characteristic in many taxa. Most pine species have two, three, or five needles per fascicle, but other numbers are also present. Only one species has one needle per fascicle: *P. monophylla*, the singleleaf pinyon of the southwestern USA. At the other extreme, four species of typically five-needled Mexican pines (*P. cooperi*, *P. donnell-smithii*, *P. durangensis*, and *P. pseudostrobus*) frequently have six needles per fascicle, and sometimes up to eight.

Needle number does not have any established ecological correlation. Adaptive radiation within specific subsections of the genus *Pinus* has taken place, both with and without modifications of needle number per fascicle. For example, almost all of the 24 Old World pines of the subsections *Pinus* and *Pinaster* have two needles per fascicle (**Table 2**) – this despite the wide range of habitats occupied by taxa in this group (e.g., *P. resinosa* and *P. sylvestris* in boreal-type forest; *P. nigra* and *P. pinaster* in lower-elevation sites in the Mediterranean Basin; *P. heldreichii*, *P. mugo*, and *P. uncinata* at high-elevation sites in the Mediterranean Basin; *P. kesiya* and *P. merkusii* in tropical savannas; and a set of eastern Asian species that occupy a wide range of habitats). The white pines occupying varied montane and subalpine habitats all typically have five needles per fascicle. At the other extreme are the pinyon species of North America which include taxa with one to five needles per fascicle, despite the arid environments in which all these species occur.

The length and form of pine needles varies greatly among pine species. The longest needles of any pine species are those of the appropriately named longleaf pine, *P. palustris*, in the southeastern USA (up to 45 cm), and *P. nubicola* in Mexico which also reach lengths of over 40 cm. At the other extreme are many pines with very short needles in the 2–8 cm range of maximum lengths. These short-needled species are almost entirely confined to the arid-adapted pinyon pines, high-elevation, or timberline pines, and pines on low nutrient sites, suggesting a relationship with environmental stress.

There are other interesting needle traits in pines that have not been studied to assess ecological significance. Several Mexican pine species have drooping, or ‘weeping’, needles that hang downward, and there are intermediate morphologies in other species with relatively flexible needles. Such long, fine needles may aid the condensation and drip of fog moisture in tropical mountain areas or in coastal fog zones, as with *P. lumholtzii*, *P. nubicola* and *P. patula* in Mexico, *P. radiata* on Cedros Island and the coast of California, and *P. canariensis* in the Canary Islands. Such hypotheses remain conjectural, however. Another unusual needle morphology in pine is that of flattened needles which are characteristic of the rare *P. krempfii* from the central highlands of Vietnam.

One strong environmental correlate of needle traits in pines does exist. Needle longevity is strongly correlated with habitat water availability and nutrient relations and/or stress. Tropical pines such as *P. caribaea* and the southern USA species *P. palustris* keep needles for no more than 2–3 years, and the Indian species *P. roxburghii* usually sheds its needles every year. Temperate forest pines commonly retain their needles for intermediate periods of 4–6 years. Pinyon pine leaves have relatively greater longevities of up to 10 years. Subalpine pines such as *P. longaeva* retain their leaves for up to 30 years or more, and even 45 years in extreme circumstances at the timberline in the White Mountains of California. This is the greatest needle longevity recorded for any conifer.

The form and morphology of pine cones is highly variable, with obvious relationships to the reproductive biology of individual species. The greatest length of cone in any pine occurs in *P. lambertiana*, where cones reach up to 50 cm in length. In terms of fresh cone weight, *P. coulteri* from California holds the record, with large globular cones 20–35 cm in diameter weighing as much as 2.3 kg. Large cones are also present in the Mexican taxa *P. ayacahuite*, *P. devoniana*, and *P. maximartinezii*. About one-third of pine species typically bear cones that are less than 5 cm long. As a broad generalization, it appears that taxa associated with stressful environments have smaller cones. *Pinus* is far more diverse in the morphology of its seeds than all other Pinaceae combined, a fact that certainly contributes to the wide range of habitats in which pines flourish. While most pines have wind-dispersed seed, the pinyon pines and many subalpine pines have large seeds dispersed by birds. It is intuitive to expect the largest seeds in species with the largest cones, but correlations between cone size and seed size is poor.

Ecophysiological Traits of Pines

Coniferous forest trees characteristically utilize a very different strategy of canopy carbon gain than do hardwood trees. Compared to deciduous hardwoods, conifers generally show a relatively low level of carbon gain per unit of leaf area, but a far higher leaf area index (LAI). Needles are retained for several to many years, and a clustered arrangement of foliage and regular canopy architecture has evolved to allow maximum irradiance of older foliage. Thus, the net primary productivity of conifer forests with high LAI is typically as great or greater than that of deciduous hardwood forests in the same climatic regime despite the lower photosynthetic rates. However, most conifers are inherently slow in becoming established in successional sequences where environmental stress is not extreme because it takes them multiple years to attain a full canopy. Under these conditions, deciduous hardwood saplings which can attain a full canopy in a single year are much more competitive.

Pines differ from the typical conifer strategy in several respects. Typical ranges of LAI in field populations of pines are only 2–4 $m^2 m^{-2}$, compared with values of 9–11 $m^2 m^{-2}$ in the more shade-tolerant genera *Abies*, *Picea*, and *Pseudotsuga*. The low LAI in pines largely results from the fact that many species carry relatively few years of needles compared to other conifers. Except in pines characteristic of environments of extreme cold or drought stress, 2–5 years of needles in the canopy at any time is typical. Thus, despite their relatively low LAI, pines are inherently more effective colonizers than many other conifers because they can attain a full canopy of foliage more rapidly early in succession. Many pines, however, can be selected for a higher LAI under plantation conditions where resources are not limiting. Highly productive plantations of commercial pine species such as *P. radiata* owe much of their productivity to LAIs two or three times those found under natural conditions.

It is interesting to speculate on the potential similarities of the rapid growth and colonizing abilities of many pines and the traits of early successional hardwood trees. The relatively low LAI of pines and their generally poor shade-tolerance are shared by such hardwoods as temperate *Eucalyptus* and many tropical pioneer trees. Shade-tolerant conifers such as *Abies*, *Picea*, *Pseudotsuga*, and *Sequoia* not only have high LAIs, but share a typical architectural form characterized by growth cycles that produce regular whorls of branches at levels determined by the height of the trunk meristem. In contrast to this pattern, most pines and many tropical colonizers (e.g., *Cecropia*, *Macaranga*, and *Musanga* spp.) are shade-intolerant and possess a canopy architecture with the cyclical addition of tiers of branches which are structurally identical to the trunk.

Considering the wide range of ecological habitats in which pines occur, it is noteworthy that there is relatively little variation in their photosynthetic characteristics. Maximum rates of photosynthetic capacity under field conditions within ecologically plastic species such as *P. contorta* and *P. sylvestris* appear to vary as much as within pines as a group. When grown under common garden conditions under nonlimiting conditions, pines from very different environments exhibit quite similar photosynthetic responses to irradiance, suggesting a considerable degree of phenotypic plasticity. This is equally true both for ecotypes of the same species and different species. Thus, variation in net primary production rates of pines in different environments is less a function of differences in photosynthetic capacity than of climatic factors of cold or drought that limit the period of positive net carbon gain throughout the year.

Seasonal patterns of low temperatures in autumn and winter are clearly important components of the potential net primary production of pine species. Thus pines in cold-temperate environments or timberline habitats have high levels of positive canopy photosynthesis limited to relatively few months of the year. Subtropical and tropical species grow throughout the year, with light, LAI, and nutrient availability as the primary factors controlling net primary production. Although pine species may tolerate habitats over a wide range of annual precipitation, the response of individual species to limited water availability is surprisingly consistent, as with almost all conifers. Net photosynthesis in pines typically falls to zero at relatively modest tissue water stress, thereby limiting the growth potential of pines in semi-arid environments.

Other aspects of the ecophysiology of pines show highly adapted traits between species that adapt them to specific climatic or environmental conditions. As logic would suggest, pines of cold habitats commonly have much lower temperature optima for photosynthesis than do species of warm climates. A stomatal response to environmental water vapour deficit is another trait showing adaptive selection. Species of semi-arid environments are highly sensitive to small changes in vapor pressure, thereby regulating summer water loss, while subtropical species are quite insensitive to such changes. Clear differences in tolerance of low nutrient conditions are also apparent in pine species whose ranges overlap.

Human Impacts on Pines and Pine Forests

Human-induced changes to pine forests have had significant impacts on the structure, dynamics, and biodiversity of these ecosystems for centuries. The consequences of human activities likely extend back thousands of years in the Mediterranean Basin where marked changes in human population numbers and far-reaching changes in land use practices have exerted major influences. Human impacts have come from logging and deforestation, land use practices that increase or decrease natural frequencies of fire, grazing, and plantation establishment outside of normal species ranges.

There is a massive literature on the history, policies, politics, and practices of logging in different parts of the range of pines. Logging takes place in natural pine forests around the world for construction-grade lumber, with varying levels of sustainability. Additionally, the need for fuelwood in many parts of the natural range of pines in the developing world still accounts for a large part of the total area of pine forest cleared every year. While pines are important lumber sources, logging of hardwood forests has often led to a stimulation of pine establishment and dominance. For example, past clearing of broadleaved forests in the southeastern USA and areas of Asia has created suitable conditions for pines. Human-induced changes to natural fire regimes have had a particularly dramatic effect on pine ecosystems. This impact has been seen most strongly where human activities have led to increased fire frequency. In Central America, Mexico, and Southeast Asia this has often arisen through the agency of slash-and-burn agriculture. However, the opposite condition of reduced fire frequencies has also been widespread and has affected pine establishment. Heavy grazing of rangelands has reduced fire frequency in many parts of the American West by reducing fuel loads, and this has had a major impact on vegetation dynamics. Fire exclusion has allowed pines to spread into some areas where the natural fire regime excluded them, and has changed the forest composition in areas where the natural fire regime allowed pines to grow, but where changed fire characteristics have altered processes affecting vegetation dynamics. Some impacts of fire suppression in pine forests through the disruption of the relationships between pines, fire, pathogens and insects are complex.

Changes in grazing pressure have triggered changes in pine distribution in many regions, but the phenomenon has been best studied in North America. Grazing facilitates pine establishment in abandoned fields by reducing the cover of vigorous grasses and thus competition with pine seedlings. Areas subjected to heavy grazing often remain susceptible to colonization by pines long after grazing pressure has been greatly reduced or eliminated. Such effects have been documented for pine forests adjoining mesic subalpine meadows and mixed grass and brush in more arid regions.

Humans have harvested pines and their products for thousands of years. There are 29 pine species whose seeds are harvested for human consumption. In some societies, pine seeds harvested from natural forests are still important economic resources, as in Pakistan, India, China, and Mexico.

Pines have been widely planted in the Mediterranean Basin since prehistoric times, and more recently throughout the world. Some pines have proved highly successful for use in plantations outside their natural ranges where there is a shortage of coniferous species to produce fibers and solid wood products. This is particularly true of temperate areas in the southern hemisphere where there are massive plantations of *Pinus radiata* and other pine species. Reasons for the widespread use of pines in exotic forestry plantations include their simple design with straight trunks and geometrical branching habitat that makes them ideal for timber production. Moreover, pines grow faster than many other potential species, are easy to manage in plantations, have easily collected seeds, and are ideally suited for planting in marginal forest lands where most plantations are desired. Many pine species – *P. caribaea*, *P. elliottii*, *P. kesiya*, *P. oocarpa*, *P. patula*, *P. radiata* and *P. taeda* – are widely grown in plantations in the tropics and subtropics.

Threats to Pine Species

One-third of all pine species are either threatened in their entirety, or have subspecies or varieties that are threatened. This includes species with naturally restricted ranges and small population sizes as well as others that owe their threatened status to human activities. Even among pine taxa that occupy large ranges, large portions of their genetic diversity have been lost; this may have reduced their ability to respond to changing environmental conditions.

See also: **Biodiversity**: Biodiversity in Forests. **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Environment**: Environmental Impacts. **Genetics and Genetic Resources**: Population, Conservation and Ecological Genetics. **Hydrology**: Hydrological Cycle. **Landscape and Planning**: Perceptions of Forest Landscapes. **Mensuration**: Tree-Ring Analysis. **Plantation Silviculture**: Forest Plantations. **Temperate and Mediterranean Forests**: Mediterranean Forest Ecosystems; Northern Coniferous Forests; Southern Coniferous Forests; Subalpine and Boreal Forests; Temperate Broadleaved Deciduous Forest. **Tree Breeding, Practices**: *Pinus Radiata* Genetics. **Tree Physiology**: Canopy Processes. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources.

Further Reading

Burns RM and Honkala BH (eds) (1990) *Silvics of North America*, vol. 1, *Conifers*, Agriculture Handbook no. 654. Washington, DC: US Department of Agriculture Forest Service.
Critchfield WB and Little EL (1966) *Geographic Distribution of Pines of the World*, US Department of Agriculture Forest Service Miscellaneous Publication no. 991. Washington, DC: US Department of Agriculture Forest Service.
Farjon A, Page CN, and Schellevis N (1993) A preliminary world list of threatened conifer taxa. *Biodiversity and Conservation* 2: 304–326.
Lanner RM (1981) *The Piñon Pine: A Natural and Cultural History*. Reno, NV: University of Nevada Press.
Lanner RM (1996) *Made for Each Other: A Symbiosis of Birds and Pines*. New York: Oxford University Press.
Millar CI (1993) Impact of the Eocene on the evolution of *Pinus* L. *Annals of the Missouri Botanical Garden* 80: 471–498.
Perry JP (1991) *The Pines of Mexico and Central America*. Portland, OR: Timber Press.
Richardson D (ed.) (1998) *Ecology and Biogeography of* Pinus. Cambridge, UK: Cambridge University Press.
Thirgood JV (1981) *Man and the Mediterranean Forest: A History of Resource Depletion*. London: Academic Press.
Van Pelt R (2001) *Forest Giants of the Pacific Coast*. Seattle, WA: University of Washington Press.

Poplars

B Stanton, GreenWood Resources, Clatskanie, OR, USA

Introduction

The genus *Populus* (family Salicaceae) comprises 29 diverse species found almost exclusively in forests of the northern hemisphere. Considered as a whole, *Populus* covers an impressive ecological amplitude from the tropics to the boreal forests. In China alone, an extraordinary number of species are found in the cold northeast, the arid northwest, and the subtropical Qinghai–Tibetan plateau. No less impressive is the close association between *Populus* forests and the development of humankind that has included their cultivation for shelterbelts, fuel, animal feed and forage, pulp, veneer, lumber, and more lately, engineered wood products. Moreover, this group of trees has lately assumed a vital ecological role in forestalling desertification in Asia and in restoring and maintaining many of the world's degraded rivers and floodplains (**Figure 1**). In the latter regard, conserving the genetic resources embodied in the natural stands of many *Populus* species is critically important. These genetic resources are also an indispensable foundation for many breeding programs that support ongoing *Populus* domestication efforts. As the global forest plantation industry becomes inexorably associated with high-yield plantations of the tropical and subtropical regions, such applied genetics programs will help to sustain *Populus* plantations as the only temperate-zone tree that can be managed for near-comparable yields.

This article is an overview of the genus *Populus* and its members, where they occur, examples of how

Figure 1 *Populus* frequently grows in riparian habitats that are also the base for much of society's agricultural and industrial sectors. The conservation of *Populus* stands in the riparian zone is an integral component of the restoration of such ecologically important habitats.

they have adapted to their environment, the particulars of their genetic recombination systems that allow for future adaptive changes, the needs inherent in their conservation, and the current genetic improvement strategies being used to domesticate *Populus* to meet the demands of a growing world population.

The *Populus* Genus

Populus is mainly found in the northern hemisphere's boreal and temperate forests but is also an inhabitant of the world's tropical and subtropical forests. The genus is divided into six sections. Three sections contain nearly all of the commercial species: section *Populus*, the aspens and white poplars (formerly known as section *Leuce*), section *Aigeiros*, the cottonwoods, and section *Tacamahaca*, the balsam poplars. Section *Populus* is distributed throughout North America, Europe, and Asia. Section *Aigeiros* is best known in North America and Europe, while section *Tacamahaca* has a North American and Asian distribution. Three less economically important sections (*Abaso*, *Leucoides*, and *Turanga*) have less extensive botanical ranges, but include species that greatly extend the class of sites occupied by *Populus* (**Table 1**).

Populus has a pioneering habit, colonizing sites after disturbances; fire and floods are often a prerequisite for good establishment. They are fairly unique among forest trees in their capacity for impressive reproduction by both sexual and asexual means. Very rapid growth rates during the juvenile phase are often exhibited. However, lifespans do not extend much beyond 100 years. In some cases, succession to ensuing seral stages may be postponed by fire or other disturbances; spruce budworm outbreaks in eastern Canada maintain the presence of *P. tremuloides*, preventing its replacement by *Abies* and *Picea*.

Table 1 Sections and species of the genus *Populus* according to Eckenwalder (1996)

Section	*Species*
Abaso	*P. mexicana*
Aigeiros	*P. deltoides*
	P. fremontii
	P. nigra
Leucoides	*P. glauca*
	P. heterophylla
	P. lasiocarpa
Populus	*P. adenopoda*
	P. alba
	P. gamblei
	P. grandidentata
	P. guzmanantlensis
	P. monticola
	P. sieboldii
	P. simaroa
	P. tremula[a]
	P. tremuloides
Tacamahaca	*P. angustifolia*
	P. balsamifera
	P. ciliata
	P. laurifolia
	P. simonii
	P. suaveolens[b]
	P. szechuanica
	P. trichocarpa
	P. yunnanensis
Turanga	*P. euphratica*
	P. ilicifolia
	P. pruinosa

[a] *Populus. tremula* includes *P. davidiana*.
[b] *Populus suaveolens* includes *P. cathayna, P. korena, P. maximowiczii*.
Source: Eckenwalder JE (1996) Systematics and evolution of *Populus*. In: Stettler RF, Bradshaw HD Jr, Heilman PE, and Hinckley TM (eds) *Biology of Populus and its Implications for Management and Conservation*, pp. 7–32. Ottawa, Canada: NRC Research Press.

The species are deciduous in all but a few cases. Their growth habit is indeterminate with the production of neo-formed leaves occurring until growth cessation occurs, triggered in many species by diminishing day length. They are largely shade-intolerant, although there are noticeable differences within the genus ranging from the intolerant (*P. balsamifera, P. trichocarpa*) to the very intolerant (*P. tremuloides, P. deltoides*). The white wood is diffuse–porous with indistinct annual growth rings and comparatively soft and light quality.

The major sections of the genus can also be broadly characterized according to the general class of sites on which they are commonly found. Sections *Aigeiros* and *Tacamahaca* are prominently adapted to lowland riparian zones along major river systems with broad floodplains, but not exclusively; *P. balsamifera* (section *Tacamahaca*) and *P. deltoides* (section *Aigeiros*) have been found respectively, on grasslands and abandoned farm fields and *P. ciliata* (section *Tacamahaca*) is found at higher elevations in the Himalayan foothills. By comparison, the aspens of section *Populus* are more frequently found on drier, less fertile, upland and montane sites; *P. tremuloides* is found at elevations of 3000 m in western North America and *P. tremula* at 3300 m in Mongolia. *Populus euphratica* (section *Turanga*) is typically found in the arid, desertlike environments of Asia, often growing on saline soils, while *P. heterophylla* (section *Leucoides*) is well adapted to prolonged inundation in swamps along the southeastern seaboard of North America.

Botanical ranges in *Populus* typically cover exceedingly wide geographic areas. For example, in section *Populus*, the range of *P. tremuloides* spans approximately 110° of longitude and over 50° of latitude in North America. Even more outstanding is *P. tremula* which grows throughout Europe and Asia, from the Atlantic to the Pacific Oceans, ranging from 70° N latitude in Norway and the tundra in Russia, south to the Mediterranean basin. Similarly, *P. alba* is distributed throughout central and southern Europe and extends southward into Afghanistan, Iran, Iraq, and Syria. In section *Tacamahaca*, *P. balsamifera* has a transcontinental range covering much of Canada, Alaska, and the Great Lakes Region of the United States. *Populus trichocarpa* spans approximately 30° of latitude from southeastern Alaska south to Baja California. The Asian *Tacamahaca* species of widest distribution, *P. suaveolens*, is found from central Asia eastward to the Japanese islands. In section *Aigeiros*, *P. nigra* spans all of Europe, northwestern Africa, western Asia, the Caucasus, and western Siberia. *Populus deltoides* ranges from the Canadian prairie southward to the coast of the Gulf of Mexico and east to the Atlantic seaboard. *Populus euphratica* (section *Turanga*) occurs over an area from North Africa and the Mediterranean through central Asia and northwestern China.

Other species have more limited or disjunct ranges. *Populus ilicifolia* (section *Turanga*) is found growing along four rivers in Kenya between 1° N and 3° S latitudes. *Populus heterophylla* (section *Leucoides*) is endemic to the coastal plain of the southeastern USA and then further inland in the Mississippi and Ohio River valleys. Separate populations of the tropical species *P. mexicana* (section *Abaso*) are located along the Pacific and Gulf coasts of Mexico.

Adaptation

The genus *Populus* has successfully adapted to the world's climatic variations. This adaptation may be expressed in a differentiation among populations and its expression is critical to the ecological and evolutionary functioning of individual species and the genus as a whole. One example, adaptive variation in phenology, is of primary importance and is often associated with a population's geographic source. The association is keyed to environmental stimuli, including temperature, photoperiod, and precipitation. In species of the temperate and boreal forests, spring growth takes place only after sufficient winter chilling has occurred which allows a response to warming temperatures, while a reduction in day length towards the end of the growing season cues the process of winter dormancy. Similarly, above-freezing cold temperatures bring about leaf abscission. Populations of *P. balsamifera*, *P. deltoides*, *P. tremuloides*, and *P. trichocarpa* from different latitudes differ in the timing of these spring and autumnal events. Northern populations typically have a lower temperature threshold required for spring growth initiation than their more southerly counterparts. Northern populations also enter the dormant phase under the influence of a longer day length than southern sources of the same species. The synchronization of these growth cycles with the change of seasons has allowed *Populus* species to achieve their characteristically wide geographic distributions.

Other examples of adaptive population variation include:

1. *Populus trichocarpa* from coastal and inland regions of the North American Pacific Northwest are differentiated in their tolerance of winter temperatures. *Populus trichocarpa* populations sampled from contrasting elevations within the same river drainage are differentially adapted to growing season length.
2. *Populus deltoides* from the lower Mississippi River valley has greater chilling requirements for flowering than more northerly populations.
3. *Populus deltoides* populations in southwest North America exhibit differences in drought tolerance that are associated with local precipitation.
4. Differences in crown architecture of Italian *P. alba* populations are correlated with latitude, from which an adaptive strategy for light interception has been inferred.

Adaptations to temperature, photoperiod, light intensity, and precipitation are sufficiently precise that populations of the same species originating from contrasting environments can be differentiated in their response to these environmental cues when tested in a single locale. In nearly all cases, the pattern of adaptive variation in studies sampling populations from latitudinal ranges has been continuous, suggesting the existence of clines. Population differences notwithstanding, genetic systems are such that the larger source of variation in most studies has been found within populations among the individual members; appreciable gene flow between populations partially counters the effects of natural selection. This reservoir of variation allows populations to accommodate yearly variations in climate as well as long-term climatic changes that alter the future adaptive landscape (**Figure 2**).

Next to the importance of climatic adaptations, the resistance to foliar, shoot, and stem diseases also plays a major role in the adaptive strategies of *Populus*. The pathogens of most significant ecological and commercial impact include *Melampsora* leaf rust, *Marssonina* leaf spot, *Venturia* shoot blight, *Septoria* canker, *Hypoxylon* canker, *Dothiciza* canker, and *Xanthomonous* bacterial canker. Pathogenic variation encompasses a range in both virulence and aggressiveness. *Populus* genetic systems have coevolved mechanisms of resistance to both as their pathogens undergo mutation and sexual recombination.

Figure 2 The timing of spring growth initiation in *Populus trichocarpa* is of critical importance to the adaptation of populations to their environment. The adaptive strategy includes differences in the earliness with which individuals of a population initiate growth, perhaps in response to yearly variation in warming spring temperature patterns.

Host–pathogen interactions of *Melampsora* leaf rust have been extensively studied in *Populus*. Resistance involves both major and minor gene systems. Qualitative resistance is expressed in the isolation of the infection by the host's hypersensitive response. If qualitative resistance is lacking and the infection moves throughout the leaf tissue, the rate at which the pathogen spreads and sporulates is controlled by the host's rate-limiting quantitative resistance mechanism. Pathogen interspecific hybridization has been observed and may progress to advanced generations with the formation of hybrid swarms potentially adding a new dimension to the range of variability and virulence; in *Melampsora* leaf rusts, there have been two occurrences of interspecific hybridization.

The strategy of disease adaptation in *Populus* is oftentimes tied to environmental conditions that determine selection pressure. *Populus trichocarpa* populations from mesic, low-elevation environments typically exhibit significantly higher overall levels of *Melampsora* resistance, compared with populations native to arid regions that lack rust populations that act as a force of natural selection to heighten host resistance levels. A similar pattern has been observed in *P. deltoides*; populations from the drier portion of the range show lower levels of rust resistance in comparison with populations sampled from more humid, wetter environments.

Recombination System

The *Populus* recombination system is efficient in both the creation of new phenotypes in succeeding generations to allow for adaptation to changing environments, and in preserving the standing adaptability of the parental generation. The recombination system is characterized by mostly dioecious species and is thus outcrossing. Staminate and pistillate flowers are grouped in unisexual inflorescences (hermaphroditism is rare but has been reported in sections *Aigeiros*, *Populus*, and *Tacamahaca*). Sex ratios are balanced in most cases, thereby maximizing the effective population breeding number (sex ratios may shift in favor of females on higher-quality sites). A higher proportion of recombinant progeny is promoted by outcrossing and a large effective breeding number. The following characteristics of *Populus* reproductive biology further promote open recombination (**Figure 3**):

1. Full reproductive maturity is achieved after 10–15 years, ensuring wide participation in the breeding population before individuals are eliminated by stand competition.
2. Periodicity seems to be an unknown in sections *Aigeiros* and *Tacamahaca* with fruiting occurring every year (production of sizable seed crops in section *Populus* occurs on 4- or 5-year intervals).
3. Pollination is anemophilous, achieving wide distribution of male gametes.
4. Each pistillate inflorescence may contain 30–40 flowers, each of which develops into a two- to four-carpelary capsule that can contain upwards of 30 ovules leading to impressive seed production by individual female trees.
5. Seeds are capable of long-distance transport by virtue of their small size and attached cotton fibers that facilitate movement by air and water. Germination is epigenous; stand establishment is prompt and fairly complete when seeds germinate on a moist mineral soil (dormancy is incomplete and stratification is not required).
6. The basic chromosome number of 19 is high in comparison to other dicotyledonous forest trees. Triploids are known in section *Populus* and probably occur in *Tacamahaca* although polyploidy is the exception rather than the rule throughout the genus. The relatively high basic number and the distinctiveness of a diploid chromosome set allows for a higher rate of recombinant gametes during reduction division.

Figure 3 Whilst *Populus* is normally dioecious and outcrossing, departures occur in many species. Shown here is *Populus trichocarpa* cv. PS-53-97 bearing pistillate (center), staminate (upper) and two hermaphroditic inflorescences (left and right) along one long and one short shoot.

7. The F_2 *P. trichocarpa* × *P. deltoides* generation typically displays large segregation variation for growth and phenology with a relatively high frequency of intermediate types as well as transgressive segregants. This may indicate a loose linkage system that furthers open recombination. Conversely, a physical clustering of genes controlling *Melampsora* leaf rust resistance may lead to an increase in parental phenotypes.

Vegetative reproduction is also highly developed in *Populus* which along with stabilizing selection counterbalances the open recombination system of *Populus* preserving the parent generation's refined adaptations. Clonal propagation from roots, stumps, and twigs commonly occurs. Extensive clonal stands of *P. tremuloides* have been established by suckering from root sprouts on upland sites. Similarly, grasslands have been colonized by *P. balsamifera* by suckering from roots of trees growing in surrounding forests. *Populus trichocarpa* reproduces clonally along riparian corridors by a process of cladoptosis. *Populus nigra* establishes along river courses by sprouting from limbs and stems buried in alluvium. Apomixis is also known to occur in the genus, although the frequency of apomictic offspring is probably low and does not significantly restrict the recombination system.

Introgression and the Recombination System

Introgression can alter the genetic composition of populations of the participating parental species. Although phenological barriers to the cross-pollination of distinct *Populus* species appear to be insubstantial in most instances, the reproduction of interspecific crosses usually functions at a lower level than their intraspecific counterparts owing to problems with either prezygotic (pollen–stigma interactions) or postzygotic (embryo abortion, low seed germination, seedling mortality) effects. Nevertheless, interspecific hybridization is known to occur in the wild between members of the same section. *Populus* × *canescens*, the hybrid offspring of *P. alba* and *P. tremula*, is widely distributed throughout Europe. *Populus grandidentata* hybridizes with *P. tremuloides* (*P.* × *smithii*) in the upper Midwest of North America. Furthermore, intersectional hybridization between *Aigeiros* and *Tacamahaca* has been observed; in California and Nevada, hybridization between *P. fremontii* and *P. trichocarpa* (*P.* × *parryi*) occurs, whilst *P. deltoides* reproduces with *P. trichocarpa* (*P.* × *generosa*) at the western limit of its range in Washington and Idaho where the two species come into contact. Hybrids of *P. deltoides* and *P. balsamifera* (*P.* × *jackii*) are found in Ontario and Alberta.

A quite large hybrid swarm involving *P. trichocarpa, P. balsamifera, P. angustifolia*, and *P. deltoides* is being studied along several rivers in southern Alberta.

Although interspecific hybrids have largely formed the foundation of commercial *Populus* plantations with vigorous growth rates and substantial disease and insect resistances, they are often less disease-resistant, less tolerant of herbaceous competition, and more palatable as herbivore browse when grown in the wild without benefit of cultivation, a phenomenon known as hybrid breakdown. But despite their reduced fitness, barriers to continuous backcrossing and introgression are not absolute. Persistent hybrid swarms are a force that opens the recombination system of the participating species, especially at the fringes of their ranges, where the pressure to adapt may be greatest. Natural hybrid zones are also of ecological significance to the degree that they foster an extensive diversity of associated plant and animal species.

Conservation

Sections *Aigeiros* and *Tacamahaca* are commonly found occupying floodplain and riparian habitats, at times growing in large contiguous, pure stands. The construction of dams, revetments, levees, and channelization projects along many of the world's rivers has reduced the frequency with which their banks are scoured and gravel bars created, both of which are essential to the establishment of a next generation of *Populus* stands. Construction of levees along the Mississippi River has eliminated much of the natural cycle of flooding and meandrous flow and, consequently, a noticeable decline in the regeneration of *P. deltoides*. The same can be said of many river systems in Europe and Asia.

The conservation of the genetic resource contained in riparian *Populus* species include *ex situ* preservation of wild *Populus* collections in cultivated arboretums. Some arboretums may incorporate a multiple population breeding system to direct and enhance within-species genetic variation. The European Forest Genetic Resources (EUFORGEN) Program to conserve *P. nigra* is perhaps the most advanced *ex situ* effort today with a collection of nearly 2800 clones from 19 countries. Similarly, an *ex situ* collection of *P. trichocarpa* from 100 stands has been assembled in the Pacific Northwest of the USA by GreenWood Resources in response to the loss of riparian forests along the Columbia and Willamette Rivers and their tributaries. Alternatively, *in situ* conservation efforts secure native *Populus* populations in large nature reserves and, in some cases, may include efforts to restore degraded habitats. A major *in situ* effort has been initiated in China's Xinjiang Autonomous Region with the establishment of the Tarim River nature reserve; a critical component is the conservation of *P. euphratica* riparian forests that have shrunk in area by nearly two-thirds.

Other conservation examples include a long-standing effort to preserve *P. nigra* in the Netherlands where it has been replaced *Populus* hybrid plantations. Similarly, the conservation of Italian *P. alba* populations has been proposed in view of the loss of native germplasm in the wake of expanding agriculture. Finally, the Indian government with support from the International Poplar Commission and the United Nations Development Program has surveyed *P. ciliata* populations in the Himalayan foothills as the first step in implementation of its conservation.

Relatively recent changes in air quality are now known to have impacted *Populus* genetic resources. A well-documented example is *P. tremuloides* in North America; populations sampled from regions with a history of chronic exposure to polluted air show significantly higher tolerances to ozone, as natural selection has eliminated sensitive individual phenotypes. The long-term effect of this narrowing of the *P. tremuloides* genetic resource is not known but no less an important concern. Natural selection and loss of diversity is likely to be occurring in polluted areas of Europe and Asia. Conservation efforts here are worthwhile to the extent that populations undergoing selection may also be losing potentially valuable alleles.

The Conservation Role of Commercial *Populus* Plantations

Production plantations established with highly selected interspecific hybrid varieties and intensive agronomic-style tending practices, are among the highest-yielding crop trees in the temperate zone. For example, growth rates of 21–33 $m^3 ha^{-1}$ have been achieved at age 7 in *P.* × *generosa* plantations in the Pacific Northwest. High-yield plantations allow for the preservation of natural forested lands while meeting the fiber and fuel needs of a growing world population.

Beyond North American *P.* × *generosa* plantations, other worldwide plantations programs include cultivation of *P.* × *canadensis* (*P. deltoides* × *P. nigra)* in France's Loire River Valley and the Po Valley of Italy, *P. simonii* × *P. nigra* in northeastern China, *P.* × *tomentosa* (*P. alba* × *P. adenopoda*) in the northern plains of China, and *P. tremuloides* × *P. tremula* in western boreal Canada. Plantations of *P. deltoides* have been established in the southeastern USA, southern Brazil, Argentina, northern India, and southern China. These plantations are managed for a range of products including fuelwood, chips for paper, and logs for veneer and sawnwood products. Intercropping with soya, ryegrass, and corn during the first several years of a *Populus* rotation is practiced in agroforestry programs in China, India, and elsewhere where labor costs are low and arable land is scarce.

A reduction in soil erosion and an increase in water quality are often claimed as environmental benefits of *Populus* cultivation. *Populus* plantations have also been used extensively in various afforestation projects in India and China to address wood shortages while also slowing desertification. Over 1 million ha of *Populus* plantings were established during the 1970s as part of China's 'Green Great Wall' project to slow the spread of the northern deserts (**Figure 4**).

Their environmental benefit notwithstanding, the degree of gene flow between plantations of exotic species or interspecific hybrids and neighboring wild *Populus* populations is an important question in the context of native species conservation. Low levels of gene flow between *P.* × *generosa* plantations and native *P. trichocarpa* stands in the Pacific Northwest have been observed. The level of gene flow between *P.* × *canadensis* plantations and *P. nigra* stands in France may be higher, however.

Domestication

As high-yield plantations become ever more important in meeting the world demand for wood and fiber, novel genetic improvement strategies become an integral component of intensive plantation management practices. A unique combination of classical plant breeding methods and contemporary molecular approaches is used in *Populus*.

Figure 4 *Populus simonii* × *P. nigra* hybrid plantation Shanxi Province, China along the Inner Mongolian frontier. *Populus* stands are being used to reduce the severity of sandstorms and to contain the spread of China's northern deserts. Courtesy of Dave Austin.

Classical *Populus* breeding strategies

Breeding and selection of *Populus* has a lengthy and distinguished history among trees, beginning with a large-scale commercial improvement program conducted in North America in the late 1920s. Successful breeding programs have since been initiated in Europe, Asia, and North America in many cases relying upon nonrecurrent, first-generation (F_1) interspecific hybridization. Hybridization brings the variation encompassed by separate species into a single generation that often exhibits heterosis for yield. Although controlled reproduction may be difficult when some species are hybridized, the ease with which superior individual selections can be vegetatively propagated promotes F_1 hybridization as a popular breeding method (**Table 2**). Advanced generation breeding into the second generation (F_2) is sometimes accompanied by diminished vigor most likely due to the disruption of coadapted linkage groups that occurs during F_1 gametogenesis or to a reduction in overdominant gene action, although transgressive segregants are occasionally found. Backcross breeding is used to introduce a single, highly heritable trait from a donor species to improve an otherwise suitable recurrent parent. For example, in the North Central region of the USA, *P. deltoides* × *P. suaveolens* F_1 hybrids are crossed (back) to unrelated *P. deltoides* selections in an attempt to introduce the strong adventitious rooting ability of *P. suaveolens* into the recurrent *P. deltoides* parent that shows superior resistance to *Septoria* canker (F_1 *P. deltoides* × *P. suaveolens* hybrids are themselves highly canker susceptible).

Given that the entire range of genetic variation can be exploited by clonal selection, a very significant advantage compared to other species that rely upon seedling-based family selection programs, *Populus* programs have frequently focused solely on the selection of superior individuals as opposed to efforts to improve the average performance of whole populations. A complete strategy incorporates recurrent breeding of parental populations so as to improve their hybridizing quality thereby more fully guaranteeing future genetic gains. The ideal is a reciprocal recurrent breeding program. But this has often proved too expensive to implement. Moreover, a lack of full reproductive compatibility between species can greatly complicate the estimation of parental hybrid breeding values required by a reciprocal recurrent

Table 2 Examples of applied *Populus* genetic improvement programs

Pedigree	*Breeding centers*
Populus alba × *P. adenopoda*	China[b]
Populus alba × *P. alba*	Italy[u]
Populus alba × *P. deltoides*	Spain[j]
Populus alba × *P. grandidentata*	Canada,[d] Serbia[f]
Populus alba × *P. tremula*	China,[c] Italy,[u] Korea[o]
Populus alba × *P. euphratica*	Iran[t]
Populus ciliata × *P. deltoides*	India[e]
Populus ciliata × *P. suaveolens*	India[e]
Populus ciliata × *P. yunnanensis*	India[e]
Populus deltoides × *P. deltoides*	Argentina,[k] Beligum,[m] Canada,[d] USA,[h,n,p,q] France[i]
Populus deltoides × *P. balsamifera*	Canada[d,r]
Populus deltoides × *P. nigra*	Belgium,[m] Canada,[d] France,[i] Italy,[l] Serbia,[f] USA[q]
Populus deltoides × *P. suaveolens*	Canada,[d,r] China,[c] USA[h,q]
Populus deltoides × *P. trichocarpa*	Belgium,[m] France,[i] USA[h,q]
Populus nigra × *P. nigra*	Belgium,[m] Italy[l,u]
Populus nigra × *P. suaveolens*	Canada,[d,r] China,[c] Korea[o]
Populus simonii × *P. nigra*	China[c,s]
Populus tremula × *P. tremuloides*	Canada,[a,d] Finland,[g] Serbia[f]
Populus tremuloides × *P. tremuloides*	Canada[d]

[a] Alberta-Pacific Forest Industries, Inc., Boyle, Alberta, Canada.
[b] Beijing Forestry University, Beijing, People's Republic of China.
[c] Datong Poplar Bureau, Jinshatan, People's Republic of China.
[d] Direction de la Recherche Forestière, Sainte-Foy, Québec.
[e] Dr. Y. S. Parmar University of Horticulture and Forestry, Solan, India.
[f] Faculty of Agriculture, Poplar Research Institute, Novi Sad, Serbia.
[g] Finnish Forest Research Institute, Vantaa, Finland.
[h] GreenWood Resources, Portland, OR, USA.
[i] Institut National de la Recherche Agronomique, Ardon, France.
[j] Instituto Nacional de Investigación y Tecnologia Agraria y Alimentaria, Madrid, Spain.
[k] Instituto Nacional de Tecnologia Agropecuaria, Buenos Aires, Argentina.
[l] Istituto di Sperimentazione per la Pioppicoltura, Casala Monferrato, Italy.
[m] Instituut voor Bosbouw en Wildbeheer, Geraardsbergen, Belgium.
[n] Iowa State University, Department of Forestry, Ames, IA, USA.
[o] Korea Forest Research Institute, Kyunggi-do, Korea.
[p] MeadWestvaco, Corporation, Wickliffe, KY, USA.
[q] Natural Resources Research Institute, University of Minnesota, Duluth, MN, USA.
[r] Prairie Farm Rehabilitation Administration, Indian Head, Saskatchewan, Canada.
[s] Poplar Research Institute of Liaoning Province, Gai, People's Republic of China.
[t] Research Institute of Forests and Rangelands, Tehran, Iran.
[u] Università della Tuscia, Viterbo, Italy.

breeding. Consequently, many *Populus* programs substitute intraspecific breeding values as a guide for the manner in which parental populations are refined for interspecific hybridization.

The traits targeted for *Populus* improvement are usually the agronomic ones of yield, stem form, pest resistance, tolerance of cold and drought, wind firmness, and adventitious rooting. All have exhibited pronounced rates of genetic variation and have responded well to clonal selection programs. Field evaluations typically involve a multistage process to sequentially refine large populations until a group of elite selections has been identified. Other selection criteria may include wood and fiber properties for the veneer and sawnwood industries and the calorific quality of biomass for the heat- and power-conversion industries.

An imperative for production programs that incorporate clonal stands is a diverse pool of operational selections to help minimize the risk of plantation failures due to unforeseen climatic and biotic events. Most plantation programs are therefore allied with an ongoing hybridization program that continuously feeds new selections into production use. Continuous turnover of the commercial pool of clones is a safeguard against catastrophic failures due to coevolution of associated pests.

Application of Molecular Tools to Tree Improvement

Populus, by virtue of its relatively small genome, ease of cloning, and use of interspecific hybridization, has emerged as the model species for the application of molecular tools (genomic mapping and genetic engineering) to more traditional tree improvement approaches. Genomic markers associated with quantitative trait loci could lead to new approaches to the evaluation of full-sib seedling populations for superior selections that normally would not be revealed until conventional field tests are conducted for a half rotation or longer. Genomics could eventually lead to map-based cloning of important genes that are then used in transformation projects. The Joint Poplar Genome project is scheduled to complete sequencing of the *Populus* genome by the end of 2003.

Genetic transformation methodologies are well developed in *Populus*. Transformation can improve existing varieties for desired traits that otherwise are unavailable to conventional hybridization programs using recombinant DNA. *Populus* varieties have been modified for herbicide resistance, altered lignin content, and leaf beetle resistance. Currently field trials of genetically modified varieties have been conducted in North America with *P. deltoides* and *P. trichocarpa* × *P. deltoides* hybrids. In Europe, more than 20 field trials have been established using genetically modified *P. tremula*, *P. tremuloides, P. deltoides*, and *P. alba* × *P. tremula* selected varieties. The use of genetically modified plants has raised concerns over the risk posed to the fitness or future adaptability of wild relatives with whom transgenic plantations might reproduce. Consequently, a major ongoing effort has been sterility transformation that would prevent completely the sexual reproduction of transgenic plantations.

See also: **Genetics and Genetic Resources**: Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance; Genetics and Improvement of Wood Properties. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts.

Further Reading

Dickmann DI and Stuart KW (1983) *The Culture of Poplars in Eastern North America*. MI: East Lansing: Michigan State University Press.

Dickmann DI, Isebrands JG, Eckenwalder JE, and Richardson J (eds) (2001) *Poplar Culture in North America*. Ottawa, Canada: NRC Research Press.

Grant V (1975) Genetics of flowering plants. New York: Columbia University Press.

International Union of Forest Research Organizations (1995) *International Poplar Symposium*, abstracts. Seattle, WA: University of Washington.

International Union of Forest Research Organizations (1999) *International Poplar Symposium II*, abstracts. Orleans, France: INRA, Station d'Amélioration des Arbres Forestiers.

International Union of Forest Research Organizations (2002) *International Poplar Symposium III*, abstracts. Uppsala: Swedish University of Agricultural Sciences.

Isebrands JG and Richardson J (comps.) (2000) *21st Session of the International Poplar Commission (IPC-2000): Poplar and Willow Culture: Meeting the Needs of Society and the Environment*, 24–28 September 2000, Vancouver. Gen. Tech. Rep. no. NC-215. St. Paul, MN: US Department of Agriculture Forest Service, North Central Research Station.

Lefevre, F. (2001) Managing the dynamic conservation networks. In: Teissier du Cros, E. (ed.), *Forest Genetic Resources Management and Conservation: France as a Case Study*, pp. 23-27. Paris: Ministry of Agriculture and Fisheries, Bureau of Genetic Resources, Commission of Forest Genetic Resources.

Stettler RF, Bradshaw HD Jr, Heilman PE, and Hinckley TM (eds) *Biology of* Populus *and its Implications for Management and Conservation*. Ottawa, Canada: NRC Research Press.

Spruces, Firs and Larches

H Wolf, State Board for Forestry (Saxony), Pirna, Germany

Introduction

Together with the genera *Pinus* (subfamily Pinoideae), *Cathaya*, *Pseudotsuga* (subfamily Laricoideae), and *Cedrus, Keteleeria, Nothotsuga, Pseudolarix, Tsuga* (subfamily Abietoideae), the genera *Picea* (subfamily Piceoideae), *Abies* (subfamily Abietoideae), and *Larix* (subfamily Laricoideae) belong to the family Pinaceae. The subfamilies are distinguished by cone and seed characters like the existence of an umbo or the existence of resin vesicles on the seed.

Species of the genera *Picea* (spruce), *Abies* (fir), and *Larix* (larch) are exclusively distributed in the northern hemisphere from 22° N in the south to 73° N forming the polar borderline of trees. Several species of these genera cover wide areas in boreal Eurasia and North America. They contribute to a major extent to the northern coniferous forests which stretch from coast to coast across these latitudes and form the greatest expanses of continuous forests. Many species of these genera are also found in mountainous regions of the more temperate zones often forming the alpine tree border line.

Picea, Abies, and *Larix* species occur in a wide range of habitats with very different soil and climate conditions. They are associated with various tree species depending on certain site conditions but they can also be found in pure stands under extreme site conditions. Mainly reproducing sexually by wind pollination, vegetative reproduction is the dominant mode of propagation if sexual reproduction is limited due to climatic limitations.

The lifetime of *Picea, Abies*, and *Larix* species ranges variously from 150 to 900 years. Under favorable conditions they grow to tall trees often forming dense forests with considerable growing stocks. Among populations of most species genetic differences can be observed in various traits. Due to their wood characteristics, the timber of spruces, firs, and larches can be used for a wide variety of purposes and is therefore of high economical importance.

Spruces

The genus *Picea* (subfamily Piceoideae) is related most closely to the genus *Pinus* (subfamily Pinoideae), but differs significantly by, e.g., cone and seed characteristics, the absence of short shoots, or the period of cone maturing. *Picea* is a very uniform genus, showing no significant differences within the genus allowing the delineation of subgenera. The genus *Picea* includes 34 species of cone-bearing, tall evergreen trees with straight stems and regularly constructed crowns with columnar or pyramidal habit. The horizontally arranged and usually rather short branches are whorled. On young trees, the bark is rather thin, on old trees scaly. The buds are conical or ovate, resinous or without resin. The spirally arranged needles are either four-sided or flat on a short petiole which remains on the shoot after needle fall. Stomatal bands can be found on all four sides or in the case of flat needles on the lower surface.

Natural Distribution

Out of the 34 species of *Picea*, eight species occur naturally in North and Central America, and 26 species are distributed in Eurasia (**Table 1**). The greatest species diversity is found in China and the Himalayas often in single species stands.

Picea species are mainly distributed in the boreal and subboreal zones of the northern hemisphere as well as to a minor extent in the mountainous regions of the more southerly zones where *Picea* can be found up to the subalpine range forming the treeline (**Figure 1**). The species of the genus *Picea* can be divided in a northern and a southern group, the differences between the groups are important from the ecological and genetical point of view. *Picea* species of the northern group occur mainly in large, often overlapping natural distribution areas either from east to west only interrupted by the Atlantic Ocean and the Bering Sea like *Picea abies, P. glauca,* and *P. obovata* or from north to south like *P. engelmannii* (**Figure 1**). In contrast, the species of the southern group grow in small, often isolated natural occurrences, for example *P. omorika*.

The northern limit of distribution of *Picea* is reached at about 69° N in Norway (*P. abies*) and the Northwest Territory of Canada (*P. glauca, P. mariana*). In the south, *Picea* stands can be found up to 23° to 27° N at the eastern (*P. morrisonicola*) and up to 23° to 25° N at the western hemisphere (*P. chihuahuana*) (**Figure 1**). In warmer regions, the water supply is the limiting factor of distribution.

In the northern part of the distribution area, the vertical occurrence of *Picea* reaches from sea level in North America and Eurasia to 2250 m above sea level in the Central Alps (*P. abies*) and about 3700 m in the southern Rocky Mountains (*P. engelmannii*). In the southern part, *Picea* species with upright growth can be found in altitudes up to 4700 m in the Himalayas forming the most upper limit of closed forests in the world (*P. asperata*).

Table 1 The intragenetic classification and distribution of species of the genus *Picea*

Distribution	*Botanical name*	*Common name*
North America	*P. breweriana*	Brewer spruce
	P. chihuahuana	—
	P. engelmannii	Engelmann spruce
	P. glauca	White spruce
	P. mariana	Black spruce
	P. pungens	Blue spruce, Colorado spruce
	P. rubens	Red spruce
	P. sitchensis	Sitka spruce
Europe and Northern Asia	*P. abies*	Norway spruce
	P. obovata	Siberian spruce
	P. omorika	Serbian spruce
	P. orientalis	Oriental spruce
Central Asia and Himalayas	*P. schrenkiana*	Schrenk spruce
	P. smithiana	Himalayan spruce
	P. spinulosa	—
East Asia including islands	*P. alcoquiana*	Alcock spruce
	P. glehnii	Sakhalin spruce
	P. jezoensis	Hondo spruce, Yezo spruce
	P. koraiensis	—
	P. koyamae	Koyama spruce
	P. maximowiczii	—
	P. morrisonicola	—
	P. torano	Japanese spruce
Central China and South Asia	*P. asperata*	Chinese spruce
	P. aurantiaca	—
	P. brachytyla	—
	P. crassifolia	—
	P. farreri	—
	P. likiangensis	Purple spruce
	P. meyeri	—
	P. neoveitchii	—
	P. purpurea	—
	P. retroflexa	—
	P. wilsonii	—

Climate and Soils

Picea species can withstand extremely cold temperatures down to −60°C. The amplitude of temperature varies from −60°C to 35°C. The mean annual precipitation ranges from 230 to 4000 mm with the maximum falling outside the vegetation period. The vegetation period ranges from 26 to 175 days, the shorter growing season in the north counterbalanced by longer periods of daylight and the ability of spruces to assimilate down to temperatures of −6 to −7°C.

Picea species are not very demanding of soil conditions with the exception of the water supply.

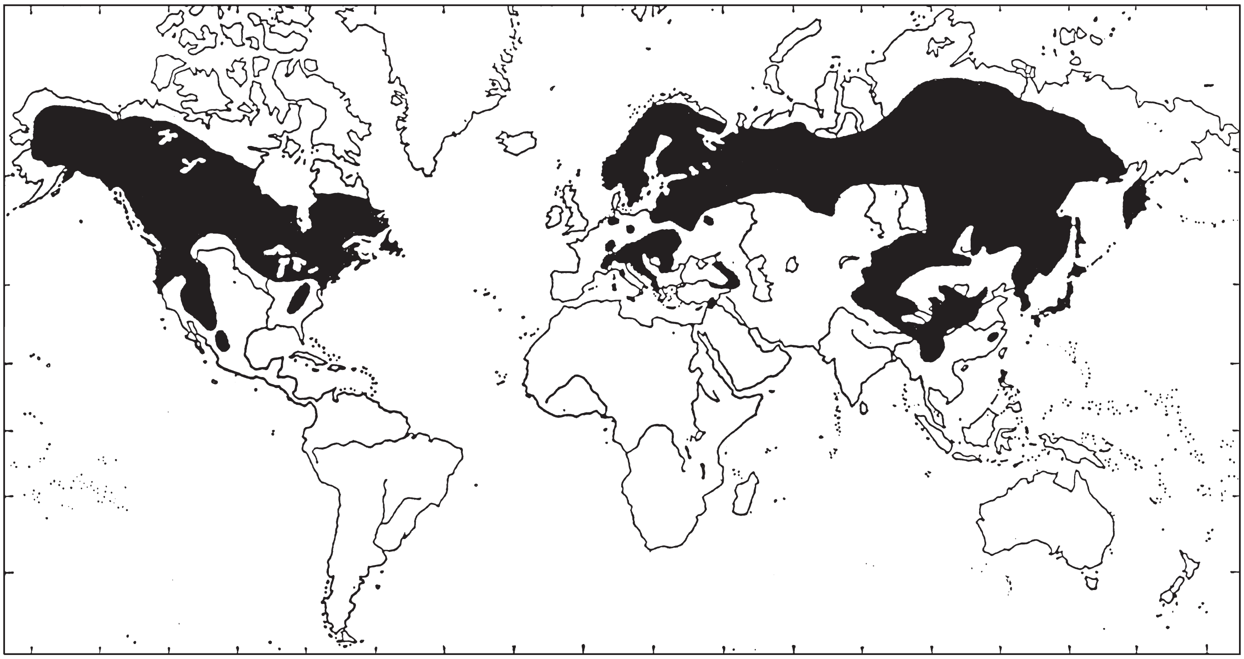


Figure 1 Natural distribution area of spruces (*Picea* spp.) Adapted with permission from Kruessmann G (1983) *Handbuch der Nadelgehoelze*. Berlin: Parey-Verlag.

In the northern part of the distribution area, *Picea* species occur on all soils showing the best growth on well-aerated, deep, acidic to slight alkaline soils with an intermediate nutrient supply and water supply over average. In the southern part, they are restricted to wet, cold or shallow soils of bogs.

Associated Forest Cover

Growing at extreme site conditions, *Picea* species can be found in pure, often uneven-aged stands. Under more favorable conditions, however, *Picea* species are associated with species of the genera *Abies, Chamaecyparis, Larix, Pinus, Pseudotsuga, Thuja,* and *Tsuga* as well as *Acer, Alnus, Betula, Populus, Prunus, Quercus,* and *Salix* in North America. In Eurasia, the species admixed to *Picea* belong to the genera *Abies, Juniperus, Larix, Pinus, Taxus, Thuja,* and *Tsuga* as well as *Betula, Fagus, Quercus, Populus,* and other deciduous broadleaved species.

Reproduction and Growth

Flowering starts between the age of 10–50 years. Male and female flowers are inserted in axils of needles of the previous year's shoots on different branches of the same tree, the female flowers inserted upright in the upper part of the crown. The flowering period varies from April to July. Peak flowering can be observed from every second year to every 13th year, in average from the third to the sixth year. Pollination is by wind over long distances due to the light weight and the low falling speed of the pollen grains which contain air vesicles. The yellowish green, crimson, or purple-colored cones ripen in the same year turning color during ripening. A ripe cone consists of brownish, woody scales, each bearing two brown to black seeds at the base. The ovate seeds are winged and mainly dispersed by wind during autumn and winter. The empty cones do not disintegrate and remain on the trees for about 1 year. Germination capacity varies from 75% to 95%. The weight of spruce seeds shows a big variation and ranges from 60 000 (*Picea torano*) to 890 000 (*P. mariana*) cleaned seeds kg^{-1}.

Seeds of most *Picea* species show no dormancy and germinate promptly without stratification. However, seeds of some species may require light for germination but prechilling will usually overcome the light requirement. Under natural conditions, seeds germinate on almost any seedbeds including rotten wood, but survival may be low. The germination is most successful on a mineral or mixed mineral and organic soil seedbed, especially under light shade, as long as drainage is adequate and the soil provides sufficient nutrients. The germination is epigeal, the four to 15 cotyledons rising above the ground.

If sexual reproduction is limited or nonexistent due to climatic limitations at the arctic or alpine tree line, vegetative reproduction of *Picea* species by layering is apparently the dominant mode of propagation.

Roots are also known to produce shoots. Artificially, vegetative propagation is easily possible by rooting of softwood cuttings from juvenile material or grafting.

Similar to that of *Abies* and *Pseudotsuga*, the root growth of *Picea* species starts before the shoot growth. The development of the root system is generally influenced by the existing soil conditions of which the oxygen supply may play an important role. Growing at sites with unfavorable soil conditions (e.g., near surface water table, clay-containing or compacted soil), *Picea* species develop an extremely shallow lateral root system near to the surface. On deep, porous, and well-drained soils, the lateral root system penetrates the soil by layer roots to a depth of 2.5 m and more.

The average age of *Picea* species varies from 250 to 800 years (*P. sitchensis*). Under favorable conditions, the average height of mature trees ranges from 25 to 40 m, some species reaching heights between 50 and 60 m (*P. sitchensis*). The mean diameter at breast height (dbh) of mature spruces ranges from 50 to 150 cm. Under favorable conditions, *Picea* forests produce timber volumes between 190 and 690 $m^3 ha^{-1}$, and at exceptionally good sites between 870 and 1200 $m^3 ha^{-1}$ (*P. abies, P. sitchensis*).

Species of the genus *Picea* have intermediate tolerance of shade, the tolerance decreasing with increasing age. Height growth is slow in the first few years but increases rapidly thereafter. When mixed with other species, *Picea* species can also survive and grow in the understory using occasional stand disturbances to rise up in the overstory.

Silviculture

Depending on the site conditions, even-aged as well as uneven-aged silvicultural systems are appropriate for the regeneration of *Picea* forests. The even-aged methods include clear-cutting and shelterwood cutting. Seed tree cuttings are not suitable for the regeneration of spruce due to its susceptibility to windthrow. Appropriate uneven-aged cutting methods are individual tree and group selection cuttings and their modifications. Thinning in young *Picea* stands enhances the growth of diameter and the crown development improving the stability of spruces.

In deep shade, lower branches soon die, decay, and break off, the resinous stubs remaining for many years. *Picea* species only exceptionally develop sprouts from adventitious buds along the stem related to light intensity, e.g., after thinning.

Pests and Diseases

Picea species are subject to damage from abiotic agents, pathogens, insects, and animals. Among abiotic agents windthrow is the most serious especially after initial or partial cuttings in old-growth stands. Species of the genus *Picea* are also sensitive to air pollution. However, most common diseases of spruces are caused by wood-rotting fungi resulting in loss of volume and predisposition of trees to windthrow and wind break. In pure stands, the mass propagation of bark beetles can cause serious damage. Due to their thin bark, *Picea* species can also be damaged by game animals that peel the bark.

Genetics

Compared to *Picea* species growing in the northern part of the distribution area, the species from the southern part show a greater systematic uniformity. Most of the *Picea* species of the northern part can be separated into geographical races or systematic varieties indicating genetic differences. The differences can be seen in phenological, morphological, quantitative, and qualitative characters as well as in resistance against pest and diseases influencing the suitability of the provenance in question for cultivation out of its natural distribution area. In North America and Asia, spontaneous hybridization between *Picea* species can be observed in common growing zones of the species in question. In Germany, the UK, and Scandinavia, *P. abies* and *P. sitchensis* in particular are the subjects of intense breeding programmes for commercial plantation forestry.

Uses

The strong, lightweight, light-colored, fine-grained, even-textured, and long-fibered wood makes most spruce species useful timber trees. The timber can be used as lumber, construction wood, rotary-cut veneer, furniture timber, posts, poles, and mine timber as well as plywood, pulpwood, and fuelwood. The high strength-to-weight ratio and the resonant qualities make the wood suitable for the construction of aircraft parts and musical instruments. Due to its wood qualities and yield, *Picea* is one of the most important commercial genus in the boreal forest. Several species like *P. abies, P. glauca, P. sitchensis,* or *P. omorika* are planted commercially outside their natural distribution area. Most *Picea* species are also important watershed protectors because of their occurrence at high elevations and on steep slopes.

Firs

Compared to the genus *Picea*, the genus *Abies* (subfamily Abietoideae) is a very heterogenous genus allowing the delineation of 10 sections with several subsections. The genus *Abies* includes 49 species of cone-bearing, tall evergreen trees with straight stems and regularly built-up crowns with pyramidal habit (**Table 2**). The horizontally arranged branches are distinctly whorled. On young trees, the bark is thin and smooth, often with resin blisters, in old trees often thick and fissured. The buds are usually resinous, globose, or ovate to fusiform. The linear–lanceolate, flat, singly borne needles are dark green above with two bluish or silvery-white stomatal bands on the lower surface. The needles which are widened like a shield at the base are inserted on long shoots usually in two ranks leaving a rounded scar after fall or removal.

Natural Distribution

Out of the 49 species of *Abies*, 15 species occur naturally in North and Central America, and 33 species are distributed in Eurasia (**Figure 2**). In contrast to *Picea* and *Larix*, one *Abies* species is found exclusively in northern Africa (**Table 2**). Similar to *Picea*, the greatest species diversity in *Abies* can be observed in China and the Himalayas.

Abies species occur from sea level to the timberline but the majority are found at middle to high elevations in mountainous areas. However, in North America as well as in North Asia, *Abies* species are found as components of boreal forests. Few species of the genus *Abies* grow as components of low-elevation, temperate forests. In North America, *Abies* species can be found from 64°30′ N in Yukon Territory, Canada (*Abies lasiocarpa*) to 14°49′ N in Central America (*A. guatemalensis*) and from 53° W in Newfoundland (*A. balsamea*) to 140° W parallel to the borderline between Alaska and Canada (*A. lasiocarpa*). The vertical distribution ranges from sea level to about 3600 m. In Eurasia and Africa, the distribution area extends from 67° 40′ N in the north (*A. sibirica*) to about 22° N in the south (*A. kawakamii*) and from 6° W in the west (*A. alba*) to 160° E in the east (*A. sachalinensis*). Vertically, firs grow at elevations from about 300 m to 4700 m in the Himalayas (*A. squamata*).

Climate and Soils

Since *Abies* species occur in very different regions of the northern hemisphere, the requirements of the climate also vary accordingly. The mean annual temperature ranges from −4°C to 11°C within the distribution area with an amplitude of temperature from –45°C to 41°C. The mean annual precipitation varies from 510 to 2540 mm with extremes between 390 and 6650 mm. In mountainous regions, between 50% and over 80% of the annual precipitation is snow and sleet. Snow packs between 3 and 12.7 m are

Table 2 The intragenetic classification and distribution of species of the genus *Abies*

Distribution	*Botanical name*	*Common name*
North America	*A. amabilis*	Pacific silver fir
	A. balsamea	Balsam fir
	A. bracteata	—
	A. concolor	White fir
	A. durangensis	—
	A. fraseri	Fraser fir
	A. grandis	Grand fir
	A. hickelii	—
	A. hidalgensis	—
	A. lasiocarpa	Subalpine fir
	A. magnifica	California red fir
	A. procera	Noble fir
	A. religiosa	—
	A. vejarii	—
Central America	*A. guatemalensis*	—
Europe and West Asia	*A. alba*	European silver fir
	A. borisii-regis	King Boris fir
	A. cephalonica	Greek fir
	A. cilicica	Cilician fir
	A. nebrodensis	Silician fir
	A. nordmanniana	Nordmann fir
Europe and North Africa	*A. pinsapo*	Spanish fir
North Africa	*A. numidica*	Algerian fir
Northern and Central Asia	*A. sibirica*	Siberian fir
Central Asia and Himalayas	*A. densa*	—
	A. pindrow	Pindrow fir
	A. spectabilis	Himalayan fir
Central China and South Asia	*A. chengii*	—
	A. chensiensis	—
	A. delavayi	—
	A. fabri	—
	A. fanjingshanensis	—
	A. fansipanensis	—
	A. fargesii	—
	A. forrestii	—
	A. recurvata	—
	A. squamata	—
	A. yuanbaoshanensis	—
	A. ziyuanensis	—
East Asia including islands	*A. beshanzuensis*	—
	A. firma	Japanese fir, Momi fir
	A. holophylla	Manchurian fir
	A. homolepis	Nikko fir
	A. kawakamii	—
	A. koreana	Korean fir
	A. mariesii	Maries fir, Shasta red fir
	A. nephrolepis	—
	A. sachalinensis	Sakhalin fir
	A. veitchii	Veitch fir, Veitch's silver fir

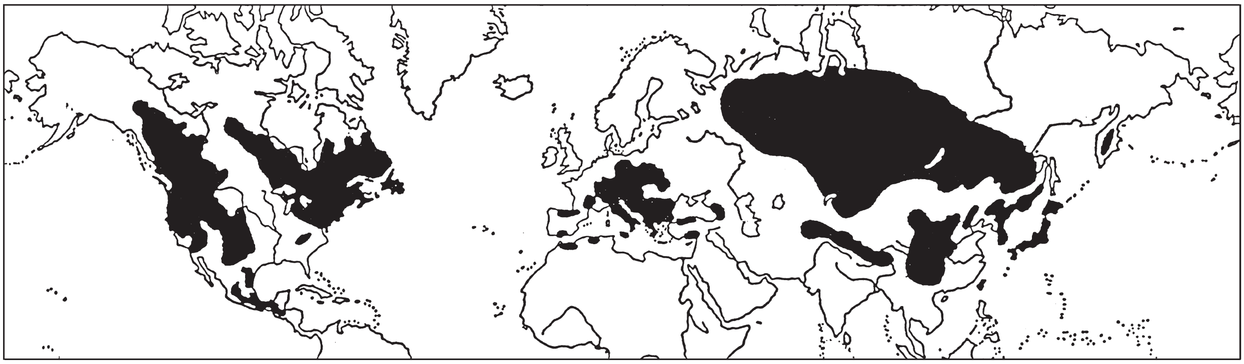


Figure 2 Natural distribution area of firs (*Abies* spp.) Adapted with permission from Kruessmann G (1983) *Handbuch der Nadelgehoelze*. Berlin: Parey-Verlag.

reported. The vegetation period ranges from 40 to 250 days, the shorter growing season in higher elevations being compensated by the ability of some fir species to assimilate down to a temperature of $-5°C$.

Due to its large distribution area with very different geological bedrocks, *Abies* species grow on a wide variety of soils developed from almost every kind of parent material. *Abies* species are tolerant of a wide range of soil conditions, nutrient content and availability as well as pH values. Species of the genus *Abies* are more dependent on moisture availability and temperature. However, the best growth of *Abies* species can be expected on deep, nutrient rich, fine to medium textured and well-drained soils.

Associated Forest Cover

Abies species seldom grow in pure, uneven-aged stands. Mainly, they can be found in mixed forests also under extreme site conditions. In North America, *Abies* species are associated more or less with the same species as *Picea* species. In Eurasia and Africa, the species mixed with *Abies* belong to the genera *Cedrus, Chamaecyparis, Juniperus, Larix, Picea, Pinus, Taxus, Thuja,* and *Tsuga* as well as *Acer, Betula, Fagus, Fraxinus, Quercus, Populus,* and other deciduous broadleaved species.

Reproduction and Growth

Flowering starts between the ages of 20 to 50 years. Male and female flowers occur separately on the same tree. The female flowers are typically inserted highly in the crown on the upper side of the previous year's shoot, the male flowers generally lower in the crown than female flowers densely along the undersides of 1-year-old twigs. The flowering period varies from April to July. Peak flowering can be observed from every second to every eighth year, on average from the second to the fourth year. Pollination by wind takes place mostly among neighboring trees due to the heavy weight and the fast sinking speed of the pollen despite the existence of air vesicles. The red or greenish conspicuous cones ripen the first year; a ripe cone consists of brownish, woody scales, each bearing two winged and typically ovate to irregularly triangular seeds at the base. The seeds with conspicuous resin blisters are mainly dispersed by wind from August to November. In contrast to other conifers, the erect cones disintegrate leaving only the spikelike cone axis on the tree. Germination capacity varies from 25% to 70% but it is very often low, around 30%. The weight of the comparatively heavy fir seeds ranges from 10 000 (*Abies cilicica*) to 200 000 (*A. koreana*) cleaned seeds kg^{-1}.

Since *Abies* seeds are disseminated in autumn under conditions which may allow an early germination, the germination is hampered by resins stored in the seed coat. Under forest conditions the dormancy is broken by evaporation of the resins during the winter after seed fall. The germination is most successful on a warm seedbed with moist mineral soil. The germination is epigeal, the three to 14 well-differentiated cotyledons rising above the ground.

Under natural conditions, most *Abies* species do not reproduce vegetatively either by sprouting or layering. Layering can be observed in few species growing in extreme conditions of the more northern and mountainous regions, e.g., *A. balsamea* or *A. lasiocarpa*. Artificially, vegetative propagation is possible by grafting or rooting of cuttings from juvenile material.

The root systems of *Abies* vary from shallow and widespread where the effective soil depth is limited by rocks or seasonable water tables, through relatively deep lateral root systems under more favorable conditions, to a deep and intensive taproot system which also develops under less favorable soil conditions.

The average age of *Abies* species varies from 150 to 500 years, exceptionally to 700 years (*A. procera*). Under favorable conditions, the average height of mature trees ranges from 20 to 50 m, several species reaching heights between 60 and 90 m (e.g., *A. alba, A. amabilis, A. grandis, A. procera, A. spectabilis*). The mean dbh of mature *Abies* trees ranges from 30 to 300 cm (*A. spectabilis*). Due to their capacity to maintain a high level of stand density and due to the generally low taper of *Abies* trees, a considerable growing stock can be observed between 450 and 600 $m^3 ha^{-1}$ on average sites. Under favorable conditions, *Abies* forests produce timber volumes between 1000 and 1600 $m^3 ha^{-1}$ (e.g., *A. alba, A. amabilis, A. concolor, A. grandis, A. procera*), and in exceptional cases up to 2300 $m^3 ha^{-1}$ (*A. magnifica*).

Although *Abies* species grow well in full sunlight, most species can survive and grow for long periods in relatively dense shade and therefore they are classified as shade tolerant. However, some species are not too tolerant of shade especially if regeneration under a closed forest canopy is considered. Due to their shade tolerance over average compared to other tree species, *Abies* species can be found in mixed coniferous and conifer–broadleaved forests as well as in pure stands.

Silviculture

For most *Abies* species, uneven-aged silvicultural systems are the most appropriate way for regeneration. Appropriate uneven-aged cutting methods are individual tree and group selection cuttings and their modifications providing the necessary growth advantage several species need in front of competing species due to their slow growth in the juvenile stage.

Pests and Diseases

Abies species are subject to damage from abiotic agents, pathogens, insects, and animals. *Abies* species are very sensitive to air pollution. Due to their thin bark, *Abies* species are susceptible to severe damages and fire. Among pathogens, mistletoe causes major damage. In old-growth trees, wood rotting fungi cause major losses. Species of the genus *Abies* are also very sensitive to browsing and bark peeling by game.

Genetics

Several *Abies* species show a high self-fertility, up to 70% and more of sound seeds being produced by outcross pollination. Since the range in elevation and latitude is large in various *Abies* species and due to different evolutionary processes, differences among populations of several species can be observed in morphology, phenology, growth rate, monoterpenes, or isozyme patterns. In North America and Eurasia, spontaneous hybridization between *Abies* species is reported in common growing zones of the species in question. In the USA, selective breeding programs are practiced, particularly for the improvement of shape, size, and color of Christmas trees.

Uses

With the exception of the absence of primary resin canals, the characteristics and uses of fir wood are similar to them of spruce wood. Young trees of most *Abies* species are preferred Christmas trees. *Abies* species growing at high elevations and on steep slopes are also important for the protection of watersheds. Only few species of the genus *Abies* are planted commercially outside their natural distribution area, for example *A. grandis* or *A. nordmanniana*.

Larches

The genus *Larix* (subfamily Laricoideae) is the type genus of the subfamily mentioned before. The genus is divided into two groups separated by the position of the bracts (exserted or nonexserted). The genus *Larix* includes 11 species of cone-bearing, tall deciduous trees with straight stems and narrow, sometimes broad, mostly regularly built-up crowns. The horizontally arranged branches are not whorled. The bark is fissured, reddish-brown to gray-brown in color. The buds are small and ovate with a little number of short and imbricate scales. The soft and thin needles are inserted in bunches on short shoots and spirally on long shoots.

Natural Distribution

Out of the 11 species of the larches, three species occur naturally in North America, and eight species are distributed in Eurasia (**Table 3**). The conifer forests around the Arctic Circle are mainly formed by

Table 3 Intrageneric classification and distribution of species of the genus *Larix*

Distribution	*Botanical name*	*Common name*
North America	*L. laricina*	Tamarack
	L. lyallii	Alpine larch
	L. occidentalis	Western larch
Central Europe	*L. decidua*	European larch
North Eurasia	*L. czekanowskii*	—
	L. gmelinii	Dahurian larch
	L. sibirica	Siberian larch
China and Himalayas	*L. griffithii*	Sikkim larch
	L. mastersiana	—
	L. potaninii	Chinese larch
Japan	*L. kaempferi*	Japanese larch

Larix laricina, L. sibirica, and *L. gmelinii* with largely extended distribution areas. Other larches occur in the mountainous regions of more temperate latitudes, distributed in smaller and more scattered areas with extreme vertically extension.

In North America, species like *L. laricina* extend from 53° W in Newfoundland to 140° W parallel to the border of Alaska and Canada and from 40° N in the south to 67° N forming the northern treeline. The vertical distribution reaches from sea level to 1220 m above sea level in eastern North America (*L. laricina*) and from 180 to 3020 m (*L. lyallii*) in the west of North America.

In Eurasia, the distribution area of *Larix* species reaches from 68° N to 73° N (*L. gmelinii*), its northern limit forming the polar treeline. The southern limit can be found at about 22° N in the Himalayas and China (*L. griffithii, L. potaninii*). The west–east distribution reaches from 5° E in the western Alps (*L. decidua*) to about 170° E in East Siberia (*L. gmelinii*) (**Figure 3**). The vertical extent varies among the different parts of the natural distribution area. In Europe and North Asia, the genus ranges from the riverine lowlands of the north (*L. sibirica, L. gmelinii*) to elevations of 2400 m forming the alpine treeline in the western Alps (*L. decidua*) or in the Manchurian Mountains (*L. gmelinii*). *Larix* species grow in altitudes between 1000 and 2700 m on the island of Hondo in Japan (*L. kaempferi*), and they can be found between 2500 and 4000 m in the Himalayas and China (*L. griffithii, L. potaninii*).

Climate and Soils

Larix species can withstand extremely cold temperatures down to −70°C as well as a large range of temperatures from −70°C to 35°C. The mean annual precipitation varies from 180 to 2500 mm. In mountainous regions, about 75–80% of the annual precipitation is snow and sleet. The vegetation period ranges from 50 to 230 days, the shorter growing season in the north being counterbalanced by longer periods of daylight.

Species of the genus *Larix* can tolerate a wide range of soil conditions. Species forming the forests at the Arctic Circle grow most commonly on wet to moist organic, boggy, and acidic sites with a shallow layer of peat or soil over permafrost. The best growth of *Larix* species can be observed on moist and deep soils rich in nutrients with high water storage capacity.

Associated Forest Cover

Growing in extreme site conditions, species of the genus *Larix* can be found mainly in pure, often even-aged stands. Under more favorable conditions, however, *Larix* species are associated with species of the genera *Abies, Picea, Pinus, Pseudotsuga, Thuja,* and *Tsuga* as well as *Acer, Betula, Fraxinus, Populus,* and *Ulmus* in North America. In Eurasia, the species associated with larch belong to the genera *Abies, Picea,* and *Pinus* as well as *Betula, Fagus,* and *Populus.*

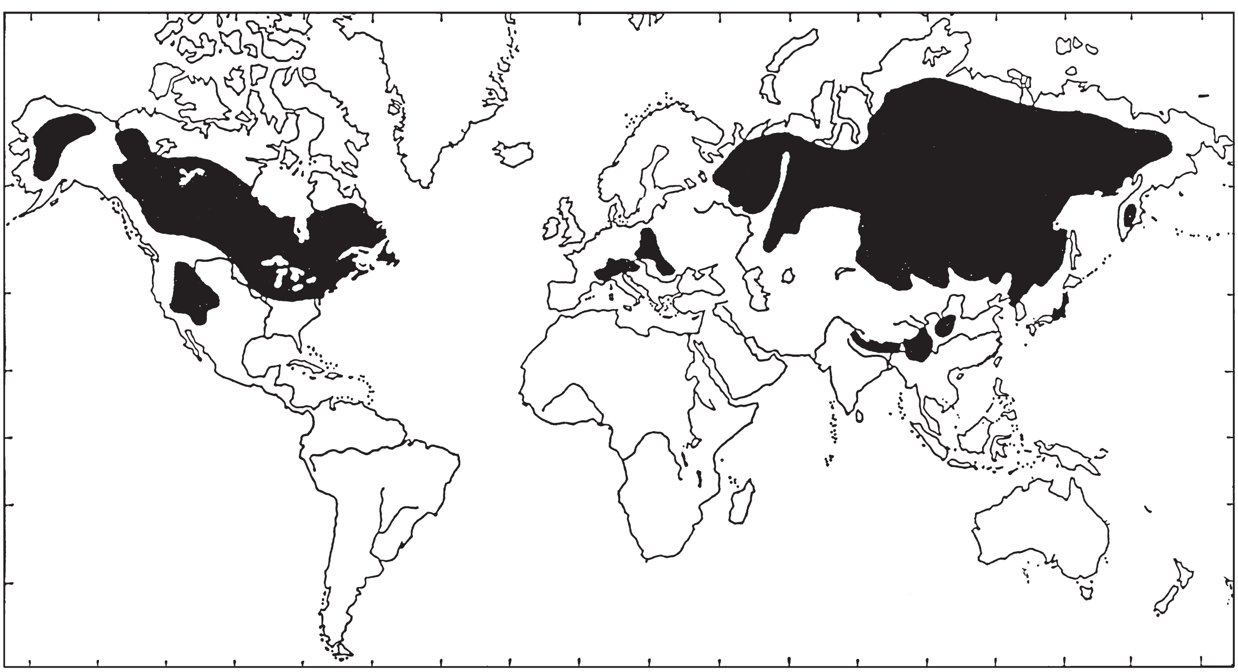


Figure 3 Natural distribution area of larches (*Larix* spp.) Adapted with permission from Kruessmann G (1983) *Handbuch der Nadelgehoelze*. Berlin: Parey-Verlag.

Reproduction and Growth

Flowering starts between the ages of 10 and 40 years. Male and female flowers occurring separately on the same tree open a few days before needle elongation or appear with the needles. The flowering period varies from March to June. Peak flowering can be observed from every year to every 10th year, on average from the third to the sixth year. Pollination by wind takes place mostly among neighboring trees due to the heavy weight and the fast falling speed of the pollen grains which lack air vesicles. The red or greenish cones ripen the first year; a ripe cone consists of brownish, woody scales, each bearing two seeds at the base. The winged and nearly triangular seeds are mainly dispersed by wind from September to spring. The empty cones do not disintegrate and remain on the trees for an indefinite period. Germination capacity varies from 15% to 50%. The small and lightweight *Larix* seeds range from 100 000 (*L. sibirica*) to 700 000 (*L. laricina*) cleaned seeds kg^{-1}.

With few exceptions internal seed dormancy ranges from none to mild. Under forest conditions any existing dormancy is broken during the winter after seed fall. The germination is most successful on a warm seedbed with moist mineral soil. Germination is epigeal, the five to seven cotyledons rising above the ground.

If sexual reproduction is limited or nonexistent due to climatic conditions along the northern limit of *Larix* species, e.g., in Canada and Alaska, layering is apparently the dominant mode of propagation. Roots are also known to produce shoots. Artificially, vegetative propagation is easily possible by rooting of softwood cuttings of juvenile material or grafting.

Species of the genus *Larix* have a very adaptable root system, coping with permafrost soil, rocky substrate, or deep and well-drained soils. Under favorable conditions, most *Larix* species develop a deep taproot with extensive and large lateral roots.

The average age of *Larix* species varies from 150 to 900 years (*L. occidentalis*). Under favorable conditions, the average height of mature trees ranges from 15 to 55 m, occasionally exceeding 60 m (*L. occidentalis*). The mean dbh of mature *Larix* trees ranges from 35 to 230 cm. In the most northern parts of the distribution area, a growing stock can be observed from 30 to 50 $m^3 ha^{-1}$. Under favorable conditions, larch forests produce timber volumes between 300 and 550 $m^3 ha^{-1}$ (*L. occidentalis*).

Larix species are highly intolerant of shade. Compared to other conifers, most *Larix* species show rapid juvenile growth, giving larches the height advantage they need to survive. When mixed with other species, *Larix* must be in the overstory and they are practically never found in the understory.

Silviculture

The requirements of *Larix* forests are best met by even-aged silvicultural systems of shelterwoods, seed tree cuttings, and clear-cuts. Thinning in young *Larix* stands enhances the growth of diameter and height during the juvenile years when response potential is greatest.

Compared to other conifers, *Larix* trees are good self-pruners, and boles of 25–30-year-old trees may be clear of branches for one-half or two-thirds their length. Older *Larix* sometimes produce sprouts from adventitious buds after thinning, the amount of sprouting increasing with the severity of thinning.

In natural forest stands located in the boreal zone, fire is essential for the maintenance of *Larix* forests. Fires thin stands, reduce fuels, regenerate the undergrowth, and prepare seed beds.

Pests and Diseases

Larix species are more resistant than other conifers to air pollution, mechanical damage or soil compaction. Some species with thin bark have low resistance to surface fire. In mountainous areas, snow avalanches and snow slides can cause serious damages. Outside the natural distribution area, *Larix* trees are very often subject to damage from pathogens and insects.

Genetics

Within *Larix* species growing over a wide range of sites as well as within species with a distribution area divided into different parts, significant differences of traits can be observed among provenances. The traits include morphological, quantitative, and qualitative characters as well as resistance against pests and diseases, influencing the suitability of the provenance in question for cultivation out of the natural distribution area. In North America and Asia, spontaneous hybridization between *Larix* species is reported in common growing zones of the species in question. In Europe, hybrids between *L. decidua* and *L. kaempferi* are planted commercially providing exceptional growth and resistance to canker.

Uses

Larix timber consists of a narrow, bright yellow sapwood and a reddish-brown heartwood which is hard, heavy, durable, and tough as well as fungi and acid resistant. The timber can be used as lumber, construction wood, fine veneer, furniture timber, posts, poles, and mine timber as well as pulpwood and fuel wood. Several species including

L. decidua, *L. kaempferi*, *L. laricina*, and *L. sibirica* are planted commercially outside their natural distribution areas.

See also: **Silviculture**: Natural Stand Regeneration. **Temperate and Mediterranean Forests**: Northern Coniferous Forests.

Further Reading

Burns RM and Honkala BH (1990) *Silvics of North America*, vol. 1, *Conifers*. Washington, DC: US Department of Agriculture, Forest Department.

Earle CJ (2002) *Gymnosperm Database*. Bonn, Germany: Rheinische Friedrich-Wilhelms-University, Department of Botany. Available online at http://www.conifers.org.

Farjon A (1998) *World Checklist and Bibliography of Conifers*. Kew, UK: Royal Botanic Gardens.

Kruessmann G (1983) *Handbuch der Nadelgehoelze*. Berlin, Germany: Parey-Verlag.

Maydell HJ and Cejchan S (1994) *Forst- und Holzwirtschaft der gemeinschaft unabhaengiger Staaten—GUS (ehemals Sowjetunion)*, Teil 5, *Die Russische Foederation*. Hamburg, Germany: Wiedebusch-Verlag.

Schmidt-Vogt H (1986) *Die Fichte: Ein Handbuch in 2 Baenden*. Berlin, Germany: Parey-Verlag.

Schuett P, Schuck HJ, and Stimm B (1992) *Lexikon der Forstbotanik*. Landsberg/Lech, Germany: ecomed Publishers.

Young JA and Young CG (1992) *Seeds of Woody Plants in North America*. Portland, OR: Dioscorides Press.

Vidaković M (1991) *Conifers: Morphology and Variation*. Zagreb, Croatia: Grafički zavod Hrvatske.

Thinning *see* **Plantation Silviculture**: Forest plantations; Rotations; Stand Density and Stocking in Plantations; Tending; Thinning. **Silviculture**: Silvicultural Systems.

TREE BREEDING, PRACTICES

Contents

Biological Improvement of Wood Properties

B Zobel, North Carolina State University, Raleigh, NC, USA

Introduction

The objective of this article is to discuss how wood can be changed either naturally or by manipulation and how these changes might affect the final product. All wood characteristics are the result of physiological effects (controls) on growth. When the physiological controls are determined by genetic or other within-plant influences, they are referred as internal. These are difficult to manipulate and require activities such as breeding to obtain the desired kind of wood. When the physiological controls are primarily influenced by forces outside the tree, such as weather, nutrient availability or other, one refers to them as external controls.

A good example of a wood property strongly controlled internally is wood density or wood specific gravity. This makes possible the development of high or low wood density races of trees within a species, when selective breeding is used. When the wood of the tree is primarily influenced by outside factors such as weather or wind, external control is indicated. If, for example, a southern yellow pine has been affected by ice or tip moth so that it is no longer straight, the reaction wood resulting will differ a great deal from wood that will result under normal growth conditions no matter what the genetic situation is.

The control of wood formation is certainly not simple or clear-cut as a definition might imply. For example, tree straightness is the result of genetic control but is also affected by environmental factors. Thus, no matter what genetic controls are acting, major environmental differences can result in wood of differing kinds. However, the simplistic way to assess what the wood in a tree will be, is to consider the result of the interaction of both internal and external influences.

General Concepts

Wood is a very pliable and variable substance and can be changed in numerous ways as described below. In the past, when a lot of old, or virgin, timber was available, there was not much need, or effort, to change the wood quality available for use. As the practice of forestry has become more widespread and important, especially since plantation forests have become a major supplier of wood, it has been necessary to grow wood most suitable for given final products; this means methods must be developed to change wood qualities to meet the needs of the intended product.

I will use the southern pine forests in the USA and eucalypt plantations in Brazil as examples of the changes and needs to modify wood properties. Initially, almost all harvesting of softwoods in the southern USA was from quite mature pine trees, from 30 to 70 years of age. There was little concern about wood variation and wood quality as the wood harvested was mature and there was little concern about variation affecting its utilization. After more intensive forestry was practiced, wood quality has become variable enough to have a major effect on its utilization. Different products were found to require different kinds of wood to make the desired product efficiently. A personal example will illustrate this:

> In 1951, I gave a talk to the pulp mill managers and executives from the southern USA about wood, how it varied, and what this variation could mean to the industry. The audience was polite enough to listen but it was evident during the talk that the attendees did not think wood variation was a very important problem since they had good wood to work with which varied only a little. After my talk, the manager of the largest group of mills in the South came to the podium, put his arm around my shoulders and said: 'Son, your talk was interesting but we do not have to worry about wood variation. We are chemists; just grow us any kind of wood and we can make usable paper from it.'

Of course, in reality, this was true, but with the changes in wood from intensive forestry, it has become neither operationally nor economically correct. The differences in wood quality with shorter rotations (harvest age) and more intensive utilization of the trees available has resulted in a large proportion of juvenile wood being used. This, along with more intensive silviculture, has resulted in the costs, quality, and expected yields of the desired products changing. Because of this, the production of substandard products sometimes has been rather dramatic. Currently, wood quality has become recognized as of key importance for efficient production of the kind and quality of product to be produced. The properties of the wood used has become of major interest for pulp as well as for lumber, in both the conifers and hardwoods.

Although the emphasis here will be on wood quality and how it affects the final product, it is necessary not to underestimate the ability of the industry to alter methodologies to adapt to differing woods. Great progress has been made in this area; methods of sawing, methods of curing timber, particleboard construction, pulping technologies, and paper manufacture have all been altered to better use the younger, different-quality wood that is becoming available. Sometimes the changes have been reasonably efficient but too often they have resulted in increased costs and/or poorer-quality final products. The first need for an industry making a given product is to have the raw material it uses reasonably uniform. When this is so, it can develop the best methods of manufacture for a reliable and stable product.

It is necessary to note that the emphasis here is on solid wood and fiber production, used in construction and for paper products. However, there are other major uses for wood; reports are available that show that more than half the wood used on a world basis is for energy production. For example, until recently, a great proportion of the hardwood produced in Brazil was for charcoal, much being utilized for energy in the steel industry. (I worked for several steel companies in this area for a number of years, with the directive to develop wood most desirable for charcoal. This was done by changing species and selecting and breeding for fast-growing trees that had the genetic potential to produce the high-density wood best used for charcoal.) It has been well proven that the *Eucalyptus* wood ideal for tissue production differs greatly from that needed to make good charcoal. Because of the large basic variation in wood properties in the eucalypts, it has been possible to develop wood in the eucalypts most suitable for charcoal, or ideal for pulp, diverse as the needs for these products are. The details as to how such changes can be made will not be covered in this article (but see my books listed in the Further Reading section).

Important Wood Properties

Before one can consider changing wood, it is essential to know which properties are the most important. Although many wood properties can be altered, only a few are of key importance; five of these are listed below:

Wood Density

Wood density, or wood specific gravity, is by far the most important wood property, affecting nearly all products. Wood density and specific gravity measure the same thing – the solid wood substance in a given volume of wood – but they are expressed somewhat differently. (They are the ratio of the dry weight of wood in a given green volume of wood; this can be expressed as dry weight/green volume. The higher the ratio the denser the wood. In pine, a specific gravity of 0.41 is low density while one with a ratio of 0.62 is considered to be very high.) Wood density is normally the term used in the industrial area, while specific gravity is more commonly used by researchers. They can easily be determined from each other. They affect strength, stability, and appearance of solid wood products and grossly affect the kind and quality of paper produced. For example, low-density wood is best for quality paper products like writing papers and tissues, while high-density wood gives the best yields when pulped and is most suitable for fiberboard containers and paper that needs good tear strength.

Wood density is easily measured and can even be roughly estimated when looking at a piece of wood. It can be altered both through silvicultural and genetic manipulation.

Spiral Grain

Spiral grain is of primary importance for stability in solid wood products such as boards while it plays only a small role in its effect on pulp. Most spiral grain is found near the center of the tree; it varies from species to species and from individual to individual. Commonly, it is considered to be important if it exceeds 4 degrees, so is not important in some species with low spiral. Some species, especially in the tropics and sometimes in those like sweet gum (*Liquidambar styraciflua*) have an extreme spirality called interlocked grain. Such wood is extremely variable and not suited for solid wood products. However, there is a reasonable genetic component so a selection program will help.

Fibril Angle

Fibril angle (correctly called microfibrillar angle) is of increasing importance as its effects become better known and methods for its measurement are improved. The wall of a wood cell is not solid, it is made up of numerous microfibrills. The orientation of these in the wall is very important to the stability and quality of the products produced. Fibril angle is greatest near the tree center; it also varies greatly from tree to tree. It has a major effect on the stability of solid wood products and can have an influence on the quality of paper produced.

Wood Uniformity

Uniformity is of great concern to the manufacturer of wood products. The more uniform the wood, the better the product produced and the greater the efficiency in manufacture. As harvest periods for trees become shorter, a greater amount of juvenile wood is obtained, resulting in increased nonuniformity of the raw material available. Currently, there is much effort to change wood properties to obtain greater uniformity, and organizations that have been successful have benefited greatly economically.

Wood uniformity can be improved by controlling the time of harvest as well as growth conditions and silvicultural treatments such as fertilization and site preparation. We have found, in species such as loblolly pine (*Pinus taeda*), that a heavy nitrogen fertilization will usually result in low-density wood being formed for a few years but normally the use of phosphorus fertilizer has only a minor effect on wood density.

General Wood Properties

If space were available, one could list many other wood qualities that can be changed by external or internal means. Some of these can be of considerable importance under certain circumstances, such as the necessity for thin-walled cells and larger cell lumina in the manufacture of tissue papers or straight grain in quality boards. Other characteristics that may be of importance are cell length, resin content of the wood, amount of heartwood present, and numerous things depending on the product desired and the species of trees being used.

Methods of Making Changes in Wood

Wood can be altered in two major ways which will be described separately below: these are external and internal. The external one includes such things as altering tree form, differences in silviculture, and choosing the most desirable species and provenances within species. Internal changes can be obtained by controlling the amount and use of juvenile wood and through genetic manipulation and silvicultural control.

External Control of Wood Properties

Tree form is the most important tree characteristic that affects wood quality. Two major aspects of tree form are straightness of the bole and limb characteristics.

Straightness of bole Straightness of the tree bole is most important. Any time a tree is not straight, it forms a kind of wood called reaction wood. One can reduce the amount and severity of reaction wood by growing straighter trees, either through silvicultural manipulation or control of parentage using a breeding program.

Reaction wood in most conifers is called compression wood. It is formed on the inside of a 'bend' in the trunk of the tree or in the underside of limbs. Its main function appears to be to straighten the tree or push up the limb by pressure on the nonstraight area.

Compression wood has many unique anatomical and chemical characteristics, most of which are adverse to good wood quality. For example, it contains an excess of lignin, often as much as 9% more than the more normal wood; this results in low cellulose yields when pulped. The cells in compression wood have fissures that cause the cell to fragment into small segments not good for the manufacture of paper. The cell walls of compression wood are often unusually thick, resulting in a coarse fiber which is not suitable when making fine papers or absorbing tissues and which result in a nonuniform surface of the paper.

The cells of compression wood have flat fibril angles so it shrinks an exceptional amount longitudinally when dried (up to 9% or more). This makes for unstable boards. Quality is especially adversely affected when a board consists partially of regular wood and partially of compression wood; the result is that one part of the board shrinks longitudinally more than another portion which causes warping, cracking, and checking in the board.

In the hardwoods, reaction wood is called tension wood. It is formed on the outside of the curve in the tree bole. Its function is to pull the tree bole straighter. Opposite to compression wood, tension wood has an excess of cellulose, otherwise the short cells and other abnormalities in compression wood such as adverse fibril angles, are present. (Since paper is made from cellulose, years ago some industrialists suggested that we breed crooked hardwoods which would increase the amount of cellulose and reduce the lignin formed. However, the cellulose in tension wood is different than that in normal wood and, when pulped, gives low yields and inferior paper qualities.)

When tension wood is used for solid wood products, the boards often have a weak plane in them (high cellulose and low lignin) causing the boards to break easily. Also, because of the flat fibril angle, it is difficult to finish the boards by planing or use of sanding, because the angle of the fibrils prevents formation of a smooth surface.

One of the most interesting things relative to the biology of wood in trees is how such opposite methods (compression wood and tension wood) have developed in the conifers and in the hardwoods, both to straighten the tree. The wood properties resulting from the two methods differ greatly. The amount of reaction wood can be reduced by producing straighter trees. This can be partially done through the use of selection and breeding straight trees since the genetic control of straightness is usually moderate to high. Natural variability in straightness is large so the combination of that plus moderately high heritability results in dramatic improvement in the population resulting from a breeding program which emphasizes tree straightness. (Put roughly, gain is the product of variability in the characteristic times its genetic control.)

Straightness can also be improved through the use of good forest management. Uniform and well-spaced, well-established plantations will result in straighter trees. As one example, if a pine tree is planted poorly so the stem of the seedling is not above the root, the resulting tree will grow crookedly, with an excess of compression wood, for the rest of its life. Planting using machines often creates serious problems when the foot of the planting machine is too shallow, resulting in the planted tree's having trailing roots. Trees from such plantations have excessive crook in their stems causing a major degrade in their wood quality. Based on my experience, the fastest and best method to improve wood quality is to develop straight trees. Frequently, detailed studies as to the cause of crookedness have been made, blaming such things as seed source, when the act of good planting would have avoided the trouble.

Limb Characteristics

Altering limb characteristics can have a major effect on the type of wood product produced. Smaller and more horizontal limbs are most suitable for the quality of both solidwood and the strength and yields of pulp. These characteristics are influenced both by the knotwood itself and by the reaction wood which is associated with the knots. Limb size can best be controlled via tree spacing in the plantation; genetic control of limb size is relatively small. However, limb angle has a much stronger genetic control, and can be improved by a breeding program. When excessively limby trees are used, limb size and angle has an effect on product quality, especially on the stability of boards and the tear strength of the paper produced. Changes in limb characteristics are not as easy to obtain or as large as for wood density, but they can be very important for certain products.

Forest Management Approaches

Variation in methods of forest management can result in differences in wood. All management activities must be done carefully if wood quality is to be as desired.

Silviculture

Silvicultural treatments that change nutrients via fertilization can have a major effect on wood properties. Especially in the conifers, but also for some hardwoods, heavy fertilization, using a high nitrogen content, often causes a considerable lowering in wood density. In the hard pines, the wood produced when a heavy nitrogen fertilization is used is somewhat similar to juvenile wood with thin cell walls resulting in lower wood density and usually in shorter cells. The response to nitrogen rarely continues for more than 5 years. As a result, there will be excessive longitudinal shrinkage in the affected annual rings of boards made from this kind of wood which will be unstable when dried. Although detailed studies on the effect of fertilization on fibril angle have not been made, I predict that the wood from heavily nitrogen-fertilized trees will have flatter fibril angles than normal, making the wood similar to juvenile wood.

Phosphorus content of the soil usually has little effect on wood density, although a shortage of phosphorus sometimes results in higher wood density. Here, the addition of this substance will reduce the higher density to that of normal wood.

Fertilization Fertilization, especially in the tropics, is often mandatory if suitable growth is to be obtained; when this is so nitrogen fertilizer should be applied slowly in small quantities at each treatment, not in large amounts at one time during the midterm of the rotation. This is especially true in the pines; when a heavy application of nitrogen is made, the trees will form a band of wood in the tree trunk that is similar to juvenile wood, resulting in unsatisfactory lumber which is difficult to cure and stabilize.

Stand density A variation in normal stand density among trees will have little effect on wood other than the width of the annual rings; this can be very important for some products and species.

Species and provenance choice Matching species and provenance to site is of key importance. Normally, reasonably small site differences, or somewhat poor adaptability to the site, do not result in unusual wood but extreme site differences can result in wood so varied that it is not usable. For example, when *Pinus caribaea var. hondurensis* is grown in certain especially good environments the wood produced can be of very low density, making it undesirable for either solid wood products or pulp. The movement of slash pine (*Pinus elliottii*) to the same environment has resulted in very dense wood, with characteristics much like that of oak, making suitability for utilization very limited.

Pruning For most species, pruning is necessary if good solidwood products are desired, especially for conifers grown in the tropics. Under the environments there, limbs will hang on and not shed for many years and become almost like little steel rods; this results in degrade of the final product. Pruning is also usually necessary for quality tropical hardwoods but there are exceptions, like some of the best eucalypts, where the limbs die early and shed naturally. Caution is necessary when pruning; if done poorly leaving stubs, or if the bark is cut into the cambium when pruning, as almost always happens when machetes or axes are the tools used, pruning becomes adverse to quality. When the cambium is cut in the conifers, the result is pitch pockets and undesirable abnormal wood grain formation. In certain of the quality hardwoods, rot will occur which ruins the pruned log for quality products when harvested.

Pest Control

Both insects and diseases can cause major changes in wood properties. An example is fusiform rust on pine which results in a high resin content (double or more of the normal) and abnormally short, and sometimes forked, cell formation. Pulp yields from rust infected wood will be reduced as much as 50%; additionally, the wood will not be suitable for production of lumber. Eucalypt canker is similar to fusiform rust in that it affects both pulp yield and quality. Suitable boards cannot be sawn from the infected stem. Until brought under control genetically by the use of rooted cuttings from disease-free parents, the eucalypt canker had a major effect on the utility of wood from disease-sensitive species. There was considerable talk in the late 1970s of not growing eucalypts in parts of Brazil because of the high incidence of the canker and its effect on wood. It is important to control insect damage and disease in the tree trunks if normal wood quality is to be obtained. Additionally, supplemental nutrients, such as nitrogen, must be used carefully or there will be a degrade in wood quality.

Effectiveness of Forest Management

A good summary relative to the effect of forest management on wood is that anything that can cause growth differences in trees can also result in changes in wood properties. Such a reaction is especially obtained in the conifers, often less than for many hardwoods.

Internal Control of Wood Properties

There are two major causes affecting the internal wood properties of a tree. The first is the time of formation and location of the wood produced, generally subdivided as juvenile and mature wood. The second is the genetic and physiological control of the anatomy and morphology of the cells produced; these can be affected by breeding, as well as by some of the external controls outlined above.

Juvenile and Mature Wood

The quality and ratio of juvenile and mature wood are key to the determination of wood quality within the bole of the tree. All trees have a zone near the tree center (the pith) where there is a change, often rapid, in wood quality from the center of the tree outward. After a number of annual rings, the changes become smaller and more or less constant, sometimes with little change from ring to ring. This is mature wood; in juvenile wood, the variation is related to the number of rings from the pith, regardless of the height in the tree or the age of the tree. This results in a juvenile wood zone that has rapid changes followed by a mature wood zone with minor changes in wood properties, regardless of height in the tree. For example, a 30-year-old loblolly pine with 30 annual rings near the base of the tree will have about the first 10 rings from the pith as juvenile wood, the next 20 as mature wood. Therefore, a log from the base of the tree will consist largely of mature wood, while a log from the upper part of the tree is predominantly juvenile wood. Closer to the top of the same tree, where there might be only 12 annual rings; the first 10 will be juvenile wood with only the last 2 rings being mature wood. Although not strictly correct, the juvenile wood of a loblolly pine tree can be considered as being in a cylinder made up of the 10 rings from the pith. The wood qualities of this core will be essentially the same regardless of the height in the tree where they are measured. Differences in wood quality of each log is therefore dependent on the proportion of juvenile wood to mature wood. The age of the tree is not relevant to the presence of juvenile wood; it is determined at any height by the location of the cambium and by the number of rings from the pith, regardless of tree age.

Juvenile wood qualities vary from the pith outward. In the conifers the wood density becomes greater, the cell length increases, and spiral grain decreases and fibril angle decreases in wood produced from the older cambium as ring number becomes greater from the pith. Juvenile wood in most conifers has low density, short cells, a high spiral grain, and high fibril angle. Such wood gives low yields of pulp with weak tear strength. It is overall considered to be of poor quality related to strength and stability for boards when compared to the mature wood in the same tree. This pattern is usual for the hard pines and some diffuse porous (soft) hardwoods like sweetgum. Many of the hard hardwoods (like oak (*Quercus* spp.) and hickory (*Carya* spp.)) have a different pattern with high wood density near the tree center but with other wood properties that follow the same pattern as described for the pines. There are some diffuse porous hardwood species, like the eucalypts or poplars, whose juvenile wood is very similar to their mature wood.

There are many other wood properties that vary between juvenile and mature wood such as extractive content, or cell size. There are so many of these that they will not be dealt with in detail in this section.

Although often considered to be of low quality, juvenile wood is preferred for some products, like printing papers and tissues, where thin-walled cells are best. Such wood produces strong mullin (bursting strength) but the tearing strength is low. Juvenile wood of some conifers is somewhat similar to mature wood of the diffuse porous hardwoods and is sometimes used to supplement the need for hardwood fibers, such as when hardwoods are in short supply or are costly to obtain.

Wood from thinnings of pine in young plantations or tops from older trees is predominantly juvenile since mature wood has not yet has a chance to be formed. In some hardwoods like the eucalypts, the effect of juvenile wood is minor since the differences between juvenile and mature wood are quite small; this enables the use of short rotations without a major sacrifice in wood quality such as one finds in the conifers.

A major effect on wood and product quality differences within a tree relate to the ratio of juvenile wood present. One major control of the effect of juvenile wood is by varying the age of harvest or the part of the tree from which the wood is obtained.

Young plantations have a large proportion of juvenile wood; despite this, the economic importance of early harvest is often assessed without a proper consideration as to the kind of wood being obtained when there is a large amount of juvenile wood present.

There have been some studies on the genetic control of the amount and kind of juvenile wood. We have found considerable genetic control in loblolly pine but little has been done with this operationally since the effect of juvenile wood can be modified by changing rotation age or by use of the part of the tree bole with the desired percentage of juvenile wood.

Genetic Control of Wood Properties

The genetic control of wood properties is usually strong to moderate and the kind of wood can be influenced using selection and breeding. A strong additive genetic control is found for wood density but there is essentially none in cellulose yield. Strong additive genetic control along with a large suitable variation pattern makes possible the changing of important wood qualities in the desired direction when a selection and breeding program is followed. There are two major categories of genetic control, generally called additive and nonadditive. When the genetic variation is largely of the additive type, and where suitably large variation occurs, improvement by selection and breeding is relatively large and quick. The amount of additive genetic variation is usually represented by the term narrow-sense heritability (h^2) (common in the literature). This is a ratio indicating how much of the characteristic is controlled by additive genetic variation and how much results from other causes, including the environment and nonadditive variation. Thus, wood density has a high narrow-sense heritability (h^2) of 0.6–0.7, straightness of the tree of 0.3–0.5, and limb size shows a heritability of about 0.1–0.2.

Although a more exact formula is used by researchers, a working relation for estimating gain from selection is

$$\text{gain} = \text{SD} \times h^2$$

In this formula SD is the selection differential which is related to the variation in the wood property and the intensity of selection used to obtain the parents which give the desirable gain. Gain in a genetics program with a wood property is dependent on the variability present within the property, the intensity of selection used, and the heritability of that wood characteristic.

Only a few wood properties, like cellulose yield per unit weight of wood, have very little additive variation, but they have considerable non-additive variation. Gains from a selection program with them will be very small. When low additive variation is present, as for cellulose yield, the use of vegetative propagation (or a complex breeding system) is necessary to capture genetic variation in the new plantation trees. (A reduction or change in the amount of juvenile wood is difficult to achieve using a genetic breeding program, because the heritabilities are low).

Wood density Wood density is a characteristic that can be improved quickly and significantly through breeding because its genetic variation is large and consists mostly of the additive type. Other wood properties that are easy to change by selection are resin content of wood and cell length. Some of the more important wood characters like spiral grain and fibril angle (along with tree straightness) have intermediate inheritance and gains through selection will be less.

Operationally, then, when a high wood density tree with high heritability is crossed with another high density tree, its progeny will have relatively high density. If a high cellulose yielder tree (with very low heritability) is crossed with a similar tree, one cannot predict the cellulose yields of the progeny, because cellulose yield is inherited nonadditively. Many wood properties are intermediate, where about half the genetic variation is of the additive type, half nonadditive. When this occurs, a selection program is not fully efficient and is dependent on the amount of variation present.

Vegetative Propagation

Although genetic gain is more difficult to obtain when the genetic control is nonadditive, the use of vegetative propagation will enable good improvement. Vegetative propagation will result in the new plant having the characteristics of the donor parent, since the new plant (propagule), usually a rooted cutting, contains all the additive as well as the nonadditive genetic variation present in the donor tree. The use of vegetative propagation in producing trees for operational planting is becoming much more widely used as methodologies for successful vegetative propagation are being improved.

The simplest way of producing improved wood for characters with a large portion of nonadditive variation is to use vegetative propagation to produce plantable trees.

Wood Uniformity

Wood uniformity, both within a tree and among trees, is a most important characteristic. When wood used in a manufacturing operation is reasonably uniform, efficiency in manufacture and quality of the final product will be greatly improved. Conversely, however, if juvenile and mature woods are both included in the same mix or board, and are treated similarly in manufacture, the final product will be variable and the efficiency and the value of the manufactured product will drop considerably.

The best way to obtain uniformity among plantation trees is to use vegetative propagation since the wood of the propagules from a given tree will all have wood similar to its donor tree. This methodology is now being much used in operational programs; one of the best examples is for the eucalypts when their wood is intended to be used for tissues. The mills have determined the best wood for making tissues and then rooted cuttings from the donor trees with these characteristics are used in establishing plantations. Both the quality and yields of tissues made from such plantations are greatly improved. This method of producing planted trees is now being applied to many other species as techniques for developing the propagules improves; in the future a great proportion of the wood available from plantations will have the desired wood uniformity and properties suited for the final product.

For the long term, the major improvement in wood, both through external and internal sources, will be to develop wood that is uniform and ideal for a given product line. Both the internal and external methodologies of changing wood must be used it such a goal is to be achieved.

See also: **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance; Genetics and Improvement of Wood Properties. **Wood Formation and Properties**: Formation and Structure of Wood; Mechanical Properties of Wood; Physical Properties of Wood; Wood Quality.

Further Reading

Allen PJ (1985) *Estimation of Genetic Parameters for Wood Properties in Slash Pine in Southeast Queensland*. Research Note no. 41. Brisbane, Australia: Queensland Department of Forestry.

Baas P (1982) *New Perspectives in Wood Anatomy*. The Hague, The Netherlands: Dr W Junk.

Bamber RK and Burley J (1983) *The Wood Properties of Radiata Pine*. Slough, UK: Commonwealth Agricultural Bureau.

Barefoot AC, Hitchings RG, Ellwood EL, and Wilson E (1970) *The Relationship between Loblolly Pine Morphology and Kraft Paper Properties*. Technical Bulletin no. 202. Raleigh, NC: North Carolina State University.

Bendtsen BA (1978) Properties of wood from improved and intensively managed trees. *Forest Products Journal* 28(10): 61–72.

Blair RL, Zobel BJ, Franklin EC, and Mendel JM (1974) The effect of tree form and rust infection on wood and pulp properties of loblolly pine. *TAPPI* 57(7): 46–50.

Burdon RD (1975) Compression wood in *Pinus radiata* clones on four different sites. *New Zealand Journal of Forest Science* 5: 152–164.

Burley J and Nikles DG (1973) *Selection and Breeding to Improve some Tropical Conifers*. Brisbane, Australia: Queensland Department of Forestry.

Campinhos E (1980) More wood of better quality through intensive silviculture with rapid-growth improved Brazilian *Eucalyptus*. *TAPPI* 63(11): 145–147.

Cown DJ (1973) Effects of severe thinning and pruning treatments on the intrinsic wood properties of young radiata pine. *New Zealand Journal of Forest Science* 3: 379–389.

Falkenhagen ER (1979) *Provenance Variation in Growth, Timber and Pulp Properties in* Pinus caribaea *in South Africa*. Technical Bulletin no. 59. City, South Africa: Department of Forestry.

Foelkel CE, Barrichelo LE, Garcia W, and Brito JO (1976) Kraft cellulose of juvenile and adult wood of *Pinus elliottii*. *IPEF* 12: 127–142.

Megraw RA (1985) *Wood Quality Factors in Loblolly Pine: The Influence of Tree Age, Position in the Tree and Cultural Practices on Wood Specific Gravity, Fiber Length, and Fibril Angle*. Atlanta, GA: TAPPI Press.

Saucier JR (1990) Forest management and wood quality. In: *Proceedings of the South Plant Wood Quality Workshop*, Athens, GA, pp. 47–56.

Senft JF, Bendtsen BA, and Galligan WL (1985) Weak wood. *Journal of Forestry* 83: 476–485.

Taylor FW (1972) Anatomical wood properties of South African-grown *Eucalyptus grandis*. *South African Forestry Journal* 80: 20–24.

van Buijtenen JP (1963) Heritability of wood properties and their relations to growth rate in *Pinus taeda*. *1st World Consul For Gen Tree Improv.*, Stockholm, Sweden.

van Buijtenen JP (1969) Controlling wood properties by forest management. *TAPPI* 52(2): 257–259.

Wright JA (1991) Impact of wood quality assessments on future fiber resources in the pulp and paper-making industry. *South African Forestry Journal* 157: 96–99.
Yang KC (1994) Impact of spacing on width and basal area of juvenile and mature wood in *Picea mariana* and *Picea glauca*. *Wood Fiber Science* 26: 479–488.
Zobel BJ and Talbert J (1984) *Applied Forest Tree Improvement*. New York: John Wiley.
Zobel BJ and Jett JB (1995) *The Genetics of Wood Production*. New York: Springer-Verlag.
Zobel BJ and Sprague JR (1998) *Juvenile Wood in Forest Trees*. New York: Springer-Verlag.
Zobel BJ and van Buijtenen JP (1989) *Wood Variation: Its Causes and Control*. New York: Springer-Verlag.

Genetics and Improvement of Wood Properties

J P van Buijtenen, Texas A&M University, College Station, TX, USA

Introduction

Wood quality must be defined in terms of the end product: what is good for linerboard is not necessarily good for newsprint. The most critical properties for breeding programs are usually wood specific gravity, tracheid length and microfibril angle, although many other properties are also important. In general, wood properties are strongly inherited, with heritabilities of 0.5 and up. This would make breeding for wood properties easy if they could be determined easily and cheaply. Unfortunately this is true only for wood specific gravity. Therefore, much effort has gone into developing assay methods suitable for small wood samples which can be taken from the tree with little damage.

Wood quality can be improved by silviculture and by breeding. Spacing, thinning, and fertilization all have major effects on the growth of the tree and the properties of its wood. Selective breeding also has a major impact. Traditionally, the selected trees are grafted into seed orchards, progeny tested, and rogued. The time between the start of the program and the harvest of the first trees is typically 50 years making it appropriate to breed for a general purpose tree. For species that can be vegetatively propagated another approach is feasible: clonal forestry. Using it with shorter rotations allows development of trees suitable for specific products.

What is Wood Quality?

This is a difficult question to answer. Many years ago some of the pioneers in forest tree improvement asked managers of the local paper mills what wood properties they considered desirable, and were unable to obtain helpful answers. It was not until the 1970s that breeders started to ask the right questions. The quality of any raw material is defined as its suitability for use and quality is affected by many properties. There is a wide range of products made out of wood and it is therefore necessary to define wood quality in terms of the end product. What is good for linerboard is not necessarily good for multiwall sack paper and might be disastrous for newsprint. This is the most important point to keep in mind when considering wood quality.

What Are the Important Products?

Wood products belong in two major groups: solid-wood products, and pulp and paper products. Solid-wood products include not only lumber, but also plywood, oriented strand board and particle board. They can be used for construction as well as furniture. Pulp and paper products can be produced by three major processes: the sulfite process, the kraft process, and mechanical pulping. The sulfite process is used extensively for spruces and firs. The kraft process is more flexible and can be used for most species, including almost any pine. Mechanical pulping is often used for lighter woods such as poplars, but can be used successfully for some pines. The sulfite process is very suitable for producing high quality writing papers. Unbleached kraft is used extensively for the production of linerboard and sack paper, while bleached kraft can be used for writing papers, computer paper and paper used in copy machines. Mechanical pulps are primarily used for newsprint.

What Are the Important Wood Properties?

First we must distinguish between the wood of two major groups of trees: hardwoods (essentially broad-leaved trees) and conifers. The two groups have distinctly different wood. That of hardwoods is more complex, and its most distinguishing feature is the presence of vessels the elements of which are connected to each other through large pores. Other elements include fibers, tracheids, and parenchyma. The hardwoods are further divided into ring-porous and diffuse-porous species (**Figure 1**). Conifers have tracheids, ray parenchyma, and resin ducts. The tracheids are much longer than those in hardwoods.

The wood in conifers usually has distinct springwood and summerwood, also called earlywood and latewood. Springwood has large-diameter tracheids

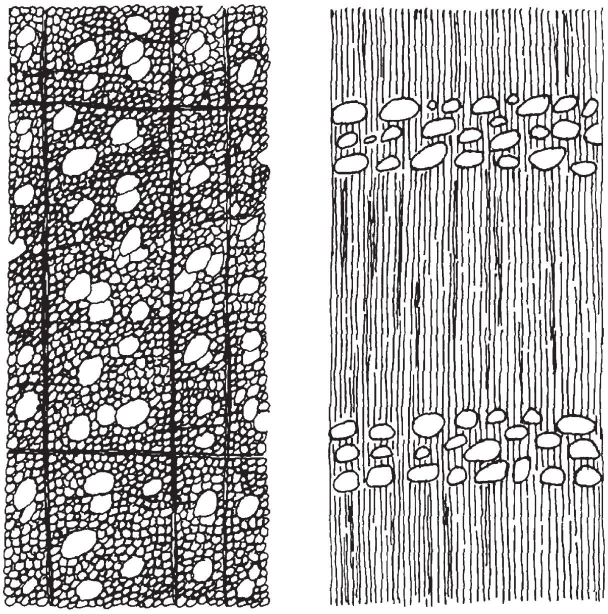

(a) (b)

Figure 1 Cross-sections of (a) diffuse-porous and (b) ring-porous wood. From Zobel BJ and van Buijtenen JP (1989) *Wood Variation: Its Causes and Control*. New York: Springer-Verlag.

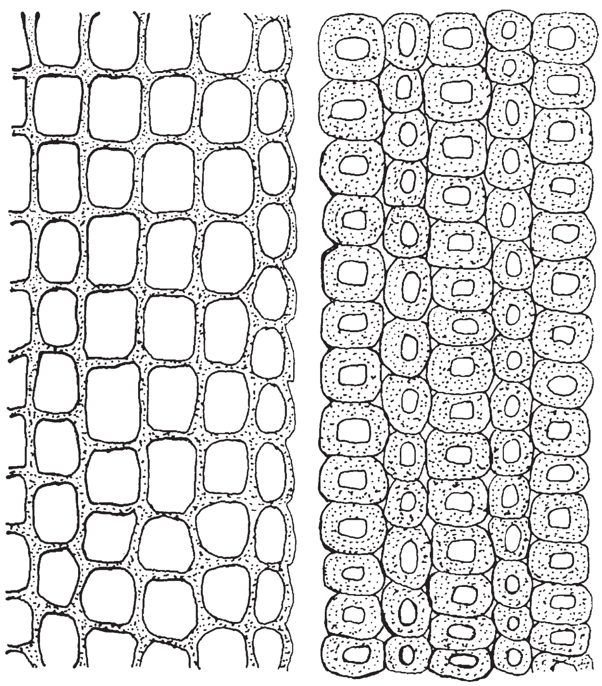


Figure 2 Cross-section of earlywood and latewood, clearly showing the difference in the cell diameter and wall thickness of the tracheids. From Zobel BJ and van Buijtenen JP (1989) *Wood Variation: Its Causes and Control*. New York: Springer-Verlag.

with thin walls and looks light on a cross-section of wood, while summerwood has narrow, thick-walled tracheids and looks dark (**Figure 2**). The most important wood properties are wood specific gravity (dry weight divided by green volume), latewood percentage, tracheid length, tracheid diameter and wall thickness, microfibril angle (the angle of inclination of the cellulose microfibrils to the long axis of the tracheid), grain spirality (the angle of the tracheids to the vertical axis of the stem), and the chemical composition of the wood.

Techniques for Determining Wood Properties Using Small Samples

In a breeding program it is most important to evaluate wood quality without destroying the tree, and much effort has been expended over the years to develop techniques to make determinations on small wood samples. The favorite method is to remove one or more small radial cores (increment cores, ≤ 10 mm diameter) from the tree, which can be used for determinations. Methods have also been developed to pulp these on a very small scale and determine the pulp and papermaking properties. It is also relatively easy to determine anatomical properties on these samples. Almost all the important properties listed earlier can be determined from an increment core. Also, new high-throughput techniques have been developed recently such as near infrared (NIR) spectroscopy, image analysis, computer tomography, X-ray densitometry, X-ray diffraction, and pyrolysis molecular beam mass-spectrometry which allow very large numbers of chemical analyses on these small samples. Several techniques have been incorporated in the Silviscan equipment developed by Robert Evans at CSIRO, Australia (**Figure 3**). These approaches are ideal for a breeding program where large numbers of individuals must be screened quickly and cheaply.

Silvicultural Improvement of Wood Properties

Spacing

The initial spacing in plantations usually has no direct effect on specific gravity and tracheid length. A wider spacing results in larger juvenile cores. In spruce closer spacing results in better pulp yield and sometimes in greater strength. On sites where water availability is a problem, wider spacing may lead to a higher wood specific gravity.

Thinning

Thinning removes the poorer quality trees and therefore increases the quality of the timber left for the final harvest. Thinning removes trees that contain little of the higher quality wood (outerwood) that is formed after the first few rings from the pith, and

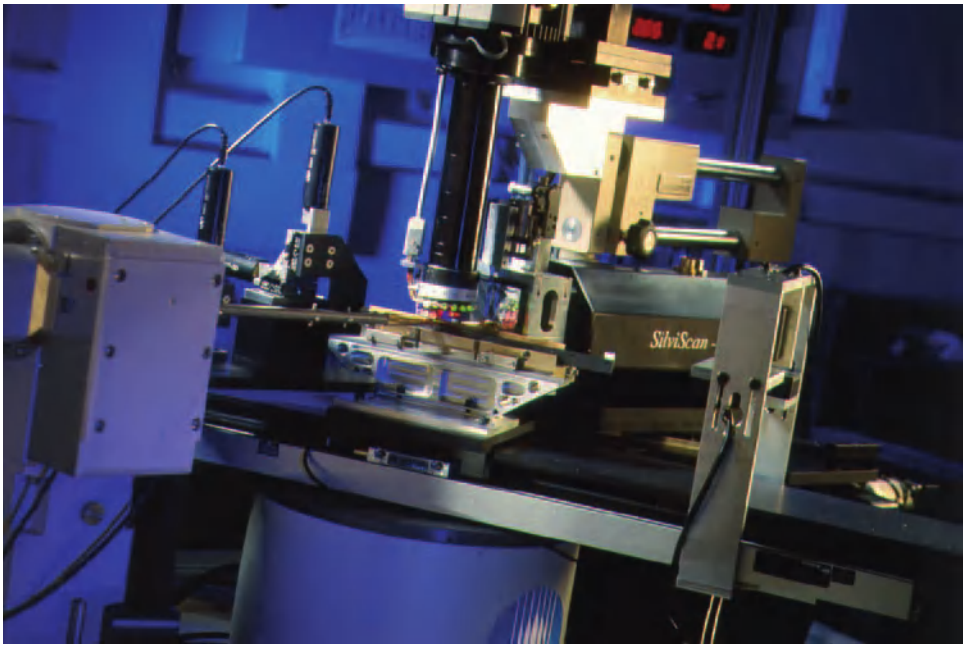


Figure 3 The SilviScan® instrument combines X-ray densitometry, diffractometry and image analysis to measure a variety of properties in a single wood sample. Photograph courtesy of CSIRO.

enhances production of such wood in the remaining crop. The effect of thinning is greatest in ring-porous species, less in diffuse-porous species, and least in conifers. Specific gravity and tracheid length are not much affected.

Fertilization

In general, soil fertilization has more effect on wood of conifers than of hardwoods. In particular, nitrogen fertilization decreases wood specific gravity in conifers and its effect may last 5–10 years. It also decreases tracheid length and increases earlywood production. To get the benefits of increased growth, while minimizing the adverse effects on wood properties, nitrogen fertilization should be light and frequent. The overall effect of fertilization both in hardwoods and conifers is beneficial, since the increase in volume more than offsets the loss in wood specific gravity. The effects of phosphorus and potassium are less pronounced than that of nitrogen. One should note that the effect of fertilization depends greatly on soil conditions. Obviously the effect is greatest when there is a nutrient deficiency.

Genetic Control of Wood Specific Gravity

The Components of Wood Specific Gravity

Wood specific gravity is a complex trait with many contributing factors. The major factor is usually the latewood percentage. Another important component is the cell wall thickness in the earlywood and the latewood. The diameter of earlywood tracheids is also important, but the diameter of the latewood tracheids is less so. The packing density, which is the specific gravity of the cell wall material itself, contributes to the actual density, but not to the variation among trees, since it is rather constant at $1.54\,\mathrm{g\,cm^{-3}}$. Extractives and insoluble deposits are the final components, which are particularly important in the heartwood.

Inheritance of Wood Specific Gravity in Conifers

Genetic variation among provenances Trends in genetic variation among provenances, if present at all, are usually weak. Specific gravity tends to be lower with increasing latitude and altitude. In the southern pines in natural stands wood specific gravity increases from the northwest to the southeast following the rainfall patterns in the southern USA. Genetic trends, determined by growing different provenances in the same location, are in the opposite direction. Clinal patterns are expected in the southern USA, the northeastern USA, and the boreal regions. This is not true, however, in the western USA with its mountainous topography. There, broad trends are expected to be less common except for elevational differences.

Tree-to-tree variation in wood specific gravity The literature on genetic differences among trees is abundant and is only outlined here. Narrow-sense heritabilities for wood specific gravity range from 0.4 to 0.7 in both corewood and outerwood. Low specific gravity species, such as Virginia pine, spruce, and silver fir, tend to have somewhat lower heritabilities than high specific gravity species such as the hard pines, larch and Douglas-fir. In general, the specific gravity of corewood and outerwood are well correlated, with genetic correlations frequently above 0.7. This makes it possible to select for specific gravity at an early age. For species that can be vegetatively propagated, the broad-sense heritability can be substantially higher than the narrow-sense heritability, which can be important for clonal forestry.

Inheritance of Wood Specific Gravity in Hardwoods

Not as much is published on the inheritance of specific gravity in hardwoods as in conifers, but the information is still substantial. Most of the work was done on eucalypts and poplars, with some on other species. In general, wood specific gravity is inherited quite as strongly in hardwoods as in conifers. In the eucalypts and poplars the heritability of specific gravity tends to range from 0.6 to 0.8, while in oak it ranges from a little below 0.4 to almost 0.6. In sycamore reported values range from 0.7 to 0.8. Juvenile–mature correlations in hardwoods are as high as in conifers.

Genetic Control of Other Wood Properties

Latewood Percentage

Differences between earlywood and latewood are so strong that they should often be evaluated separately. A fair amount of information is available on the relationship between latewood percentage and specific gravity, but far less on the genetics of it. There is no general trend in the earlywood : latewood ratio, although the higher latewood percentage is usually associated with high wood specific gravity. The heritability of latewood percentage is rather variable with reported values ranging from 0.25 to over 0.9. The narrow-sense heritability is often around 0.5, while the broad-sense heritability may be around 0.8. One should note that latewood percentage is related to other factors such as fertilization and it also affects the average cross-sectional tracheid dimensions which are very important for pulp and papermaking. On the average, latewood cells are slightly longer than earlywood cells.

Cell Dimensions

Tracheid length is moderately to strongly heritable, but information is somewhat limited, particularly in hardwoods. Most of the work in hardwoods has been with eucalypts and poplars. Estimated heritabilities ranged from 0.36 to 0.86. It has also emerged that polyploidy has a major effect on fiber length in both natural and artificially produced polyploids, increasing fiber length by 21% to 26%. Reported narrow-sense heritabilities in conifers range from 0.28 to 0.9 and broad-sense heritabilities from 0.56 to 0.86. In some species such as Scots pine (*Pinus sylvestris*), lodgepole pine (*P. contorta*), and shortleaf pine (*P. echinata*) differences among provenances have been reported.

Tracheid diameter and wall thickness are in general fairly strongly inherited, but information is quite limited. In loblolly pine (*Pinus taeda*) heritabilities up to 0.8 were reported. Inheritance in *Eucalyptus viminalis* was equally strong.

Spiral Grain

Spiral grain is probably related to wind resistance, but is difficult to measure accurately. If severe it can be a problem for solid-wood products, but generally it is not economically important. It has been intensively studied in *P. radiata* where it can cause problems. Heritability is strong enough to make genetic improvement feasible. There are also some data for eucalypts and beech indicating the same situation. Some species, such as sweetgum (*Liquidambar styraciflua*), have interlocking grain, which can be very troublesome but is also amenable to genetic improvement.

Chemical Properties

Genetic control of wood chemistry is topical, for two reasons. Much work is going on with control, at the molecular level, of lignin synthesis, and new techniques have been developed to analyze small wood samples in large numbers.

Traditionally the lignin, cellulose, and extractives content have been studied most extensively. Lignin content is very strongly inherited but its range of variation is small, indicating that it is very important and natural selection maintains it in a very narrow range. It can be determined extremely accurately. Cellulose cannot be measured as accurately; this lowers the heritability and makes genetic improvement more difficult. In eucalypts, however, considerable progress has been made in increasing cellulose content in clonally propagated trees.

Oleoresin components are quite often under the control of individual genes of large effect, and could be manipulated readily. There has been limited interest, with the exception of overall resin yield in pines, and the presence of limonene, which conveys insect resistance. In the decade 1970–80 some terpenes were used as a form of early genetic marker in studies of forest tree populations.

Other Wood Properties

Compression wood is rather strongly inherited both in loblolly pine and radiata pine. Surprisingly the relationship with form is rather weak, so factors other than straightness must play a major role. Another important property is heartwood formation, but its heritability is rather low.

A trait that is currently of major interest is microfibril angle. It is inherited rather strongly and is related to the strength of individual fibers as well as solid-wood stiffness. Bark percentage is rather variable in loblolly pine, being very important in young trees, where it can occupy as much as 50% of their volume. It is much less so in mature trees and it has a strong geographic component.

Finally, in eucalypts it has been found that collapse during drying, a rather common defect, is highly heritable.

Interrelationships among Traits

Interrelationships among traits are of great importance to the breeder. To select for one trait, but accidentally cause an adverse change in another, may be fruitless. For instance, if wood specific gravity and volume growth were negatively correlated, then selection just for wood specific gravity would decrease growth. This could be good or bad. Selection for low wood specific gravity could result in increased volume and wood that is more suitable for newsprint. On the other hand, selection for increased growth could result in wood less suitable for sack paper. In principle, one copes with this by using a selection index. Knowing the economic value of the traits under selection and their genetic and phenotypic relationships, one can assign a weight to each trait, to give a best estimate of the overall genetic value. A way to show the interrelationships among traits is by use of the so-called coefficient of genetic prediction. This shows the purely incidental change in trait 2 from a change of one standard deviation in trait 1. An example is given in **Table 1**.

Specific Gravity and Growth Traits

In general, there tends to be a weak negative correlation between specific gravity and height and diameter growth. Since in general the correlations between specific gravity and growth are not strong, it is usually not difficult to find individuals with desirable combinations for both traits. Specific gravity and date of bud break have a noteworthy correlation based on research done in Norway spruce. Early flushing is associated with less latewood, lower wood specific gravity, and greater ring width.

Wood Specific Gravity and its Components

Because of the totally different anatomy of the wood of conifers and hardwoods, they will be discussed separately. In loblolly pine latewood percentage, latewood specific gravity, earlywood specific gravity, and latewood tangential tracheid width showed the strongest genetic relationships to overall wood specific gravity. The first three factors have a positive association, while the tangential tracheid width has a negative relationship to overall wood specific gravity. Compression wood has a strong positive relationship with specific gravity.

In hardwoods little is known about the genetic relationships among the proportions of different cell types, but the important cell types are tracheids, libriform fibers, vessel elements, and medullary ray parenchyma.

Relationships among Other Wood Properties

In a few conifers tracheid length has a negative genetic correlation with wood specific gravity and growth rate and positive correlations with other

Table 1 Coefficients of genetic prediction (CGP). Selecting a population of parents one standard deviation above or below the average for a trait listed in one of the columns, will change the genotypic values of the progeny traits by the CGP times one standard deviation (based on data from the Western Gulf Forest Tree Improvement Program). The CGP is calculated as the phenotypic covariance of trait 1 and trait 2 divided by the product of their genetic standard deviations

	25-year height	*25-year DBH*	*25-year volume*	*Juvenile SG*	*Mature SG*	*Average SG*
25-year height	0.22	0.16	0.18	– 0.06	– 0.06	– 0.08
25-year DBH		0.25	0.26	– 0.12	– 0.11	– 0.14
25-year volume			0.26	– 0.12	– 0.11	– 0.13
Juvenile SG				0.19	0.16	0.21
Mature SG					0.36	0.30
Average SG						0.30

DBH, diameter at breast height; SG, specific gravity.

fiber dimensions such as lumen diameter, tangential and radial width, and wall thickness in the latewood.

In loblolly pine the microfibril angle in the earlywood is greater than in the latewood. It is fairly constant in the earlywood, but decreases from the pith to the cambium in the latewood.

In loblolly pine and eucalypts moisture content is negatively correlated with wood specific gravity. Hence, while wood specific gravity increases, the green weight stays relatively constant, since water is replaced with wood substance.

Controlling Wood Properties by Breeding

First one should consider the breeding objectives in terms of the end product. Since the trees will be harvested 50 to 75 years after the selections are made, it seems advisable to breed for properties that are generally desirable, because future wood technology is so uncertain. Increased specific gravity would be particularly suitable, since the use of thinnings and shorter rotations associated with plantation management depresses wood specific gravity (along with other components of wood quality), and it will be important to compensate for this, especially in corewood, which will make up a larger portion of the wood harvested. Another useful strategy is to try to reduce wastage and/or processing costs, e.g., by reducing lignin or by modifying lignin so it can be more easily removed by pulping. Significant reductions in lignin content probably cannot be achieved without major modifications in the system of growing, harvesting, and processing the trees. Wood uniformity within and between trees is also of great importance to the users of wood.

When designing a long-term breeding program for wood quality two key decisions must be made: (1) how to cope with the correlations among traits and (2) how to deal with the selection and progeny test phases. Index selection is, in principle, the best way to deal with adversely correlated traits. In order to cope with the negative correlations between specific gravity and growth, a multiple-population breeding strategy may be considered as an alternative to simultaneous improvement within a single population. Differentiated 'breeds' may be used for different end products or even for different categories of site.

Progeny testing is actually not necessary for traits as highly inherited as wood properties. Just selecting the individuals with the most desirable wood properties would suffice. Since selection for wood properties is generally combined with selection for other properties, such as growth rate, form, and disease resistance, progeny tests will be available anyway, and thus one only has to evaluate the best individuals already selected for other reasons. The age of testing is another major consideration. Since juvenile and mature wood properties are highly correlated, early selection is desirable. Another possibility is to use selection for wood properties in a stepwise screening program, where trees are evaluated first for the traits that can be measured easily and cheaply and are subsequently tested for properties that are progressively more expensive to determine.

Breeding for Wood Specific Gravity

A main consideration when breeding for wood specific gravity is whether wood specific gravity is a main objective or a secondary trait. Most breeding programs opt for the second alternative. One needs to consider, however, that it has a high economic worth, and the fact that an increase in quality generally means higher economic returns than increases in yield. Specific gravity should therefore be a high priority. An additional attractive feature of high wood specific gravity is that in the production of pulp and paper it allows a better combination of tensile strength and tear factor, which is desirable for some products such as multiwall sack paper. The economic effect of per-hectare fiber yield can vary according to the ownership. Since the weight of the green wood is not affected by wood specific gravity and pulpwood is often sold by weight, there is little incentive for a small private landowner to increase wood specific gravity. On the other hand, a company that grows wood on its own holdings has several incentives: increased dry matter production, increased quality, and reduced transportation cost.

Breeding for Other Wood Properties

This is not often done, because they are more expensive to evaluate and often less important. Tracheid length and microfibril angle are the two traits sometimes considered. However, owing to recently developed methods for high-throughput analysis of wood properties the situation is rapidly changing. There is an increased interest in microfibril angle, because of its effect on wood stiffness and pulp properties. Many chemical properties can be determined by the same methods as well.

Chemical properties can also be modified indirectly through improvement in stem straightness and branch size. This results in a reduction in reaction wood, which in conifers reduces lignin content and microfibril angle.

How Are Genetic Gains Obtained Operationally?

There are two major approaches: the seed orchard approach and clonal forestry. The seed orchard approach involves selecting the best individuals, grafting them in seed orchards, progeny testing the orchard to remove the less desirable clones and providing a new generation to select in. Operational plantations are generated from the seed produced by the orchards.

Clonal forestry depends on the availability of efficient vegetative propagation methods, usually rooted cuttings, sometimes tissue culture. A few highly selected individuals can than be propagated to reforest substantial acreages. Because of the cost involved this is most economical on the best sites, located close to manufacturing facilities. Because the time to deployment is shortened this method lends itself to tailor-making trees for specific products. For example the Aracruz company in Brazil has achieved rotations of 6 to 7 years with eucalypts. With *Gmelina arborea* 4 year rotations are possible. With blocks of well characterized clones, it is possible to fine-tune processing to the individual clones.

See also: **Genetics and Genetic Resources**: Molecular Biology of Forest Trees. **Papermaking**: Overview; World Paper Industry Overview. **Pulping**: Chemical Pulping; Mechanical Pulping. **Tree Breeding, Practices**: Biological Improvement of Wood Properties. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts. **Wood Formation and Properties**: Formation and Structure of Wood.

Further Reading

Helms JA (ed.) (1998) *The Dictionary of Forestry*. Bethesda, MD: Society of American Foresters.

Tuskan GA, West D, Bradshaw HD, *et al.* (1999) Two high-throughput techniques for determining wood properties as part of a molecular genetics analysis of loblolly pine and hybrid poplar. *Applied Biochemistry and Biotechnology* 77–79: 1–11.

Zobel BJ and Jett JB (1995) *Genetics of Wood Production*. New York: Springer-Verlag.

Zobel BJ and Sprague JR (1998) *Juvenile Wood in Forest Trees*. New York: Springer-Verlag.

Zobel BJ and Talbert J (1984) *Applied Forest Tree Improvement*. New York: John Wiley.

Zobel BJ and van Buijtenen JP (1989) *Wood Variation: Its Causes and Control*. New York: Springer-Verlag.

Zobel BJ, van Wyk G, and Stahl P (1987) *Growing Exotic Forests*. New York: John Wiley.

Breeding for Disease and Insect Resistance

B B Kinloch, Institute of Forest Genetics, Berkeley, CA, USA

Introduction

Pest resistance historically has been the single most important trait in crop breeding, reflecting the vast number of biotic agents that challenge domesticated plants. The number of diseases and insects that afflict forest trees may be even greater than their agricultural counterparts, but no comparable investment to combat them has been made, in spite of the fact that some forest trees have been victims of some of the most spectacular and disastrous epidemics known. Virtual elimination of American chestnut to chestnut blight and extirpation of large populations of American and European species of elm to Dutch elm disease, and white pines to white pine blister rust are textbook examples, as are the depredations of gypsy moth on North American hardwoods. Other important epidemics that started in the last century, some recently, include dogwood anthracnose, butternut canker, Port-Orford cedar root rot, pitch canker of pines, sudden oak death in North America, and the pinewood nematode in Japan. Almost all, of course, are the result of introduced pests. More will undoubtedly follow.

Exotic pests have caused immense economic and ecological damage, and, with few exceptions, are the only ones that merit serious attention. A few pathosystems that exhibit properties of both endemic and exotic diseases are often disturbed, or 'degenerate,' as a result of human intervention (for example, offsite planting, narrow genetic base, dysgenic selection). The same applies to insect pests. The far greater number of endemic forest pests has been regulated by natural selection over epochs of mutual adaptation through coevolution with their hosts.

While much basic understanding of pest resistance and breeding strategies have come from agronomic crops, distinctive properties of tree populations make the former incomplete models. The most important of these properties is the extension of trees in space and time. This has several important biological and practical consequences, especially for disease resistance. Great size projects a tree's parts into different microenvironments above and below ground, providing diversity of niches and habitats, while great longevity provides a perennial source of energy for different forest organisms, including pathogens and predators. Ontogenetic changes occur in morphology, physiology, and susceptibility to pests. Extension also imposes great logistical constraints to the breeder in time required for trees to reach sexual maturity, as well as access to flowers high in the crown. Great diversity (heterozygosity) of wild tree populations provides an abundant resource of variability, but is accompanied by high genetic load and inbreeding depression. This inhibits use of conventional agronomic breeding tools of selfing and backcrossing, complicating analysis of heritable traits, including resistance.

Mechanisms and Inheritance of Resistance

In comparison with crop pathosystems, relatively little is known about mechanisms and inheritance of resistance in trees to specific pests, especially insects, but several general characteristics are shared, such as hypersensitivity, partial resistance, ontogenetic (age-related) resistance, and tolerance. Morphological traits (e.g., leaf toughness, bark or cuticle thickness, trichomes, hairs) that impede pest feeding or ingress, or phenological traits that put host tissues out of synchrony with the life cycle of the pest are particularly important in host–insect interactions. Constitutive products of secondary metabolism (e.g., phenolics, tannins, monoterpenes) protect against herbivory. Behavioral characteristics (e.g., host preference, apparency, predator attraction) add a dimension of complexity to insect–tree interactions.

Genetic resistance is conditional: it depends as much on the genotype of the pathogen as it does on that of the host. The same is true of pathogen virulence and aggressiveness. Although emphasis is most often placed on host resistance, as if it were independent of the pathogen, it is the interaction phenotype that is inherited, and this is a property of both symbionts. This is made especially clear in gene-for-gene systems.

Hypersensitive reactions (HR) are often controlled by single, dominant, major resistance genes (R genes) in gene-for-gene systems. These systems exhibit precise specificity between interacting gene loci of host and pathogen, in which the resistant interaction phenotype is conditioned by an R allele in the host and a complementary allele for avirulence (AVR) in the pathogen. R alleles function in pathogen recognition and activation of host defenses, often leading to HR. HR causes necrosis in host cells immediately surrounding the lesion, effectively arresting further pathogenesis. The outcome is virtual immunity for the host. Virulence (vR) alleles function to avoid or suppress this recognition, thus genetically restoring a compatible (i.e., susceptible) interaction phenotype. R genes can impose intense selection pressure on pathogen vR genes, which may cause them to increase exponentially in frequency until the usefulness of the R genes deployed in the host population is nullified. However, except when selected for by R genes, vR genes are thought to be less fit than AVR genes, which may explain why they do not become fixed in natural pathosystems. HR and R genes are more likely to be found in specialized, biotrophic pathosystems, such as leaf rusts of poplars and stem rusts of pine. HR is also common in tree–insect interactions, but the genetic basis has not been determined.

Partial resistance (PR), as the name implies, restrains pathogen development and/or reproduction without entirely excluding disease. Epidemiologically, PR functions to reduce the rate of infection, and has often assumed names more descriptive of particular kinds of diseases (e.g., 'slow rusting,' 'slow mildewing'). The degree of protection PR affords ranges widely, but can be highly effective in ensuring survival and mitigating damage. It is usually more complexly inherited than major gene resistance (MGR), and may involve several to many genes. Although much less dramatic than MGR, resistance conferred by PR is likely to be more stable, because it is not vulnerable to pathogen races with specific virulence to it. MGR and PR can exist together and act synergistically.

Ontogenetic resistance (OGR) and tolerance are the least understood mechanisms, but may be the most widespread and important in regulating forest diseases and predators in natural ecosystems. These two mechanisms may represent the greatest contrasts with annual plants in disease interactions. OGR is resistance that increases with age (occasionally decreases, but not to be confused with senescence). It has both a seasonal component, similar to annuals, wherein tissues become morphologically or physiologically less susceptible to pathogenesis or herbivory, and a perennial component that extends over the tree's lifetime. Tolerance implies the ability of a tree to survive, grow, and reproduce despite harboring the pest. Although conceptually clear, it is often difficult in practice to separate tolerance from low levels of resistance.

Unique to woody perennials is the inherent capacity to create barriers that wall off and compartmentalize invading pathogens in living sapwood. Upon injury, parenchyma tissues in rays react, synthesizing phenolic and other toxic compounds that discolor wood in a zone surrounding the site of infection and confine spread of invading microorganisms to the limits of the reaction zone. Trees also protect living bark from injury from abiotic or biotic origin by formation of a nonsuberized impervious layer of cells in phloem and cortex tissues at the site of the lesion, temporarily isolating invaders from water and nutrients. Necrophyllactic periderms are then laid down behind the injury site which seal the wound. Although both of these reactions are nonspecific, reaction rates are genetically determined and amenable to selection.

General Considerations

Because tree breeding is expensive, there must be a clear economic benefit to justify a program. Usually, only pests of severe epidemic potential will justify the effort, and these are usually ones that have been introduced to a susceptible host population (or vice versa), although in some circumstances, such as widespread off-site planting, dysgenic selection, or crowded monocultures, endemic pests can become epidemic.

There should be some indication that selection and breeding for resistance to the pest will work. Addressing some of the following questions should assist in making a determination:

1. Is there a pattern of infection? Natural stands under strong epidemic pressure from the pest may reveal resistant phenotypes that are unlikely to be chance escapes. Provenance or family trials in established plantations may also show clear genetic differences that can be exploited.
2. Is there an efficient screening technique in place to evaluate candidate parental genotypes? Criteria for resistance should be clear, and expression of the traits selected for unambiguous. Most important, if artificial inoculation/infestation techniques are used, results should be consistent with field performance throughout the length of the rotation.
3. Is the pest more or less specialized in its host range? Usually, there are better chances of finding host genetic variation in resistance to specialists than generalists, and to biotrophs than heterotrophs.
4. Do exotic relatives of the host exist, especially at the pest's gene center, with resistance to the same or related pest? These may be able to be used as resistance donors in interspecific hybridization and backcross breeding.
5. How well is the genetic structure of the pest population known, both in its places of origin and introduction? Is its breeding behavior predominantly outcrossing or inbreeding (or clonal)? The amount of diversity and its potential for recombination will suggest the level of risk to races of wider virulence.

The goal of selection and breeding should always be for durable resistance. R genes, while highly effective in the short term, can be completely overcome by virulence genes with the appropriate specificity. Developing pyramids ('stacking') of different R genes in breeding lines, or buffering MGR with PR, are alternative breeding strategies to prevent or dampen exponential increases in pathogen virulence frequencies.

As detailed an understanding as possible of mechanisms and inheritance of resistance/virulence will always assist in making gene deployment strategies more effective. Nevertheless, resistance can still be used without such knowledge.

A clear distinction must be kept between breeding for production and for information. For example, if it is deemed necessary to understand the inheritance of resistance mechanisms, strict genetic control of both inoculum source and host material must be exercised in an appropriate mating design. If on the other hand the objective is simply to 'pick the winners' with as broad a base of resistance possible, bulk inoculum from throughout the range of intended deployment is more appropriate for screening candidates.

Maintaining as broad a genetic base as possible is probably the most essential requirement of any breeding program. Selection, by definition, narrows the genetic base. But sufficient diversity in either program breeding or archival populations is necessary as a hedge against the risk of new pests arising, or races of the same one with wider virulence. How much diversity is enough is a difficult and controversial issue, and will depend on the specific circumstances. Gene frequencies for resistance to exotic pests can be extremely rare, as for example those that confer resistance to white pine blister rust and root rot of Port-Orford cedar in North America. In such situations, availability of large, wild populations are the best solution, especially if natural selection is being imposed by the pest.

Examples of Active Resistance Breeding Programs

Table 1 lists seven major forest tree disease or insect epidemics that have motivated breeding programs. These include canker diseases, a vascular wilt,

Table 1 Examples of major pests with active breeding programs

Disease/pest	*Host*	*Pathogen/pest*	*Type of disease*	*Origin*	*Type of resistance (parameter)*
Chestnut blight	*Castanea dentata*	*Cryphonectria parasitica*	Canker	Exotic	PR (canker size)
Dutch elm disease	*Ulmus americana*	*Ophiostoma ulmi*, *O. novo-ulmi*	Vascular wilt	Exotic	Tolerance (% crown damage)
White pine blister rust	*Pinus* (subsect. *Strobi*)	*Cronartium ribicola*	Canker	Exotic	MGR, PR (infection frequency; canker abortion, size)
Leaf rusts	*Populus, Salix*	*Melampsora* spp.	Leaf rust	Exotic, Indigenous	MGR, PR (slow rusting)
Fusiform rust	*Pinus taeda*, *P. elliottii*	*Cronartium quercuum* f.sp. *fusiforme*	Canker	Indigenous (degenerate)	MGR, PR (% infection, canker size)
Port-Orford cedar root rot	*Chamaecyparis lawsonia*	*Phytophthora lateralis*	Root rot	Exotic	MGR?
White pine weevil	*Picea sitchensis*, *P. glauca*	*Pissodes strobi*	Shoot feeder	Exotic, indigenous	PR (% infested)

foliage rusts, a root rot, and a shoot-feeding insect. Thumbnail sketches of problems and progress in four of these follow, illustrating some of the general principles discussed above. Some are also covered in other articles in this volume (*see* **Pathology**: Vascular Wilt Diseases; Leaf and Needle Diseases; Stem Canker Diseases; Pine Wilt and the Pine Wood Nematode; Rust Diseases; Insect Associated Tree Diseases).

Chestnut Blight

Chestnut blight is responsible for one of the worst epidemics of trees, if not all plants, in history, having destroyed the dominant species (*Castanea dentata*) of an entire ecosystem that reached from Maine to Georgia. Caused by *Cryphonectria parasitica*, introduced from Asia, the disease also severely impacted European chestnuts (*Castanea sativa*). After a century of frustrated efforts, the biological tools and knowledge seem to be in place to make restoration of the American chestnut a real possibility. Critical elements consist of high crossability of American chestnut with Asian congeners; simple inheritance of effective partial resistance; a reliable and consistent screening technique; and sexual precocity enabling short intervals (5–6 years) between breeding cycles. It will nevertheless be a long-term endeavor.

No silviculturally useful variation in resistance was found in native chestnut stands, and early breeding efforts sought to exploit the inherent resistance of chestnuts from Asia, where the disease is endemic. The Chinese chestnut (*C. mollissima*), the most wide-ranging and resistant species, was used as the principal source of resistance. Although significant resistance was observed in F_1 hybrids in early trials, it was not adequate for deployment. Further backcrossing to the Chinese parent could increase resistance, but only exacerbate the problem of undesirable growth and form inherited from the Chinese parent.

However, early analysis of certain F_1 and backcross progenies suggested the possibility of relatively simply inherited resistance. Subsequent quantitative trail loci (QTL) mapping with molecular markers of progeny of an F_2 cross confirmed this, and indicated the presence of two or three partially dominant, independently inherited genes responsible for the phenotypic resistance observed. Resistance was expressed as a marked reduction in canker growth rate following artificial inoculation of stem bark with defined cultures of the pathogen. Now the stage was set for a new breeding approach: backcrossing could be done on the recurrent susceptible American parent, to introgress the few genes for resistance from the *C. mollissima* donor, while continually purging remaining Chinese background genes affecting the desired American phenotype. After three backcross (BC) generations from the F_1, only one-sixteenth of the genome, on average, remains Chinese. Each BC generation is screened in field inoculations, using uniform blight cultures placed in drill holes in the bark. Partial resistance is measured by the area of canker expansion after 9–11 months. After the most resistant offspring are selected in each round, a final cross between two BC3 trees ('BC3 F_2s') with partial resistance should theoretically result in one of 16 trees having two copies of both resistance genes, making them as resistant as the Chinese parents in their pedigree.

Diversity for local adaptation will be provided by including at least 20 different American parents in the BC3 breeding population for any given area. This model, currently being tested and implemented in Virginia, could eventually be applied to a large portion of American chestnut's range. It would involve pollinating American chestnut flowers on sprouting stumps in the wild to produce F_1 seed before they become lethally infected.

Dutch Elm Disease

The impact of Dutch elm disease on American elms has been almost as severe as chestnut blight on American chestnut, and has affected many more species worldwide. It is a more difficult and insidious disease to deal with, because of its complexity. It is a systemic vascular wilt, caused by a species complex of at least two fungal pathogens (*Ophiostoma ulmi*, *O. novo-ulmi*) from uncertain origin in Asia, each with different races spanning a wide range of virulence; it has a saprophytic stage, extending survival of the fungus beyond the disease cycle; it is vectored by several different species of elm bark beetles (Scolytidae), with all the problems of host preference, resistance, and environmental interactions that they entail; and resistance mechanisms and inheritance are difficult to assess and interpret. It is a breeder's nightmare, and were it not for the extremely high aesthetic and amenity value of some elm species for urban and landscape forestry, the nearly century-long effort to develop resistance might never have been attempted. Success has been elusive in both North America and Europe, yet some significant progress has been made.

The American elm (*Ulmus americana*) is the most susceptible of over 40 species in the genus, and over 40 million trees are estimated to have been killed by the disease, including 70% of landscape elms. Sources of resistance are abundant in Asia, especially in populations of *U. pumilla*, *U. parviflora*, and *U. japonica*. However, the relative ease with which resistance genes can be introgressed from Asian chestnuts into American chestnut does not apply to the corresponding elms, because *U. americana* is tetraploid, resulting in severe barriers to breeding with potential Asian donors. Additionally, Asian species tend to be highly susceptible to other diseases and insects, can be climatically maladapted, and generally lack the irreplaceable vaselike architecture that defines American elm. Nevertheless, a few promising *U. parviflora* × *U. americana* hybrids have been made in the University of Wisconsin program that seem to combine resistance traits of the Asian parent with morphological features of the American. Many more such hybrids from diverse sources will be needed for a successful breeding program, but these results are encouraging.

Like the experience with chestnut blight, early selection and testing of American elm were disappointing. Of many thousands of candidate phenotypes tested, only a handful survived for further breeding. These are usually referred to as having tolerance, rather than resistance, and perhaps only 1 in 100 000 American elms have this in useful amounts. To efficiently screen selections, the University of Wisconsin program uses artificially inoculated seedlings or rooted cuttings and measures the volume of discoloration in stems as an index of relative tolerance. Seedlings with less than 50% discoloration, with or without foliar symptoms, usually correlate well with field performance. The criterion for acceptable tolerance in the field was $<20\%$ crown damage. A few long-term survivors, intercrossed with each other and susceptible controls, have produced up to 50% of offspring with less than 20% crown damage after 1 year in the field. Recent results of tests conducted by the National Arboretum showed the ability of a few earlier as well as new selections to respond and then recover from heavy artificial inoculation in the field, equaling performance of some non-American tolerant clones. This suggests that extended evaluation of candidates in the field may be more rewarding in the long term than relying completely on artificial inoculation.

White Pine Blister Rust

The nine white pine species native to North America are highly susceptible to blister rust, and most have been severely damaged in parts of their native range since the disease was introduced over a century ago. All species have important ecological functions, but breeding has been focused on the tall timber species, western white pine (*Pinus monticola*) and sugar pine (*P. lambertiana*).

Unlike most other exotic diseases, a surprising number of resistance mechanisms have been found in white pines to blister rust, even though hosts and pathogen have not coevolved. Three general types of resistance are recognized:

1. MGR, causing classic hypersensitive necrosis in needles on challenge by the pathogen. R genes have been found in several white pines, and exist in a gene-for-gene relationship with cognate genes

for avirulence in the rust. Thus, virulence gene *vcr1* in *Cronartium ribicola* neutralizes resistance gene *Cr1* in sugar pine but not *Cr2* in western white pine, and vice versa for *vcr2*. Single recessive genes are also thought to contribute high levels of resistance in western white pine.

2. PR has two main components in white pines: reduced infection frequency, and different kinds of bark reactions that abort infections after they establish in stem tissues. These mechanisms are more complexly inherited, but can still give effective, if incomplete, resistance. Most important, they are not specifically vulnerable to major virulence genes in the rust.
3. OGR is recognized in adult trees that are free of rust when surrounded by heavily infected cohorts, either in natural stands or seed orchards, but which produce highly susceptible offspring. It is genotype specific, and appears to be very strong and stable. OGR would be useful in stabilizing a crop in later parts of a rotation, but is the least understood and probably most difficult of all the mechanisms to develop.

The problem for breeding is how to recognize, concentrate, and deploy these different mechanisms and the genes that control them into synthetic populations to effect durable resistance. Dominant R genes are easy to breed with and confer immunity to all rust biotypes that lack specific virulence to them. But they place severe selection pressure on the rust for these virulent mutants, which are usually rare in natural populations. When this happens, the selected virulence alleles increase exponentially in frequency in the ambient inoculum, nullifying the protection conferred by populations deployed with only R gene resistance. A strategy devised for sugar pine is to prevent or dampen sudden increases in virulence gene frequency by buffering MGR with different PR mechanisms. This is accomplished in a two-stage process. Seedlings are screened first for MGR by artificial inoculation. Those selected are then outplanted in a field location where the frequency of virulence has been maintained at high levels by continuous natural selection from planted MGR. Since MGR is neutralized in this environment, seedlings surviving have both PR and MGR, and by forward selection will constitute the new parental generation when they mature. Concentration of both MGR and PR genes are effected and increased in subsequent generations (**Figures 1–3**).

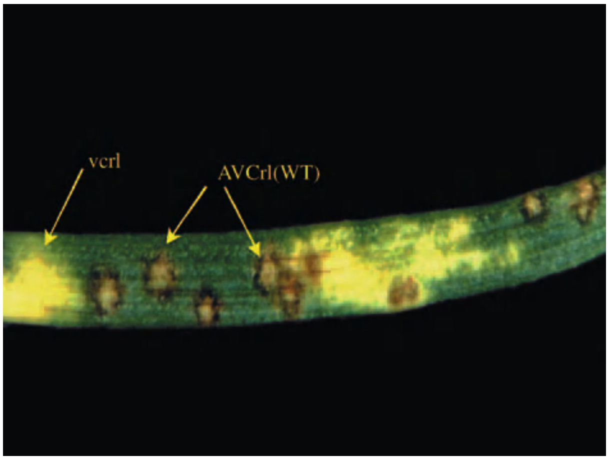


Figure 1 Interaction phenotypes in the white pine–blister rust pathosystem: needle symptoms on sugar pine with the Cr1 gene express as hypersensitive necrotic spots to inoculum carrying avirulence allele AVCr1 (wild type), but as normal yellow spots to inoculum with virulence allele vcr1.

Figure 2 Sugar pine families susceptible and resistant to white pine blister rust in a field trial. The resistant family (far right) has the major gene Cr1 in homozygous condition.

Phytophthora Root Rot of Port-Orford Cedar

Phytophthora lateralis was introduced into western North America from an unknown source over half a century ago, and has since caused widespread mortality in Port-Orford cedar (*Chamaecyparis lawsonia*), a narrow but valuable endemic of northwest California and southwest Oregon. Spread by motile zoospores is rapid and unstoppable – by water coursing through infested stands, or carried by vehicles, people, or animals passing through. Roots are the main infection courts, but foliage can also serve. Environmental variance is high, with low areas being most vulnerable, but root grafts extend infection foci uphill more gradually. The resulting pattern is a mosaic, making assessment of phenotypic resistance ambiguous and difficult.

Figure 3 Partial resistance in sugar pine to white pine blister rust. (a–c) Bark reactions of varying size; (d) low infection frequency. Both trees have Cr1, but have been exposed to natural inoculum with a high frequency of vcr1. b–d reproduced with permission from Kinloch BB Jr. and Davis D (1996) Mechanisms and inheritance of blister rust resistance in sugar pine. In: Kinloch BB Jr., Marosy M, and Huddleston M (eds) *Sugar Pine: Status, Values, and Role in Ecosystems*, pp. 125–132. Davis, CA: University of California, Division of Agriculture and Natural Resources.

Yet, this seemingly intractable problem has recently been overcome by exploiting Port-Orford cedar's unusual reproductive characteristics: precocious flowering (2–4 years) enables rapid turnover of generations compared with other conifers; breeding can be done in containerized orchards in greenhouses; seed is produced abundantly in the same season as pollination; and ease of vegetative propagation by rooted cuttings, even of older trees, permits establishment of ramets of selected candidates, or rapid multiplication of selected progeny genotypes.

Efficient screening is accomplished in two stages. Candidate trees are prescreened by dipping detached branches into zoospore suspensions, then measuring the length of the lesion formed under the bark after a few weeks. The most promising candidates are then rooted, dip inoculated in the same way, planted in nursery beds, and monitored for survival. Most mortality occurs within a year.

The high throughput enabled by these techniques has uncovered rare but highly effective resistance. Although the exact mechanism is not known, progeny of controlled crosses among a few highly selected parents have shown Mendelian segregation of healthy/living : dead offspring, implicating a single dominant gene for resistance. This will greatly facilitate deploying resistant genotypes for restoration of this species. Whether or not the pathogen harbors virulence capable of overcoming this resistance is unknown, but its overall diversity, based on molecular markers, is very low. Partial resistance or tolerance may also be found in the host that could be combined with MGR to mitigate the effect of wider virulence arising. The distribution of MGR is not known, and its rarity could be an impediment to restoring locally adapted, resistant Port-Orford cedar throughout its range. However, the ability to rapidly turnover breeding generations in Port-Orford cedar renders this problem soluble by introgressing nonlocal sources of resistance into local populations through backcrossing.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Entomology**: Bark Beetles; Defoliators; Foliage Feeders in Temperate and Boreal Forests; Population Dynamics of Forest Insects; Sapsuckers. **Pathology**: *Phytophthora* Root Rot of Forest Trees; Diseases of Forest Trees; Insect Associated Tree Diseases; Leaf and Needle Diseases; Pine Wilt and the Pine Wood Nematode; Rust Diseases; Stem Canker Diseases; Vascular Wilt Diseases.

Further Reading

Alfaro RI, Borden JH, King JN, *et al.* (2002) Mechanisms of resistance in conifers against shoot infesting insects. In: Wagner MR, Clancy KM, Lieutier F, and Paine TD (eds) *Mechanisms and Deployment of Resistance in Trees to Insects*, pp. 101–126. London: Kluwer Academic Publishers.

Anagnostakis SL (1999) Chestnut research in Connecticut: breeding and biological control. *Acta Horticulturae* 494: 391–394.

Bingham RT (1983) *Blister Rust Resistant Western White Pine for the Inland Empire: The Story of the First 25 Years of the Research and Development Program*. US Department of Agriculture Forest Service General Technical Report no. INT-146. Ogden, UT: US Department of Agriculture, Intermountain Forest and Range Experiment Station.

Brasier CM (2001) Rapid evolution of introduced plant pathogens via interspecific hybridization. *BioScience* 51: 123–133.

Burdon RD (2002) Genetic diversity and disease resistance: some considerations for research, breeding, and deployment. *Canadian Journal of Forest Research* 31: 596–606.

Carson SD and Carson MJ (1989) Breeding for resistance in forest trees: a quantitative genetic approach. *Annual Review of Phytopathology* 27: 373–395.

Crute IR (1997) *The Gene-for-Gene Relationship in Plant–Parasite Interactions*. Oxford, UK: Oxford University Press.

Guries RP and Smalley EB (2000) Once and future elms: classical and molecular approaches to Dutch Elm Disease resistance. In: Dunn CP (ed.) *The Elms: Breeding, Conservation, and Disease Management*, pp. 231–248. Boston, MA: Kluwer Academic Publishers.

Hansen EM and Sutton W (eds) (2000) *Phytophthora Diseases of Forest Trees*, Proceedings from the 1st International Meetings on Phytophthoras in Forest and Wildland Ecosystems. Corvallis, OR: Forest Research Laboratory, Oregon State University.

Heybroek HM, Stephan BR, and Weissenberg K (eds) (1982) *Resistance To Diseases and Pests of Forest Trees*, Proceedings of the 3rd International Workshop on the Genetics of Host–Parasite Interactions in Forestry, Pudoc, Wageningen, The Netherlands.

Kinloch BB Jr. and Davis D (1996) Mechanisms and inheritance of blister rust resistance in sugar pine. In: Kinloch BB Jr., Marosy M, and Huddleston M (eds) *Sugar Pine: Status, Values, and Role in Ecosystems*, pp. 125–132. Davis, CA: University of California, Division of Agriculture and Natural Resources.

Namkoong G (1991) Maintaining genetic diversity in breeding for resistance in forest trees. *Annual Review of Phytopathology* 29: 325–342.

Shigo AL (1984) Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. *Annual Review of Phytopathology* 22: 189–214.

Zobel BJ and Talbert JT (1984) *Applied Forest Tree Improvement*. New York: John Wiley.

Genetic Improvement of Eucalypts

B M Potts, University of Tasmania, Hobart, Tasmania, Australia

Introduction

Eucalypts are virtually endemic to Australia; they are the tallest flowering plants on earth and the most widely grown hardwood plantation species. No sector of world forestry has expanded as rapidly as the industrial use of eucalypts and, while they are still at the early stages of domestication compared with crop species, they are fast becoming amongst the most advanced genetic material in forestry. This article overviews (1) the unique biological features of the genus, including its distribution and taxonomy, breeding systems, and natural regeneration mechanisms; (2) the history of its domestication, from its first discovery in the late eighteenth century, through its rapid dispersal around the world in the nineteenth century to its prominent role in the industrial plantations of the late twentieth century for the pulp and paper markets; (3) the genetic improvement of species, from provenance selection to advanced generation breeding strategies, including definition of breeding objectives and large-scale assessment of key biological traits affecting profitability; (4) the important role played by eucalypt hybrids, particularly in tropical and subtropical zones; (5) deployment options through seed and clonal propagation systems; and (6) progress towards molecular breeding and genetic engineering.

The Genus

Eucalypts are generally long-lived, evergreen hardwood species belonging to the predominantly southern hemisphere, angiosperm family Myrtaceae. They range in habit from shrubs and multistemmed mallees to enormous trees some which include the tallest flowering plants on earth (*Eucalyptus regnans*, up to 96 m). Most species are endemic to Australia but five tropical species are confined to islands north of Australia (e.g., *E. urophylla* and *E. deglupta*). A small group of species also extends outside of Australia into Papua New Guinea (e.g., *E. alba* and *E. tereticornis*). Eucalypts are the dominant species in open forests and woodlands throughout Australia but extend into a great diversity of habitats. They occur naturally from sea level to the alpine treeline, from high rainfall to semi-arid zones, and from the tropics to latitudes as high as 44° S, but they are absent from true arid and rainforest environments in Australia.

In the broad sense, eucalypts include the genera *Eucalyptus, Corymbia,* and *Angophora*. A key feature of the majority of eucalypts is the fusion of either the petals and/or sepals to form an operculum from which the eucalypts derive their name (from a Greek root *eu* – well and *calyptos* – covered). The operculum appears to have evolved independently in different eucalypt lineages and has not evolved in *Angophora*. There is some debate as to whether the *Corymbia* and *Angophora* genera (bloodwood taxa) warrant separation from the genus *Eucalyptus* in the strict sense (non-bloodwood taxa), but this split is supported by several independent DNA studies and is adopted herein. This dichotomy appears to be associated with differences in the structure of raised oil glands (termed bristle glands), wood properties (the bloodwood lineage for example only has solitary vessels in the xylem), leaf venation, and ovule arrangement. The latest taxonomic revision of the eucalypts recognizes just over 700 species that belong to 13 main evolutionary lineages (**Table 1**) but still treats the bloodwood eucalypts as subgenera of *Eucalyptus*. Most species belong to the subgenus *Symphyomyrtus*, and it is mainly species from three sections of this subgenus that are used in plantation forestry.

Eucalypts have several noteworthy biological features. Many species are heteroblastic, with leaves changing from a sessile, horizontally orientated juvenile form to a petiolate, vertically orientated adult form. This is also accompanied by changes in leaf anatomy, physiology, and chemistry. The timing of this heteroblastic transition is under strong genetic control and susceptibility to many pests is dependent upon the leaf type present in the canopy. Eucalypts also have well-developed mechanisms for vegetative recovery from defoliation arising from factors such as fire, drought, frost, or herbivory. The bark often protects numerous dormant vegetative buds that sprout to form epicormic shoots after defoliation. If the whole stem is killed by, for example fire, many species also have the possibility of resprouting from lignotubers. Lignotubers are organs that develop as swellings in the axils of the cotyledonary and early seedling nodes and comprise a mass of vegetative buds, vascular tissue, and food reserves. They usually become buried and allow the plant to regenerate after the death of the main stem. Epicormic or coppice shoots exhibit varying degrees of reversion to the juvenile leaf form. Other vegetative regeneration mechanisms such as rhizomes or root suckering have been reported in *Corymbia*. Regeneration usually occurs by seed that is stored in woody capsules, 5–30 mm in diameter, and often held on the

Table 1 Major evolutionary lineages[a] within the eucalypts

Pryor and Johnson's subgenera/genera	*Brooker's subgenera*	*Number of species*	*Examples of well-known forestry species*
Angophora (genus)	*Angophora*	7	
Blakella	*Blakella*	15	
Corymbia	*Corymbia*	67	*C. torelliana*, *C. citridora*, *C. maculata*
Eudesmia	*Eudesmia*	19	
Gaubaea	*Acerosa*	1	
Gaubaea	*Cuboidea*	1	
Idiogenes	*Idiogenes*	1	*E. cloeziana*
Monocalyptus	*Primitiva*	1	
Monocalyptus	*Eucalyptus*	110	*E. regnans*, *E. delegatensis*, *E. obliqua*, *E. marginata*, *E. fastigata*
Symphyomyrtus	*Cruciformes*	1	*E. guilfoylei*
Symphyomyrtus	*Alveolata*	1	*E. microcorys*
Symphyomyrtus	*Symphyomyrtus*	474	*E. camaldulensis*, *E. exserta*, *E. globulus*, *E. grandis*, *E. nitens*, *E. paniculata*, *E. robusta*, *E. saligna*, *E. tereticornis*, *E. urophylla*, *E. viminalis*
Telocalyptus	*Minutifructus*	4	*E. deglupta*

[a]The alignment of Pryor and Johnson's (1971) genera and subgenera with Brooker's (2000) subgenera. Pryor and Johnson's classification was informal, but widely used for 30 years. The number of species in each of Brooker's subgenera is indicated and examples of well-known forestry species are given. The subgenera *Blakella* and *Corymbia* had previously been treated as a separate genus *Corymbia* Hill and Johnson (Hill and Johnson 1995) and the subgenus *Angophora* treated as a genus and this treatment has been adopted in the text.

Sources: Pryor LD and Johnson LAS (1971) *A Classification of the Eucalypts*. Canberra: Australian National University Press; Brooker MIH (2000) A new classification of the genus *Eucalyptus* L'Her. (Myrtaceae). *Australian Systematic Botany* 13: 79–148; Hill KD and Johnson LAS (1995) Systematic studies in the eucalypts 7. A revision of the bloodwoods, genus *Corymbia* (Myrtaceae). *Telopea* 6: 185–504.

tree for several years. In good years, large numbers of seed are shed, particularly following wildfire. The seeds generally have no special adaptation for dispersal and, with the exception of a few cases of water dispersal (e.g., *E. camaldulensis*), seed dispersal is mainly by wind and normally occurs over short distances. Eucalypt seed is short-lived in the soil seed bank.

Eucalypt flowers are occasionally solitary (e.g., *E. globulus*), but often occur in clusters of three or more in umbels (**Figure 1**) or terminal inflorescences. The eucalypt flower is normally bisexual, with numerous stamens that expand outwards after the operculum is shed to form the conspicuous floral display. Eucalypts are predominantly animal-pollinated, with vectors encompassing a wide variety of insects, birds, and marsupials, and a few bat species. They have a mixed mating system, but are generally preferential outcrossers, with high levels of outcrossing maintained by protandry and various incomplete pre- and postzygotic barriers to self-fertilization. The postzygotic barriers include intense selection against the products of inbreeding. For example, inbreeding depression for growth in selfed *E. globulus* is nearly 50%, and this is quite typical. Consistent with most myrtaceous genera, eucalypts are diploids with virtually all having a chromosome

Figure 1 Flowers and flower buds of *Eucalyptus nitens*. *Eucalyptus nitens* bears its flowers in umbels of up to seven flowers. The figure shows buds just about to shed their inner operculum and those from which the operculum has been shed. In this group of eucalypts, the inner operculum is derived from fused petals and shed just before the anthers expand and shed pollen. The outer operculum is derived from the fused sepals and is shed early in bud development. The stigma of this species becomes receptive 5–7 days after operculum shed, at a stage when most pollen has been released from the anthers. Photograph courtesy of Dean Williams.

number of $2n=22$. While the major eucalypt subgenera do not hybridize, reproductive barriers between species within subgenera are often weak. Hybridization and intergradation between recognized taxa are common in nature, often making delineation of species difficult. Many artificial hybrid combinations have been produced. In general, hybrid inviability tends to increase with increasing taxonomic distance between the parents, but there are exceptions.

History of Domestication

Eucalypts are the most planted hardwood trees in the world. Following their discovery in the late eighteenth century, they were spread rapidly around the world and were early introduced into countries such as India (*c.* 1790), France (*c.* 1804), Chile (1823), Brazil (1825), South Africa (1828), and Portugal (1829). Initially they were introduced as botanical curiosities but, as the potential for some species to grow fast was quickly recognized, they were grown for windbreaks, land reclamation, and leaf-oil production, but mainly for fuel wood and timber production. Plantations were established, for example, to provide railway crossties and fuel for wood-burning locomotives in Brazil and South Africa, mine props in Chile and South Africa, and charcoal in Brazil for iron and steel production. One factor causing their rapid early spread appears to be the belief that growing eucalypts could banish diseases such as malaria, and they became known as 'fever gums' in the latter half of the nineteenth century.

Eucalypts became renowned for species with fast growth, straight form, valuable wood properties, wide adaptability to soils and climates, and ease of management through coppicing. They are now found in more than 90 countries where the various species are grown for products as diverse as sawn timber, mine props, poles, firewood, pulp, charcoal, essential oils, honey, and tannin as well as for shade, shelter, and soil reclamation. The exotic eucalypts became an important source of fuel and building material in rural communities in countries such as India, China, Ethiopia, Peru, and Vietnam. However, it was the great global demand for short-fiber pulp that drove the massive expansion of eucalypt plantations throughout the world during the twentieth century. Their high fiber count relative to other wood components, coupled with the uniformity of fibers relative to other angiosperm species, has caused high demand for eucalypt pulp for coated and uncoated free-sheet paper, bleach board, sanitary products (fluff pulp), and secondarily for top liner on cardboard boxes, corrugating medium, and as a filler in long-fiber conifer products such as newsprint and containerboard. New technologies are also increasing interest in the use of plantation eucalypts for sawnwood, veneer, medium density fiberboard, and as extenders in plastic and molded timber.

No sector of world forestry has expanded as rapidly as the industrial use of eucalypts. While precise global figures are difficult to obtain, it is estimated there were 9.5 million ha of industrial eucalypt plantations in the world in 1999 (**Table 2**), with the vast majority of these established since the 1950s. This area is predicted to reach 11.6 million ha in 2010 (**Table 2**). Other less conservative global estimates suggest that there were nearly 16 million ha of general eucalypt plantations by the 1990s which would reach 20 million ha by 2010. These figures compare with the estimated 30 million ha of tall (>30 m tall) and 240 million ha of open (10–30 m tall) native eucalypt forest in Australia in 2001. The majority of plantations consist of only a few eucalypt species and hybrids. The most important plantation eucalypts around the world are *E. grandis, E. globulus,* and *E. camaldulensis*, which together with their hybrids account for about 80% of the plantation area; these are followed by *E. nitens, E. saligna, E. deglupta, E. urophylla, E. pilularis, Corymbia citriodora*, and *E. tereticornis*. In the case of pulpwood, the market favorites are *E. grandis, E. urophylla*, and their hybrids in tropical and subtropical regions and *E. globulus* in temperate regions. However, eucalypt plantations of the traditional pulpwood species as well as other species (e.g., *C. citriodora, C. maculata, E. cloeziana*, and *E. nitens*) are increasingly being managed for solidwood production. While there are reports of eucalypt plantations achieving growth rates of over $60\,m^3\,ha^{-1}\,year^{-1}$, with intensive management, typical growth rates reported for the *E. grandis* plantations in Brazil and South Africa are $40\,m^3\,ha^{-1}\,year^{-1}$ with a harvest age of 6–8 years,

Table 2 Area of industrial plantations of eucalypts (millions of hectares)

Region	*1999*	*2010*	*Change*
Africa	1.08	1.00	−7%
Asia	2.43	3.20	32%
Europe	1.32	1.40	6%
North and Central America	0.08	0.10	30%
South America	4.09	5.00	22%
Oceania	0.48	0.90	89%
Total	9.48	11.60	22%

Source: Wood resources international cited in Raga FR (2001) Perspectiva para el eucalipto chileno. In *Developing the Eucalypt of the Future*, IUFRO International Symposium, 10–15 September 2001, pp. 13. Valdivia, Chile: INFOR.

and 20–22 $m^3 ha^{-1} year^{-1}$ for *E. globulus* plantations in Portugal and Chile with a harvest age of 8–10 years. The world average is suggested to be more like 20 $m^3 ha^{-1} year^{-1}$, but it is anticipated that this could reach 25–30 $m^3 ha^{-1} year^{-1}$ in the future with better silviculture and breeding.

Initially, the botanical gardens of southern Europe played a major role in the introduction of eucalypts to other parts of the world, including Africa and South America. Later in the nineteenth century eucalypts were introduced directly from Australia with, for example, large quantities of seed being sent out of Australia by Ferdinand von Mueller, a government botanist and eucalypt specialist. These early introductions were often used as the base to establish large-scale plantings, resulting in narrow, potentially inbred, genetic bases in some cases (e.g., *E. globulus* in South Africa and Ecuador). In other cases, seed for plantation establishment was collected from ornamentals or multispecies plantings, and appears to have contained high frequencies of interspecific hybrids. In the latter case, F_1 generation hybrids may have performed well but subsequent seed collection from these hybrid plantations resulted in F_2 and subsequent generations with poor growth and form as well as extreme variation (e.g., those derived from the Rio Claro *E. urophylla* hybrids in Brazil 'Brazil alba,' or Mysore *E. tereticornis* hybrid in India). In many countries where eucalypts have been introduced for a long time and continually reproduced from local seed sources, they have formed landraces that are adapted to the specific environment of the country. However, there are many examples where the initial use of a limited sample of the genetic diversity in the native gene pools, the use of suboptimal provenances, inbreeding, or hybrid breakdown have led to landraces being outperformed in field trials by seedlots from some native-stand provenance collections (e.g., *E. globulus* in Argentina, *E. grandis* in South Africa). The planting of suboptimal germplasm is particularly problematic in rural communities where seed obtained for new plantings has been collected with no or only little phenotypic selection from local plantings, generation after generation. In a few cases, where more active breeding has occurred the local landrace has outperformed newly imported native stand seedlots (e.g., *E. grandis* in Florida).

Some of the earliest breeding of eucalypts was undertaken by French foresters in Morocco in 1954–1955. Coincident with the increasing interest in industrial plantations of eucalypts, the 1960s saw a more formal approach to genetic improvement with, for example, the commencement of the Florida *E. grandis* breeding program in 1961, *E. globulus* breeding in Portugal in 1965, and establishment of large provenance tests of *E. camaldulensis* in many countries. Major advances in domestication of the genus occurred in the 1970s with, for example, the first commercial plantings of selected clones derived from hardwood cuttings at Pointe Noir in the Congo followed by Aracruz in Brazil (many of which were spontaneous hybrids), and the establishment in many countries of the first large base-population trials of species such as *E. urophylla* and *E. globulus*. These trials were established from open-pollinated seedlots collected from range-wide provenance collections and formed the bases for deployment and breeding populations in many countries. Many other major international base-population trials were established through the 1980s for species such as *E. grandis, E. tereticornis*, and *E. viminalis*, and using more intensive collections of elite provenances identified in earlier collections.

While eucalypts are still at the early stages of domestication compared to crop species, they are fast becoming amongst the most advanced genetic material in forestry, with stock originating from the *E. grandis* program in Florida already in its sixth generation. In Brazil, around 500 000 ha of plantation were apparently established with 'Brazil alba' seed between 1940 and 1970 before it was realized that the quality of the new plantations was much inferior to earlier plantations and *E. grandis* due to hybrid breakdown. The company Aracruz Celulose S.A. has subsequently doubled yields from its Brazilian plantations through species and provenance selection, breeding, and the use of proven clones. Domestication of eucalypts has proceeded faster in countries like Brazil that rely on plantations for their eucalypt wood than in Australia, where up until the 1990s wood products of eucalypts were derived almost entirely from native forests. However, major provenance trials of species such as *E. regnans, E. delegatensis, E. globulus*, and *E. nitens* were established in Australia in the late 1970s, and major breeding programs for *E. globulus* and *E. nitens* were started in the 1980s.

Species Improvement

A key feature of eucalypt species is the great diversity of the native gene pools. Large, genetic differences between provenances are the rule rather than the exception. In some cases, provenances of a single species may vary from tall forest forms to small trees and even shrubs when grown in common environment trials (e.g., *E. globulus*). This diversity may occur for all traits of interest to breeders such as growth and survival, pest resistance, and wood properties, as well as flowering season and precocity. Such provenance variation makes it important that, firstly, species-elimination trials are based on adequate provenance representation and, secondly, when establishing base populations for breeding the full range of genetic diversity is assessed. This is further complicated by the large provenance × environment interactions that have been revealed in multisite field trials of species such as *E. camaldulensis, E. deglupta, E. delegatensis, E. nitens, E. urophylla*, and *E. viminalis*. Increasing information is available for environmental matching of species and provenances to sites through comparison of local environmental profiles with native ranges in Australia as well as exotic environments where they have been successfully grown. However, a traditional approach for formation of base populations for breeding has been the establishment of large rangewide provenance trials, supplemented with more intensive collection from elite provenances in a second stage. While early provenance trials pooled individual-tree seedlots, later trials have tended to maintain family identity to allow better pedigree control and conversion of trials to seed orchards. Increasing international exchange of eucalypt germplasm amongst breeding programs now means that base populations are comprising not only seedlots from native stand collections in Australia but also material from landraces and more advanced breeding programs.

A focus of eucalypt breeding in recent years has been the clear definition of breeding objectives and identification of relevant selection traits. Major developments were made in the 1990s in clarifying breeding objectives for kraft and mechanical pulpwood production using eucalypt wood. Wood density, pulp yield, and volume per hectare were identified as the key biological traits influencing the economics of pulpwood production. Economic weights have been determined to allow estimation of total breeding value in terms of monetary value to the industry sector. Wood density and pulp yield were rarely considered in earlier selection programs, yet they can account for over 70% of the benefits from breeding for pulp production. Approaches have now been developed for the quick, cheap, and nondestructive measurement of many key wood properties (e.g., pilodyn, mechanized coring (**Figure 2**) and near-infrared reflectance analysis (NIRA)), allowing their widespread application in breeding programs. Extending such work beyond pulp to paper is the next step. There is increasing work being undertaken on identifying breeding objectives and selection traits for solidwood products; however, this is complicated by the greater range of products involved from sawn timber, composites, and veneer, and changing technologies, as well as the fact that plantations may be required for multiple products through thinning or changes in product pricing.

Figure 2 Coring *Eucalyptus globulus* for wood density assessment using a mechanized coring machine. Photograph courtesy of Carolyn Raymond, Cooperative Research Centre for Sustainable Production Forestry.

The amount of genetic variation and intercorrelation among selection traits in the breeding population has a major effect on genetic progress. The genetic correlation between growth and wood density, for example, is probably slightly adverse in species such as *E. globulus* and *E. nitens*, but estimates are variable ranging from zero to significantly adverse. Most genetic parameters such as heritabilities and genetic correlations published for eucalypts to date refer to the additive genetic variation within provenances and have been calculated based on open-pollinated progeny trials. As eucalypts have a mixed mating system and the male parent is unknown, the accuracy of these genetic parameter estimates is questionable, particularly from native-stand seed collections where outcrossing rates may vary markedly. In *E. globulus*, for example, no correlation has been observed between open-pollinated and control-pollinated breeding value estimates for growth traits, but the correlation is significant for traits of higher heritability such as wood density and disease-resistance traits. The other types of heritability often reported include additive and nonadditive components of genetic variation and are the clonal and family heritability (or repeatabilities of their means). This is a measure of the relative differentiation between genotypes or families and is a measure of the repeatability of performance for clonal or family deployment respectively.

Traditionally, eucalypt breeding has involved open-pollinated breeding strategies using single populations or sublines, possibly coupled with open- or controlled-pollinated nucleus populations of the most elite selections or specialized breeds (**Figure 3**). In programs where clones are deployed, the standard approach has involved progeny testing, and phenotypic or genetic selection of elite genotypes, followed by various stages of selection on cloning potential and clonal elimination trials. Selected clones are frequently used as parents in the subsequent generations. Traditionally, breeding programs have involved discrete generations. However, programs in Australia and Portugal are now implementing a 'rolling front' breeding strategy that has overlapping generations with selection, crossing, and trial planting done each year. This strategy is believed to be more flexible in the face of changing breeding objectives, technologies, resource allocation, and industry reorganization, which are becoming increasingly common. In this scheme, decisions are defined in terms of dynamic rules, where a general objective function guides the

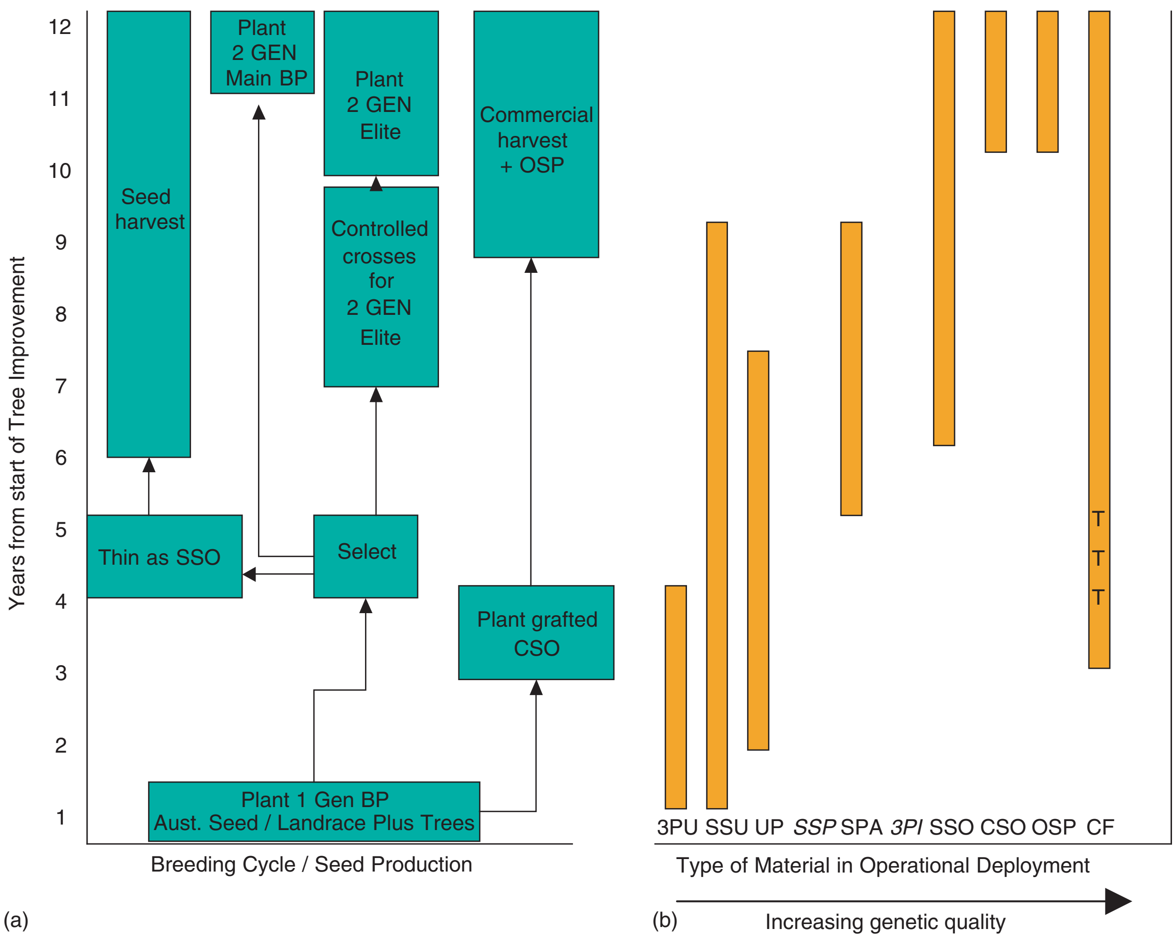


Figure 3 Elapsed time for first generation breeding and take-up of deployment options for *Eucalyptus globulus* in the company Forestal y Agricola Monteaguila S.A. in Chile (year 1 = 1990). (a) The type of genetic material deployed. The breeding population contained two sublines, a large Australian native stand collection and the other the Chilean landrace. The breeding populations (BP) were planted on multiple sites, the majority of the landrace selections from which seed was collected were also grafted and used to develop a clonal seed orchard (CSO) and a mass controlled pollination system based on 'one-stop pollination' (OSP). One site of the Australian subline was converted to a seedling seed orchard (SSO). (b) Planting started with importation of Australian seed (3PU), supplemented by harvests from the best trees in the plantations of the Chilean landrace (SSU). Within 3 years the superiority of the Jeeralang provenance in Australia (UP) was demonstrated and imported native stand seed formed a main component of the plantations established for the next 5 years until SSO and CSO seed came on stream. In 2000, backward and forward selected families from OSP contributed 30% of plantings and was expected to yield 30% volume improvement relative to Jeeralangs (UP). A clonal program (CF; T, test scale) was commenced in 1991, with cloning high rooting, selected families from the landrace and cold tolerant selection and later selections from the first generation breeding population (1GEN BP) trails. Commercial planting started in year 6 and by year 11, 20% of the total planting used clonal stock. Seed stands derived from plantations of selected provenance (SSP) or third party improved seed (3PI) were not utilized. From Griffin AR (2001) Deployment decisions: capturing the benefits of tree improvement with clones and seedlings. In *Developing the Eucalypt of the Future*, IUFRO International Symposium, 10–15 September 2001, pp. 16. Valdivia, Chile: INFOR.

selection and crossing done each year. Such a strategy exploits advances in genetic evaluation through best linear unbiased prediction (BLUP) methodology using individual-tree models that allow for overlapping generations, and complex pedigree- and field-trial structures. The costs of controlled pollination of many eucalypts have now been reduced substantially, through the development of techniques requiring only a single visit as opposed to three visits to the flower. Such reductions in costs have now made controlled crossing of the breeding population viable in species such as the large-flowered *E. globulus*, allowing improved accuracy of genetic evaluation over open-pollination where the male parent is unknown and breeding values could be biased by selfing and nonadditive genetic effects. Other major advances in genetic evaluation have come through improved trial designs such as incomplete-block and row–column designs, as well as including clonal information into evaluation models.

Interspecific Hybridization

Interspecific eucalypt hybrids have been used in forestry for decades and are a significant component of eucalypt plantation forestry, particularly in the tropics and subtropics. While some multiclonal seed orchards are used for F_1 hybrid production, cost-efficient clonal propagation is the key to their successful exploitation. Failures to develop such systems has limited deployment and hence reduced use of many desirable species combinations, particularly in temperate regions.

Clones of *E. urophylla* × *E. grandis* are easy to propagate and are widely planted in Brazil and Congo (**Figure 4**). Most eucalypt hybrids tested or deployed are either F_1s or composites derived from spontaneous hybridization (e.g., 'Brazil alba,' or Mysore hybrid in India) or more recently manipulated F_1 hybrids. The main hybrids used in industrial plantations are *E. grandis* × *E. urophylla, E. grandis* × *E. camaldulensis* (**Figure 5**), and cultivars including at least one of *E. saligna, E. pellita, E. exserta*, and *E. tereticornis*. Such hybrids are planted on a relatively large scale in Brazil and Congo, although sizeable plantations also occur in China, Indonesia, and South Africa. While hybrids are less utilized in more temperate zones, eucalypt hybridization programs involving controlled crossing were undertaken early in countries such as Russia and France, but hybrid development was curtailed by extreme frosts. Such artificial hybridization was undertaken early in temperate Australia, mainly aimed at understanding trait inheritance and the reproductive barriers between species. Hybrid development has focused on F_1 hybrids and has aimed to combine species with complementary attributes. However, as most traits are inherited in a more or less intermediate manner in the F_1s there is increasing interest in backcross and other advanced generation eucalypt hybrids to provide desirable combinations of traits. Some desirable species combinations produce high proportions of inviable/uncompetitive hybrids (e.g., *E. grandis* × *E. globulus, E. camaldulensis* × *E. globulus, E. urophylla* × *E. dunnii, E. dunnii* × *E. grandis*) and the key to hybrid selection appears to be rapid production and testing of large populations and application of high selection intensities. There are also advantages in selecting seed parents for both sexual and vegetative propagation traits.

Figure 4 Clonal plantation of an elite *Eucalyptus urophylla* × *E. grandis* hybrid at Pointe Noire, Congo. Photograph courtesy of Rod Griffin, Shell Forestry.

Deployment

Seedlings

In rural communities outside Australia, eucalypts have historically been propagated from the most accessible seed that is often derived from ornamentals or local plantations, with little attention paid to its

Figure 5 A phenotypically outstanding *Eucalyptus grandis* × *E. camaldulensis* F_1 hybrid in a family trial in Guangxi Dongmen Forest Farm, China. At 10 years the diameter at breast height of this tree was 32 cm compared with the adjacent tree in the foreground that measured only 11.3 cm. Such individuals are damaged at the base to cause coppice shoots that are multiplied by tissue culture to provide sufficient stock plants for production of hardwood cuttings for clonal tests.

Figure 6 Seed production stand of landrace *Eucalyptus globulus* near Lota, Chile after seed-bearing branches were harvested by climbers.

genetic quality. However, seed with varying levels of improvement has been obtained for deployment in industrial plantings from the best native-stand provenances in Australia, seed production areas (**Figure 6**), seed orchards, and more recently, mass controlled or supplementary pollination. The main problem with collection of seed from native stands is that genetic gain, from even the best provenances, may be limited due to varying degrees of inbreeding from selfing or crossing between related individuals which often grow in close proximity in the forest owing to limited seed dispersal. Self-fertilization is particularly a problem when seed is collected from isolated trees. Nevertheless such an approach has been a means of rapidly obtaining genetic gain in plantations during the early stages of domestication (**Figure 3**). Similarly, seed-production areas were often established early by visually thinning even-aged exotic plantations to leave large trees of good form for seed collection in subsequent years (**Figure 6**). While this will avoid the problem of the neighborhood inbreeding that may occur in native forests, it does not avoid problems of inbreeding due to selfing or a narrow genetic base, and genetic gain may also be limited by the low heritability of growth and some tree-form traits.

A large component of improved seed for the main plantation species is now available from open-pollinated seedling or clonal seed orchards established in many countries (**Figure 3**). Seedling seed orchards can be rapidly obtained by thinning pre-established progeny tests based on phenotypic selection, or preferably breeding-value estimates. In species such as *E. globulus*, large genetically based differences in the season and age of flowering may limit outcrossing and the number of effective pollen parents. To improve flowering synchrony, specialized thinning or planting designs are often employed. Higher genetic gains are expected from the more expensive, clonal seed orchards established by either forwards or backwards selection of elite genotypes. Mature scion wood of most commercial eucalypt species can be grafted onto seedling rootstocks using a variety of techniques including bottle-, top-cleft-, patch-, and micrografting, but the success rate is variable at the species and genotype level. Loss of trees due to late-acting graft incompatibility can be a significant cost with such clonal orchards and can be overcome by the use of cuttings or micropropagated clones.

Two major advances have occurred in the production of improved eucalypt seed in the last decade. One was through the discovery that the gibberellin inhibitor paclobutrazol could be used not only to reduce tree growth and allow easier canopy management, but also to enhance flowering. The other advance has been the discovery that the stigma is not necessary for successful pollination and that the pollen will germinate on the surface of the style when it has been cut either just after or even just prior to operculum shed, which often occurs about a week before stigma receptivity. This development has enabled pollination to be undertaken at the same time as emasculation and, coupled with single-flower or style-isolation procedures, has allowed controlled pollination to be undertaken in a single visit to the flower (termed 'single-visit pollination' (SVP) or 'one-stop pollination' (OSP)) (**Figure 7**). The traditional approach involved three visits – emasculation and isolation at operculum shed, pollination at stigma receptivity, and then removal of isolation bags. In the large-flowered species, *E. globulus*, orchards are now established for the manual production of elite full-sib families for deployment using SVP, with or without style isolation and emasculation (**Figure 8**). This approach is also being widely adopted with small-flowered species such as *E. grandis*, for the large-scale production of interspecific hybrids for clonal testing.

Figure 7 One-stop pollination of *Eucalyptus globulus*. (a) Emasculation of the flower just prior to operculum shed before pollen is released; (b) isolation of the style after it has been cut transversely just below the stigma and pollen applied. Photograph courtesy of Dean Williams.

Vegetative Propagation

Industrial-scale clonal propagation of eucalypts is widespread, particularly in the tropics and subtropics. Selected eucalypt clones are now used routinely in countries such as Brazil, Congo (**Figure 4**), Morocco, and South Africa. Most clonal systems use hardwood (ripened-shoot) cuttings. Micropropagation is mainly used to rejuvenate adult material or rapidly bulking up mother plants for hardwood cutting production. Embryogenesis is still in the research stage with eucalypts. Cuttings can be obtained relatively easily from seedlings or from basal coppice of most eucalypts, but the ability of shoots to produce roots rapidly declines with tree age and with a few exceptions (e.g., *E. deglupta*), adult shoots will not root. Maturation usually occurs rapidly and appears to be due to the production of a rooting inhibitor in mature apical or epicormic leaves. However, rejuvenation of shoots from the crown of mature trees is possible through rapid, 'cascade' grafting (including micrografting) on juvenile rootstocks or micropropagation (five to six transfers are usually required). Felling mature

Figure 8 Grafted seed orchard of *Eucalyptus globulus* of Bosques Arauco S.A., Chile. The orchard is being used for the production of controlled cross seed using one-stop pollination procedures similar to those shown in **Figure 7**.

trees will usually result in stumps producing juvenile coppice shoots from which cuttings can be obtained and used to establish mother plants for subsequent harvesting. The rooting potential of cuttings is generally increased in the next phase when shoots are harvested directly from well-maintained mother plants. Rapid multiplication is often achieved by using sequential generations of cuttings for mother plants. Clone banks of mother plants from which basal shoots are regularly harvested are either maintained in containers or in field plots.

Cuttings are usually obtained by dipping stem cuttings of one or two nodes into 1–3% indole butyric acid (IBA) rooting hormone. Rooting is usually obtained within 6–12 days and aided by high humidy (e.g., misting) and bottom heating. However, species vary in their propensity to form well-rooted cuttings and the conditions to achieve their maximum rooting potential, particularly mother-plant environment and handling. Species such as *E. globulus, E. nitens*, and *E. regnans* have a reputation for being difficult to root, whereas *E. camaldulensis, E. deglupta, E. grandis*, and *E. robusta* are easy. Even within species, there is considerable variation between families and genotypes. Genotypes of a species may vary in the proportion of cuttings that root from 0% to 90%. For example, in *E. globulus* only 25% of selections have been reported to root at rates of over 75%. In *E. deglupta*, the mean success is between 85–90%. However, good rooting does not ensure high growth rates and there are many examples of good rooting clones which have below-average growth rates. High rooting ability is essential for the successful exploitation of eucalypt hybrids, and most indications to date suggest that it will be inherited in a predominantly additive manner in most interspecific combinations. For economic production of clones, rooting success greater than 70–80% is usually required, which often results in a large number of individuals initially selected on breeding-objective traits being discarded.

Recent advances in technology for industrial-scale clonal propagation of eucalypts have occurred with the development of intensive micro- and minicutting systems in Brazil. Microcuttings use apices obtained from micropropagated plantlets, while the minicutting is based on the rooting of axillary shoots derived from rooted stem-cuttings. In both systems, field clonal hedges are replaced by intensively managed minihedges grown indoors using hydroponic systems (**Figure 9**). This reduces costs and can also make the propagation cycle less dependent on weather conditions.

Figure 9 Indoor hydroponic, minicutting systems developed at Klabin Riocell, Brazil. Mother plants (left bottom) are grown indoors in hydroponic beds (left top) from where shoots are harvested for minicuttings. Cuttings are set in indoor rooting facilities (right top) and well-rooted cuttings obtained by 30 days (right bottom). Photograph courtesy of Teotônio Francisco de Assis.

Genetic Modification and Molecular Breeding

Development of genetically modified (GM) eucalypts has been slow compared with *Populus* species. Traits being considered for modification are no different from those being examined in other forest tree genera. Most transformation has involved marker genes, although genes of commercial significance including herbicide and insect resistance have been stably inserted. Genetic engineering of sexual sterility has been a major focus of research in Australia where eucalypts are native. Transgenic plantlets have been recovered from species such as *E. grandis, E. camaldulensis, E. globulus, E. saligna, E. urophylla, E. dunnii*, and various hybrids of these species. Field trials were established in the UK in 1995 and in Spain, Portugal, and South Africa in 1997. However, the development of fully tested GM clones to the stage of large-scale planting is likely to be a slow process, taking up to 12 years, and owing to regulatory problems research has, for the moment, shifted more towards molecular breeding through marker- or gene-assisted selection.

The first eucalypt gene sequenced was the important lignin gene CAD of *E. gunnii*, published in 1993 by French researchers working at the University of Toulouse. The first genomic maps of *Eucalyptus* appeared in the early 1990s and were based on random amplified polymorphic DNA (RAPDs) which are dominant polymerase chain reaction (PCR) markers or codominant restriction fragment length polymorphisms (RFLPs), and were used to study the genetic control of quantitative traits in species such as *E. grandis, E. urophylla, E. nitens*, and *E. globulus*. There are now hundreds of codominant (more informative) microsatellite loci developed for eucalypts that are transferable across species and have allowed alignment of genome maps from different studies and species. High consistency in marker order (synteny) is being revealed, and generic maps are emerging with candidate genes (e.g., for flowering and wood properties) positioned. Considerable progress has been made toward identifying genomic regions and markers associated with variation in quantitative traits (quantitative trait loci, QTL). QTL have been detected for numerous traits of economic significance including growth, propagation and wood properties, and in several cases these have been shown to colocate with candidate genes (e.g., *cinnamoyl* CoA reductase (CCR) gene with pulp yield, cellulose yield, and lignin quality (S/G ratio)). Research is now focusing on identifying genes and alleles responsible for the variation in traits of economic significance, particularly the highly heritable and expensive-to-measure wood property traits, through QTL and association studies. The next decade will see major advances in our understanding of the eucalypt genome and molecular breeding. There are now several privately owned databases containing partial sequences of many of the genes expressed in various tissues (e.g., cambium) of *Eucalyptus*, microchips have recently been produced to study eucalypt gene expression, and there is growing interest in large-scale sequencing of the eucalypt genome.

See also: **Genetics and Genetic Resources**: Genetic Systems of Forest Trees; Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Genetics and Improvement of Wood Properties. **Tree Breeding, Principles**: Breeding Theory and Genetic Testing; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tropical Ecosystems**: Eucalypts.

Further Reading

Boland DJ, Brooker MIH, Chippendale GM, *et al.* (1985) *Forest Trees of Australia*. Melbourne, Australia: Australian Government Publishing Service.

Borralho NMG, Cotterill PP, and Kanowski PJ (1993) Breeding objectives for pulp production of *Eucalyptus globulus* under different industrial cost structures. *Canadian Journal of Forest Research* 23: 648–656.

Doughty RW (2000) *The Eucalyptus: A Natural and Commercial History of the Gum Tree*. Baltimore, MD: John Hopkins University Press.

Downes GM, Hudson IL, Raymond CA, *et al.* (1997) *Sampling Plantation Eucalypts for Wood and Fiber Properties*. Melbourne, Australia: CSIRO.

Eldridge K, Davidson J, Harwood C, and van Wyk G (1993) *Eucalypt Domestication and Breeding*. Oxford, UK: Clarendon Press.

Grattapaglia D (2000) Molecular breeding of *Eucalyptus*: State of the art, operational applications and technical challenges. In: Jain SM and Minocha SC (eds) *Molecular Biology of Woody Plants*, pp. 451–474. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Griffin AR, Burgess IP, and Wolf L (1988) Patterns of natural and manipulated hybridization in the genus *Eucalyptus* L'Herit: a review. *Australian Journal of Botany* 36: 41–66.

Jacobs MR (1979) *Eucalypts for Planting*. Rome: Food and Agriculture Organization.

Keane PJ, Kile GA, Podger FD, and Brown BN (eds) (2000) *Diseases and Pathogens of Eucalypts*. Melbourne, Australia: CSIRO.

Moran GF, Thamarus KA, Raymond CA, *et al.* (2002) Genomics of *Eucalyptus* wood traits. *Annales des Sciences Forestières (Paris)* 59: 645–650.

Potts BM and Dungey HS (2004) Interspecific hybridization of eucalypts: key issues for breeders and geneticists. *New Forests* 27: 115–138.

Potts BM, Borralho NMG, Reid JB, *et al.* (eds) (1995) *Eucalypt Plantations: Improving Fibre Yield and Quality*, Proceedings CRCTHF-IUFRO Conference, 19-24 February, Hobart, Tasmania.

Potts BM, Barbour RC, Hingston A, and Vaillancourt RE (2003) Turner Review no. 6. Genetic pollution of native eucalypt gene pools: identifying the risks. *Australian Journal of Botany* 51: 1–25.

Turnbull J (1999) Eucalypt plantations. *New Forests* 17: 37–52.

Williams JE and Woinarski JCZ (eds) (1997) *Eucalypt Ecology: Individuals to Ecosystems*. Cambridge, UK: Cambridge University Press.

Nitrogen-fixing Tree Improvement and Culture

J L Brewbaker, University of Hawaii, Honolulu, Hawaii, USA

Introduction

This review focuses on the genetic improvement and culture of important tree species that fix nitrogen. About 700 tree species are known to fix nitrogen, among approximately 3000 suspected to do so. They represent 11 plant families. Most N-fixing trees (NFTs) are multipurpose and tropical in origin. They are often as valuable as fuelwood, green manure, or forage as they are for lumber or craftwood, and they are cultivated in a great diversity of agroforestry systems. A majority are legumes nodulated by *Rhizobia* or *Bradyrhizobia* bacterial species. However, 10 dicotyledonous families fix nitrogen with the aid of actinomycetes of the genus *Frankia*. Legume trees that fail to fix nitrogen are primarily in the subfamily Caesalpinioideae and include highly selected tropical ornamentals, commonly grown as clones, in genera such as *Bauhinia, Caesalpinia, Cassia, Delonix, Haematoxylon*, and *Parkinsonia*. The great majority of significant NFT species can be thought of as newly domesticated. Only a few NFT genera (e.g., *Acacia, Casuarina, Erythrina, Leucaena, Prosopis*, and *Robinia*) have attracted the investment of provenance collections and strategic plant improvement. The review is in alphabetic order by genus, and within genera by species. An especially useful reference is the book by K.G. MacDicken (see further reading list).

The Genus *Acacia* (Mimosoideae: Leguminosae)

This large genus dominates NFT literature and embraces three great groups of species – about 850 Australian (now assigned by some authors to a genus *Racosperma*), 200 African, and 200 American. Most American species are shrubs and most African species are thorny trees. Diploid species are largely outcrossing, often due to self-sterility, but about one-third of acacias studied are polyploid, and polyploidy in legumes is often associated with self-fertility. Many species of great forestry potential are in early phases of domestication, provenance collection, and evaluation, among them the moist tropical species *A. aulacocarpa, A. cincinnata, A. crassicarpa, A. holosericea, A. leptocarpa*, and *A. polystachya*. Only limited provenance studies or genetic improvement is reported for many important acacias, including the following:

- *A. albida* ($2n = 26$) (= Faidherbia albida): this large, slow-growing tree of dry African tropics is widely distributed for its use as shade and forage on arid lands.
- *A. confusa* ($2n = 26$): 'Formosan koa,' a native of the Philippines and Taiwan, is a small tree grown as fuelwood and as an ornamental and soil-stabilizer, especially on wetter, acid soils. As with many other acacias, some selection has occurred for ornamental use.
- *A. farnesiana* ($2n = 52$): as with other polyploid legume trees, this small, thorny, tropical American tree is widely adapted, self-fertilizing, and often weedy. It has been grown for fuelwood and forage, and provides gum for glue and black dye for ink. It was planted and selected for flowering in France, as the 'cassie' flowers yield a pleasant perfume.
- *A. nilotica* ($2n = 52, 104$): 'Babul' is a thorny Indian and African tree used as firewood, fodder, charcoal, gum, and tannin. A polyploid, it is extremely variable genetically, and several varieties are recognized commercially. These probably include both self-fertile and self-sterile types.
- *A. saligna* ($2n = 26$): this small tree of south-west Australia is highly variable and grows rapidly in a wide range of ecosystems. It provides fodder and fuel and has been planted widely for sand-dune and mine-dump stabilization.
- *A. senegal* ($2n = 26$): this slow-growing, thorny African tree is the source of gum arabic and can be used for fuel, charcoal, and feed. Limited selection has been made to optimize productivity of gum under severe harvest stress conditions.
- *A. tortilis* ($2n = ?$): this thorny, polymorphic African tree (**Figure 1**) provides firewood and fodder in the dry, hot tropics. It tolerates alkaline soils and is often shrubby in growth.

Widely cultivated acacias that have been the subject of provenance and family evaluations and of other genetic improvement include the following species.

Acacia auriculiformis and *A. mangium*

These are related, rapidly growing trees from Australia to New Guinea, whose hybrid is of increasing genetic interest. The former is a smaller, rather crooked tree widely adapted and grown since 1900 throughout the tropics for shade, fuelwood, furniture, and pulpwood. The latter is taller but less forked and has large phyllodes and branches with much fluting; wood is lower in specific gravity. Both are diploids ($2n = 26$) that can be selfed and show low isozymic heterozygosity values, although outcrossing by bees

Figure 1 Naturalized stand of *Acacia tortilis* in Kenya, often coppiced for fuelwood and fodder.

Figure 2 *Acacia mangium* trial in Chumphon, Thailand, age 3 years.

Figure 3 High-value hardwood trials of *Acacia koa* in Hamakua, Hawaii, age 8 years.

occurs (pollen is in polyads). Both can be cloned from cuttings, and both thrive on acidic soils. *A. mangium* (**Figure 2**) was introduced into Malaysia for pulpwood in 1967 (to 25 000 ha) as seeds from a single tree. A broader sample of germplasm was introduced in the 1980s to overcome the loss of form and vigor that occurred due to inbreeding. Extensive provenance collections have been made and evaluated throughout the world for both species. Vigorous hybrids of good form among the two species were then observed and came to dominate scientific interest. As yet the marketing of hybrid seeds or clonal propagules from hybrids is not economic. Provenances from Papua New Guinea have generally dominated yield trials, and growth habit shows startling differences on different sites. Related, interfertile species of interest include *A. aulacocarpa, A. crassicarpa*, and *A. leptocarpa*.

Acacia koa Gray ($2n = 52$)

Koa (**Figure 3**) is a high-value hardwood that is endemic to Hawaii, polyploid, and largely or completely self-sterile. Among 700 accessions evaluated since 1989 in Hawaii, 40 were chosen as parents for seed orchards. Genetic advance through selection was seen in degree of forking, improved bole form, tolerance of koa wilt (*Fusarium oxysporum*), and high wood yield. Seed orchards began bearing in 3–4 years. Genetic advance is sought particularly for tolerance of wilt, a limiting factor in growing koa at lower elevations.

Acacia mearnsii ($2n = 26$)

Australia's black wattle is a temperate tree now found worldwide as a source of tannin (35–40% recovery from bark), fuelwood, charcoal, poles, windbreaks, and other benefits. This self-sterile species is aggressive, however, and can become weedy. Provenance selections in the mid-1900s for high bark tannin contents at the Wattle Research Institute in South Africa (now the Institute for Commercial Forestry) and in Zimbabwe's Rhodesian Wattle Co. led to varieties preferred for production of tannins. Trees were felled after approximately 10 years, selection focusing on rapid growth. Provenance evaluations and plantations for wood also developed extensively in China. Selected provenances also proved of major value in the reforestation of Korea after the Korean war. With the advent of synthetic tannins and leather substitutes, bark tannin production greatly declined. It is agreed that genetic diversity is great and selection for wood productivity could be profitable, but limited investment is currently made in improvement. Related wattle species of less value for tannins include the green wattle (*A. decurrens*) and silver wattle (*A. dealbata*) that have also been planted widely in the tropics.

Acacia melanoxylon ($2n = 26$)

Australian blackwood is a fine hardwood of the quality of kauri or walnut that occurs over a wide latitudinal range on the east coast of Australia. It is noted for its environmental plasticity and for the importance of locally adapted provenance evaluations. It was introduced widely into East Africa and Sri Lanka in the 1950s.

The Genus *Albizia* (Mimosoideae: Leguminosae)

This is a genus of 150 tropical species of trees, shrubs, and lianas. Many have been domesticated and widely planted but little studied for genetic improvement (e.g., *Albizia chinensis* of the Himalayas, *A. odoratissima* and *A. procera* from South and Southeast Asia). Also important but little bred is *A. lebbek* ($2n = 26$), the 'siris tree,' a widely adapted tree evidently native from Africa to Australia. Limited variation among local and very seedy populations suggests that it is self-pollinated, with abundant dried pods that rattle 'like a woman's tongue.' It is used as an ornamental, for timber and fuelwood, and for fodder. The following species have been the subject of some provenance evaluation, selection and improvement.

Albizia falcataria ($2n = 26$)

Also known as *Paraserianthes falcataria,* albizia (**Figure 4**) is one of the fastest-growing trees of the world. This Southeast Asian tree is planted widely in the tropics as a shade tree and favors moist and acid to neutral soils. Its wood is of low density and of low caloric value, but it is used for pulpwood, boxes, and particle board. Varieties have been selected for use as matchsticks and other products in the Philippines, where plantations are harvested on 10–15-year cycles.

Figure 4 Naturalized stand of *Albizia falcataria* on acid soils in Hawaii.

Albizia saman ($2n = 26$) (= *Samanea saman*)

The classic parasol-shaped 'raintree' or 'monkeypod' shares with many legumes a host of Latin and common names. It was distributed worldwide from its Central American center of origin as an ornamental, timber tree, craftwood, and shade tree. It was distributed throughout the tropics from unknown sources and from narrow gene bases, not unlike most tropical trees. Almost no genetic variation occurs, for example, among Hawaii's beautiful, spreading raintrees, that appear to be highly self-pollinated and abundantly seedy in our fuelwood trials. Several accessions of the raintree were included in the gene conservation program of Oxford Forestry Institute.

The Genus *Alnus* (Betulaceae)

This amazingly widespread genus of alders is largely temperate. It includes 35 species, all NFT through association with *Frankia* actinomycetes. They grow rapidly and aggressively (to 30 m in 10 years), and are often considered weeds, although they provide significant soil improvement for forests. Most are $2n = 28$ and outcrossing. Like many NFTs, the alders are widely planted, fully domesticated, poorly represented by forest genetic resources, and managed with little view to genetic improvement. Among these are:

- *A. acuminata*: a Central and South American species planted extensively throughout Latin America for timber and fuelwood.
- *A. glutinosa*: black alder, a widely distributed European species that provided wood for early violins and that is grown as a fuelwood and craftwood and as a stabilizing tree along rivers and roadsides.
- *A. nepalensis*: the Nepal alder of Himalayan origin, planted extensively worldwide for timber, forage, and firewood.
- *A. rubra*: the red alder of northwest North America, a tree up to 40 m tall that is used for construction and furniture, as fuel and in pulpwood mixtures. It can become annoyingly weedy in young stands of pines. As with other alders, the red alder varies greatly in ecosystem adaptability (latitudinal, elevational).

The Genus *Calliandra* (Mimosoideae: Leguminosae)

Most of the 132 species of this predominantly American genus are shrubby, and few enter commerce, but the genus is noted for growth on acid tropical soils. Several are common as ornamental shrubs or trees selected for red, pink, or white flowers, including *C. inaequilatera* and *C. haematoma*.

Calliandra calothyrsus (2*n* = 22)

Calliandra is a small, clonable, rapidly growing tree used less in its native America than in countries like Indonesia, where it serves as fuelwood, green manure, and fodder. It is sparsely seedy due to its nocturnal flowering habit and cross-pollination largely by bats and moths. The US National Academy of Science supported an early publication on calliandra, and Oxford Forestry Institute provided seed collections for >120 international trials of different seedlots and species. Wide variations were recorded in wood yield, branching, and growth habits. Selection in Australia and Costa Rica has focused on variations in fodder utility and digestibility, which are very low in fresh foliage due to high condensed tannin contents.

The Genus *Casuarina* (Casuarinaceae)

This Australian genus is now recognized to include 17 tree species, with about 70 related polymorphic species assigned to the genera *Allocasuarina*, *Ceuthostoma*, and *Gymnostoma*. The true casuarinas are noted for hardwood, fuelwood, and shade on tropical beaches and waterways. Major shelterbelts occur along coastlines in China and in Pacific islands. N fixation is by *Frankia,* pollination is by wind, and some species are dioecious. The species below have been hybridized and evaluated widely in China.

Casuarina cunninghamiana and the related (and cross-fertile) *C. glauca* (2*n* = 18)

These are of less significance as plantation species than *C. equisetifolia*, but their genetic variation is much better studied. *C. glauca* can be weedy due to root-sprouting. These species have a broad ecological range as riverine species of eastern Australia, and extensive provenance collections have been made and studied, e.g., in California, China, and Egypt. Genetic diversity was similar to that of other tropical wood species (0.2–0.3, probabilities that any two alleles are different) with unusually large between-provenance variations. Significant variations are reported in traits like freezing survival, tree height, and diameter. Clinal variations by latitude were very significant. Selected families and species hybrids dominate modern plantings.

Casuarina equisetifolia (2*n* = 18)

The ‘ironwood’ is the most extensively planted casuarina, noted for fuelwood, pulp, and timber, and as a shade tree. Provenance collections are somewhat limited and significant variations occur among them. Clones based on its stately hybrid with *C. junghuniana* (= *C. montana*) are prominent in Thailand and India (**Figure 5**).

The Genus *Dalbergia* (Papilionoideae: Leguminosae)

The ‘rosewoods’ of fame occur among the 100 species of this tropical papilionoid genus of trees, shrubs, and lianas. Many species are known for their high-value hardwood and widely planted, but have been the subject of no major genetic improvement. These include *D. decipularis* (Brazilian tulipwood), *D. latifolia* (Indian rosewood, blackwood), *D. melanoxylon* (African blackwood), and *D. nigra* (Brazilian rosewood). The rosewoods are often endangered by deforestation and major genetic erosion.

Dalbergia sissoo Roxb. (2*n* = 20)

‘Sissoo, shisham’ is a widely planted high-value hardwood endemic to the Himalayas (**Figure 6**). It is also recognized for shade, soil enrichment,

Figure 5 Three years' growth of hybrid *Casuarina equisetifolia* × *C. junghuniana* in Chumphon, Thailand.

Figure 6 Logs of *Dalbergia sissoo* with Director C. Sheikh of Pakistan Forest Institute.

fuelwood and charcoal, honey, and traditional medicines. While it thrives on gravelly outcroppings in the terai at the foot of the Himalayas, it also grows under a wide range of stressing environmental factors, including aridity, mild frost, and very high temperatures. Sissoo is self-fertile but appears to be partially outcrossed in nature and provenance variations are large. Like most legume trees, sissoo is light-seeking and invariably crooked, and genetic variability is high for stem form and growth habit. Estimates of heritability for stem form are high (40–50%) but these assume complete outcrossing. They have led to optimistic projections for expanded use of genetically improved sissoo throughout the tropics, despite its relatively slow growth and lack of institutional investment.

Figure 7 Hawaii's largest tree is the Costa Rican earpod, *Enterolobium cyclocarpum*.

The Genus *Elaeagnus* (Elaeagnaceae)

This European genus includes 40 species of shrubs and trees that fix nitrogen through association with the actinomycete *Frankia*. Similar American NFTs occur in the genera *Shepherdia* and *Hippophae*, often noted as fodder trees but 'armed' with spines for protection. *Elaeagnus angustifolia*, the Russian olive, is commonly cultivated as an ornamental and has been planted widely as a shelterbelt companion of trees that do not fix nitrogen. Selected cultivars and clones are reportedly of better form and appearance.

The Genus *Enterolobium* (Mimosoideae: Leguminosae)

A small genus of five tropical American species, this is related to the genus *Albizia*. A widely cultivated rapidly growing ornamental (**Figure 7**) is the giant, spreading *Enterolobium cyclocarpum*, known as 'guanacaste' or 'elephant's ear.' Like *Albizia saman*, its roots are often superficial and it is undesirable as a street tree. The wood ranges widely in density and quality, and the wood dust causes allergies. Foresters favor trees with dark walnut-like wood, but there is no evidence that these selections are prominent in plantations. Fuelwood plantings in Hawaii (1×1 m spacing) yielded well but showed great intraprovenance variations.

The Genus *Erythrina* (Papilionoideae: Leguminosae)

The 112 species of 'coral trees' are tropical and worldwide in origin, with *E. fusca* native to three continents, its seeds surviving in sea water. Most are small thorny trees with soft wood and high alkaloid contents in leaves. Truly multipurpose but low in value, their uses range from fodder, food, and medicinal to fencepost, shade tree, green manure, and ornamental. Interspecific hybrids were evaluated widely and proved highly interfertile. All appear to be $2n = 42$ and outcrossed by hummingbirds. Many are American in origin, with one endemic to Hawaii, *E. sandwicensis*. *E. abyssinica* and *E. crista-galli* are grown as ornamentals worldwide. Erythrinas are easily cloned from stakes or cuttings. Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE) in Costa Rica maintains a clonal and provenance collection, and the following species are largely grown as locally adapted clones selected for specific use.

- *E. berteroana*: a coral tree that is highly tolerant of aluminous clays, and is often cloned to serve as fence posts in its native tropical America.
- *E. fusca*: the most international species, a classic multipurpose tree. It often serves as shade and green manure for coffee and cocoa and as fenceposts.
- *E. poeppigiana*: a tall South American tree that serves widely as a shade or nurse tree for coffee and as fodder (despite high alkaloid contents).
- *E. variegata* (= *E. indica*): used as a thorny living fence, ornamental, shade for coffee, and support for viny crops. A fastigial, erect cultivar is widely cultivated throughout the Pacific as hedgerows.

The Genus *Gliricidia* (Papilionoideae: Leguminosae)

This small meso-American genus (four species) is known primarily for the species *G. sepium*.

Gliricidia sepium ($2n = 20$)

Gliricidia (**Figure 8**) is a small, rapidly growing, and thornless tree with bright pink flowers in the spring that appear to be entirely outcrossing. It has been spread internationally as an ornamental, green manure, fodder, and firewood tree. The trees clone easily from stem cuttings but develop better roots from seedlings. Planting of gliricidia clones as living fences, as support trees for peppers and yams, and as shade for cacao and coffee, often involves 'seat of the pants' selection of erect, less-forked types. A joint series of provenance collections was made in the 1980s, with inputs from International Livestock Center of Africa, University of Hawaii, Nitrogen Fixing Tree Association, Oxford Forestry Institute, Food and Agriculture Organization of the UN and other organizations. Genetic variations were great both between and within provenances. An outstanding provenance, Tequisate, from Guatemala, was observed in trials from Hawaii and the Philippines to Nigeria. Its superior growth was evident in both fodder and total biomass. Extensive studies were conducted in Nigeria of gliricidia in alley farming systems with crops like maize, and as a leguminous fodder supplement in animal diets. The fresh fodder was not palatable to animals, but palatability increased upon drying, and digestibility of the pure legume was relatively low (55%) but increased when in grass mixtures. Improvement in forage quality with selection was predicted among gliricidia provenances and clones.

Figure 8 *Gliricidia sepium* managed for alley farming trials at Ibadan, Nigeria.

The Genus *Inga* (Papilionoideae: Leguminosae)

Over 200 species of tropical American origin are in this genus of woody shrubs and trees, studied taxonomically by the Oxford Forest Institute. The species *Inga laurina* ('icecream bean') is used as a food and shade tree in Latin America, *I. vera*, *I. edulis*, and others serve variously as shade, fuelwood, and food (sweet pulp), notably on acid soils in humid tropics. Seeds are recalcitrant, restricting the cultivation and improvement of these species.

The Genus *Intsia* (Caesalpinioideae: Leguminosae)

This tropical Asian genus of three species includes *Intsia bijuga* ($2n = 24$), a handsome timber tree called 'ipil' in the Philippines. The hard, rot-resistant timber of this and *I. palembanica* (Borneo teak) are noted for use in decking and truck bodies. Ipil is believed to be highly variable genetically in the Philippines but there is little evidence of selection and breeding. Debate also exists about its ability to fix nitrogen.

The Genus *Leucaena* (Mimosoideae: Leguminosae)

No NFT genus has been selected or bred more extensively than this American genus of 22 species ranging from Peru to Texas, from sea level to 3000 m. Among the fastest-growing trees, all are woody and most will flower the first year. All are polyploids, ranging from $2n = 52$ to $2n = 112$. The predominant diploid species ($2n = 52$, 56) are self-sterile, while three of the four polyploids ($2n = 104$, 112) are self-fertilized. A single self-pollinated variety of the $2n = 104$ species, *Leucaena leucocephala*, circumnavigated the world four centuries ago, accounting for early interest in this model multipurpose tree for agroforestry systems. Cultivation and management systems differ greatly for leucaenas; some are maintained as shrubs for fodder, some as trees for a wide variety of uses. All species have been included in >2500 seed collections made by University of Hawaii, Oxford Forestry Institute and Commonwealth Scientific and Industrial Organization (CSIRO) of Australia, with evaluations in Hawaii, Queensland, and Nicaragua. In Hawaii, 232 interspecific hybrids were made among 16 species, resulting in 77% interfertility. Many of the 73 hybrids grown were heterotic for growth rate and involved attractive combinations of parental traits. Many species are widespread, at least partially domesticated and of use as fodder or fuelwood, e.g., *L. collinsii*, *L. lanceolata*, *L. macrophylla*, *L. shannonii*, and *L. trichandra*. Much current breeding is based on populations from interspecific hybrids, involving taxa such as *L. pallida* ($2n = 104$), *L. diversifolia* ($2n = 104$), and *L. pulverulenta* ($2n = 56$). Species fully domesticated and of breeding interest include the following:

- *L. diversifolia* ($2n = 104$): self-fertile tree of highland Mexico, now widespread, used as coffee shade, fuelwood, and green manure. Fertile hybrids with *L. leucocephala* are being evaluated for timber and fuelwood.
- *L. esculenta* ($2n = 52$): widely grown outcrossing food tree (edible pods) of highland Mexico, also used as shade. Seedless hybrids with *L. leucocephala* are attractive as high-value hardwood, widely adapted in elevation and resistant to psyllid insects.

Leucaena leucocephala ($2n = 104$)

Leucaena leucocephala is the familiar leucaena throughout the lowland tropics on less acid soils, known by a hundred vernacular names. Among 700 international collections of this self-fertile species grown in Hawaii, most were identical seedy shrubs, the 'common type' widely used for fodder and fuelwood in warm tropics. In contrast, seed collections in its native Mexico and Central America range widely in ideotype, including arboreal types from which 'giant' cultivars have been bred and are now international in use. These are distributed largely as pure lines, e.g., K8, Cunningham, K636, and Tarramba, for fodder and wood uses, and are not inclined to be weedy. Hybrids among pure lines show some heterosis, and one F_2 population (K636 × K584) is marketed. However, interspecific hybrids with highland species are of great commercial interest. KX2 derives from the fifth cycle of recurrent selection following the crossing of *L. leucocephala* with a small Mexican tree, *L. pallida*, a self-sterile polyploid that confers resistance to psyllids and to cold weather. Another, KX3 (**Figure 9**), is from hybrids with *L. diversifolia*, described above. An attractive, clonable, seedless triploid hybrid is K1000 (**Figure 10**) showing impressive hardwood quality and growth rate derived from the cross with *L. esculenta*.

Figure 9 High-value hardwood from 12-year old hybrid, *Leucaena leucocephala* × *L. diversifolia*, in Waimanalo, Hawaii.

Figure 10 Seedless triploid clone K1000, *Leucaena esculenta* × *L. leucocephala*, age 7 years, Waimanalo, Hawaii.

The Genus *Millettia* (Papilionoideae: Leguminosae)

This genus of 90 African and East Asian species now embraces the genera *Pongamia* and *Derris,* and includes a number of lesser-known fuelwood and timber trees. The pongam or Indian beech is *Millettia* spp., formerly known as *Pongamia pinnata* and as *Derris indica*. It is a native of East Asia that is now widespread and used in many ways, providing a seed oil as fuel and medicinal, fuelwood, postwood, shade, and ornamental. Profuse root suckers and weediness limit its use.

The Genus *Mimosa* (Mimosoideae: Leguminosae)

Few arboreal species occur in this large genus of 400 species, and these are often thorny and shrubby. *Mimosa scabrella* ($2n = ??$), bracatinga, is an exception. It is a fast-growing Brazilian legume of good form with diverse use as fuelwood, lumber, charcoal, ornamental, pulpwood, and shade for coffee. It is believed to be outcrossing and one study showed wide provenance variations.

Figure 11 Variegated-leaf clone of *Pithecellobium dulce* as ornamental, Honolulu, Hawaii.

The Genus *Parkia* (Mimosoideae: Leguminosae)

Forty species of this genus range from Africa to Southeast Asia, and a few are now worldwide. They are bat-pollinated and probably self-sterile, and have recalcitrant seeds. They are observed to vary genetically, but with no evidence for breeding and selection. Two species are outstanding:

- *P. javanica* (= *P. roxburghii*): an imposing tree to 40 m with umbrella crown, used as ornamental or timber tree, with seeds used medicinally.
- *P. speciosa*: a source of food in Southeast Asia (seeds, from the large pods), known to produce hybrids with *P. javanica*.

The Genus *Pithecellobium* (Mimosoideae: Leguminosae)

The 20 tropical American trees of this genus are largely thorny and best known as sources of sweet fruit. It was earlier treated by early botanists as a much broader taxon, including genera like *Albizia*.

Pithecellobium dulce ($2n = 26$)

Manila tamarind is a thorny American tree up to 15 m tall that can be found throughout the drier tropics (**Figure 11**). Its multiple roles include food use of the pods and seeds, honey, postwood, fuelwood, shade, and ornamental. It is alternately planted and cursed, as its thorns and weediness (seeds are spread by birds) reduce its utility and attractiveness. Variegated mutants are selected as ornamental trees, and thornless mutants (as in *Prosopis*) are known to occur.

The Genus *Prosopis* (Mimosoideae: Leguminosae)

The 44 species of this genus are American in origin, and most are drought- and salt-tolerant, thorny,

$2n = 28$ and self-sterile. They include the mesquites of fuelwood and charcoal fame (*Prosopis glandulosa* in North America) that add flavors to many a grill. They are also known as honey and fodder trees and occasionally provide high-value hardwood. Among species that are fully domesticated and widely planted but little studied genetically are *P. cineraria* (= *P. spicigera*), a widespread Indian tree of the hot tropics used as firewood, fodder, green manure, and charcoal. It segregates for thorns, and thorny trees are favored for goat-proof fences. Also of fame is *P. tamarugo*, a slow-growing Chilean species widely planted locally for its saline tolerance under annual rainfall <100 mm. It has not been adapted effectively outside of Chile. The following two species complexes have been more widely evaluated as provenances or localized selections. However, as with most NFTs, expert panels routinely recommend the increased availability of genetically improved materials, if research money could accompany the recommendations.

Prosopis alba ($2n = 28$) and *P. chilensis*

These are algaroba trees from a related complex largely found in highland subtropics that also includes *P. flexuosa* and *P. nigra*. All serve as sources of honey, firewood, and charcoal, and the sweet succulent pods are used for food and cattle fodder. Seedlot variations are reported for growth rate, limbiness, stem form, and thorniness. Phenotypic selection in natural stands was declared ineffective, due to environmental plasticity, a phenomenon with which all NFT breeders are familiar.

Prosopis pallida ($2n = 28$) and *P. juliflora*

These ($2n = 28$, 56) are two closely related mesquites from Peru north into Central America that are now abundant worldwide; their awkwardly forking trees often dominate arid landscapes and seascapes (**Figure 12**). Known best for their excellent charcoal and dense fuelwood, they were also planted internationally as animal fodder (pods). The wood has very high calorific value (4200–4800 kcal kg^{-1}), and the relatively slow-growing trees offer a durable postwood and an excellent source of honey. *Prosopis pallida* in Hawaii segregates about 1/8 thornless, suggesting single-gene control based on the presumed two-tree origin (introduced from Paris Botanical Garden in 1828). Such a narrow gene base is undoubtedly common in many countries. Trees are coppiceable and cuttings and grafts take fairly well, permitting some use of clones. Thornless trees are universally favored for tropical beaches but do not breed true due to self-sterility. Some selection has also occurred for pod yields, tree form, and growth, but serious genetic improvement awaits financial support.

Figure 12 The Peruvian *Prosopis pallida* dominates Pacific beaches, such as this in Molokai, Hawaii.

The Genus *Pterocarpus* (Mimosoideae: Leguminosae)

Many fine timbers (bloodwood, narra, padouk, Philippine mahogany, vermilion wood) derive from the 20 species of this tropical Indian and African genus of tall leguminous trees. Narra is probably the best known and most widely cultivated. Timber, dye, and shade use are also made of many other taxa, notably *Pterocarpus erinaceus* (kino, Burmese rosewood), also referred to as *P. angolensis* and *P. echinatus*. Other important species include *P. dalbergioides* (Andaman padauk), *P. macrocarpus* (Burma padauk), *P. marsupium* (malabar kino, source of astringent resin), *P. santalinus* (red sandalwood), and *P. soyauxii* (West African padauk). All are characterized by winged pods, presumed outcrossing, clonability, and extensive natural variability.

Pterocarpus indicus ($2n = 22$)

This majestic spreading tree (up to 40 m tall) is known as narra, Burmese rosewood, and Andaman redwood, and is native over a wide ecological range from Myanmar to Borneo and the Philippines. It is cultivated as an ornamental and street tree and is harvested as a choice timber for furniture and flooring. Flowering occurs in short intervals and pod set appears to be due to self-pollination. Much variation is seen in tree form, fluting, forking, and growth rates of narra. Cuttings root easily from trees of all ages and clones have been selected for adaptability to location, ecology, and use. It responds well to deep, high-quality soils of reduced acidity.

The Genus *Robinia* (Papilionoideae: Leguminosae)

Four interfertile species make up this North American temperate genus, a relict of tropical origin related to gliricidia and sesbania that becomes deciduous only upon frost. Like sesbania, it has a unique N-fixing spectrum of rhizobia. The shrubby species *Robinia hispida*, rose acacia, is planted as an ornamental but has little selection history. In contrast, the black locust is among the most intensively studied and bred NFTs.

Robinia pseudoacacia ($2n = 20$)

The black locust (or false acacia) is widely naturalized throughout North America, where the borer *Megacyllene robiniae* has restricted commercial plantings to erosion control, land stabilization, and as postwood. It is nodulated by both *Rhizobium* and *Bradyrhizobium* bacteria and can become weedy. Away from the borer, black locusts have been planted worldwide and cultivated intensively in Eastern Europe as a pulpwood, postwood, and fuelwood tree. Its outcrossed papilionoid flowers also serve as a bee pasture for honey and cultivars have been selected for use as an ornamental. It was introduced to Europe in the 1700s, where 'shipmast locust' arboreal types were selected and grown intensively (250 000 ha in Hungary) as a timber tree on a 30-year harvest cycle. Great genetic variability (average heterozygosity 0.30) and breeding progress were recorded for height, yield, spinelessness, and coppiceability. In contrast, much less variation was observed in specific gravity (average 0.62 at age 20 years). Intensive studies have been made to accelerate planting of uniform clones from vegetative and root cuttings, tissue cultures, and from grafts.

The Genus *Sesbania* (Papilionoideae: Leguminosae)

This genus includes 50 species of shrubs and small trees in the section Robinieae, now scattered worldwide. Most species are annuals, of which many are important as fodder (**Figure 13**) and ornamental. All nodulate aggressively, some having nodules on the stems. A very fast-growing fodder and multipurpose species is *Sesbania sesban* (= *S. aegyptica*; $2n = 12$) a short-lived shrub or tree now planted worldwide, and a similar shrub called 'ohai' is native to Hawaii, *S. tomentosa*.

Sesbania grandiflora ($2n = 24$)

S. grandiflora, called 'agati,' is a small polyploid tree from Southeast Asia or Indonesia with showy flowers that are self-fertile but largely outcrossed. It is planted internationally as a multipurpose tree for fodder, fuelwood, ornamental use and often for food (flowers, young pods, and leaves). It is recognized by farmers as a source of fixed nitrogen and green manure. It coppices vigorously for use as fodder or fuel (fast-burning), and selections have been made for ornamental or food use, e.g., with larger flowers or with red (versus white) flowers.

Figure 13 Forage trials in Maseno, Kenya, of several arboreal and shrubby species of the genus *Sesbania*.

The Genus *Sophora* (Papilionoideae: Leguminosae)

This genus includes 52 species of temperate and tropical origin, several noted as ornamentals or as source of hardwood and of toxic or medicinal chemicals. *Sophora japonica* ($2n = 28$; Japanese pagoda tree) is a large deciduous tree native to China and Korea that has been cultivated for more than 30 centuries in China as an ornamental, dye, and medicinal plant. Flowering begins only on very old trees and the outcrossed flowers cause stains to form where they fall. Genetic variations exploited by horticulturists include weeping, fastigiate, and variegated-leaf trees, and cloning or grafting is common.

The Genus *Tipuana* (Papilionoideae: Leguminosae)

This is a monotypic South American genus with *Tipuana tipu* ($2n = 20$) as the sole species. The 'pride of Bolivia' is a fine timber (rosewood) and ornamental, and is widely planted for fodder, windbreak, and as a street tree to 20 m height in Argentina and Bolivia (to 3000 m elevation). The outcrossed large yellow flowers produce winged one-seeded pods, and it can be weedy. It has an irregular bole similar to most legume trees and it is coppiceable and clonable. Limited studies suggest major provenance variations in ecosystem adaptability (elevation and cold tolerance).

See also: **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species; Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Tropical Hardwoods Breeding and Genetic Resources; A Historical Overview of Forest Tree Improvement; Forest Genetics and Tree Breeding; Current and Future Signposts.

Further Reading

Awang K and Taylor DA (eds) (1993) Acacias for rural, industrial, and environmental development. In *Proceedings of 2nd Meeting of the Consultative Group for Research and Development of Acacias*, Udorn Thani, Thailand.

Brewbaker JL and Sorensson CT (1994) Domestication of lesser-known species of the genus *Leucaena*. In: *Tropical Trees: The Potential for Domestication and Rebuilding of Forest Resources*, pp. 195–204. Institute of Terrestrial Ecology Symposium no. 29. Edinburgh Centre for Tropical Forests. London, UK: HMSO.

Carron LT and Aken KM (eds) (1992) Breeding technologies for tropical acacias. In: *Proceedings of a Workshop*, July 1991, Tawau, Sabah, Malaysia, July 1991. ACIAR proceedings no. 37.

El-Lakany MH, Turnbull JW, and Brewbaker JL (eds) (1990) Advances in Casuarina research and utilization. In *Proceedings of the 2nd International Casuarina Workshop*, January 1990, Cairo, Egypt.

Evans DO (ed.) (1996) International workshop on the genus *Calliandra*. In *Proceedings of a Workshop*, January, 1996, Bogor, Indonesia.

Gutteridge RC and Shelton HM (eds) (1994) *Forage Tree Legumes in Tropical Agriculture*. Wallingford, UK: CAB International.

Hughes CE (1998) *Leucaena, A Genetic Resources Handbook*. Oxford, UK: Oxford Forestry Institute, Department of Plant Sciences.

MacDicken KG (1994) *Selection and Management of Nitrogen-Fixing Trees*. Morrilton, AR: Winrock International Institute of Agricultural Development.

Pasiecznik NM, Felker P, Harris PJC, *et al*. (2001) *The* Prosopis juliflora–Prosopis pallida *complex: A Monograph*. Coventry, UK: Henry Doubleday Research Association.

Roshetko JM (ed.) (2001) *Agroforestry Species and Technologies: A Compilation of the Highlights and Factsheets Published by NFTA and FACT Net 1985–1999*. Taiwan: Taiwan Forestry Research Institute and Council of Agriculture; Morrilton, AR: Winrock International.

Shelton HM, Piggin CM, and Brewbaker JL (eds) (1995) Leucaena–opportunities and limitations. In *Proceedings of a Workshop*, January 1994, Bogor, Indonesia.

Turnbull JW (ed.) (1987) Australian acacias in developing countries. In *Proceedings of an International Workshop*, August 1986, Gympie, Australia.

Westley SB and Roshetko JM (eds) (1994) Dalbergia. In *Proceedings of an International Workshop*, Winrock International, Morrilton, AR.

Withington D, Glover N, and Brewbaker JL (eds) (1987) *Gliricidia sepium* (Jacq.) Walp.; management and improvement. In *Proceedings of a Workshop*, June 1987, CATIE, Turrialba, Costa Rica.

Genetics of Oaks

A Kremer, L A Xu, and A Ducousso, INRA, UMR Biodiversité Gènes et Ecosystèmes, Cestas, France
L A Xu, Nanjing Forestry University, Nanjing, Jiangsu, China

Introduction

Oaks (*Quercus* spp.) belong to the most widely distributed genus of forest trees. Besides their economic and ecologic importance, oaks are also considered in many countries as cultural and patrimonial resources. Despite their value, they have received very little and spasmodic attention in genetic research in comparison to other forest trees. They were some of the earliest species that were investigated for inheritance studies in Europe, but were neglected in genetics for almost a century. The first international conference on oak genetics was organized in 1991, whereas international working groups in conifers had been well established for decades. This conference synthesized the state of knowledge in oak genetics. Over the past 10 years, significant contributions have been made in population and evolutionary genetics of oaks. This contribution adds to the 1991 synthesis the genetic knowledge of oaks that has accumulated over the past decade.

Biogeography

The genus *Quercus* is distributed over the northern hemisphere in Asia, North America, Europe, and Africa. There are more American than Eurasian species. The highest oak species diversity exists at 15–30° N, in Central America and Mexico and in Southeast Asia (Yunnan province in China). Species richness decreases northward and southward from both Mexico and southern China. The northern limit of distribution is at 50° N, except for the European *Q. petraea* and *Q. robur*, which extend up to 60° N. The southern limit of the genus is reached in the southern hemisphere in Colombia and Indonesia, where oak species exist at higher altitudes. Oak species grow from sea level to very high altitudes, up to 4000 m in Yunnan province in China.

Throughout its natural range, the genus has differentiated into numerous species adapted to extremely variable habitats, from swamps to deserts. For example, evergreen species have differentiated under Mediterranean climates as *Q. agrifolia* and *Q. wislizenii* in California, and *Q. coccifera* and *Q. ilex* in southern Europe. Typical examples of extremely wide distribution are *Q. rubra* and *Q. alba* in North America, *Q. acutissima* and *Q. mongolica* in Asia, and *Q. robur* and *Q. petraea* in Europe. In most cases the widely distributed species are those that have received the most intensive genetic studies.

Taxonomy and Phylogeny

Depending on the authors, there are between 300 and 600 reported oak species. Since the beginning of Linnaean taxonomy, classification within the genus *Quercus* has been controversial, and more than 20 classifications have been proposed. Disagreements involve the characters to be used for the classification, the infrageneric subdivisions adopted (subgenera or sections), and species delineation. There is so much variation within some species that several authors have questioned the concept of species, and further complications in taxonomy are due to frequent interspecific hybridization. The most complete classification is that proposed by Camus (1936–1954), which has recently been supported by molecular approaches. Classification criteria are mostly based on foliar and fruit characteristics. In Camus' classification, the genus *Quercus* (*sensu lato*) is subdivided into two subgenera: *Euquercus* (*Q. sensu stricto*) and *Cyclobalanopsis*. About 150 species belong to *Cyclobalanopsis*; these only exist in South Asia, whereas species belonging to *Euquercus* are the more familiar oak species. The subgenus *Euquercus* (now called subg. *Quercus*) has been further subdivided into six different sections by Camus, and into three sections in a more recent review based on phylogenetic inferences of morphological characters. Earlier taxonomists considered *Cyclobalanopsis* and *Quercus* (*sensu stricto*) as two separate genera. Recently taxonomy in the genus *Quercus* has benefited from phylogenetic approaches based on molecular data. Analysis of nuclear and chloroplast DNA sequences showed that the genus was composed of three major clades: *Cyclobalanopis*, *Cerris*, and the remaining three main sections that form one monophyletic group (*Protobalanus*, *Erythrobalanus* (red oaks), and *Lepidobalanus* (white oaks) *sensu* Camus). A major finding of the DNA data in comparison to previous morphological data was the ancient evolutionary separation of *Cerris*.

Genomics

Although a few cases of naturally occurring triploids have been mentioned in the literature, oaks are diploid species, bearing $2n = 24$ chromosomes. Extra chromosomes ($2n = 24 + 1$, 2, or 3) have been reported as consequences of irregular segregation in mitoses. The diploid DNA content per cell is remarkably homogeneous across species and botanical sections, as reported values only vary between 1.88 and 2.00 pg ($= 10^{-12}$ g per cell). The DNA content of two widely separated sections was 1.88 pg for *Lepidobalanus* (*Q. petraea* and *Q. robur*) and 1.91 pg for section *Cerris* (*Q. cerris* and *Q. suber*), and these species are representative of the most widely separated sections (*Lepidobalanus* and *Cerris*). The genome of oak species contains 40% guanine + cytosine (G + C) base composition, which is similar to most higher plants. Genetic mapping in *Q. robur* resulted in 12 linkage groups and a total map length ranging between 1200 and 1800 cM. The map length of the different linkage groups in *Q. robur* varies between 10 and 200 cM. Eighteen percent of the genetic markers used in the mapping study deviated from Mendelian segregation as a result of a high genetic load in the species. The physical characteristics of the oak genome (number of chromosomes, physical and genetic size, genetic map length) are similar to tomato (*Lycopersicon*)! The oak genome is six times larger in physical size and three times larger in genetic size than *Arabidopsis*, the prime model species in plant genomics.

Genomic research has further addressed the molecular differentiation among species and gene discovery. Phylogenetically closely related oak species exhibit limited molecular variation among species, as a result of their interfertility. In the case of *Q. robur* and *Q. petraea*, the interspecific differentiation, regardless of the molecular markers used, is only slightly larger than the intraspecific variation. Hence genomic regions responsible for species variation are extremely rare. As a result of the similarity between genomes, molecular markers as microsatellites could easily be transferred across species and botanical sections.

Evolutionary Biology

Origin and Diversification

Fossil remains of oaks are common and have been discovered on the three continents. Earliest remains found in China, Europe, and North America come from the Eocene. The almost simultaneous appearance of the genus on the three continents has raised the question of its geographic origin and radiation.

Two scenarios were proposed to reconstruct the history of the species. In the first, the genus appeared in Southeast Asia, deriving from a sister genus *Trigonobalanus* during the Palaeocene, and migrated in two directions: to Europe and America via the North Atlantic land bridge before the Eocene, and via the Bering strait after the Miocene. In the second scenario, the genus *Quercus* derived from the widely distributed boreal–tropical deciduous forest that occupied the northern hemisphere at the beginning of the Tertiary. The genus further differentiated as the continents separated further. As a result, oak species arose 'simultaneously' on the different continents and differentiated from the ancestral group composing the boreal–tropical forest. Between the Oligocene and Miocene, oaks diversified extremely rapidly as a response to important climatic changes. Most fossil remains of that period are similar to extant samples. Hence it is believed that most of the extant species already existed at the mid-Miocene.

Postglacial Migration

During the Quaternary, oaks underwent important migrations in response to climatic changes. There were about 17 Milankovitch climate oscillations (alternation of glacial and interglacial periods) when oak species, like other plants, were subjected to successive contractions and expansions of their distributions. A glacial period lasted 50–100 thousand years, whereas interglacial periods were much shorter and lasted 10–20 thousand years. Climatic oscillations were strong selective forces, favoring species that were vagile enough to track their moving habitats. They were most likely responsible for the selection of a reduced number of species that occupy today large continental distributions (*Q. robur* in Europe, *Q. alba* in America, or *Q. acutissima* in Asia). These movements have profoundly influenced the genetic diversity of the species, but in rather different ways between North America and Europe. A large survey conducted recently in Europe comparing the remaining historical footprints (pollen deposits) with genetic fingerprints (chloroplast DNA (cpDNA) polymorphisms) demonstrated how the extant distribution of genetic diversity was shaped by the dynamics of postglacial colonization. At the end of the last glaciations, European oaks were restricted to three major refugia (southern Iberian peninsula, central Italy, and southern Balkan peninsula). As glacial periods lasted up to 100 000 years, species were most likely genetically differentiated among these refugial zones, as shown by the completely different haplotype lineages (=cpDNA variant) occupying these regions. In less than 7000 years (from 13 000 to 6000 years ago), oaks recolonized the majority of their modern ranges. On average, the migration was extremely rapid (300–500 m year^{-1}). Rare long-distance dispersal events contributed significantly to the rapid spread of the species. These dynamics had various consequences for the diversity of the species. Despite the strong founder effects that accompanied the recolonization, oaks were able to maintain high levels of genetic diversity. Although the highest neutral diversity is restricted to the southern areas of Europe, the level of diversity is still important in the central part of Europe, where the different migration fronts originating from the refugial zones merged. However, today's distribution of adaptive diversity is not correlated with neutral diversity; there is no footprint left by the maternal origin on the variation of adaptive traits. Genetic variation for adaptive traits resulted from more recent local selection pressures. Interspecific hybridization was a key migration mechanism as it facilitated the introgression of late-successional species (*Q. petraea*) into the pioneer species (*Q. robur*). The systematic sharing of the same cpDNA haplotype by different white oak species occupying the same stands indicates that hybridization was extremely important during recolonization. Postglacial colonization dynamics in North America were quite different from Europe. Species were not restricted to genetically separated refugial zones. Furthermore, oak stands persisted as low-density populations close to the Laurentide ice sheet. Hence postglacial recolonization was more diffuse than in Europe.

Reproduction and Mating System

Reproduction in oaks can be either vegetative or sexual. Coppicing has been a widely used vegetative system to regenerate oak stands. Stump sprouting is also a natural way of propagation for oaks after forest fires and, when repeated over generations, creates clonal structures in natural stands. The production of root suckers is a less frequent natural means of propagation, but has been reported in *Q. pyrenaica* and *Q. ilex*. Oaks are predominantly monoecious species with distinct male and female flowers, although cases of floral hermaphroditism have been reported. *Quercus* is anemophilous (wind-pollinated) whereas other genera of Fagaceae (except *Fagus* and *Nothofagus*) are entomophilous. There are important differences among species groups in the lag between pollination and fertilization. In the *Lepidobalanus* section (white oaks), acorns mature at the end of the growing season in which the pistillate flower is pollinated. In contrast, in the

Erythrobalanus and *Cerris* sections, fertilization occurs more than 12 months after pollination.

Oaks are also predominantly outcrossing species. All reported values of effective outcrossing rates using the mixed-mating model exceed 0.90. Hence it has often been suggested that a self-incompatibility mechanism existed in oaks, although no experimental data have yet been published on the subject. Mating studies have also indicated that crosses among related trees are rare.

Hybridization

There is much literature on oak hybridization. Hybridization was first investigated by using morphological traits as diagnostic markers, but this has raised controversy as the range of within-species variation of morphological features remains largely unknown. During the past 10 years, gene markers have been applied to study introgression that provided new interpretations on the ecological and evolutionary role of hybridization in sympatric oak species. In two examples, one in European oaks (*Q. petraea* and *Q. robur*) and one in North American oaks (*Q. grisea* and *Q. gambellii*), hybridization was shown to be asymmetric. In the European example, *Q. petraea* preferentially pollinated *Q. robur*, whereas in the other example *Q. grisea* was the predominant male parent. As indicated earlier, asymmetric hybridization can reinforce the succession of species replacing the pioneer species (*Q. robur*) by a late successional species (*Q. petraea*) and is thought to have facilitated the dispersal of species during the postglacial recolonization. The use of molecular markers also permitted estimation of the level of introgression and revisiting of former interpretations of the geographic distribution of hybrids. Occurrence of hybrids has been reported more frequently at the margins of the natural distributions of sympatric species where typical parental habitats are less frequent. The hypothesis of higher fitness of hybrids under nonparental habitats has recently been challenged by an alternative interpretation. In the *Q. grisea*/*Q. gambellii* example, it was suggested that the mate-recognition systems can be impaired under stress conditions prevailing at the margin of a species' range. It was found in this example that the formation of a hybrid zone resulted from the diminishing male function due to environmental stress.

Hybridization in natural stands was further confirmed by artificial crossings. Extensive controlled crossing was done within and between species belonging to the three sections *Lepidobalanus*, *Erythrobalanus*, and *Cerris*. Among the 75 intersectional crosses, only three resulted in viable seedlings (*Q. turbinella* (section *lepidobabanus*) × *Q. cerris* (section *cerris*), *Q. turbinella* (section *lepidobabanus*) × *Q. suber* (section *cerris*), and *Q. turbinella* (section *lepidobabanus*) × *Q. marilandica* (section *erythrobabalnus*)), and were confirmed by segregation analysis of the progeny. Hence hybridization is mostly intrasectional, as has been extensively reported in the *Lepidobalanus* section. Artificial controlled crosses also confirmed the preferential asymmetric crosses between *Q. petraea* and *Q. robur*, and challenged the use of morphological features for hybrid identification. Hybrids resulting from controlled crosses between *Q. petraea* and *Q. robur* exhibited foliar characteristics that were not intermediate between the parental forms, as they resemble more the female parent.

Gene Flow in Natural Populations and Neighborhood Size

Oaks have small pollen grains that can be physically transported over long distances. Physical models of oak pollen dispersal pointed to maximum theoretical distances of several hundreds of kilometers. Investigations on oak pollen production and dispersal in California indicated that pollen grains can be transported at least 16 km. In Finland, at the northern margin of *Q. robur*, pollen grain capture on traps along a gradient was recorded at 7 km from the source stand. However, pollen may lose viability quite rapidly. Effective pollen dispersal has recently been measured using parentage analysis with microsatellite fingerprinting obtained in *Q. macrocarpa* and in *Q. petraea* with *Q. robur*. In both examples, it was shown that more than half of the male parents contributing to pollination of female parents on a 5-ha study stand were actually located outside the stand, and that the mean distance of pollen dispersal exceeded several hundred meters. Although nearest neighbors contributed preferentially to pollination in these two examples, pollen dispersion curves are clearly composed of both a short- and a long-distance contribution, most likely related to different wind-transport mechanisms. These data were obtained in rather dense stands (10–100 trees ha^{-1}), and contrasted sharply with those obtained in a savanna landscape where oak trees are more sparsely distributed. In a pollen-dispersal study of the Californian *Q. lobata* (1–2 trees ha^{-1}), effective pollen flow was much more limited (mean dispersal distance = 65 m) as a result of the low density of trees. There is an important asymmetry between pollen and seed dispersal: the ratio of the number of gene migrants by pollen and seed between populations amounts to several hundreds, even though parentage analysis has indicated that long-distance seed dispersal can also occur. Based on dispersal curves from gene-flow data, attempts were made to estimate neighborhood sizes. In dense stands (100–200 trees ha^{-1}), as with *Q. petraea* and *Q. robur*, the neighborhood size was estimated at 12–20 ha, representing 1200–4000 trees. However, these numbers are lower for more sparsely distributed species, as for *Q. lobata* where a male neighborhood size of 3 ha was inferred.

Genetic Diversity

Genetic variation for morphological and adaptive traits has been investigated in oaks for more than a century. Provenance tests were established in Europe at the end of the nineteenth century, and progeny tests in the 1950s. Similar efforts were made in North America in the second part of the twentieth century. During the past 15 years, genetic surveys have been conducted in many oak species to monitor the level and the distribution of genetic diversity with various molecular tools in response to conservation issues. While investigations of phenotypic traits were mostly concentrated on economic important species for which provenance tests were established, molecular diversity was assessed for a greater range of species.

Diversity of Phenotypic and Adaptive Traits

Levels of diversity Phenotypic and adaptive traits exhibit extremely high levels of diversity, even for fitness-related traits. Heritability values (h^2) were estimated by many authors in progeny and clonal tests for the commercially important species (*Q. petraea, Q. robur, Q. rubra*, and *Q. acutissima*). The highest estimated heritabilities were for phenological characters like bud burst (0.35–0.80) and leaf retention (0.35–0.65), and for wood quality (0.15–0.87). Genetic variability for height growth is extremely variable among species and case studies (in *Q. petraea* estimated h^2 ranges from 0.15 to 0.78, in *Q. acutissima* from 0.43 to 0.44, and in *Q. rubra* from 0.15 to 0.25). Most of the crown-architecture characters of oaks have given low estimates of heritability (<0.05) except for the presence of epicormic shoots (0.38). These heritability values are statistical estimates and their range of variation does not correspond to confidence intervals but rather variation between estimates made among different experiments.

Geographic distribution of diversity Phenotypic traits exhibit important population differentiation but not as much as for the chloroplast genome. However, differentiation values (Q_{st}) reach 0.06–0.6 for height and phenological traits in *Q. petraea*. Geographic trends of variation exist for phenological growth, and form traits. Geographic gradients are, however, most evident in phenological traits (dates of bud break and growth cessation). In the European species, *Q. petraea*, there is a clinal trend of variation with latitude and altitude, with southern origins flushing earlier than northern origins; these trends are consistent across the different, widely scattered provenance tests that were established. In the widely distributed American species, *Q. rubra*, there are contrasting patterns depending on the site where the provenance test was established. Longitudinal clines were observed in tests planted in Nebraska whereas an altitudinal cline was found in tests established in Tennessee. These trends are different from those observed in widely distributed north temperate conifers, suggesting that not only climatic factors may impose selection pressures, but most likely also biotic factors, such as defoliating insects. For other traits such as growth and form, no consistent geographic gradient of variation was observed in either American or European species.

DNA and Protein Diversity

Levels of diversity There is now evidence that, in respect of their DNA features, oaks are among the most diverse species of forest trees. This is particularly so for species with large continental distributions, such as *Q. robur* and *Q. petraea* in Europe, *Q. macrocarpa* in North America, or *Q. acutissima* in Asia. These can exhibit high levels of heterozygosity both within a population and throughout their ranges. For microsatellites, the number of identifiable alleles present at a locus within a population can frequently exceed 20. There is also evidence that levels of diversity differ between the two major botanical sections: white oaks (section *Lepidobalanus*) are more variable than red oaks (section *Erythrobalanus*), as shown by a comparative allozyme analysis between these two sections. High levels of diversity are most likely due to the maintenance of large population sizes, the ability for long-distance gene flow, and prevalent interspecific hybridization. Long generation intervals may be advocated for managing oak populations, to minimize the allele losses associated with genetic drift.

Geographic distribution of diversity Most nuclear genetic diversity resides within populations, as is usual for wind-pollinated species. With a few exceptions, genetic differentiation among populations (F_{st} or G_{st}, which are analogs of Q_{st}) is less than 10%. Earlier results obtained with allozymes were confirmed by other molecular markers, random amplified polymorphic DNA (RAPD), amplified fragment length polymorphisms (AFLPs), or microsatellites (simple sequence repeats). As for the level of diversity, substantial pollen flow, large populations, and long generation intervals may account for these results. The geographic distribution of genetic diversity of chloroplast genomes is strikingly different from those of nuclear markers. Oak stands tend to be completely fixed within populations for the chloroplast genome but fully differentiated among stands. Hence differentiation values (F_{st} or G_{st}) in most cases exceed 0.80. The discrepancy between nuclear and chloroplast genome differentiation is due to their different inheritance. As chloroplast genomes are maternally inherited, and as seed exhibits restricted dispersal, diversity within a stand rapidly becomes eroded as a result of stochastic effects. These trends are facilitated during the initial establishment of the stand, which is often associated with low population sizes due to founder effects. Fixation of chloroplast genomes is enhanced by the limited number of founder individuals and the restricted dispersal of seed. When these mechanisms are extended to larger geographic scales, they lead to strong geographic patterns of cpDNA diversity that reflect the colonization dynamics of the species, resulting in strong phylogeographic structures. In conjunction with historical records gathered from fossil pollen, phylogeography of cpDNA permitted reconstruction of postglacial colonization pathways of oaks throughout Europe.

Genetic Improvement

Oaks have several features that limit operational breeding. Besides the biological constraints of longevity, such as delays in the onset of flowering, and the impossibility of seed storage, the uncertainty of long-term breeding objectives makes the implementation of improvement programs economically questionable. Hence research in breeding and improvement has been much less intensive than in shorter-rotation species, even for highly valuable tree species. The general understanding is that tree improvement would be a rather risky initiative for such long-lived species and that research in genetics should be oriented towards a sustainable management of oak stands rather than to the improvement of the existing resources by breeding and selection methods. Hence objectives of tree improvement initiatives were limited to the selection of seed stands, or the installation of first-generation seed orchards.

Europe

There is a long tradition of oak improvement in Europe, although it has not taken the typical form of a modern tree-breeding program. In the Netherlands, it was traditional to raise *Q. robur* for several years in the nursery and to select for stem form. These procedures resulted in the selection of various cultivars that were used in horticulture. Classical tree breeding started in the early 1950s in Germany, and even earlier in Eastern European countries when the earliest plus-tree selection was done and clonal seed orchards were established. Ongoing activities in tree improvement are being conducted on three species: *Q. petraea*, *Q. robur*, and *Q. suber*. For these species, European countries have selected seed stands which are clustered in provenance regions following European Community regulations on reproductive material. For *Q. petraea* and *Q. robur*, progeny tests associated with seed orchards were installed in Belgium, Croatia, Denmark, Hungary, Germany, Ireland, Lithuania, Netherlands, Slovakia, Ukraine, and the UK. Objectives of improvement are wood quality (including the quality of cork for *Q. suber*), stem form, and adaptation to the site. Research to solve the problems posed by the poor storage ability of seed was also pursued. Besides improvement of seed-storage protocols, techniques were developed for vegetative reproduction either by traditional cutting propagation or by using *in vitro* techniques and somatic embryogenesis.

North America

At the first international conference on oak genetics held in 1991, 27 ongoing oak improvement programs were reported on a total of nine species (*Q. alba, Q. falcata, Q. macrocarpa, Q. nigra, Q. phellos, Q. prinus, Q. robur, Q. rubra*, and *Q. velutina*). These programs were mainly conducted by public agencies and institutions in the eastern USA, whereas two projects in Canada were mentioned. In this period, some of the oldest provenance and progeny tests were established for *Q. rubra*. Objectives of breeding programs were timber and veneer for *Q. rubra* but more generally, juvenile growth and plantation success. Other objectives were also pulp production or use as shelterbelts (for *Q. macrocarpa* in the Great Plains). Breeding efforts varied from only plus-tree selection (in about half of the programs) to also producing seedlings or clonal seed orchards. However, owing to the decline of oak plantations and to reduced public budgets (national or state agencies), these projects have all been reduced in the past 10 years. Recent initiatives have, however, revitalized tree improvement activities in northern red oak, such as the creation of the Hardwood Tree Improvement and Regeneration Center (HTIRC) in Purdue (Indiana). HTIRC aims to improve the genetic quality and regeneration of *Q. rubra* through application of classical breeding, genomics, and advanced propagation technology.

Exotics

Oaks have been transferred to various regions in the world. Red oaks from the eastern USA have been introduced in Europe, and *Q. rubra* is currently used throughout western Europe, not only as an ornamental tree but also as a plantation species for veneer or timber production. Hence tree improvement activities in *Q. rubra* were implemented in France, Germany, and the UK, starting with the installation of combined provenance and progeny tests. As the introduction in Europe began at the end of the eighteenth century, there have been only a few generations since the species was introduced in Europe but landraces (a landrace is a population that became adapted in a new environment to which it was transferred) have already been genetically differentiated in Europe. Similarly, *Q. robur* was introduced in many countries throughout the world, but no genetic improvement program has been reported outside its natural range and Europe.

See also: **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species; Genecology and Adaptation of Forest Trees; Genetic Systems of Forest Trees. **Genetics and Genetic Resources**: Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics. **Temperate Ecosystems**: Fagaceae. **Tree Breeding, Principles**: Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes.

Further Reading

Axelrod DI (1983) Biogeography of oaks in the Arcto-Tertiary province. *Annals of the Missouri Botanical Gardens* 70: 629–657.

Camus A (1936–1954) Les chênes, Monographie du genre *Quercus* et Monographie du genre *Lithocarpus*. Encyclopédie Economique de Sylviculture. Paris, France: Editions Le Chevallier.

Guttman SI and Weight LA (1989) Electrophoretic evidence of relationships among *Quercus* (oaks) of eastern North America. *Canadian Journal of Botany* 67: 339–351.

Kremer A (ed.) (2002) Range wide distribution of chloroplast DNA diversity and pollen deposits in European oaks: inferences about colonisation routes and management of oak genetic resources. *Forest Ecology and Management*, Special issue, 156(1–3): 224.

Kremer A, Savill PS, and Steiner KC (eds) (1993) Genetics of oaks. *Annales des Sciences Forestières* 50(1): 1s–469s.

Manos PS, Doyle JJ, and Nixon KC (1999) Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (*Fagaceae*). *Molecular Phylogenetics Evolution* 12: 333–349.

Turok J, Kremer A, and de Vries S (eds) (1998) *Proceedings of the first EUFORGEN meeting on Social Broadleaves*. Rome, Italy: IPGRI.

Pinus radiata Genetics

R D Burdon, New Zealand Forest Research Institute, Rotorua, New Zealand

Introduction

Pinus radiata is arguably the most domesticated of all forest trees. It is grown in exotic plantations occupying over 4 million ha, an area roughly 500 times its natural extent. Overall these plantations are highly productive, and many are intensively managed. Associated with the intensive management, several large-scale, intensive genetic improvement programs have developed, which have prompted a large volume of genetic research on the species. Indeed, this genetic research, and commercially motivated research on most other aspects of the species' biology, have led to the species assuming the role of a model species for research into forest trees. The genetics of the species are of twofold interest. On the one hand, the story typifies that of many conifers, and pines in particular, in respect of karyotype, genomic characteristics, and genetic system in general. On the other hand, there are a number of features that are highly distinctive of the species. Notable among these are the biogeography, with five discrete natural populations that are differentiated by a combination of adaptive features and apparent founder effects, and the conspicuously high level of functional genetic variation from tree to tree. Intensive genetic improvement began from around 1950, and is now being pursued at varying levels of sophistication in at least five countries. It has delivered major genetic gains, in growth rate, tree form, and disease resistance. Improvement work is shifting in emphasis towards improving wood properties, while differentiated breeds are being developed. Challenges remain in the management of gene resources.

The Genetic System

Breeding System

Like almost all pines (*Pinus* spp.), *P. radiata* is an outbreeder. Effective self-fertility, reflected in filled seed produced upon selfing, is very incomplete, but highly variable from tree to tree. This is consistent with the postulated mechanism of a fairly high 'load' of recessive embryo lethal genes, combined with the archegonial polyembryony – with this polyembryony, the set of viable seed can be much higher than the percentage incidence of viable zygotes resulting from inbreeding.

The viable offspring produced by self-pollination show, on average, marked inbreeding depression, with poorer growth and competitive ability than outcross progeny. This inbreeding depression reflects sublethal deleterious recessive genes. It varies markedly according to parents and individual offspring. This variability, in both effective self-fertility and inbreeding depression in viable offspring, is consistent with random variation among parents in the load of deleterious recessive genes.

Matings between relatives that are less extreme than selfing also cause inbreeding depression, roughly in proportion to the relatedness between the seed- and pollen parents.

Seed collections made from natural stands show appreciable inbreeding depression, resulting from neighborhood inbreeding whereby neighboring trees tend both to be related to each other and to interpollinate. In plantations, the natural neighborhood structures are typically broken down, and seed collections from plantations show negligible signs of inbreeding. Self-thinning evidently eliminates inbred individuals preferentially during the life of a natural stand.

Genomic Characteristics

Pinus radiata is strictly diploid with a haploid chromosome number of 12. Any departure from the diploid state evidently reduces natural fitness to zero. Regarding the karyotype, the chromosomes are extremely large, all of similar size and metacentric, with only subtle distinguishing features. In these respects the species is typical of pines (*Pinus* spp.) in general, and also of most other conifer genera.

In keeping with the size of the chromosomes, the genome is enormous, around 2×10^{10} basepairs, but over 95% noncoding. However, despite the extremely stable karyotype, it appears that there is a relatively high mutation rate, judging from the level of the genetic load and the general sensitivity of pines to gamma rays. In keeping with the genomic stability, DNA analysis has revealed a very high level of homologies, in respect of functional genes and their loci within chromosomes, between *P. radiata* and *P. taeda*, which has become another main 'model-species' pine.

Crossing-over of chromosomes in meiosis is high – estimated map length is around 1800–2000 centi-Morgans – and is evidently slightly higher in male than female meiosis.

Genetic Architecture

Taxonomic Position and Crossability

Pinus radiata belongs within the subgenus *Pinus* (syn. *Diploxylon*) or the 'hard pines.' It has recently been assigned to a section Attenuatae van der Burgh (the 'California closed-cone pines') which has recently been separated from the section Oocarpae, which now comprises a group from Mexico–Central America. Within the Attenuatae, it is readily crossable with *P. attenuata* and moderately crossable with some southern populations of *P. muricata*, but tends to be reproductively isolated from both species by pollination season and distance. However, there is one area where hybrids with *P. attenuata* occur naturally, but without conclusive signs of long-term introgression. *Pinus radiata* is also known to be weakly crossable with three or four members of the Oocarpae.

Population Differences

The pattern of natural population differences reflects the distinctive natural distribution. The species occurs in just five discrete natural populations (**Figure 1**). While all populations exist in a particular variant of a Mediterranean climate, created by a cold ocean current reducing summer temperatures and causing summer sea fogs, the habitats of the populations differ significantly (**Table 1**). In addition, the geographic separation between populations varies widely. In keeping with that, the degree of taxonomic separation varies. The southernmost populations, from Cedros and Guadalupe Islands, are recognized as separate varieties, vars *cedrosensis* and *binata* respectively, both having their needles usually in pairs rather than threes. The three northern populations, on the mainland, are assigned to var. *radiata*; that from Cambria is apparently the most distinct.

Chemotaxonomic information is very incomplete, but it serves to reinforce a picture of highly multidimensional differentiation among the various natural populations. In this pattern, the apparent affinities between individual populations can depend greatly on the trait in question, such that many traits have to be considered simultaneously, preferably in common-garden experiments, for the overall pattern to become clear. However, immunoassay techniques have been used to give a measure of genetic distances between populations, with results that generally match the classical taxonomic picture.

The populations differ not only in traditional taxonomic traits and phytochemistry but also in tree morphology, growth rate, site tolerances, and pest and disease resistance (which are often the effective manifestations of site tolerances).

Some population differences for morphological traits, turpentine composition, and wood density are summarized in **Table 2**. Corresponding differences in growth rate, site tolerances and disease and pest resistance are summarized in **Table 3**. In some morphological features, such as cone size and branching pattern, marked population differences are superimposed upon large tree-to-tree differences. However, for needles per fascicle (except on vigorous shoots of young trees) and bark thickness (except in old trees), tree-to-tree differences are totally subordinate to population differences.

The pattern of population differences can in part be interpreted in terms of adaptation to the different environments. For example, the strong taproot development of the Cedros population, and to a lesser extent the Guadalupe population, are presumably an adaptation to more intense drought on the islands. The greater palatability of Guadalupe to browsing animals can be readily interpreted as reflecting a lack of browsing mammals on the island. However, there are other population differences that are difficult to interpret as being adaptive. It therefore appears that some of the differences reflect founder effects and genetic drift occurring in the processes of colonizations, local extirpations, and coalescences that evidently resulted from climatic fluctuations and eustatic sea-level changes that have occurred since the Pleiocene.

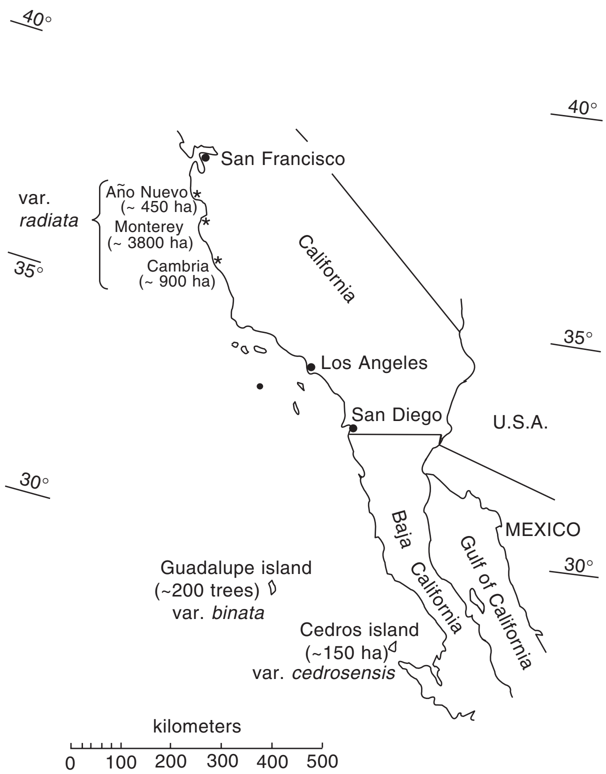


Figure 1 Map showing natural distribution of *Pinus radiata*. Current extent is shown for each population, being reduced by urbanization at Monterey and Cambria and grossly reduced on Guadalupe island. Adapted with permission from Burdon RD (2000) *Pinus radiata*. In: Last FT (ed.) *Ecosystems of the World*, vol. 19. *Tree Crop Ecosystems*. Amsterdam, The Netherlands: Elsevier.

Marker and Genomic Differentiation

Some strong population differences exist within *P. radiata* with respect to the standard isozyme systems, in contrast to the norm of isozyme variation within species being almost entirely among individuals within populations. Indeed, there are electromorphs that represent high-frequency private alleles for some of the populations. Actual DNA marker differentiation has not been studied thoroughly. Markers (simple sequence repeats or SSRs) have been developed that give excellent 'fingerprinting' of individual genotypes and pedigree verification, but such markers, because they are so polymorphic within populations, are inherently unsuited to differentiating among populations. Thus, while populations will surely be differentiated by DNA markers,

Table 1 Natural occurrence and habitats of *Pinus radiata*

Population	*Latitude (°N)*	*Altitude (m)*	*Exposure*	*Rainfall (mm)*	*Geology/soil*	*Extent (ha)*	
						Historic	*Current*
Año Nuevo	37	0–330	Very varied	675–900?	Argillite-derived, slightly calcareous	450	450
Monterey	$36\frac{1}{2}$	0–420	Generally moderate	400–650?	Very varied geology and soils	7400	3800
Cambria	$35\frac{1}{2}$	0–180	Varied	450–575?	From single sandstone formation	1400	900
Guadalupe	29	330–1200	Severe	150–500?	Basaltic, rocky	250?	200 trees
Cedros	28	380–640	Locally severe	150–250?	Skeletal, old sediments and metamorphics	150	150

Adapted from Burdon RD (2000) *Pinus radiata*. In: Last FT (ed.) *Ecosystems of the World*, vol. 19: *Tree Crop Ecosystems*, pp. 99–161. Amsterdam, The Netherlands: Elsevier.

Table 2 Native-population differences within *Pinus radiata* in some morphological traits, turpentine composition, and corewood density

Trait	*Population*				
	Año Nuevo	*Monterey*	*Cambria*	*Guadalupe*	*Cedros*
Bark thickness (young trees)	Thinnish	Thickish	Medium	Thin	Thin
Cone length (cm)	8–15	5.5–13	10–19	5–11.5	3.5–9.5
Mean seed weight (mg)	42	23	48	29	29
Needles per fascicle	3	3	3	2	2
Persistence of juvenile features	Low	High	Very high	Very low	Low
α-pinene (% pinenes) in wood turpentine	23	35	34	21	14
Inner corewood density (site-dependent)	325	330	320	360	360
Sinker root development	Medium	Medium	Least	Strong	Greatest

(Adapted from Burdon RD (2000) *Pinus radiata.* In: Last FT (ed.) *Ecosystems of the World,* vol. 19: *Tree Crop Ecosystems,* pp. 99–161. Amsterdam, The Netherlands: Elsevier.)

Table 3 Differences between natural populations of *Pinus radiata* in growth potential, site tolerances, and resistance to pests and pathogens

Feature	*Grade of evidence*	*Population*				
		Año Nuevo	*Monterey*	*Cambria*	*Guadalupe*	*Cedros*
Growth potential	a	+	+	+	−	− −
Ease of transplanting	bc	+	o	−	+(+)	− −
Resistance to/tolerance of:						
Frost	b	+ +	+	−	o?	− −
Snow damage	c	+	o	−	n.d.	n.d.
Boron deficiency	b	+	+	+	−	− −
Phosphorus deficiency	b	−	+ +	+ +	−?	n.d.
Soil salinity	bc	o	+	+ +	− −	−
Damage by pathogens						
Dothistroma pini	ab	+ +	+ +	− −	o	− −
Cyclaneusma minus	a	+	+ +	− −	−	−?
Sphaeropsis sapiniea	b	+ +	+ +	− −	− −	−
Phytophthora cinnamomi	b	− −	+	+ +	n.d.	n.d.
Endocronartium harknesii	b	o	−	− −	+ +	+
Damage by invertebrates						
Pineus pini	c	+	+	− −	− −	+
Damage by mammals						
Deer/rabbit browse	bc	o	o	o	−	+
Deer browse	b	−	o	+	n.d.	n.d.
Porcupines	b	+	+	− −	n.d.	n.d.

o, average; +, better than average; + +, markedly better than average; −, worse than average; − −, markedly worse than average; n.d., no firm data available.
a–c denote decreasing weight of evidence.
(Reproduced with permission from Burdon RD (2000) *Pinus radiata*. In: Last FT (ed.) *Ecosystems of the World,* vol. 19: *Tree Crop Ecosystems*, pp. 99–161. Amsterdam, The Netherlands: Elsevier.)

there are not yet the markers identified whereby a tree can be assigned unequivocally to a single native population, let alone to its correct hybrid ancestry.

Within-Population Genetic Variation

Tree-to-tree genetic variation, both visible and cryptic, is a striking feature of *P. radiata*, which has led to much past confusion among taxonomists. Cone size and shape show much variability, which is superimposed upon the considerable population differences. Dramatic variation exists in branching pattern (**Figure 2**), with neighboring trees often ranging from being monocyclic or uninodal (with only one cluster of branches produced in a year's growth on the leader) to highly polycyclic (with up to six such clusters); this variability is of profound importance for breeding programs and wood utilization. Considerable tree-to-tree genetic variation is also evident for growth rate, resistance to some diseases, stem straightness, a wide range of wood properties, turpentine composition, rate of onset of

(a) (b)

Figure 2 *Pinus radiata* trees of contrasting branching patterns. (a) This tree has a highly polycyclic (or multinodal or short-internode) branching habit, producing several quite closely spaced branch clusters on each year's growth of the leader. In consequence, the branches are relatively small, giving a dispersed pattern of knots in timber, which favors producing structural grades. It is usually associated with less susceptibility to malformation and often better straightness and faster growth, at least early in the rotation. This sort of habit has been favored for the main breeding programs of New Zealand and Chile. Preferable for structural timber, it requires pruning in order to produce clear timber, which has been widely practiced in New Zealand. (b) This tree has an essentially monocyclic (or uninodal or long-internode) branching habit. The branches are large and steep-angled, but clearcuttings can be obtained between branch clusters without pruning. Prone to malformation and general poor form on many sites, this habit has been pursued in a subsidiary breeding program in New Zealand to produce a long-internode breed. This variation is strongly heritable, with the two trees representing extremes of an essentially normal distribution. For many sites, the ideal might be two co-equal branch clusters per year's leader growth, but that can only be expected reliably through mass propagation of well-proven clones. Courtesy of New Zealand Forest Research Institute Ltd.

some adult characteristics, and soil tolerances. Soil tolerances can generate substantial genotype–site interactions among phosphorus-deficient sites and elsewhere.

Estimated heritabilities and additive genetic coefficients of variation (which between them encapsulate the scope for genetic improvement) are shown for a range of traits in **Table 4**. While some of the values relating to branching pattern and cone characteristics may be exceptional, those for other traits seem fairly typical for the genus. For many additional wood properties only broad-sense estimates are available; while generally very high, they are unlikely greatly to exceed narrow-sense heritabilities. Some of the wood properties, e.g., grain spirality and percentage heartwood, can show very high coefficients of variation, but such figures need to be interpreted with caution. As always, heritabilities for individual traits can depend, to varying degrees, on both the populations and the environments.

Relatively few between-trait genetic correlations are known at all well (**Table 5**), although, as with heritabilities, the values may vary according to both population and environment. Those best known involve positive associations between growth rate, frequency of branch clusters, light, wide-angled

Table 4 Estimated heritabilities and phenotypic coefficients of variation among individuals within base populations in *Pinus radiata* for different traits, together with likely economic significance for genetic improvement

Trait	*Heritability*	*Coefficient of variation (%)*[a]	*Economic significance*
Turpentine composition	>0.9		Negligible
Wood density (cores or disks)	0.7	7	Sometimes major
Cone characters[b]			
Volume, seed weight	>0.5	20–35	Minimal
Length, shape, scale no.	>0.5	12–18	Minimal
Grain spirality	0.3–0.7	~45	Sometimes major
Branch clusters on bole	>0.5	20–30	Often high, but indirect
Stem sinuosity[c]	0.4		Not major (−ve)
Wood density (penetrometer or torsiometer measurements)	0.3–0.4		As for wood density
Branching habit overall[c]	0.3		Generally high
Height to first cone	0.3	20–30	Little direct importance
Dothistroma attack[c]	0.3		Locally major
Cyclaneusma needle cast[c]	0.1–0.35		Considerable (−ve)
Branch angle (steepness)[c]	≤0.2		Considerable (−ve)
Height	0.2	12	Limited in itself
Stem diameter	0.1–0.3	15	Major
Stem volume	0.1–0.3	30	Major
General stem straightness[c]	0.1–0.3		Generally major
Branch diameter	0.2		Major (−ve)
Frost resistance (growth room)	0.2		Minor overall
Butt sweep[c]	0.1–0.2		Often major (−ve)
Forking, etc.	0.05–0.1		Major (−ve)
Wind damage	0.05		Locally major (−ve)
Leader dieback	0.05		Sometimes important

[a] Where measurement scale allows valid estimate.
[b] Broad-sense heritability, instead of narrow-sense, but unlikely to be much greater than narrow-sense.
[c] Based on visual scores, with observer error depressing effective heritability values.
Reproduced from Burdon RD (1992) Genetic survey of *Pinus radiata*. Part 9. *New Zealand Journal of Forestry Science* 22: 275–298, with permission.

Table 5 Approximate values of the better-estimated between-trait genetic correlations in *Pinus radiata*

	Height	*Wood density*	*Stem straightness*	*Branching frequency*	*Forking (incidence)*	*Branch diameter*	*Branch angle*
Stem diameter	0.7	−0.2 to −0.4	0.1	0.15–0.45	0.1		0.1
Height		0.15	0.2	0.2–0.45	0.35		0.25
Wood density			0	−0.05	0		
Stem straightness				0.4	0.5		0.15
Branching frequency					0.3–0.5	0.75	0.6
Forking						0.3	0.4
Branch diameter							0.65

Note: Positive signs denote favorable genetic correlations in relation to ideal of fast growth, high wood density, small, wide-angled branches, zero forking, and polycyclic (multinodal or short-internode) branching habit. Hence there are a number of adverse correlations in relation to an ideal of long internodes that would allow significant clear cuttings without pruning, more so on some sites than others.
After Burdon RD (1992) Genetic survey of *Pinus radiata*. Parts 1–9. *New Zealand Journal of Forestry Science* 22: 275–298.

branching, stem straightness, and freedom from malformation, and a negative association between wood density and stem diameter. Significant constraints therefore face the breeder in trying to pursue long internodes (which offer clear cuttings without pruning) along with improved growth and form, or both increased wood density and volume production.

Genotype–environment interactions are evident in respect of both variation among sites in expression of genetic variation and rank changes among sites in performance of genotypes. Differences in tree form can be more strongly expressed on fertile sites. Rank changes are strongly evident between phosphorus-deficient sites and elsewhere (pointing to genetic variation in tolerance of this deficiency) but otherwise tend to be limited.

Within-population variation in genetic markers (isozymes, restriction fragment length polymorphisms

(RFLPs), randomly amplified polymorphic DNA (RAPDs), amplified fragment length polymorphisms (AFLPs), SSRs) is significant, but it does not stand out from other conifer species in the way that much of the morphological variation does.

Early Domestication Genetics

Domesticated stocks of the species have arisen since the species was first introduced as an exotic, around 1850–1860 for South Africa, Australia, New Zealand, and Spain, and in 1885 for Chile. New Zealand evidently became self-sufficient for seed by the early 1880s, and made significant exports of unimproved seed to South Africa at least in the 1920s and to Australia until the middle of the twentieth century. Documentation of follow-up seed importations by Chile and Spain has not been traced. It appears that the two northernmost of the natural populations, Año Nuevo and Monterey, have been the progenitors of almost all the domesticated stocks, with a disproportionate contribution from the small Año Nuevo population. For many purposes these are the natural populations that are best adapted to the exotic environments, but even broader adaptation can presumably be obtained from drawing germplasm from the other populations.

While domesticated stocks may have come from a very incomplete and unbalanced representation of the natural range, seed importation records for New Zealand and genetic evidence indicate a fairly broad ancestral base in terms of numbers of individuals.

Even before intensive breeding began, some genetic improvement occurred in a process of landrace development. Release from the 'neighborhood inbreeding' of natural stands has evidently been a positive factor. There have also been some genetic shifts in response to pressures of natural and silvicultural selection in the adoptive environments, although it is difficult to quantify these shifts accurately. Heterosis, or hybrid vigor, from crossing between two natural populations, has been postulated but not proven.

Intensive Genetic Improvement

General History

Pioneering research on genetic variation in *P. radiata* began in Australia during the 1930s, under the auspices of the (Commonwealth) Forestry and Timber Bureau, Canberra. Intensive breeding programs began in New Zealand, Australia, and South Africa in the 1950s. These were based on local stocks, in the belief that provenance variation would not be important. This decision was put to the test in parallel or subsequent provenance or provenance/progeny trials. In fact, it proved to be justified, despite initial underestimation of provenance variation and the likelihood that additional germplasm from the natural range could bring long-term benefits. However, some of these benefits may only be realizable in segregating generations, after the F_1.

Improvement began with very intensive selection of 'plus trees,' mainly in commercial stands (**Figure 3**). Selection criteria varied significantly among agencies according to perceptions of whether growth rate or form was the higher priority for improvement. The plus trees were grafted into archives prior to establishing grafted clonal seed orchards. This put tree breeders on a long 'learning curve' in the siting, establishment, and management of the orchards. Difficulties arose with delayed incompatibility of grafts (or else obtaining cuttings from postjuvenile trees), achieving good pollen isolation, and with seed yields.

An interim improvement measure, pending self-sufficiency for orchard seed, has been collection of seed from the best trees in stands, either at felling or on standing trees. This was much helped by the serotinous cones which could store several years' seed crops on the trees. In addition, progeny trials were available as back-up seed sources.

Figure 3 One of the original *Pinus radiata* plus trees selected in a closed stand in New Zealand, shown well after the selection age. The outstanding vigor of this parent ('Clone 55') characterizes almost all its progeny. The wood of the progeny, while of low density, has some very desirable technical properties. Courtesy of New Zealand Forest Research Institute Ltd.

Progeny testing was embarked upon from the outset, with varying thoroughness and success. However, it became appreciated, by the late 1960s, that the extremely intensive selection of plus trees left little scope for reselection on the basis of progeny-test information, and severely restricted the genetic base for long-term breeding. Further selection of first-generation plus trees was done, making vastly more selections.

Despite the technical problems, clonal seed orchards came close to meeting planting requirements, and actually exceeded them in some areas. However, the slow and incomplete capture of genetic gain prompted the development of new delivery systems. Selection of orchard sites was greatly improved. Hedged seed orchards were adopted in some quarters, which allowed controlled pollination with full capture of genetic gain and greater flexibility, and they are easier and safer to manage and harvest. Other types of orchard that allow controlled pollination have also been developed (**Figure 4**). Vegetative multiplication of small amounts of top-quality seed is a slightly more recent development that can further speed up the capture of genetic gain. It is being done on a large operational scale using nursery cuttings, and on a smaller scale using tissue-culture plantlets, while embryogenesis from seed embryos is being pursued. Embryogenesis, while more difficult to achieve in pine than in spruces (*Picea* spp.), offers a platform for future genetic transformation. Clonal forestry, based on mass propagation of well-characterized, intensively select clones, is being pursued by a few agencies, and is close to being fully developed, although there still remain some problems of long-term storage of clones to retain full vigor and ease of propagation.

Figure 4 Clonal seed orchard of *Pinus radiata* designed to produce seed of superior genetic quality by controlled pollination. This is one of several types of orchard that has been developed to avoid the operational problems of producing seed on tall, tree-form grafts or cuttings, and is an adaptation of the meadow orchard system of producing apples. A site has been chosen that favors early and profuse seed production on the grafts. Often such seed is now produced in limited quantities for mass vegetative multiplication, still mainly by nursery cuttings. Courtesy of New Zealand Forest Research Institute Ltd.

As befits the species' commercial importance and its model-species status, it is the subject of a full-scale genomic sequencing project, but the information is proprietary.

Early improvement work was directed mainly at improving growth rate and tree form, in varying emphasis on the two. Genetic gains achieved have generally been large (**Figure 5**), typically reflecting

Figure 5 Trees of *Pinus radiata* produced by early pair-crossing between intensively select parents on a very high-quality site in New Zealand. Tree form is strikingly good for the site and stocking. Planted at 750 stems ha^{-1} in pasture, and thinned at age 8 to 215 stems ha^{-1}, 18-year predominant mean height was 33.5 m, mean breast height diameter 54 cm, with 480 m^3 stemwood ha^{-1}. The better pair-crosses of similar material, kept at higher stockings but on a similar site, gave mean annual increments approaching 50 $m^3\,ha^{-1}\,year^{-1}$ at age 27, compared with an expected value of 30–35 $m^3\,ha^{-1}\,year^{-1}$ for unimproved stock. With large genetic gains achieved in growth and tree form, attention is shifting to improving wood properties to help produce high-quality raw material on short rotations. Courtesy of New Zealand Forest Research Institute Ltd.

the relative emphasis on growth and form respectively. Since then there has been some focus on resistance to needle-cast diseases, with local or sporadic efforts directed at resistance to some other diseases. More recently has come increasing emphasis on improving wood properties (**Figure 6**), to offset the impacts of various measures that cut effective growing costs, viz. shorter rotations, fertilizer use, heavier thinning regimes.

Genetic Improvement in Individual Countries

New Zealand The breeding program was initiated by the Forest Research Institute (FRI) within the New Zealand Forest Service. FRI also conducted associated research, gathering up some earlier work. A national program was effectively operated until 1987, when the Forest Service was dissolved. Following that, the New Zealand Radiata Pine Breeding Cooperative was created, with FRI doing the breeding and genetic research, but with increasing in-kind contributions from member companies after corporatization and then privatization of Forest Service plantations. Cooperative members have come to include some from Australia, the Forestry Commission of New South Wales and some smaller concerns. During 2000–2002, the Cooperative became a limited-liability company. In the meantime, some companies have developed their own propagation and clonal programs as their own intellectual property. In 2003 a decision was made to terminate state funding of breeding and gene-resource work and immediately associated research.

Intensive plus-tree selection began in the early 1950s, for establishing regional seed orchards, although the regionalization proved to be unnecessary.

Figure 6 Sampling a *Pinus radiata* candidate for selection for determining several key wood properties by taking a core of 12 mm diameter. Courtesy of New Zealand Forest Research Institute Ltd.

The first block of orchard was planted in 1958, to start producing seed in 1968. Orchards produced enough seed for the whole country by 1986. Since then, control-pollinated orchards have become predominant, with considerable vegetative multiplication. Fully clonal systems, while still hampered by imperfect control of maturation, are being implemented on a significant scale by two companies.

Following the initial round of plus-tree selection, many more first-generation plus trees were selected in 1968–1970, to give a broadly based breeding population, with a further round during 1984–1987.

Selection was initially for growth and form, arriving at a strongly polycyclic (or multinodal or short-internode) ideotype (**Figure 2a**), although a side-program pursued a long-internode ideotype (**Figure 2b**) as an insurance. Recently a portfolio of differentiated breeds has been created, to serve different sites and end-uses as well as addressing market uncertainties.

Australia Although the federal organization (Forest and Timber Bureau, later the Division of Forestry and then Forestry and Forest Products) of the Commonwealth Scientific and Industrial Research Organisation (of Australia) (CSIRO) started the research, breeding programs began under the auspices of individual states and Australian Capital Territory (ACT). Of the states, New South Wales, Victoria, and South Australia had a major involvement in the species, with lesser involvements on the part of Western Australia, ACT, Tasmania, and Queensland. All the states and ACT began intensive breeding by 1960 or soon after, with two programs in Victoria, although some programs have effectively lapsed or been absorbed. Lack of coordination among the states, and the consequent thin spread of expertise, hampered progress, but some coordinated efforts were eventually achieved under the auspices of the Australian Forestry Council. The Council established a research working group that met biennially to address forest genetic improvement in general, and New Zealand participants were eventually admitted.

Selection emphasis has been more on growth rate and less on tree form than in New Zealand, but some shifts towards establishing new plantations on more fertile ex-pasture sites call for greater emphasis on improving tree form.

In 1978 CSIRO led a major initiative to collect seed from natural stands for *ex situ* gene resources. Numerous plantings resulted from that, but are in need of active management. Further seed collection was done on Guadalupe island in 1991.

In 1983, after disastrous fires in South Australia, the Southern Tree Breeding Association was formed, initially to address a crisis of availability of seed of acceptable genetic quality. Members now include, in addition to various South Australian agencies, ones from Victoria, Western Australia, and Tasmania.

South Africa Despite an early start with breeding, in the 1950s, activity has been limited by the restricted areas over which the species succeeds.

Chile An abortive start by Instituto Forestal in the early 1970s was followed by the successful establishment of a Cooperative (initially Convenio) between the Southern University of Chile and industry parties. Established along the lines of the Industry/North Carolina University Tree Improvement Cooperative, it began with individual members setting up their own seed-orchard programs. However, it appears not to have led to a coordinated national program based upon free exchange of genetic material, although some interregional integration has occurred within large corporate structures.

Initial plus-tree selection was intensive, aimed at much the same short-internode ideotype as in New Zealand. Each member company established a 42-clone grafted seed orchard. Choice of orchard site was guided by experience in New Zealand and Australia, and was mostly very successful, leading to orchards meeting most members' seed requirements in about 10 years.

Among major member companies there have been separate developments, pursuing vegetative multiplication, and sophisticated biotechnology for appropriating intellectual property.

Spain In the late 1980s a breeding program was set up for the Basque autonomous region, on the northern coast just west of the Pyrenees, based in Vitoria. By far the main emphasis has been on breeding for diameter growth. Problems in finding a suitable seed-orchard site within the region have led to the establishment of an orchard far to the south, in Andalusia.

Hybridization

Experimental hybridization of *P. radiata* was undertaken as early as the 1930s, the main success being crossing with *P. attenuata*. While this hybrid had advantages, difficulties of mass production, and limited availability of sites where it had a decisive advantage prevented its large-scale planting. Interest in interspecific hybrids has been rekindled by a combination of availability of technology for vegetative multiplication of seeds or seedling stock, combined with a desire to extend site tolerances and/or improve resistance to diseases that are threats.

Genetic Transformation

Genetic transformation is being researched in *P. radiata*, initially as proof of concept, with current emphasis on control of reproduction and herbicide resistance, but with a view to other goals, notably manipulating wood properties. It is serving as a research tool. Operational use is envisaged as being in the context of clonal forestry.

See also: **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species; Genetic Systems of Forest Trees; Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics; Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Genetics and Improvement of Wood Properties. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts.

Further Reading

Burdon RD (2000) *Pinus radiata*. In: Last FT (ed.) *Ecosystems of the World*, vol. 19: *Tree Crop Ecosystems*, pp. 99–161. Amsterdam, The Netherlands: Elsevier.

Burdon RD (2001) *Pinus radiata*. In: CAB International (compil.) *Pines of Silvicultural Importance*, pp. 359–379. Wallingford, UK: CAB International.

Burdon RD and Moore JM (eds) (1997) *IUFRO '97 Genetics of Radiata Pine*. Proceedings of NZFRI-IUFRO conference 1–4 December and workshop 5 December, Rotorua, New Zealand. FRI Bulletin no. 203.

Burdon RD (1992) Genetic survey of *Pinus radiata*. Parts 1–9. *New Zealand Journal of Forestry Science* 22: 275–298.

Burdon RD, Hong SO, Shelbourne CJA, *et al.* (1997) International gene pool experiments in *Pinus radiata*: patterns of genotype–site interaction. *New Zealand Journal of Forestry Science* 27: 101–125.

Burdon RD, Firth A, Low CB, and Miller MA (1998) *Multi-site Provenance Trials of* Pinus radiata *in New Zealand*. Forest Genetic Resources no. 26, pp. 3–8. Rome: FAO.

Jayawickrama KJ and Carson MJ (2000) A breeding strategy for the New Zealand Radiata Pine Breeding Cooperative. *Silvae Genetica* 40: 82–90.

Millar CI (2000) Evolution and biogeography of *Pinus radiata* with a proposed revision of quaternary history. *New Zealand Journal of Forestry Science* 29: 335–365.

Moran GF, Bell JC, and Eldridge KG (1988) The genetic structure and conservation of the five natural populations of *Pinus radiata*. *Canadian Journal of Forest Research* 18: 506–514.

Rogers DL (2002) *In situ* conservation of Monterey pine (*Pinus radiata* D. Don): information and recommendations. Report no. 26. Davis, CA, USA: University of California Division of Agriculture and Natural Resources, Genetic Resources Conservation Program.

TREE BREEDING, PRACTICES

Breeding and Genetic Resources of Scots Pine

O Savolainen, University of Oulu, Oulu, Finland
K Kärkkäinen, Finnish Forest Research Institute, Vantaa, Finland

Introduction

This article covers Scots pine (*Pinus sylvestris*) genetic resources and breeding, and especially contrasts issues in this species to those in other important species of conifers. The emphasis is on results on northern countries, where this species is very important and has been intensively studied. As most pines are at early stages of domestication, breeding is still largely aided and/or constrained by the natural features of the species. Breeding programs have not advanced beyond F_2 generation seeds and advanced generations are not yet available. Commercially sold improved seed is still based mostly on first-generation seed orchards. Further, the silvicultural production populations are in cultivated forest-like situations rather than intensively managed plantations. In these conditions Scots pine has to grow for the full rotation, even 80–100 years.

Biological Characteristics of Scots Pine

Scots pine's natural distribution ranges from western Scotland to eastern Siberia and from northern parts of Scandinavia to central Turkey or southern Spain. It has the widest distribution of all pine species, and, in relation to its range, the discontinuities in its distribution are minor. The species is wind-pollinated and predominantly outcrossing. Very efficient pollen flow has been documented through direct measurements of radioactively labeled pollen or by measuring seed set in isolated young stands that do not yet produce any own pollen. Early on, it was evident that seemingly functionless (nonadaptive) variation in seed cone morphology is not differentiated across populations, consistent with the high gene flow. Many studies on a wide range of populations have shown that at neutral (or near-neutral) genetic markers, such as isozymes or repeat sequences of DNA (microsatellites), allelic frequencies in populations over the whole area of distribution are quite uniform, with less than 5% of the total variation between populations. The same finding has also been made in initial studies of nucleotide sequence variation. Thus, all available evidence suggests that the whole distribution area of Scots pine functions in many ways as a single enormous population, with very minor differentiation at marginal very isolated populations, e.g., in Spain. Initial studies of maternally inherited markers, in mitochondria, confirm that seed migration is not as efficient, but thorough studies of maternally inherited markers are still lacking. This picture of the enormous population size with efficient gene exchange gains further support from the fact that the levels of variation, e.g., at the standard isozyme loci, have been among the highest in any organism. Further, even if quantification of variation at the DNA level has not been done extensively, it has been rather easy to detect genetic variation for genetic mapping with various DNA techniques.

The broad area of distribution covers a wide range of climatic conditions. Even within Finland the length of the thermal growing season ranges from 120 days in the north to 170 days in the south (latitude 60° N to 68° N). Consistent with the large range of environmental variation, many adaptive traits, such as timing of growth or the development of frost tolerance show steep clines, correlated with the environmental gradients. In common-garden experiments in greenhouses, first-year seedlings of northern populations form the terminal buds and become frost-tolerant several weeks before the southern Finnish strains. Such clines extend also south of the Finnish populations. While populations in different latitudes are highly differentiated, they still contain much genetic variation in these traits, as documented by quantitative genetic studies. The adaptive significance of the variation has been demonstrated by extensive transfer experiments between latitudes and altitudes in Sweden. Results from large-scale provenance trials suggested that 1° of latitudinal transfer northward causes a decrease in survival of approximately 10%, while an increase of 100 m in elevation results in a reduction of survival of approximately 3%. The evidence thus suggests that the patterns in quantitative traits are due to intense natural selection that overcomes the high level of gene flow at the relevant loci, and creates a pattern of detailed adaptation to the climate. In the north the relevant trait is adaptation to the short growing season and survival in cold conditions, in the southern margin (e.g., Spain) traits like drought resistance may be most important. This high differentiation for quantitative traits affecting survival has to be taken into account when breeding the species. Note that the parallel selection for, e.g., early cessation of growth and early frost tolerance results in high correlation of these traits among populations. However, this does not imply that the traits are genetically correlated at the within-population level. In fact, initial quantitative trait locus (QTL) mapping studies have shown that different loci are responsible for growth cessation and the development of frost tolerance.

Many other conifer species are much less sensitive to such transfers between areas, and breeding for specific geoclimatic zones may not be as important, e.g., in *Pinus radiata* or *P. taeda*.

Breeding System

Another important trait of Scots pine is its breeding system. There is no self-incompatibility system, and wind pollination results in considerable proportions of self-pollination and self-fertilized zygotes. Direct measurements at the zygote stage have not been made, but it can be inferred that the primary selfing rate must be often at least 20%. In the mature seed, however, there are usually only a low percentage of selfs. There seems to be little occurrence of other kinds of inbreeding. Several studies have shown that adult Scots pine populations do not have any selfs. Thus, between the zygote stage and the adult tree stage the selfs are preferentially eliminated by usually severe inbreeding depression. Much of the elimination takes place very early, during seed development. At the age of a few years natural populations show little evidence of inbreeding. When selfs survive in experimental conditions, they show a cumulative decline in relative survival with lowered fitness over several decades due to poorer growth, which results in size-specific elimination of selfs by competition. The inbreeding depression is presumably due to a large number of deleterious recessive genes in the Scots pine genome. The average tree is heterozygous for 8–10 so-called embryo lethals, which means that Scots pine is among the species with the very highest genetic loads. Scots pine reproduction is exclusively sexual. Note that the generation time is very long; the trees do not become fully reproductively mature before the age of 20. Not only is there no asexual reproduction in the natural populations, but Scots pine has also proved a very recalcitrant species for various modes of vegetative propagation.

Natural versus Artificial Regeneration

A large proportion of Scots pine forests is still naturally regenerated. In some areas, e.g., in Russia, the huge annual requirement for Scots pine seed still exceeds the supply of genetically improved seed. Artificial regeneration is either with seedlings or through sowing of unimproved seed. In Scandinavia, natural regeneration has an established role in forest management practices even in areas with ample breeding material available. Natural regeneration is preferred over artificial regeneration mainly because of the lower cost. Moreover, problems in the development of planted seedlings have resulted in decreased use in some areas. Furthermore, problems in producing seeds adapted to the intended area (owing to problems with background pollen contamination in seed orchards) have slowed the use of improved material in northern areas. This has forced foresters to use natural regeneration and/or seeds from natural seed-tree stands in artificial regeneration in the northern areas.

Breeding Goals

The boreal flora with only a few tree species is challenging for tree breeders: seedlings of Scots pine may be planted, e.g., on dry and poor or relatively moist and nutrient-rich soils. The rotation age of Scots pine is much longer (80–100 years) than in some other conifers, e.g., loblolly pine in the southern USA (25–28 years). Enough genetic variation must thus be maintained in Scots pine populations to meet the requirements of spatially and temporally heterogeneous environments.

When breeding for northern environments, survival is the most important trait. In line with the large effects on survival of provenance transfers, several breeding zones have been established for Scots pine in northern countries: 11 in Finland and as many as 24 in Sweden where altitudinal variation is much more important than in Finland (**Table 1**). Growth rate has also been an important trait in breeding programs. Furthermore, stem and wood quality, crown shape and size, and pest resistance are other traits that have been taken into consideration in most breeding programs of Scots pine.

Breeding programs of Scots pine in Finland are national and use only domestic material. However, several international large-scale provenance studies have been established and maintained by the International Union of Forest Research Organizations (IUFRO). The first IUFRO trial was established as early as 1907, and it was followed by several other international trials. These experiments have documented the ample genetic variation that exists within and among populations in many quantitative characters. Recently, international provenance trials and progeny tests of Scots pine have been used for studies on resistance to air pollution and adaptation to climate change.

Scots Pine Breeding and Seed Production

Genetically improved material in Scots pine is produced by sexual reproduction. No clonal material

Table 1 Breeding activities of Scots pine in Finland and Sweden; estimates were obtained with permission from Haapanen and Mikola (2002)

	Finland	*Sweden*
Agency running the program	Finnish Forest Research Institute (Metla)	Forestry Research Institute of Sweden (Skogforsk)
Basis of subdivision of program	Mainly latitudinal gradation	Latitudinal and altitudinal gradations
Number of breeding populations	11	24
Proportion of regeneration of Scots pine served by breeding program	50% (proportion varies between areas being high in the southern parts and very low in northern parts of Finland)	66%
Number of planted seedlings in 1999	60 million	124 million
Seed orchards, ha	2000	924

for regeneration purposes is currently available. Cloning by somatic embryogenesis, which succeeds only with immature seed embryos, is difficult in Scots pine, which lowers the efficiency of cloning as a breeding tool in this species. The material of the production populations is generated in seed orchards, where genetically and/or phenotypically superior trees intermate and produce seed. These seeds are used in nurseries to produce seedlings to be planted at 1 to 2 years of age.

Actual breeding takes place in breeding populations. Selection of phenotypically superior "plus" trees has taken place in virtually all countries cultivating Scots pine. These phenotypes have been vegetatively propagated by grafting to establish the first-generation seed orchards. Several criteria have been used in selecting plus trees. Growth rate has been one of the major criteria, others including stem and wood quality and self-pruning. The first-generation seed orchards have been in full seed production already for several decades, and the genetic gain over wild seed has been estimated to be about 5–10% in growth and somewhat lower in quality characteristics.

The performance of plus trees has been evaluated by progeny tests, and the proven best parents with respect to, e.g., hardiness, growth, and stem and wood quality have been selected to establish 1.5-generation seed orchards. This work has started, for example in Finland and Sweden, and some of the 1.5-generation seed orchards are already functional. In Sweden, crosses between most superior trees have already started to produce elite trees for new-generation seed orchards.

The long-term breeding programs of Scots pine try to maximize genetic gain, avoid inbreeding in production populations, and maintain enough genetic variation for potentially changing environments. In Sweden, a multiple-populations breeding approach has been adopted, where double-paired matings produce material for within-family selection experiments. In Finland, breeding will proceed with a rather similar approach where double- and multiple-pair matings produce material for among- and within-family selection experiments. The genetic gain in growth may be as high as 20–24% in the second-generation seed orchards.

Because of the long generation times, these breeding populations are still at a very early stage of development compared to those of *P. radiata* and *P. taeda*.

Genetic Functioning of Scots Pine Seed Orchards

High genetic gain and maintenance of genetic diversity are two demands that clonal Scots pine orchard designs should meet. These aspects have been studied empirically and theoretically by Scots pine breeders.

The loss of genetic variation is not a major problem in present seed orchards of Scots pine. The first-generation seed orchards of Scots pine consist of many clones with a few ramets per clone. In Finland the average clone number in a Scots pine seed orchard is 121 and in Sweden 80. The number of clones will be substantially lower in advanced-generation seed orchards. Furthermore, variation in fertility among clones lowers the effective population size, thus reducing the expected genetic variability in the seed crop. Fertility variation is most pronounced in young seed orchards, reducing effective population size to half of the actual (census) number of clones. However, the loss of genetic variability due to fertility variation is much less serious in seed orchards with full pollen and seed production. Furthermore, the numbers of clones in present-day orchards, and also in the planned advanced-generation orchards, should be high enough to maintain much genetic variability.

The major factor reducing capture of genetic gain of seed-orchard material is background pollination. Orchards producing seed should be spatially isolated from surrounding Scots pine forests. In Finland, the orchards producing seed for northern areas were established in more southern areas to improve seed set, and thus it was expected that they should be genetically isolated from local forests, not only due to spatial separation but also due to temporal separation because of the earlier flowering of northern seed-orchard clones compared to local populations. Long-distance pollen dispersal, however, has been observed to be much more common than was earlier believed. The estimates of background pollination in Scandinavia vary between 6% and 75%, being as high as 25–35% in many old seed orchards with full pollen and seed production. In southern orchards, background contamination reduces the genetic gain expected from the seedlot. The situation is much worse in northern seed orchards, where background pollination (north × south crosses) makes seed lots unsuitable for regeneration in planned areas due to low hardening and high mortality. The area suitable for regeneration with seed orchard material has been estimated to be between the origin location of clones and location of a seed orchard. Suitable areas for different seedlots have also been estimated by freeze tests of the seedlings. Attempts have been made to solve the problem of background pollination with various methods, e.g., by supplemental pollination or selective seed collection, but the problem persists without a clear solution.

Genetic Resources and Gene Conservation

Although large natural populations of Scots pine maintain ample genetic variation, some measures have been taken to assure the maintenance of genetic variability for potentially changing environments, for instance, in planning long-term breeding programs. The Swedish multiple-populations breeding scheme is considered to serve both breeding and gene-conservation purposes. In Finland, several gene-reserve areas of Scots pine have been established in addition to breeding populations. In gene-reserve stands only natural regeneration is allowed, and seed from these stands may also serve as natural-population control material in genetic studies.

Future Aspects

The impending climate change will be an important issue for Scots pine breeding. The core of Scots pine breeding will be the production of seed material that survives for 80 years in the forests. Breeding for climate change has also already started. For instance, all testing is done in several breeding zones, in order to detect genotypes that are preadapted to the future conditions. Recently, more emphasis has also been placed on understanding and breeding for wood physical and chemical properties.

See also: **Genetics and Genetic Resources**: Genetic Systems of Forest Trees; Propagation Technology for Forest Trees. **Silviculture**: Natural Stand Regeneration. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Forest Genetics and Tree Breeding; Current and Future Signposts.

Further Reading

Danell Ö (1991) Survey of past, current and future Swedish forest tree breeding. *Silva Fennica* 25: 241–247.

Eiche V (1966) Cold damage and plant mortality in experimental provenance plantations with Scots pine in northern Sweden. *Studia Forestalia Suecica* 36: 1–218.

Eriksson G, Ilstedt B, Nilsson C, and Ryttman H (1987) Within and between-population variation of growth and stem quality in a 30-year-old *Pinus sylvestris* trial. *Scandinavian Journal of Forest Research* 2: 301–314.

Giertych M and Mátyás C (1991) *Genetics of Scots pine*. Budapest: Akademiai Kiado.

Haapanen M (2002) *Evaluation of Options for Use in Efficient Field Testing of* Pinus sylvestris (*L*), Research Paper no. 826. City: Finnish Forest Research Institute.

Haapanen M and Mikola J (2002) Integrating tree breeding and forestry. *Proceedings of the Nordic Group for Management of Genetic Resources of Trees*, Mekrijärvi, Finland, March 23–27, 2001, Research Paper no. 842. Helsinki: Finnish Forest Research Institute.

Koski V (1970) A study of pollen dispersal as a mechanism of gene flow in conifers. *Communicationes Instituti Forestalis Fenniae* 70: 1–78.

Koski V (1971) Embryonic lethals of *Picea abies* and *Pinus sylvestris*. *Communicationes Instituti Forestalis Fenniae*. 75: 1–30.

Mikola J (1982) Bud-set phenology as an indicator of climatic adaptation of Scots pine in Finland. *Silva Fennica* 16: 178–184.

Mikola J and Haapanen M (2003) *Tree Breeding 2050: Long-term Breeding Strategy in Finland*. Helsinki: Finnish Forest Research Institute.

Rosvall O (1999) Enhancing gain from long-term forest tree breeding while conserving genetic diversity. *Acta Universitatis Agriculturae Suecica, Silvestria* 109: 65–94.

Ruotsalainen S (2002) *Managing Breeding Stock in the Initiation of a Long-Term Tree Breeding Program*. Research Paper no. 875. Helsinki: Finnish Forest Research Institute.

Sarvas R (1968) Investigations on the flowering and seed crop of *Pinus sylvestris*. *Communicationes Instituti Forestalis Fenniae* 53: 1–198.

Savolainen O and Kärkkäinen K (1992) Effect of forest management on gene pools. *New Forests* 6: 329–345.

Williams CG and Savolainen O (1996) Inbreeding depression in conifers: implications for breeding strategy. *Forest Science* 42: 102–117.

Southern Pine Breeding and Genetic Resources

J P van Buijtenen and T D Byram, Texas A&M University, College Station, TX, USA

The Southern Pines

The southern pines include four major and six minor species. Together, they make up much of the commercial wood production in the USA supplying approximately 56% of the overall wood consumed (**Table 1**). Southern pine is used for both solid-wood products such as dimensional lumber, plywood, and engineered structural beams and panels and for various pulp and paper products of which linerboard is a main application.

Loblolly pine (*Pinus taeda*) occurs throughout the South and ranges from Texas to Delaware, with only one major discontinuity, in the Mississippi River valley (**Figure 1**). It does not occur in the southern part of Florida. It has acceptable wood quality, is widely adapted and grows rapidly.

Loblolly pine seedlings account for over 80% of the annual nursery production in the South.

Slash pine (*P. elliottii* var. *elliottii*) occurs naturally only in the coastal plain east of the Mississippi River although it has also been widely planted as an exotic west of the Mississippi River in the coastal plains of Louisiana and Texas (**Figure 2**). It is popular for its rapid early growth, resistance to fire and tipmoth (*Rhyacionia frustrana*), and adaptability to phosphorus-deficient sites. Despite its rapid early growth and excellent form, it is ultimately outgrown by loblolly pine on most sites. However, its importance has declined primarily because of its susceptibility to fusiform rust (*Cronartium quercuum f. sp. fusiforme*) and its limited geographic range. Although rust-resistant varieties are now available, the species has not regained its former popularity.

Shortleaf pine (*P. echinata*) has the widest natural range of all southern pines. It occurs from New York to Texas, and is better adapted to heavy soils than some of the others. It also is well adapted to somewhat higher elevations, occurring in the Appalachian and Ozark Mountains as high as 1000 m. Very little shortleaf pine is planted commercially, because of its slow early growth and its susceptibility to tipmoth.

Longleaf pine (*P. palustris*) occurs in the coastal plain from Texas to Florida and north to Virginia. It forms a rosette, called the 'grass stage,' after germination. Under natural conditions, the grass stage will persist until a fire eliminates needles infected with brownspot disease (*Scirrhia acicola*), and reduces the surrounding competition and accumulated fuel. It will then grow very rapidly and become tall enough to be fairly resistant to the next fire. The species is difficult to plant, but is making an appreciable comeback with the use of containerized seedlings. It is prized for its straight stems and high-quality wood.

Southern pines are widely planted around the world as exotics. Many of the planting programs are supported by breeding efforts. Continents include South America (Argentina, Brazil), Australia, Asia (China), and Africa (South Africa, Zimbabwe, Swaziland, Malawi). The techniques used are similar to those described for the southern USA, but in slash pine somewhat more emphasis is placed on hybridization.

The minor southern pines include pitch pine (*P. rigida*), pond pine (*P. serotina*), sand pine (*P. clausa*), spruce pine (*P. glabra*), table mountain pine (*P. pungens*), and Virginia pine (*P. virginiana*). There are limited breeding programs to improve Virginia pine, which is widely planted for Christmas tree production. Most of the southern pines are closely related and belong to the subsection Australes

Table 1 Volume of roundwood products by southern pine species and type of product, 1996. Data from "National forest inventory and analysis," USFS.

Species group	*Saw logs*	*Veneer logs*	*Pulpwood*	*Composite products*	*Fuelwood*	*Post – poles – pilings*	*Other products*	*All products*
(a) Volume in millions of (m^3)								
Loblolly – shortleaf pine	56.5	17.5	45.4	2.2	2.3	0.9	0.1	125.0
Longleaf – slash pine	14.4	2.6	17.0	0.2	0.5	0.8	0.3	35.7
Major southern pines	70.9	20.1	62.4	2.4	2.8	1.7	0.4	160.7
Total US softwoods	146.1	31.8	80.7	3.2	14.0	4.7	3.7	284.2
(b) Volume as a percentage of total US grown softwoods								
Loblolly – shortleaf pine	38.7	54.9	56.2	67.7	16.3	20.5	2.9	44.0
Longleaf – slash pine	9.9	8.3	21.1	5.4	3.5	16.2	8.4	12.6
Major southern pines	48.6	63.2	77.3	73.1	19.8	36.6	11.2	56.5

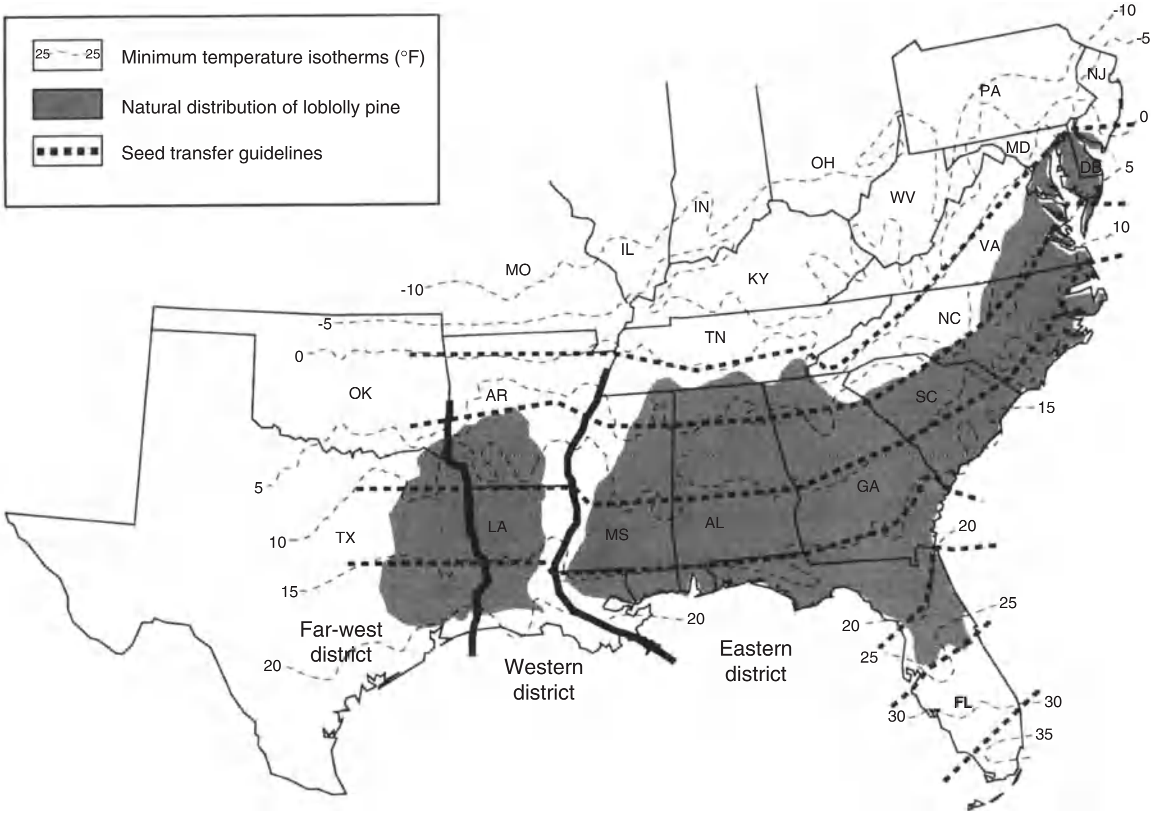


Figure 1 Natural range of loblolly pine with guidelines for the transfer of seed. From Schmidtling RC (2001) *Southern Pine Seed Sources*, General Technical Report no. SRS-44. Asheville, NC: USDA, Forest Service.

(southern yellow pines) of the genus *Pinus*. The exceptions are Virginia pine and sand pine, which belong to the subsection Contortae. As a result many of the southern pines can be crossed readily.

The Southern Pines as a Genetic Resource

Natural Variation

The southern pines have much natural variability, which is basically intact because domestication has just begun. As a result both natural stands and current breeding programs are rich genetic resources. Genetic variation exists at various levels: regional, stand-to-stand, and among trees within stands. In natural stands, the tree-to-tree variation is most striking, while variation among stands is much less. Regional variation is also of major importance, particularly in species with large natural ranges. Elevational races are only important in species such as shortleaf pine whose range includes mountainous areas. Of the major species, loblolly pine and shortleaf pine are the most variable, while slash pine is most uniform. The variability (**Figure 3**) has been studied extensively, by means of *in situ* studies, geographic variation studies, heritability studies, and progeny tests done in the course of breeding programs.

Since natural regeneration is practiced on much of the public and nonindustrial private land, which comprises more than half of the forest land in the South, a major portion of the gene pool is preserved in its natural condition. In addition the breeding programs are making a concerted effort to preserve a large number of genotypes in test plantations and grafted scion banks.

Geographic Races

Loblolly pine and shortleaf pine, as discussed earlier, have very large ranges and the resulting geographic variation presents opportunities for spectacular successes and disasters. Loblolly pine from Livingston Parish, Louisiana, has done extremely well over a very large area, combining good growth rate with resistance to fusiform rust, while most southern pines from east of the Mississippi River do very poorly in East Texas. A major geographic variation study was undertaken to provide a scientific basis for the geographic movement of seed and seedlings.

The so-called Southwide Geographic Seed Source Study (SGSSS) was the first organized attempt to delineate these geographic trends. This study was

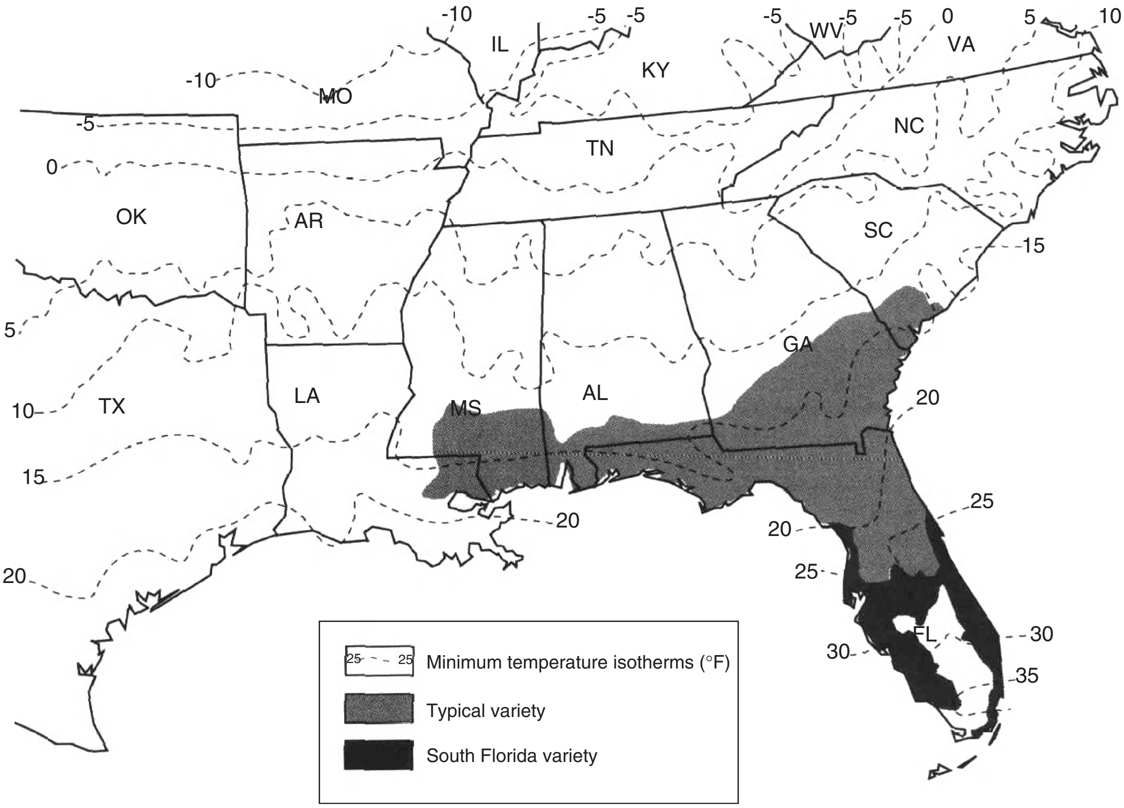


Figure 2 Natural range of slash pine with minimum temperature isotherms. From Schmidtling RC (2001) *Southern Pine Seed Sources*, General Technical Report no. SRS-44. Asheville, NC: USDA, Forest Service.

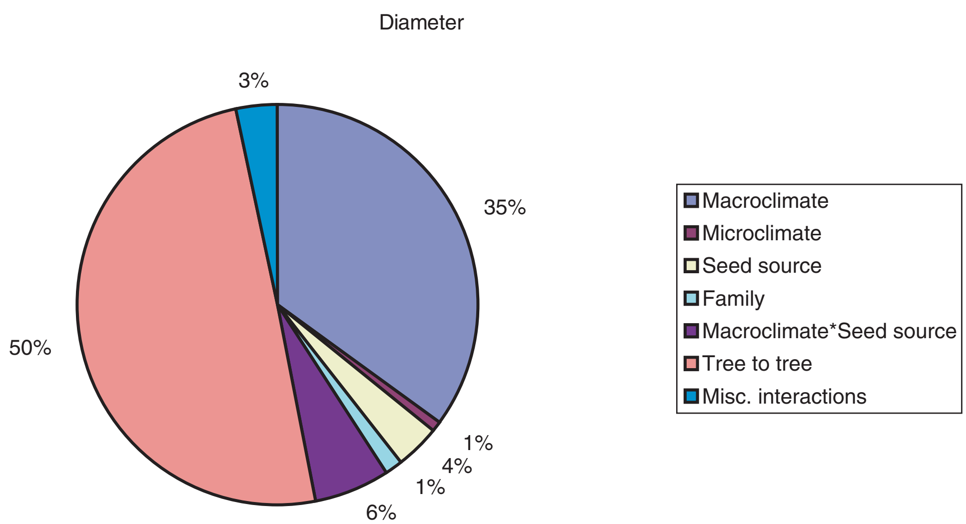


Figure 3 Breakdown of the total variation within the western part of the loblolly pine range into its variance components. Results are based on Western Gulf Forest Tree Improvement Program Geographic Variation Study Series 1.

undertaken in 1951 by the Southern Forest Tree Improvement Committee, with the Southern Experiment Station of the US Forest Service playing a major role. It was a truly cooperative effort with 17 organizations including industries, forestry schools, State agencies, and the US Forest Service participating. The study was nonintensive, with one or two seed collections and a similar number of plantings from each State, but it provided extremely important results that still provide the guidelines for the movement of southern pine germplasm throughout the South (**Figure 1**).

The SGSSS was followed up by individual studies using a finer grid. The most recent general guidelines provided on the basis of these studies are:

> Seedlings will survive and grow well if they come from any area having a minimum temperature within 5°F of the planting site's minimum temperature. Seedlings from an area with warmer winters will grow faster than seedlings from local sources; seedlings from an area with cooler winters will grow slower…. The difference in winter lows can be as much as 10°F, but with increased risk of damage at the cold end of the range and growth loss at the warm end. East–west transfers within districts are usually successful, and in some instances may be desirable if improved stock is available.

History of Southern Pine Tree Improvement

Several factors contributed to the establishment of large-scale breeding programs in the South. The virgin forest had largely been cut over by early in the twentieth century and large scale-planting programs had been undertaken partly in response to the Great Depression and the soil erosion that resulted from drought and poor farming practices. At the same time, research in Sweden, Denmark, and the USA was showing that choosing the right seed source was important for successful regeneration of forest stands.

As told by Zobel and Sprague, one crucial event galvanized the forestry community of the South into action. At that time the Swedes were most advanced in the study of forest genetics. In 1950, Dr Åke Gustafsson gave an inspiring lecture on his accomplishments as a crop breeder, which was attended by the State Governor of Texas, the director of the Texas Forest Service, and a number of forest industry leaders. As a result the Texas Forest Service started a cooperative tree improvement program in 1951, hiring Bruce Zobel to lead the effort, and as they say: the rest is history. About that time, the University of Florida Cooperative Forest Genetics Research Program was started under the direction of Tom Perry. In 1956, Bruce Zobel moved to North Carolina, starting the cooperative at North Carolina State University. At the time, the model of a cooperative tree improvement program was novel, based on some very good biological, economic, and psychological reasons. It allowed the participants to pool their genetic and financial resources and their technical expertise. The free exchange of genetic material and information among the members was crucial to the success of the individual programs. The cooperative spirit of those early days was very different from the competitiveness frequently fostered by the current research and economic climate. Genetic expertise was scarce, the task was too large for the resources of one organization, forests were not seen as profit centers, and the critical mass achieved in the early cooperative programs generated a spirit of enthusiasm.

Approach to Breeding

The Seed Orchard Approach

Most tree improvement programs for the southern pines followed the seed orchard approach to forest tree breeding (*see* **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement). This consisted of mass selection of superior phenotypes in natural stands, followed by the concurrent establishment of seed orchards for the production of commercial seed and progeny tests to determine the genetic value of the selected parents. When results of the progeny tests became available, these data were used to 'rogue' the seed orchards (i.e., remove clones of poor genetic value). With this genetic base established, the breeding programs continued as recurrent selection programs.

Major Phases of the Breeding Programs

Initially, a major effort was expended in locating superior trees in natural stands. The selection criteria reflected the breeding objectives with the relative merit of the candidate trees judged by an elaborate grading system that compared their performance to that of their neighbors. Selection efforts were eventually extended to locating candidate trees in unimproved plantations to serve both as infusions and expansions of the original breeding populations.

The breeding objectives differed somewhat depending on the species, the intended deployment zone, and the desired product. Initially, there was great emphasis, particularly in loblolly pine, on the improvement of stem straightness. Rust resistance was a major criterion in areas where rust was a major problem. This was the case for loblolly pine for planting in Georgia, and for slash pine in some parts of its natural range and in all the areas where it was planted as an exotic. Of course, height and volume growth were of major importance in all programs and for all species. In some programs, great effort was also expended on wood quality research, although the selection pressure exerted to improve wood quality was actually very mild.

The grading systems were basically a form of index selection, rating the merits of various traits, but without the benefit of known heritabilities or genetic correlations between traits. The candidate tree was compared to a number of check trees in the immediate neighborhood and given points according to its degree of superiority. After a candidate was identified, a grader employed by one of the tree improvement cooperatives would evaluate the tree to make the final judgment as to whether it should be included in the breeding population. A great many trees were rejected in the process. In any case, hundreds of thousands if not millions of trees were screened to identify the individuals that were ultimately included in the breeding population.

Plantation selections were depended on heavily for the base populations, which caused some concern because the geographic origin of many of the plantations was not known. Fortunately the results of extensive geographic seed source studies of plantation selections have paralleled those of seed source studies from natural stands.

Simultaneously with this tree selection effort a great deal of time was devoted to developing grafting techniques. Grafting the southern pines was not easy, and it took several years before a high success rate was obtained. The most successful types of grafts today are cleft grafts, side grafts and side-veneer grafts. Using these techniques thousands of hectares of seed orchards were established (**Figure 4**). Progeny test procedures also went through a long period of evolution. Initially, mostly open-pollinated or wind-pollinated progeny tests were established as this could be done quickly and cheaply. Gradually these were replaced by control-pollinated tests, as pollination procedures were developed (**Figure 5**). The most popular scheme in the early days was the four-tester scheme in which all clones in an orchard were pollinated with the same four 'males'. This scheme accurately evaluated the genetic quality of the female parents, but it soon became clear that advanced-generation selections from this scheme would be highly interrelated and that inbreeding would be a serious problem in the next cycle of orchards. As a result most organizations shifted to various types of diallel schemes. A complete diallel is the set of all possible crosses among the parents to be evaluated. Since the number of crosses goes up as the square of the number of parents it rapidly becomes unwieldy. A 30-clone orchard, for example, would require 900 controlled crosses. Various types of partial diallel are obtained by systematically sampling the complete diallel to get a good representation of all parents, while keeping the number of crosses within reason.

The field layout of the progeny tests also changed dramatically over the years. Row-plots and block-plots of as many as 100 trees were popular in the 1950s, but it soon became apparent that these tests were statistically inefficient. Also, they took up excessive land, since trees cannot be spaced anywhere near as closely as agricultural crops. The scheme evolved to short rows repeated many times and the whole test repeated at three to four different locations. Currently, many tests are laid out as single tree plots, where each cross in a block is represented by one individual. Randomized complete blocks are commonly used but incomplete blocks where entries are randomized with some restrictions are also used by some programs.

Advanced-generation breeding presented some new hurdles. The age of selection was the first. Ideally, one should select trees at maturity, when all harvest-age characteristics are known. However, this would be an extremely slow process. Theoretical considerations based on available progeny test data showed that genetic gain per year could be maximized by making selections much earlier. The consensus was that selection some time between ages 5 and 10 would be optimal. Considerable research was done to move the selection age even earlier by selecting families based on seedling measurements. At this time it would be very risky to select individual trees on this basis. However, some traits can be measured quite early on seedlings, and

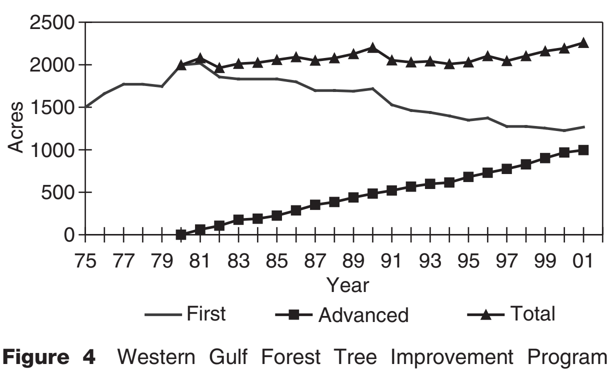


Figure 4 Western Gulf Forest Tree Improvement Program seed orchard acreage from 1975 through 2001.

Figure 5 Bucket trucks are widely used in southern pine seed orchards for pollination (shown here) and cone collection. Photograph courtesy of Texas Forest Service.

one can eliminate some families based on early testing data. Some cooperatives adopted stepwise screening, whereby measurements on greenhouse grown seedlings are used to eliminate poorly performing families before field testing. This resulted in considerable cost savings. Traits that have proven amenable to this procedure include rust resistance in loblolly and slash pine, and growth rate in some provenances of loblolly pine.

Inbreeding and potential inbreeding depression also presented a major problem. This is being managed by subdividing the population into smaller populations called breeding groups or sublines. By limiting crosses made for breeding purposes to matings among members of breeding groups, but designing the orchards so that mating would occur between individuals from different groups, one could confine inbreeding to the breeding population and ensure that seed produced in seed orchards would be largely outcrossed. The approach is somewhat similar to the use of inbred lines in corn, but in corn the lines are purposely inbred and specific crosses are made to combine hybrid vigor (heterosis) with crop uniformity. In southern pines, inbreeding is still avoided as much as possible, even within sublines, while the seed orchards are composed of the best available parents arranged in unrelated groups.

Several organizations have initiated elite breeding populations, or super breeding groups, consisting of only the very best individuals from all the sublines or combinations of breeding groups. These populations are generally a supplement to the mainstream breeding program, being intended to capture additional genetic gain for use in the production population.

Recently increased emphasis is being placed on genetic conservation as an integral part of long-range breeding. The preferred method of conserving genotypes is through grafting into scion banks: a strategy of *ex situ* conservation. Long-term seed storage, commonly used in agriculture, is not very practical for the southern pines. It is not very reliable and would require that stands of trees would be established periodically to replenish the seed. In the absence of inbred lines there is a substantial risk that rare genes would be lost in the process. This approach complements *in situ* conservation through natural regeneration, which is still widely practiced in the South particularly on public and nonindustrial private land.

Accomplishments

The scale at which the tree improvement programs operate is truly staggering. Loblolly pine serves as a good example, since it is the most important species and figures are most readily available. In the initial phase, thousands of selections were made. Over 10 000 have now entered the breeding population (**Table 2**). Individual breeding populations are of course smaller, since breeding is a localized effort, but they are generally of the order of 1000 trees per population (**Figure 6**). Seed orchard acreage increased rapidly in the early years and reached a maximum of about 3900 ha (10 000 acres), leveling off and decreasing after that time because of increased efficiency of seed production as orchards aged. The initial orchards have now largely been replaced by newer selections. Many cooperative member organizations are operating on the advancing-front concept, where every few years an old section is replaced with the best selections currently available.

Southwide, over 1 billion improved seedlings are produced annually. These are sufficient to regenerate about 800 000 ha (2 million acres) per year (**Figure 7**). The genetic gains reported for volume growth range from 10% to 35%. The combined

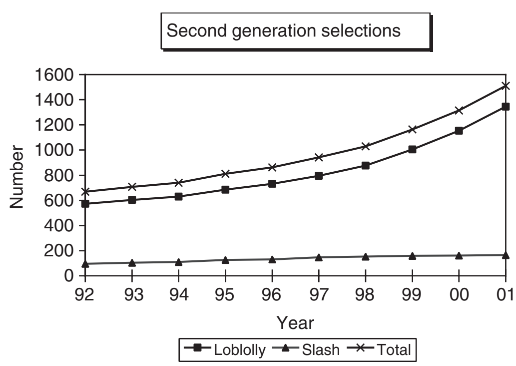


Figure 6 Western Gulf Forest Tree Improvement Program second generation selections from 1992 through 2001.

Table 2 Loblolly selections forming genetic base of North Carolina State and Western Gulf Forest Tree Improvement Program Cooperatives

	1st generation	*Plantation selections*	*2nd generation*	*3rd generation*	*Total*
Western Gulf Forest Tree Improvement Program	3350		1345		4695
North Carolina State	580	3120	680	778	4578
Total	3350	3120	2025	778	9273

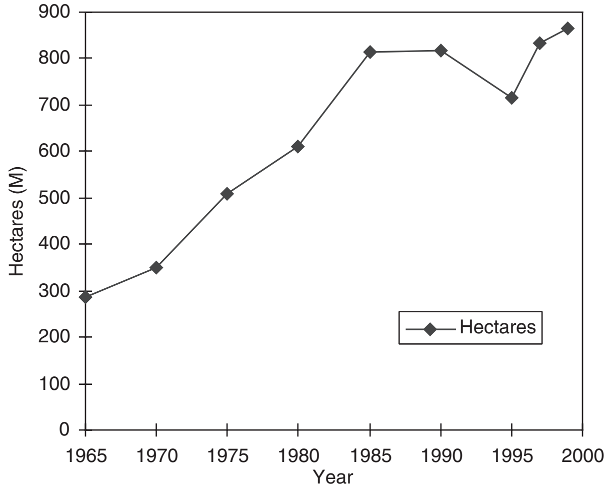


Figure 7 Area planted annually in the southern USA from 1965 through 2000. Based on data in Southern Forest Resources Assessment Draft Report. Data from USDA Forest Service, Southern Research Station.

effect of genetic improvement and more intensive management has far exceeded expectations, to the point that the timber shortages predicted less than a decade ago are not materializing.

The cooperatives are making a concerted effort to preserve all the genotypes included in the breeding population forming a genetic base far greater than the trees included in the production orchards. These so-called scion banks combined with the genetic tests form an invaluable genetic resource in addition to the extensive natural stands.

See also: **Genetics and Genetic Resources**: Molecular Biology of Forest Trees. **Tree Breeding, Practices**: Genetics and Improvement of Wood Properties. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources.

Further Reading

Byram TD, Lowe WJ, and Gooding GD (2000) Western Gulf Forest Tree Improvement Program gene conservation plan for loblolly pine. *Forest Genetic Resources* 27: 55–59.

Dorman KW (1976) *The Genetics and Breeding of Southern Pines,* Agriculture Handbook no. 471. Washington, DC: US Department of Agriculture.

Dvorak WS, Jordan AP, Hodge GR, Romero JL, and Woodbridge WC (2000) The evolutionary history of the Mesoamerican Oocarpae. In: *Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative*. Raleigh, NC: North Carolina State University.

Lowe WJ, McKinley CR, and Toliver JR (eds) (1986) *Advanced Generation Breeding of Forest Trees,* Southern Cooperative Series Bulletin no. 309. Baton Rouge, FL: Louisiana Agricultural Experiment Station.

Schmidtling RC (2001) *Southern Pine Seed Sources,* General Technical Report no. SRS-44. Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station.

Schulz RP (1997) *Loblolly pine,* Agriculture Handbook no. 713. Washington, DC: US Department of Agriculture.

van Buijtenen JP(ed.) (1983) Progeny Testing of Forest Trees, Proceedings of workshop on progeny testing, 15–16 June 1982, Auburn, AL. College Station, TX: Department of Agricultural Communications, Texas A&M University.

van Buijtenen JP (1984) Genetic improvement of forest trees through selection and breeding. In: Wenger KF (ed.) *Forestry Handbook*, pp. 457–488. New York: John Wiley.

Wells OO (1983) Southwide pine seed source study: loblolly pine at 25 years. *Southern Journal of Applied Forestry* 7(2): 63–71.

Wells OO and Wakeley PC (1966) *Geographic variation in survival, growth, and fusiform infection of planted loblolly pine,* Forest Science Monograph no. 11. Bethesda, MD: Society of American Foresters.

Williams CG and Byram TD (2001) Forestry's third revolution: integrating biotechnology into *Pinus taeda* L. breeding programs. *Southern Journal of Applied Forestry* 25(3): 116–121.

Zobel BJ and Sprague JR (1993) *A Forestry Revolution: The History of Tree Improvement in the Southern United States*. Durham, NC: Carolina Academic Press.

Zobel BJ and Talbert J (1984) *Applied Forest Tree Improvement*. New York: John Wiley.

Tropical Hardwoods Breeding and Genetic Resources

E D Kjaer, The Royal Agriculture and Veterinary University, Hoersholm, Denmark

Introduction

The tropical flora includes thousands of tree species that have proven to be of high value to humans. Products from trees include an almost endless number of goods: timber, fuelwood, edible fruits, medicinal compounds, fibers for clothing, latex, and oils. The genetic diversity of these species represents an enormous biological resource in terms of options for human utilization. Research into the application and conservation of this genetic resource has provided important guidelines on its sustainable genetic management. Tree breeding has focused on relatively few hardwood species considered to have high potential in industrial plantations. However, more recently a broader scope has been applied, and the research and development have focused on a substantially larger number of species including domestication of trees planted by farmers.

Genetic Resources

The term 'genetic resources' refers to genetic variation in trees of potential or present benefit to humans. Variation of genetic origin is due to DNA polymorphisms as such (genes) but the genetic patterns of variation are also of major importance. Genetic variation can thus be seen as organized at different levels: variation between different species, between different populations (forests) within a given species, and between different individual trees of the same species within a given population. The idea of a genetic resource is that this genetic variation – in the broad sense stated above – is of potential value for humankind at present or in the future.

In addition to the genetic diversity as such, a subject of considerable interest is the evolutionary processes (e.g., natural selection in favor of healthy trees) that continuously work within and between populations, and assure continued adaptation to changing climatic conditions, competition with other species, or infections from new pests. This is based on the perception that populations need to be able to respond to changing environments and new competitors in order to maintain their relative fitness. It does hold true that most if not all tree species are exposed to constant competition from other species in a changing environment. Rapid coadaptation and development are thus believed to be necessary for any species in order to maintain fitness and ultimately to avoid extinction in the long run. This perception is sometimes referred to as the 'Red Queen hypothesis' after Van Valen, who chose the name from *Alice in Wonderland*, where the Red Queen tells Alice that 'she needs to run as fast as she can just to stay in the same place.' One can say that the genetic diversity is a dynamic feature of a species being constantly shaped by its environment through ongoing evolutionary forces. Therefore, management of genetic resources of tropical forest trees normally (although not always) aims at protection of the genetic processes as well as the resource itself.

The genetic resource of tropical hardwoods is considered to be especially valuable due to the vast array of potentially harvestable crops from the thousands of species. An important feature of many (although far from all) tropical trees is that they grow in very diverse ecosystems and therefore have a scattered distribution, and/or are found at low densities. This complicates large-scale harvest of the products and therefore in principle favors some kind of domestication of the species through planting activities. However, successful planting programs require planting material in sufficient amount and of high genetic quality. Aspects of characterization, identification, propagation, and breeding of tropical hardwood species have therefore been important research topics for many species for a number of decades.

Provenance Trials and Breeding Programs for Industrial Plantations of Tropical Hardwoods

For practical reasons, the initial focus was on breeding hardwood species with some kind of pioneer characteristics, i.e., shade-intolerant species with fast juvenile growth. Such species are easier to cultivate in plantation regimes compared to the more difficult shade-tolerant, mature-phase species that require shade and exhibit less vigorous juvenile growth. Some of the earliest tree improvement activities focussed on teak (*Tectona grandis*). Teak is considered to be one of the world's most prominent timber species due to its valuable wood but it is also easy to establish in plantation regimes. The juvenile growth rate is high but rapidly moderates with age and more than 50 years are in general required in order to obtain valuable teak logs. Selection and vegetative propagation of superior teak trees on a commercial scale in India, Indonesia, and Thailand go back to the 1950s. Large-scale international provenance tests were initiated in the 1960s as a joint effort between a number of teak growing countries in Africa, Asia, and Central and South America. This comprehensive series of trials has since shown that large differences exist between seed sources and that the selection of the best origin of the seed is therefore important in order to obtain vigorous growing trees (see **Table 1**). Variation in stem form was also found to be important.

Provenance trials have been established for a number of other tropical hardwoods including a number of widely planted species such as *Milicia excelsa*, *Dalbergia sissoo*, *Dalbergia* spp. (rosewoods), *Swietenia humilus* and *S. macrophylla* (mahoganies), *Gmelina arborea*, but also many lesser known species such as *Vochysia guatemalensis*, and *Zeyheria tuberculosa*. The general finding is that variation between populations is important for almost all investigated species.

Breeding in principle consists of continuous cycles of initial selection of superior trees according to their phenotypic performance, testing by growing the trees under relevant conditions in repeated field trials, analysis of the field trials and selection of superior trees or progenies of trees based on these results, crossing of the selected trees (formation of the next generation breeding population), and initiation of the next breeding cycle by selection in the progenies for second-generation testing. Breeding in terms of such selection and testing for tropical hardwoods have in general not progressed beyond the early stages (first generation). Experiences from fairly intensively bred *Gmelina arborea* and *Tectona grandis* have however indicated that at least selection for stem form and insect resistance are likely to provide good response (**Figure 1**). Breeding of rosewood (*Dalbergia sissoo*) in India and Nepal has also shown that a high level of genetic control exists for growth rate and that good response from selection can be obtained from breeding for both growth and especially stem form. This finding has been repeated in a number of species

Table 1 Relative growth rates (basal area at age 17 years) of 12 teak provenances grown in field trials at Aracruz, Brazil

Origin	*Provenance (location of collection site)*	*Estimated annual rainfall*	*Average growth relative to the fastest growing (%)*
Southern India	Mount Start, Tamil Nadu	2032 mm	100
Southern India	Nilambur, Kerala	2565 mm	96
Southern India	Konni, Kerala	2540 mm	91
Indonesia	Ngliron, Java	1200 mm	86
Ghana (African landrace)	Jema	Not available	69
Laos	Khong Island	1925 mm	58
Northern India	Purunakote, Orissa	1350 mm	58
Laos	Vientienne Town	1570 mm	55
Thailand	Ban Pha Lai	1100 mm	54
Thailand	Ban Mae Pam	1200 mm	47
Northern India	Munda Reserve Forest	1350 mm	47
Laos	Savannakhet	1300 mm	44

Note: The trial site at Aracruz in Brazil has an annual rainfall of approximately 1400 mm. Still, the most vigorous provenances at this planting site come from parts of Southern India, where the rainfall is substantially higher. It is a general observation that the genetic patterns of variation often are difficult to predict without proper testing in field trials. Use of planting material from healthy stands of local origin is therefore often preferred when results from provenance trials are lacking. Adapted from Kjær, E.D., E. Lauridsen & H. Wellendorf 1995. *Second Evaluation of an International series of Teak Provenance Trials*. Danida Forest Seed Centre, Humlebaek, Denmark, 117p.

Figure 1 Clonal seed orchard in Northern Thailand. These trees are vegetatively propagated graftings (clones) from so-called plus-trees (very straight trees identified and selected in natural forests in Thailand during the 1960's), and established in order to collect improved seed for planting programs. In front Verapong Suangtho of the Royal Forest Department, Bangkok.

and revealed a pattern that indicates that gains from selection in the early stages are often surprisingly high in many tropical and subtropical species compared to similar findings in temperate species. Over the years, breeding has therefore been accepted as an important means to improve the productivity of plantation species (**Figure 2**).

Propagation

Large-scale propagation of the selected and improved genetic material has proved to be a severe obstacle for large-scale application of many tropical hardwoods. Technically successful breeding programs have in many cases not led to the expected increase in productivity in the plantations, simply because the improved planting material has not been applied at any substantial scale. The problem of effective multiplication is most complicated for species with large fruits, moderate seed, and/or seed that are sensitive to desiccation and therefore difficult to handle and transport. One or more of these features unfortunately characterizes the seed biology of many valuable hardwood species from moist or semimoist tropical conditions, and has by itself limited large-scale application of such species altogether for large-scale planting purposes.

The traditional propagation of improved genetic material is in seed orchards based on seed collection from graftings of the superior trees. However this approach has proven to be much more difficult for many tropical hardwoods compared to the experience from temperate conifers. Thousands of hectares of seed orchards of teak have been established in India, Indonesia, and Thailand, but they have produced only limited commercial seed.

Much research has therefore focused on development of alternative propagation methods to seed. Development of rooted cuttings through application of growth hormones has proven to be a feasible option for a large number of species including several of the difficult dipterocarp species. Development of tissue culture has also been successful for a number of species. Although important findings and important tools for breeding, the vegetative propagation techniques have in general proven to be associated with additional costs that have limited their commercial-scale application with only a few exceptions.

Breeding a Wider Range of Tropical Hardwood Species

Given the thousands of valuable tropical hardwoods, breeding has until recently focused on surprisingly few species. This is probably due to a combination of lack of resources, the partly mythical view that most tropical hardwoods are slow growing (this is often not the case), the preference for growing plantations as monocultures without nurse species, and the fact that many of the species have complicated breeding systems.

Research into Genetics and Population Dynamics of Tropical Hardwood Species

Basic research into the often complicated breeding systems of tropical hardwoods has over the last three decades generated important knowledge for a much larger number of tropical hardwood species. Understanding of pollination ecology is often an important

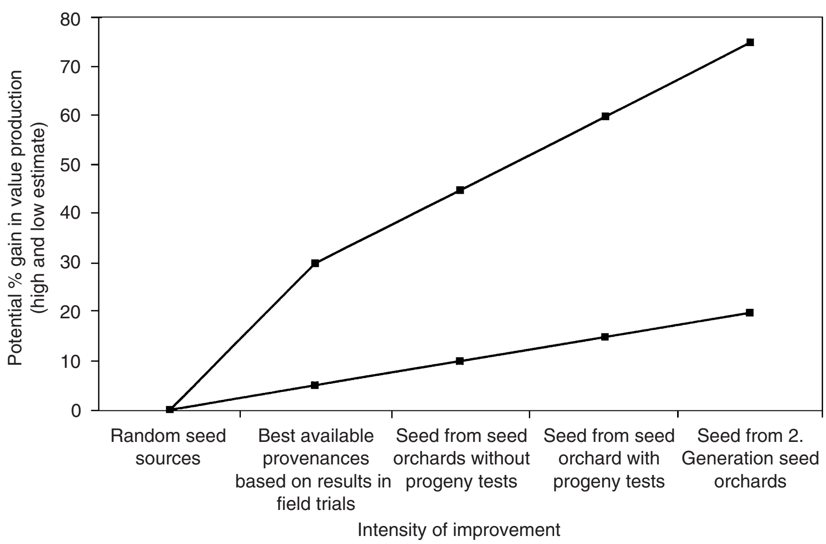


Figure 2 Expected gains from tree breeding. Based on estimates in Foster GS, Jones N, and Kjaer ED (1995) *Economics of Tree Improvement in Development Projects in the Tropics*. In: Environmental and Economic Issues in Forestry: Selected Case Studies in Asia. Edited by Shen S and Converas-Hermosilla A. World Bank Technical Paper no. 281. The World Bank, Washington D.C.

prerequisite for effective breeding programs, and for good management of the genetic resource as such. Formal studies of pollinators and estimation of selling rates and gene flow are time consuming, but results from a number of tropical hardwood species with different pollination syndromes has allowed some important generalizations to be drawn that are valuable for practical management of the genetic resources of tropical hardwoods. These include the recognition that most species are predominately outcrossing and pollen is often dispersed over large distances depending on the pollinators. For example, fig wasps have been found in general to have a pollination radius on the scale of several kilometers whereas beetles often move pollen less than 100 meters. For some species such as some understory woody species, the average pollen movement distance has been found to be only a few meters. The research programs into genetic processes and population dynamics of tropical hardwoods have in most cases been initiated based on concern for their conservation status, where increasing fragmentation of natural habitats is a major concern. However, the findings have also proven very useful for practical breeding and domestication because a basic understanding of the reproductive ecology is important in order to develop effective propagation and genetic management programs.

Breeding of Hardwoods for On-Farm Plantings in Heterogeneous Environments

The large number of potentially important species, combined with the general development towards joint forest management of tropical forest, has in recent years challenged traditional breeding techniques. Further, focus in many forestry programs has moved from industrial plantations to support farmers planting on their own farms in wood lots and agroforestry systems.

Large-scale international provenance trials of dry zone acacias were initiated in the 1980s and these trials have revealed substantial differences in survival and biomass growth according to the origin of the seeds. They indicate that choice of the right seed source is even more important for species growing under dry or semi-dry conditions. Results from domestication of species grown for fodder and fallow (e.g., *Bauhinia* sp. *Sesbaria sesbar*, and *Gliricidia sepium*), gum arabic (*Acacia senegal*), oils (e.g., *Melaleucas*), and other non-wood products (e.g., *Azadirachta indica*) have also proven that these characteristics are often under as high genetic control as growth and stem form. Breeding for non-timber forest products thus seems to be an important option, although often more difficult to select for in practice. On-going research into this issue will contribute important information in the coming years.

New Concepts for Breeding Tropical Hardwoods

The introduction of two important concepts – (1) multiple population breeding and (2) breeding seed orchards – has been an important contribution to development of low-input, genetically diverse breeding programs. The point of departure in multiple population breeding is that a number of smaller, low-input, breeding programs are run in each separate ecologically based breeding zone. This supports local adaptation to ecological conditions and thereby manages the genetic diversity in the breeding program without a number of expensive, repeated tests. The breeding seed orchard is a special planting that serves multiple purposes: it produces seed (seed orchard), tests the genetic entries (progeny trial), and provides the base population of next generation selection (breeding population). This is obtained by establishing a seed orchard based on progenies from selected trees in a repeated block design. The design in terms of plot size, number of progenies and replications, are chosen in breeding seed orchards in ways that accommodate the combined requirements (**Figure 2**).

Interdisciplinary Approaches and Farmer-Based Domestication

Many programs have proven that breeding of tropical hardwoods cannot be done in isolation from the plantation technology and indeed not in isolation from the socioeconomic context. Genetic improvement and propagation remains an academic exercise unless the improved germplasm is distributed and applied by the tree planters. Tree improvement of tropical tree species has therefore gained much in recent years from an interdisciplinary approach that include institutional aspects and participatory methods. Participatory breeding and gene resource management programs for tropical hardwoods enables practical schemes to build on the local knowledge that are essential for breeding for number of non-wood products. Also, participatory breeding is required in order to deal with species cultivated through natural regeneration rather than plantings as is the case in the West African parkland, or species management by farmers at landscape level as is the case with many fodder species in the Nepali middlehills.

See also: **Genetics and Genetic Resources**: Propagation Technology for Forest Trees. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance; Breeding Theory and Genetic Testing; Economic Returns from Tree Breeding.

Further Reading

Bawa KS (1990) Plant-Pollinator Interactions in Tropical Rain Forests. *Annual Review of Ecology and Systematics* 21: 399–422.

Dieters MJ, Matheson AC, Nikles DC, Harwood CE, and Walker SM (eds) (1996) *Tree Improvement for Sustainable Tropical Forestry*. Caloundra, Australia: International Union of Forest Research Organizations.

FAO (2002) *Proceedings from the South Asian Moving Workshop on Conservation, Management and Utilization of Forest Genetic Resources*. Forspa Publication no. 31. Bangkok, Thailand: Food and Agriculture Organization.

Foster GS, Jones N, and Kjaer ED (1995) *Economics of Tree Improvement in Development Projects in the Tropics*. In: Environmental and Economic Issues in Forestry: Selected Case Studies in Asia. Edited by Shen S and Converas-Hermosilla A. World Bank Technical Paper no. 281. The World Bank, Washington D.C.

Gibson GL, Griffin AR, and Matheson AC (1989) *Breeding Tropical Trees: Population Structure and Genetic Improvement Strategies in Clonal and Seedling Forestry.* Oxford, UK: Oxford Forestry Institute.

Leakey RRB and Newton AC (1994) *Tropical Trees: The Potential for Domestication and the Rebuilding of Forest Resources*. London, UK: HMSO.

TREE BREEDING, PRINCIPLES

Contents

A Historical Overview of Forest Tree Improvement

J Burley, University of Oxford, Oxford, UK

Introduction

Genetic principles have been applied widely in the practice of forest management within the last 100 years although elements of breeding operations were practiced earlier. Various terms have been used to describe the discipline, particularly forest genetics and tree breeding, but a collective term, tree improvement, is useful since it incorporates genetic change, silvicultural improvement, and better use of the end products and services derived from trees.

The twentieth century saw changes in the objectives of forest management and hence of tree improvement, in the species of interest, in the benefits sought, in the nature and number of individual characteristics improved, and in the techniques used. Recently emerging issues include the concept, conservation, and control of the genetic resources that underlie tree improvement, and the application of modern techniques of biotechnology. A number of contributions to this Encyclopedia summarize the state of knowledge of these issues and the progress in genetic understanding and practical improvement of many species.

Concepts of Forest Genetics, Tree Breeding, and Tree Improvement

Forest genetics is generally considered to include Mendelian (traditional) genetics, population genetics and quantitative genetics. Gregor Mendel, an Austrian monk, established the basis for traditional genetics in 1866 with his famous experiments on peas in a monastery at Brno (now in the Czech Republic); these led to his famous laws of heredity (segregation and independent assortment of discrete genes), dealing with the inheritance of traits in relatively small groups of individuals over short periods of time. They concern descendant generation segregation, progeny–parent relationships, linkage of genes and characteristics, and individual gene action (additive, dominance, and epistatic effects).

The implications of Mendel's results were not appreciated by the scientific community until the early 1900s but then agricultural plant and animal breeders effected rapid advances in productivity by the application of these principles. However, they were not applied to forest trees on a significant scale because of the long generation intervals of most trees, especially in commercial rotations; it proved difficult to determine these genetic controls without long-lasting field trials until the development of biochemical methods allowed the identification and tracking of individual genes and character controls. Although some efforts were made earlier, it is reasonable to consider that the start of major tree breeding occurred at the end of World War II (1945) when selective tree breeding began.

Population genetics concerns the genetic behavior, distribution, and changes in large groups or populations of individuals over relatively longer time periods, including responses to natural and artificial selection. It incorporates such concepts as survival, fitness, the Hardy–Weinberg equilibrium for allele frequencies, and polymorphism. Statistical analysis improved dramatically with the enhanced capacity of computers. This is crucial to an understanding of population genetics within a species which itself is essential for guided tree breeding, for comprehending past evolutionary change, and for predicting future responses to political, environmental, management-related, and economic changes.

Many traits of productive and economic importance are controlled by several genes and their interactions (polygenic inheritance). Quantitative genetics deals with the assessment of genetic and environmental parameters including phenotypic and genetic variances, covariances and correlations, the estimation of heritability, and the response to selection.

Tree improvement can thus be taken strictly to include enhancement of silviculture and management systems as well as genetic improvement (tree breeding), together with the enhancement of processing and use of products and benefits derived from trees; however, the Encyclopedia contributions concentrate mainly on the breeding aspects and their underlying genetic principles. Genetic changes must be seen in the framework of appropriate management practices. For instance, a genotype that is good for low-altitude sites with dry sandy soils requiring fertilization or irrigation is not necessarily the optimum for wet clays needing drainage and/or subject to windthrow at high altitudes. Similarly a genotype that has wood structure and properties suitable for newsprint may not be appropriate for fine furniture.

Traditional Tree Improvement

The traditional stages of tree improvement include the following.

Species and Provenance Trials

Many species originate in environments that resemble the conditions of a given planting site and they can be evaluated in comparative (common garden) experiments on a range of sites (homoclimal comparison). For species that naturally occur over a wide geographic range with varying environmental conditions, natural selection may have caused heritable differences to evolve between populations (termed variously, and often loosely, origins, original provenances, or seed sources); some degree of difference may also occur when trees are introduced to a site and seeds subsequently collected from that site (termed provenances, derived provenances, and sometimes landraces, although in a different sense to that used for agricultural crops by Otto Frankel). These different origins and provenances also require evaluation in comparative trials and the interpretation should take into account all available information about the genetic history of each population beginning with the native origin of its parental stock. Many countries have decades of experience of the most suitable exotic species but surprisingly little information on the genetic variability between or within populations of their indigenous species, with the notable exceptions of Canada and the USA where plantation forestry is based largely on indigenous conifers.

Seed Stands (UK) or Seed Production Areas (USA)

When the demand for local seed of exotic species is high (to reduce dependency, risks, and costs of imports from original sources) silviculturists and tree breeders identify phenotypically superior stands and thin or fertilize them to stimulate flower and seed production. Although the phenotypic superiority does not prove genetic superiority, this is the simplest and earliest step that can be taken to obtain some genetic gain and it is successful if the stand identification is careful and the traits of interest are under some degree of genetic control. Such source-identified material costs more to produce and should be saleable by nurseries at slightly higher costs.

Phenotypic Selection of Parent Seed Trees

When sufficient areas of plantation are established the tree breeder screens all trees systematically for individual phenotypic superiority, those chosen being termed plus trees. Again if individual characteristics are under a reasonable degree of genetic control, open-pollinated seed from these selections will yield somewhat improved offspring.

Seed Orchards

Greater improvement can be obtained if the selections are propagated (by grafts, cuttings, or seedlings) into seed orchards. The clonal orchards are special plantations with many copies of each selected phenotype randomly allocated and widely spaced to encourage wide crossing among all possible combinations of the parents and heavy seed production. The seed produced is then genetically superior to forest-collected seed of seed stands or individual plus trees. Seedling seed orchards permit the use of the stock as progeny tests and breeding populations (then known as breeding seedling orchards or BSOs) in addition to seed production.

Progeny Tests

The growth and properties of plants derived from seed stands or from the original parents in the plantations can be compared with commercial seedlots or new imports. However, information about the genetic value of each individual plus tree can only be derived from carefully designed, managed, assessed, and analyzed progeny trials. A wide range of designs and analyses exists and the availability of modern computing facilities makes the use and analysis of unbalanced and incomplete designs possible. The ultimate aim is to obtain information on the breeding value of each individual, the extent of correlations between all traits of interest, and the use of individuals in recurrent selection cycles over successive generations to continue the process of genetic gain while avoiding such problems as inbreeding depression or increased disease risk through narrowing the genetic base.

Use of Improved Material

Genetically improved material arising from seed orchards is usually distributed to commercial plantation agencies as seed, seedlings, or vegetative propagules. Techniques for clonal propagation were developed for many species centuries before genetic principles were understood. A famous Japanese geneticist, Ryookiti Toda, reported in the 1970s on work undertaken in Japan in the seventeenth century on the selection and propagation of sugi (*Cryptomeria japonica*).

Program Sequences

Early tree breeding programs attempted to follow these steps sequentially, often following nearly complete commercial rotation periods to complete each phase; the time required to complete the different stages of tree breeding became the main constraint to genetic advance. However, the gap between these steps progressively shortened as the demands placed by human populations on natural resources increased and as early selection methods, flower induction techniques, sophisticated statistical routines, and modern computing power were developed.

Some breeding programs proved abortive because the steps were not followed adequately; for example, programs with *Pinus sylvestris* in Britain and *Cupressus lusitanica* and *Pinus patula* in Colombia failed because they were essentially the wrong species for the sites. New Zealand efforts with *Pseudotsuga menziesii* failed initially because of failure to identify the optimum provenance whereas relatively little attention was given to the origins of the now hugely successful *Pinus radiata*.

Early Forest Tree Improvement

Tree breeding is not new. It is sometimes argued by botanists that palms are not strictly trees because they do not have persistent cambia and do not therefore technically produce wood; however, if this technicality is overlooked, then the Assyrians and Babylonians can be credited with the first hand-pollination of trees since they improved date palms 3000 years ago. It was not until Hooke's invention of the microscope in the seventeenth century that it was possible to see the pollen grain.

One of the American leaders in the postwar field of forest genetics and tree breeding, Bruce Zobel, published with his coauthor, John Talbert, a widely available list of early forest geneticists and their topics; this list was based on an historical review by the Hungarian–Canadian tree breeder, Oscar Sziklai (see **Table 1**). Beginning with Bradley in England they listed some 30 outstanding individuals who had worked variously from 1717 to 1935 on different components of tree improvement – seed sources, inheritance, hybridization, vegetative propagation, reproductive biology, seed production stands and orchards, and a few specialized characteristics such as stem straightness and wood properties.

Work on provenance variation and self-fertilization of larch was started at the Institute of Forest Genetics in Sweden during 1902. In Placerville, California, in 1924, the Eddy Tree Breeding Station was established largely conducting pine hybridization. However, among the developed countries, the bulk of work related to tree improvement was undertaken in the Southern USA with four major pine species. For instance, also in 1924, Philip Wakely began work at the Southern Forest Experiment Station of the US Forest Service on range-wide seed source collection and testing that was fundamental to all subsequent selective breeding work and he also conducted pine hybridization. In the 1930s, work on poplars was conducted in the US Forest Service North East Forest Experiment Station by Ernest Schreiner and in Sweden by Nilsson-Ehle and coworkers. This work on poplars, especially on interspecific hybrids, precipitated the considerable but often uncritical work on pine and spruce hybridization that took place before and after 1945.

Not all of the work was done in the countries now considered 'developed.' Sir Harry Champion who subsequently became Professor of Forestry at Oxford, published in the 1920s and 1930s on the seed source and genetic control of stem form and wood

Table 1 Some of the early forest geneticists and their areas of interest

Year	*Geneticist and country*	*Area of interest*
1717	Bradley (England)	Importance of seed origin
1760	Duhamel de Monceau (France)	Inheritance: oak
1761	Koehlreuter (Germany)	Hybridization
1787	Bursdorf (Germany)	Plantation for seed production
1840	Marrier de Boisdhyver (France)	Vegetative propagation
1840	De Vilmorin (France)	Fir hybrids
1845	Klotzsch (Berlin)	Intraspecific hybrids: oak, elm, and alder
1904	Cieslar (Austria)	Provenances: larch and oak
1905	Engler (Switzerland)	Elevation differences of species: fir, pine, spruce, larch, and maple
1905	Dengler (Germany)	Provenance tests: fir and spruce
1906	Andersson (Sweden)	Vegetation propagation
1907	Sudworth, Pinchot (USA)	Breeding nut and other forest trees
1908	Oppermann (Denmark)	Straightness: beech and oak
1909	Johannsen (Sweden)	Elite stands
1909	Sylven (Sweden)	Self-pollination: Norway spruce
1912	Zederbauer (Austria)	Crown form: Austrian pine
1918	Sylven (Sweden)	Seed orchards
1922	Fabricius (Austria)	Plantation for seed production
1923	Oppermann (Denmark)	Seedling seed orchards
1924	Schreiner (USA)	Poplar breeding
1928	Burger (Switzerland)	Pine selection
1928	Bates (USA)	Seed orchards
1930	Larsen S. (Denmark)	Controlled pollination: larch
1930	Heikinheimo and M. Larsen (Finland)	Curly grain: birch
1930	Nilsson-Ehle, Sylven, Johnsson, Linquist (Sweden)	Pine and aspen breeding
1935	Nilsson-Ehle (Sweden)	Triploid aspen

Reproduced with permission from Zobel BJ and Talbert J (1984) *Applied Forest Tree Improvement*, Caldwell, NJ: The Blackburn Press, and based on the previous work of Oscar Sziklai (University of British Columbia).

properties (twisted grain) in the Indian chir pine (*Pinus roxburghii*).

Tree Improvement after 1945

Following World War II, systematic tree breeding programs based on a good understanding of genetic principles were initiated in Europe, Japan, and North America; in Europe the species were both indigenous and exotic while in Japan work was concentrated initially on the indigenous *Cryptomeria japonica*. In both Canada and the USA attention was focused on indigenous Douglas-fir (*Pseudotsuga menziesii*), pines (*Pinus* spp.), and spruces (*Picea* spp.) with some work on timber and nut-bearing hardwood species. Tree breeders were appointed and tree breeding stations were established or expanded in Denmark, Finland, France, Germany, Italy, Norway, Sweden, and the United Kingdom. In Europe and Japan most of the research and development were conducted by governmental and academic institutions. Among the outstanding and most influential pioneers was C. Syrach Larsen in Denmark.

Starting in the 1950s, in the USA Bruce Zobel pioneered not only tree improvement *per se* (in his commercial and academic appointments) but also the concept of tree improvement cooperatives; these facilitated the sharing of research costs, genetic material, and benefits between a number of industrial forestry companies, which were commercial competitors yet which saw the value of precompetitive collaboration. These collaboratives were coordinated by universities notably Florida, North Carolina State and Texas for southern pines. A detailed history of these cooperatives written by Zobel and Sprague was published by the Forest History Society and is a significant, insightful review of the personnel and administrative procedures of these initiatives.

Many other universities conducted forest genetic research and an international tree improvement cooperative was established under the coordination of North Carolina State University and involving countries interested in central American tree species (CAMCORE). In addition to legally constituted cooperatives, throughout the latter half of the twentieth century regional tree improvement conferences were held annually and biennially in several regions of the USA; these brought together geneticists, breeders, nursery and forest managers, and academic staff and students. They provided a valuable forum for the rapid dissemination of findings and practices and they became models for regular associations and conferences in other parts of the world.

In the 1960s tree improvement programs were initiated in Australia (federal and State-oriented), New Zealand (Forest Research Institute, Rotorua), South Africa (De Wet Tree Breeding Station), and Zimbabwe (then Rhodesia) (Forestry Commission); these have become outstanding examples of highly planned, efficiently conducted, and economically effective tree breeding. Subsequently many other countries in the British Commonwealth initiated programs with the initial guidance of the Commonwealth Forestry Institute (now the Oxford Forestry Institute); francophone countries in Africa and the Pacific region were assisted by the Centre Technique Forestier Tropical (CTFT, Nogent-sur-Marne, France). These were all concerned primarily with exotic pines and eucalypts for industrial plantations and in most of these countries they are still fundamental to the forest industry.

The International Union of Forestry Research Organizations (IUFRO) was established in 1892 to encourage collaboration, the sharing of information and material, and mutual support for forest research; initiated by a few countries in Europe, it progressively enlarged and formed several hundred specialist Working Parties, several of which dealt with provenance research on temperate species before and after 1945. However, it was not until 1972 that a specific tropical group was established by Garth Nikles (Australia) and Jeff Burley (UK) to deal with the genetic improvement of tropical species.

Breeders and geneticists from many tropical countries participated thereafter in international provenance trials coordinated by the agencies described above, by the Food and Agriculture Organization of the United Nations (FAO, Rome, Italy, the United Nations Agency created in 1948 with responsibility for forestry activities within the UN), by the Danish Tree Seed Centre (DTSC, Humlebaek, Denmark) and by the Commonwealth Scientific and Industrial Research Organization (CSIRO, Canberra, Australia).

Regular meetings of up to 300 participants from more than 30 countries also shared their experience on all aspects of tree improvement. Advanced breeding programs were developed in several South American countries, particularly Argentina, Brazil, and Uruguay; a team of researchers in the Aracruz Company in Brazil received the Marcus Wallenberg Prize (the most prestigious award related to forestry) in 1983 for their work on the improvement of eucalyptus growth and properties for the paper industry.

The eventual target of these institutions, programs was the clonal seed orchard as the major seed production unit to disseminate the products of the selective breeding effort. These encountered major problems that varied between species. Many early orchards failed to produce significant quantities of seed; sites had to be identified that favored flower and seed production, not necessarily the same as sites that promoted the traditional forester's goal of stem wood production. In grafted seed orchards, late incompatibility between stock and scion caused many clones to be rejected from the breeding program. The behavior of scions after grafting was often influenced adversely by factors dependent on the age of the parent from which the scion was taken (cyclophysis) and the position in the parent's crown from which the scion was collected (topophysis). Gradually these problems were overcome by physiological and management research and sometimes by the use of rooted cuttings rather than grafts; in other cases, seedling seed orchards were adopted to avoid incompatibility problems.

Recent Changes in Tree Improvement Objectives and Methods

There have been significant changes in the policy, institutional, and technical aspects of forestry in the last half-century and tree improvement has changed accordingly. In the 1950s the primary target was simply the production of large volumes of industrial wood. In the 1960s more attention was given to the quality of such wood and this was refined further in the 1970s to address the quality of pulp and paper. These targets continued in the new millennium with increasingly refined techniques for evaluating quality.

However, at the same time as industrial forestry escalated, in tropical and developing countries more attention was given to rural development forestry and the role of trees in supporting agriculture and human welfare. Many research institutions in developing countries and several in developed countries have begun the evaluation of species, populations, and selected individuals for inclusion in breeding programs to enhance the production of human food, animal fodder, fuelwood, construction poles, pharmaceuticals, and chemical exudates. These generally follow the same principles as those for industrial conifers or eucalypts but on the basis of less initial knowledge, more political problems, and fewer resources of finance and skills.

For tree improvement, in the 1950s much work concentrated on the choice of species and provenance with some simple mass selection and occasional species hybridization. Through the 1960s there was considerable debate and practice of different progeny test methods and seed orchard designs; as the sophistication of design and analysis improved, there was also an increased awareness of the need for large numbers of selections and test plantings to obtain precise estimations of genetic parameters and to provide material for recurrent selection.

The 1970s saw the planning and implementation of recurrent selection strategies; in many organizations these replaced the traditional single-generation approach in which individual parents were selected, propagated in seed orchards, and culled on the basis of progeny tests that evaluated their genetic worth; the resulting culled orchards produce seed that Zobel termed '1.5 generation material' although strictly it was still based on selections made in the first generation. The development of recurrent multi-generation plans required the development of intensive recording, maintenance of large databases, and the training and dedication of career geneticists.

The 1980s focused attention on cloning through cuttings and tissue culture. The perfection of cutting techniques led to the ability to propagate hybrids, especially in the eucalypts. Hybridization and cloning together probably led to the biggest increase in productivity of all time because combinations of species' attributes could be put together to match new plantation environments that have never existed in the wild. Outstanding wood production and stem form were obtained in Brazil, Congo, South Africa, and Uruguay and many other countries have emulated these successes. Typical annual yields of eucalypt wood per hectare in Brazil rose from 4 m^3 at the start of the twentieth century to over 40 m^3 by the end; the role of research in integrating selection, hybridization, cloning, and silviculture was recognized by the award of the Marcus Wallenberg Prize in 1983 to a team of four from the Aracruz Company at Victoria, Espiritu Santo, Brazil.

In the 1990s three major sets of techniques and strategies emerged: molecular genetic methods, multiple population breeding strategies (for which Gene Namkoong received the Marcus Wallenberg Prize in 1994), and breeding seedling orchards (pioneered in developing countries by Richard Barnes).

Throughout the 1980s and 1990s terpenoids and isozymes were used for a variety of genetic purposes, sometimes inappropriately; this led to some bad management decisions about optimum breeding strategies. It also identified the need to determine and separate the diversity of genetic markers from functional diversity. The recent development of molecular techniques facilitates several fields of enquiry in ecology, genetics, and tree breeding. These include:

- taxonomic identification and classification
- evolution of species and individuals
- genecology and habitat-related genetic variation between populations of a given species
- population genetic structure
- identification of breeding systems (for breeding, gene flow, conservation, and habitat fragmentation)
- evaluation and prediction of genetic differences among species, populations, individuals, and clones
- genetics and functional genomics of pest resistance, environmental tolerance, growth pattern, and chemical and wood properties
- 'finger-printing' of individual genotypes and verification and reconstruction of pedigrees
- monitoring of biological diversity.

Subject to public acceptance, genetic modification of trees themselves can contribute significantly to rapid and progressive improvement over recurrent generations. The challenge for the future, following a century of traditional tree improvement, is to achieve this technically and politically without reducing the resources for traditional breeding; genetic modification must always be based on the material and knowledge achieved in classical tree improvement.

Dissemination of the results of research and of information on the development of theory and practice was a vital element of the rapid expansion and progress of tree improvement throughout the world. In the postwar era one of the most influential books was written by Syrach Larsen in Denmark; despite some scientific deficiencies, it provoked the rapid growth of interest in the possibilities of tree breeding. Initially one journal, *Silvae Genetica*, was established specifically to cover all fields related to forest genetics and tree breeding. Subsequently the literature related to the subject expanded with innumerable textbooks, journals, and conference proceedings plus many series of committee reports, booklets, and technical notes from national breeding stations and international agencies such as FAO. This literature, coupled with graduate university research and specialized training courses by such institutions as CSIRO, CTFT, DTSC, FAO, and OFI, enhanced the development of the corps of effective forest geneticists and tree breeders throughout the world. Within the academic area, initially principally in the USA, the pioneers in the immediate postwar period who set the standards for academic education included Bruce Zobel in North Carolina State, Francois Mergen at Yale, Jonathan Wright at Michigan State, and Bill Libby at the University of California, all ably supported and succeeded by a large number of scientists and students from many countries.

Genetic Resources

Underlying all forest genetic improvement are the genetic resources of forest ecosystems, species, populations, individual trees, chromosomes, genes, alleles, and all their variation. They include populations and individual genotypes resulting from artificial selection and breeding efforts. They constitute an intergenerational resource for all forest-based demands of products and services. The various benefits sought by humankind are controlled to different extents genetically and information on this variability is fundamental to obtaining genetic advance from selection and breeding. This wide diversity of resources requires a range of methods for its exploration, evaluation, conservation, improvement, and dissemination. Modern tree improvement programs deliberately target the conservation of representative natural diversity in addition to the production of genetically restricted populations for high productivity of benefits.

Conservation of natural forest populations is traditionally undertaken through the establishment of parks and reserves (*in situ*) but it is also effected by exotic plantings (e.g., arboreta, botanic gardens, conservation stands, *ex situ*). Many of the international trials of species and provenances have been used for *ex situ* conservation. Temporary but relatively long-term conservation is also practiced through the storage of seed under appropriate conditions (commonly low temperature and moisture, depending on the species requirements). Tree breeders are now well aware of the values, needs and methods of the conservation of forest genetic resources.

See also: **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species; Forest Management for Conservation; Genecology and Adaptation of Forest Trees; Genetic Aspects of Air Pollution and Climate Change; Genetic Systems of Forest Trees; Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics; Propagation Technology for Forest Trees; Quantitative Genetic Principles. **Tree Breeding, Practices**: Breeding and Genetic Resources of Scots Pine; Breeding for Disease and Insect Resistance; Genetic Improvement of Eucalypts; Genetics and Improvement of Wood Properties; Genetics of Oaks; Nitrogen-fixing Tree Improvement and Culture; *Pinus Radiata* Genetics; Southern Pine Breeding and Genetic Resources; Tropical Hardwoods Breeding and Genetic Resources. **Tree Breeding, Principles**: Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources

Further Reading

Adams WT, Strauss SH, Copes DL, Griffin AR (eds) (1992) *Population Genetics of Forest Trees*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Barnes RD (1995) The breeding seedling orchard in the multiple population breeding strategy. *Silvae Genetica* 44(2–3): 81–88.

Burley J and Styles BT (eds) (1976) *Tropical Trees: Variation, Breeding and Conservation*. Linnean Society Symposium Series no. 2. London: Academic Press.

Eldridge K, Davidson J, Harwood C, and van Wyk G (1994) *Eucalypt Domestication and Breeding*. Oxford, UK: Clarendon Press.

Fins L, Friedman ST, Brotschol JV (eds) (1992) *Handbook of Quantitative Forest Genetics*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Kanowski PJ (1993) Forest genetics and tree breeding. *Plant Breeding Abstracts* 63(6): 719–726.

Larsen CS (1956) *Genetics in Silviculture*. Edinburgh, UK: Oliver & Boyd.

Mátyás C (1999) *Forest Genetics and Sustainability*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Namkoong G, Barnes RD, and Burley J (1980) *A Philosophy of Breeding Strategy for Tropical Forest Trees*. Tropical Forestry Papers no. 16. Oxford, UK: Commonwealth Forestry Institute.

Namkoong G, Bawa K, Burley J, and Shen SS (1991) *Managing Global Genetic Resources: Forest Trees*. Forest Genetic Resources Work Group, Committee on Managing Global Genetic Resources, National Research Council. Washington, DC: National Academy Press.

Simons AJ (1992) Genetic improvement of non-industrial trees. *Agroforestry Systems* 18: 197–212.

Thielges BA (1975) *Forest tree improvement: the third decade*. Baton Rouge, LA: School of Forestry and Wildlife Management, Louisiana State University.

Wright JW (1976) *Introduction to Forest Genetics*. New York: Academic Press.

Young A, Boshier D, Boyle T (eds) (2000) *Forest Conservation Genetics: Principles and Practice*. Canberra, Australia: CSIRO Publishing.

Zobel BJ and Talbert J (1984) *Applied Forest Tree Improvement*. Caldwell, NJ: The Blackburn Press.

Zobel BJ and van Buijtenen JP (1989) *Wood Variation: Its Causes and Control*. New York: Springer-Verlag.

Zobel BJ and Sprague JP (1993) *A Forestry Revolution: The History of Tree Improvement in the Southern United States*. Durham, NC: Forest History Society and Carolina Academic Press.

Forest Genetics and Tree Breeding; Current and Future Signposts

R D Burdon, New Zealand Forest Research Institute Ltd., Rotorua, New Zealand

Introduction

The context of forest tree improvement is changing and will continue to change. Upgraded processing technology, the development of new products, global economic changes and associated changes in markets, biotic events, plus changes in crop management systems, will all tend to change breeding goals. The classical breeding methodology is likely to undergo basically incremental changes made possible by a combination of more refined algorithms, upgraded software, and continued increases in computing power. Advances in propagation technology, some more or less classical, some much more radical, will favor updating of both breeding goals and crop management systems. Management of the populations used in total breeding programs will become a more pressing issue as genetic advances continue, with the associated tendency to narrow genetic bases. Novel gene technology, directed at identifying existing genes or at introducing new ones, is being widely explored, yet remains unproven. Genetic modification has many attractions, including reducing lead times and expanding the range of prospective breeding goals, but in forest trees poses some special risks and requires prolonged testing of transformants. While new biotechnology promises much, it is widely seen as a powerful supplement to classical breeding rather than a substitute for it. Institutional and economic changes, along with rapid changes in technology, are changing the ways in which forest genetic improvement is pursued. Collaborative structures are coming under severe pressure, planning horizons are becoming shortened, and field-based work is tending to lapse in the face of stagnant funding combined with a shift towards biotechnology.

At the same time, and counter to the genetic improvement that is a key part of intensive domestication, there is a movement away from interfering with natural genetic processes and towards management of natural ecosystems. Yet to retain this option may require the productive capacity of intensive, highly domesticated plantations; and to implement it effectively may require research information from modern gene technology.

Plantation Crop Improvement

Evolution of Breeding Goals

Breeding goals initially tended to focus on growth rate and tree form, with general health and adaptation as prerequisites. However, the goals have almost always evolved as breeding has progressed, with new information on biotic factors, genetic parameters, market demands, and the underlying wood characteristics that meet those demands. The goals will surely continue to evolve.

Disease and pest resistance Intensive plantation culture, plus increased and more rapid global travel, make diseases and pests more of a risk. So too will the favored status of a few intensively domesticated species that people may seek to grow over extended ranges of environments. Thus increased emphasis on improved pest and disease resistance is likely.

Wood properties Impetus for achieving genetic improvement of wood properties can be expected from several directions. On the one hand, there is greater sophistication among wood processors and in the markets. On the other, there is a widespread tendency for practices that reduce the effective growing costs, notably use of fertilizers and lower stockings in order to shorten rotations, plus genetic gains in growth rate, to militate directly and indirectly against wood quality. Thus there is a call both to tailor wood properties better to market needs and to offset adverse impacts of reducing growing costs, to improve net value.

Portfolio approach Despite the greater sophistication, market requirements will remain uncertain, especially for species that are unsuited to extremely short rotations. One way of addressing such uncertainties is to deliberately grow a 'portfolio' of well-characterized but differentiated breeds in the hopes that one or more may eventually command a high premium in a market niche while the others are all routinely marketable by virtue of being well characterized.

Targeting by hybridization Early on in tree breeding, interspecific hybridization was pursued widely and somewhat uncritically, probably because many poplar hybrids gave strong, often almost unconditional heterosis (superior hybrid vigor) and were readily amenable to mass vegetative propagation. Many species hybrids, however, show no clear heterosis, and/or pose major problems of mass propagation. More recently, it has become appreciated that careful choice of parental populations or genotypes can strongly influence the merit of hybrids, that there are specific situations where heterosis can result from complementarity of site tolerances or pest or disease resistance, and that economic advantages can accrue from certain combinations of attributes even in the absence of actual heterosis, while advances in propagation technology can overcome the historic difficulties in mass propagation. Even with past difficulties, some nonpoplar hybrid combinations have proved successful, and there is likely to be a resurgence of experimental hybridization, both interspecific and interprovenance.

Impacts of new propagation systems and other biotechnology Improved vegetative propagation systems are making possible mass propagation of individual clones in a wider range of species. The consequent clonal systems can change breeding goals in several ways. They will facilitate the selection of ideotypes that may not be strong competitors but can, as pure crops, be especially productive. This would be matching long-term trends in much crop breeding, whereby certain features that can militate against competitive ability can actually favor high economic productivity. Thus some long-term gains in production may stem from exploiting divergences between competitive ability and productivity, although the scope for this is necessarily relatively limited when trees are grown for stemwood production. Yet in future the divergence that exists may become the basis for wringing out further gains in productivity. Moreover, various features of stem architecture that favor competitive ability also represent highly undesirable within-log variation in wood properties. For some traits, like resistance to climatic damage, clonal selection may be much more powerful, since much wind damage may reflect physical interactions among neighboring genotypes rather than the inherent susceptibility of each and every genotype to such damage. Routine screening of large numbers of candidate genotypes for such crop-performance traits is prohibitively costly and time-consuming, so a major challenge is to develop the capability to characterize the appropriate ideotypes for improving such traits.

Less radical is the potential for clonal forestry to target ideotypes that represent intermediate expression of traits, since use of clonal material avoids the variation arising from genetic segregation. This, however, will only be worthwhile for traits of high heritability.

Genetic engineering, which is addressed later, can of course make it possible to address breeding goals that are basically inaccessible when using naturally occurring material. It can also be used as a research tool, to provide information with a range of applications.

Classical Breeding

Quantitative methodology

Selection Algorithms for estimating (or predicting) genotypic values from data are likely to undergo some incremental refinement. However, the limiting factors may remain information on economic-worth functions and genetic intercorrelations, poor economic information being a major problem in the presence of adverse genetic correlations; this calls for good understanding of cost and price structures in production systems, although uncertainty concerning future markets will bedevil longer-rotation species. To some extent, this problem can be finessed by deploying differentiated breeds, which exploit differences between environments and end-uses in the comparative economic weights of different traits. In effect, this is a means of exploiting global nonlinearities in economic-worth functions for different traits. However, with clonal forestry systems there is the prospect of exploiting various nonlinearities to a greater degree.

Trial layout Theoretical efficiency of experimental layouts for selection has been widely studied, but often in relation to fixed total numbers of individuals planted. Optimality in terms of cost-efficiency of genetic gain, however, remains the ideal. While it is almost always the subject of operational guesses, explicit quantitative analysis has seldom, if ever, been published.

Data analysis While experimental layouts can be refined, the efficiency of selection therefrom may remain limited by the inherent effectiveness of block layout schemes for partitioning environmental effects. Another approach is to use the data to estimate both the local environmental effects and the genotypic effects, in order to achieve better estimates of genotypic values. Such neighborhood-adjustment or spatial analysis has already been significantly developed, but guidelines as to optimal algorithms in given situations remain to be established with any high degree of confidence. Establishment of better guidelines and more extensive use of such analysis are foreseen, especially with continued improvements in software and computing power.

As tree-breeding programs progress, population structures are typically becoming more complex, with overlapping generations and multiple classes of relatives. This increases the call for sophisticated data analysis for selection, thus strengthening the traditional affinities with animal-breeding methodology.

Stochastic simulation For general optimization studies, increased stochastic simulation is foreseen, since it is a powerful tool not only for predicting outcomes but also for assessing associated risks by characterizing distributions about the most likely outcomes.

Genotype–environment interaction ($G \times E$) Genotype $\times$ environment interaction, whereby the comparative performance of different genotypes will vary according to the environment, remains an important issue for genetic management of forest trees. It involves: (1) geographic transference rules for deploying material; (2) possibly structuring breeding populations into units to serve different environments; and, (3) even without such differentiation of breeding populations, selective deployment of planting-stock genotypes in different environments. A challenge remains to characterize the roles of environments in generating interaction, so that candidate genotypes can be tested more efficiently by choosing near-optimal subsets of environments for testing. In that way, it should be possible to maximize the efficiency of screening candidates for performance across the range of environments over which the species may be grown. Such an approach will contrast with much of the traditional methodology for studying $G \times E$ in crop plants, which has focused on the interactive behavior of finite numbers of stabilized cultivars and is the subject of a voluminous literature. More specifically, a challenge exists to make joint use of data on both test performance and environmental particulars for characterizing the roles of environments in generating interaction.

Forwards versus backwards selection The term 'backwards selection' is classically applied to selection on the basis of progeny-test performance, as in roguing or reconstituting seed orchards. Forwards selection applies classically to selection of seedling ortets within families created by crossing between superior parents, as in turning over generations in a long-term breeding population. While backwards selection gives high confidence in individual selections, it may sacrifice too much in terms of the genetic gain that can be virtually assured from forwards selection. Moreover, the distinction between forwards and backwards selection can become blurred in clonal selection, where either there can be dedicated clonal trials or seedling offspring in the breeding population can be clonally replicated. The latter case effectively allows forwards selection while reducing exposure to $G \times E$.

Population management

The status of controlled pollination Controlled pollination and the associated control of pedigree have been cornerstones of many existing breeding programs. However, full control of pollination can either limit the number of combinations in which parents can be crossed or incur excessive cost. Full control of pedigree, while it maximizes control of nominal inbreeding, effectively limits the manageable size of a breeding population, which can lead to loss of low-frequency alleles and severely limits the chances of capturing the infrequent to very rare favorable mutations. Sacrifice of full pedigree, however, need no longer be the irreversible step that it has been, thanks to DNA marker technology.

Refining of population structure Management of domesticated genetic resources has not usually reached the stage at which appreciable inbreeding is unavoidable. Neighborhood structures make mild inbreeding a natural feature of the genetic systems of many, if not most, forest tree species, so such inbreeding should be easily enough accommodated. However, there are signs of rekindling interest in some quite close inbreeding as a breeding tool, in order to purge genetic load and to build up frequencies of desired alleles more rapidly — only by selfing is it possible to achieve perfect assortative mating for all traits.

Breeding populations, where programs have elaborated beyond relatively simple variations of mass selection, have basically been structured around the production of seed orchards. However, where clonal forestry systems are the norm, the tendency has been for little to be developed in the way of formally structured breeding populations. In future, we must look to structuring breeding populations in the expectation that they will provide clonal material. Two likely implications are: (1) that individual offspring genotypes may be clonally replicated, particularly across sites; and (2) that some inbreeding may be more readily tolerated, because associated bias in family-mean information may matter less for selection.

In any event, a breeding population with clonal replication allows a closer integration of elements of both forwards and backwards selection.

Allowing for climatic change Since climatic change is a near certainty and, from latest knowledge of quaternary history, an ever-present risk, any management of genetic material should make some provision to accommodate such change. Even without the human influences that are currently driving global warming, recent climatic changes have sufficed to create widespread suboptimality of local populations. While most natural populations, with high rates of natural mortality and the consequent 'soft,' density-dependent selection, are sufficiently heterogeneous to allow considerable natural wastage of maladapted segregants, plantation forestry which is based on low ratios of final-crop trees to trees planted will not accommodate such wastage so readily. It seems logical to anticipate likely climatic change in locating at least some of the breeding-population and gene-resource material.

Deployment Issues

Family and clonal forestry Genetic uniformity has in principle enormous advantages for growing and utilization, although clonal monocultures are subject to notorious biotic and bioclimatic risks. For many species, therefore, single clones cannot safely be regarded as crop cultivars in their own right; rather, they should be components of a composite cultivar population, akin to the multiline cereal cultivars that have been synthesized to provide durable disease resistance in the face of mutation and adaptive shifts in pathogen populations. It remains to be seen what proportions of such clonal assemblages in forest trees will be deployed in mosaic or mixture respectively. For clonal material, management regimes can be precisely tailored to individual clones, or even to mixtures of clones that may be silviculturally similar but diverse with respect to ancestry and cryptic traits such as resistance to new pathogens.

Short of deploying specific clones, specific families are already used in some cases to match the management and utilization of crops to genetic composition but, with the genetic segregation that can even occur within pair-crosses, such matching is likely to fall well short of what is possible with clones.

Application of Molecular Biology

Molecular biology, involving DNA technology, has already reached initial applications in tree improvement. Most of the major potential applications and the basic underpinning science, however, are still being researched. Some of that work is being done with new sources of funding. However, with stagnant funding levels, much of it is being done at significant opportunity costs in terms of gains available from conventional breeding. Yet the successful application of much of the DNA biotechnology will be strongly dependent on the field plantings of the genetic material of conventional breeding programs. Using such biotechnology will intensify the domestication process that begins with plantation forestry and continues with classical breeding, and the essence of domestication is increasing inputs in order to obtain better returns. While biotechnology can substitute for some classical breeding measures, no prospect is seen of satisfactory net overall substitution within the short term.

Markers and expressed sequences

Verification/determination of genetic identity Use of simple sequence repeats (SSRs), also called microsatellites, has enabled verification of both clonal identity and pedigree. It has also revealed an embarrassing rate of errors in genetic identity, such errors becoming more and more crucial as a breeding program advances, on account of the increasing levels of genetic gain that are dependent on correct identity.

Determination of population origins While verifying an intended pedigree may now be relatively straightforward, there can be much greater challenges in identifying population origins of material, because the polymorphisms (presence of different alleles or forms of genes at individual loci within the genome) that differentiate individual genotypes or pedigrees represent noise variation in trying to differentiate populations. Such a capability, however, may be crucial for addressing problems of genetic contamination, which may be acute in the gene resources that underpin breeding populations.

Pedigree reconstruction Pedigree reconstruction, as opposed to the verification of a specific pedigree, has been proposed in respect of paternity as a means of saving on the costs associated with multiple pair-crosses per parent. However, there are likely to be situations where reconstruction of pedigrees, from large numbers of possible parents, may yet be needed, as in a biotic crisis when it may be necessary to select for disease resistance in unpedigreed commercial stands. For that, it appears that much more powerful marker systems will be needed in order to give essentially unambiguous answers.

Use of DNA markers for selection Use of neutral genetic markers to locate and characterize quantitative trait loci (QTL) in the genome (see below), as an aid to selection, has already been the subject of much experimental and theoretical research. Such information may be used in conjunction with phenotypic information on the trait(s) concerned, in true marker-aided selection (MAS) or, if practiced before phenotypes can be expressed, can be done entirely on marker information. Even after some theoretical pitfalls have come to light it appears promising, and it has worked well in some crop plants but not others. However, its efficacy in forest trees remains to be demonstrated. Because forest trees are outbreeders the general linkage disequilibrium (LD) that forms the ideal condition cannot be expected, except perhaps in hybrids between species that are fixed (having zero or 100% gene frequencies) with respect to different QTL and linked markers.

Genomics Genomics, the study of the physical arrangement of genes and noncoding DNA in the chromosomes, and the base sequences and gene functions, has become the focus of major research efforts.

Comparative The close genomic similarities between genomes of various important forest trees will favor collaborative efforts, since findings in one species can often be applied, in various possible ways, to one or more other species. The very high degree of synteny among certain species, e.g., within the genus *Pinus*, with the same genes at the same genetic loci having the same function, allows information to be readily applied from one such species to another. Quite remarkable, however, are the orthologies between very distantly related organisms, whereby very similar DNA sequences can code for closely homologous gene action despite wide differences in general plant structure and organization. Commonalities between the roles of the same genes (or close homologs) in different organisms can provide the basis for what S.H. Strauss refers to as genomics guided transgenes for exploratory use in genetic engineering.

Functional Study of pathways of gene action, based on expressed sequence tags, can, apart from yielding fundamental knowledge, help identify the effects of particular genes, and the feasibility of various prospective breeding goals. Genetic modification can be a powerful research tool, allowing the study of the metabolic and phenotypic impacts of altering the expression of existing genes or introducing alien genes.

Targeting breeding goals While there may arise some conditions that allow general LD in outbreeders, these conditions are often unlikely to obtain. This creates an additional call for the ideal situation of being able to identify readily the genes of interest by the base sequences, which would allow true gene-assisted selection (GAS).

Applications of genetic engineering Genetic engineering, or genetic modification (GM), entails inserting DNA sequences to modify the activity of existing genes, or introduce new functional genes. Much of the research to date has aimed at proving the concept for the species concerned. Several operational applications are being widely pursued, notably pest resistance, herbicide resistance, and reproductive sterility. GM is also being explored as a means of improving certain wood properties. It promises certain gains that may substantially exceed those already promised by the typically high heritabilities of wood properties. However, there remain great attractions in using GM essentially as a research tool, using the insertion of DNA sequences to probe the roles of certain genes and their pathways of action. Indeed, this could yield some information that may eventually be applied in conventional breeding. GM, however, is intensely dependent on *in vitro* culture systems.

While all technologies have their own risks, the risks of GM attract special public attention, and in the case of forest trees they have some special features. They must therefore be addressed as part of the research on developing GM technology for forest trees, and be seen to be so.

Propagation Technology

Seed propagation will remain necessary, at least to produce the genetic recombinants that provide the candidates for the next cycle of recurrent selection. For many species, however, seed production will continue to be needed for mass production of commercial stocks, either directly or as a platform for mass vegetative multiplication. Pending, or failing, the development of mass vegetative multiplication, incremental improvements can be expected in seed-orchard technology, to improve yields and physical quality of seed and to avert unwanted external pollination. Care may be needed, however, in the choice of environment for seed production. In some spruces, in particular, the inherent growth rhythms and climatic tolerances of seedlings have been found to be affected by climatic conditions during a particular phase of seed production. Thus the choice of a congenial climate for producing seed may compromise adaptation to the harsher climates for which the seedlings are intended.

Rooting of cuttings has become a mature technology for mass-producing planting stock in many species, including some that were traditionally propagated as seed. Its development will surely continue in some quarters. Micropropagation, or tissue culture, will be refined further in many cases and developed for additional species, often for initial rapid multiplication to complement cuttings production. Embryogenesis, the other *in vitro* system, offers even higher multiplication rates, and has special promise as a means of providing recipient material for GM. Often, however, *in vitro* systems need to be refined in order to work with any genotypes of choice within a species.

Full control of maturation state in clonal material is extremely desirable, if only to allow clones to be mass-propagated after their merit has been proven. Several technologies exist to check the process of maturation (or physiological aging), with cryogenic storage looking increasingly promising. However, achieving true reversal of maturation, or rejuvenation, in somatic tissue would have enormous strategic significance. Still unrealized for a great many species that do not sprout from stumps, it remains perhaps the biggest single challenge in propagation technology.

Technology Portfolios

New biotechnologies are developing rapidly, and the many prospective technologies for individual steps in the process of genetic improvement can lead to large numbers of potential technological pathways for delivering enhanced genetic gains. Individual technologies typically have risks, of not performing as hoped, at least for the species in question. Even if a technology succeeds in itself, it may fail because it belongs in a pathway that is outflanked by another pathway. The problem is that, while each technology needs a concerted research effort, there needs to be a portfolio of alternative and complementary technologies under investigation in order to spread risks.

Interactions with Other Disciplines

Wood science, processing technology, and product development Increasing emphasis is being placed on genetic improvement of wood properties, for a number of reasons. Easily obtainable genetic gains have often been already captured for traits involving silvicultural performance and tree form. At the same time the pursuit of shorter rotations, fertilizer use, and lower stockings, all to reduce effective growing costs, call for genetic improvement to offset consequent declines in wood quality. Furthermore, wood processors and end-users are often demanding tighter quality specifications. Wood properties often appear to be very amenable to conventional breeding, but can be very expensive to evaluate (especially product-performance properties), while the role of specific basic properties in governing product performance is often little known. Major research efforts are afoot to study wood chemistry and ultrastructure in relation to product-performance properties, and the developmental pathways in expression of genes significantly affecting wood properties, with comparative genomics and genetic modification as research tools. Such work is directed at the full range of existing wood products, and the possibilities of new products.

Pathology Improved disease resistance is often needed for plantation crops, in the face of additional hazards posed by monocultures and growing preferred species over a range of sites. Such resistance often needs to be durable against genetic shifts in pathogen populations. Use of DNA markers promises to detect the various genetic resistance factors in the host, to help aggregate the multiple resistance factors needed to assure durability.

Other disciplines Of note are the overlapping areas of physiology and biochemistry, as essential adjuncts of functional genomics.

Impacts of Institutional Changes

Forest genetics research and tree breeding have historically been done largely under government agencies, or else multiparty cooperatives. Governments have tended to withdraw from such activities, with global pressures to reduce taxes. The development of biotechnology, particularly relating to DNA, has encouraged much more proprietary attitudes towards intellectual property. That in turn, along with many recent changes in forest ownership, is placing tree-breeding cooperatives under pressure. All these factors are also exerting pressure on the long-term strategic management. Also discouraged by proprietary attitudes toward individual technologies, which militate against collaboration, are adequate risk-spreading technology portfolios.

Species for Domestication

The list of forest tree species that have been subject to intensive domestication, including elaborate breeding programs, is relatively short, rather like the main food crops. The cost of intensive breeding will tend to focus domestication on a limited number of forest tree species. On the other hand, the perenniality and lifespan of forest trees make environmental adaptation much less flexible, which may tend to stop the list of domesticated forest tree species from remaining extremely short. Nevertheless, pines, eucalypts, and acacias seem likely to predominate among the intensively domesticated species.

Management for Conservation

Plantation forests have assumed great economic importance, despite occupying only a small area relative to native forests. They also have potentially great ecological importance, in that they may serve to relieve exploitation pressures that might otherwise affect natural forests (although clearance for agriculture is another matter). However, preserving and managing native forests, either for controlled exploitation or pure conservation, is often far from straightforward. Monitoring breeding systems and measures of genetic diversity can help indicate the likely impacts of population size and of cutting and regeneration regimes on long-term viability of populations. For this, information on reproductive biology will be very important. Some indications are being obtained of the impacts of certain exploitation regimes on the structure and diversity of populations. However, the most appropriate measure of genetic diversity is problematic. Diversity reflected in neutral genetic markers is often poorly correlated with the functional diversity that is often crucial to site adaptation and to response to artificial selection, such that common-garden field trials are often needed to relate functional diversity to marker diversity as well as elucidating genecology and within-species taxonomy. Common-garden experiments, however, while they can reveal much, will often need to be complemented by ecophysiological studies. Such studies can identify the specific environmental factors that cause stress, and the ways in which stress arises. As such, they can be powerful tools for applying results of the common-garden experiments beyond the particular environments where they are located. Of interest are indications that major functional diversity can be governed by promoter regions rather than coding regions of genes.

The genetic component of conservation management is likely to depend on the ecological validity of management regimes. Misguided exclusion of fire has often proved very counterproductive. Questions must now arise concerning the appropriateness of trying to impose uneven-aged and essentially continuous canopy structures on each and every species.

See also: **Genetics and Genetic Resources**: Genetic Systems of Forest Trees; Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics. **Tree Breeding, Practices**: Breeding for Disease and Insect Resistance; Genetics and Improvement of Wood Properties. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Economic Returns from Tree Breeding. **Tree Physiology**: Stress.

Further Reading

Burdon RD (2003) Genetically modified forest trees. *International Forestry Review* 5(1): 58–64.

Dutkowski GW, Costa e Silva J, Gilmour AR, and Lopez GA (2002) Spatial analysis methods for forest trials. *Canadian Journal of Forest Research* 32: 2201–2214.

Kibblewhite RP and Shelbourne CJA (1997) Genetic selection of designer trees for different paper and pulp grades. In: *Transactions of the 11th Fundamental Research Symposium Fundamentals of Papermaking Materials*. Cambridge, UK, pp. 439–472.

Lambeth C, Lee B-C, O'Malley D, and Wheeler N (2001) Polymix breeding with parental analysis of progeny: an alternative to full-sib breeding and testing. *Theoretical and Applied Genetics* 103: 930–943.

Lambeth C, Lee B-C, O'Malley D, and Wheeler N (2001) Polymix breeding with parental analysis of progeny: an alternative to full-sib breeding and testing. *Theoretical and Applied Genetics* 103: 930–943.

Mátyás C (ed.) (1999) *Forest Genetics and Sustainability*. Dordrecht The Netherlands: Kluwer Academic.

Muller-Starck G and Schubert R (2001) *Genetic Response of Forests to Changing Environmental Conditions*. Dordrecht, The Netherlands: Kluwer Academic.

Plomion C (2001) Wood formation in trees. *Plant Physiology* 127: 1513–1523.

Skrøppa T and Johnsen Ø (1999) Patterns of adaptive variation in forest tree species: the reproductive environment as an evolutionary force in *Picea abies*. In: Mátyás C (ed.) *Forest Genetics and Sustainability*. Dordrecht, The Netherlands: Kluwer pp. 49–58.

Strauss SH (2003) Genomics, genetic engineering, and domestication of crops. *Science* 300: 61–62.

Strauss SH and Bradshaw HD (eds) (2004) *The Bioengineered Forest: Challenges for Science and Society*. Washington, DC: RFF Press.

Stroup WW (2002) Power analysis based on spatial effects mixed models: a tool for comparing design and analysis strategies in the presence of spatial variability. *Journal of Agricultural, Biological and Environmental Statistics* 7: 491–511.

Unifying perspectives of evolution, conservation and breeding (2001) Proceedings (eight papers), Symposium in Honour of Dr Gene Namkoong. *Canadian Journal of Forest Research* 31: 561–632.

Walter C and Carson MJ (eds) (2004) *Plantation Forest Biotechnology for the 21st Century*. Trivandrum, Kerala, India: Research Signpost.

White TL, Neale DB, and Adams WT (2003) *Forest Genetics*. Wallingford, UK: CAB International.

Yanchuk AD (2001) The role and implications of biotechnological tools in forestry. *Unasylva* 204(52): 53–61.

Conifer Breeding Principles and Processes

A D Yanchuk, British Columbia Ministry of Forests, Victoria, BC, Canada

Introduction

Conifers or gymnosperms occupy many important forest ecosystems and are some of the oldest known species on the planet. Of the thousands of conifer species known to exist on earth, probably fewer than 100 have received even preliminary genetic studies, and only a dozen or so are under any kind of intensive tree improvement and breeding efforts. Some of these species, such as Monterey pine (*Pinus radiata*), have provided some of the most successful commercial forest tree plantations in the world. According to the Food and Agriculture Organization, of the approximately 187 million ha of forest tree plantations around the world, 31% are coniferous and of these approximately 20% are pine species.

Relative to genetic improvement in agricultural species, forest tree genetic improvement programs are very new. However, many changes to classical breeding approaches used in domesticated plants and animal species have had to be made in order to accommodate the unique biological features of forest trees. The reproductive biology, geographic patterns of genetic variation in the species, preservation of adaptive genetic variation, and the maintenance of wild forest reserves are issues that are unique to forest tree genetic resource management.

Genetic Surveys and Selection in Natural or Naturalized Populations

As far back as the early and mid twentieth century emphasis was placed on range-wide genetic surveys (i.e., provenance testing) using 'common garden' experiments, first established by research ecologists. Samples (seed) were collected from natural populations of interest (i.e., provenances) then raised and planted together in several environments to test performance of the local provenance versus nonlocal.

These studies showed that most conifers have large amounts of genetic variation, both within and among populations, and local populations are generally slightly suboptimal (e.g., adaptational lag can be present, among other factors). However, forest trees, in general, do show that patterns of adaptation are reasonably well associated with the climate from which they originated. More importantly, there are differences among and within species in this type of adaptation. Conifers can be classified as generalists, intermediates, or specialists in their level of adaptation to climatic and environmental gradients. For instance, species such as western white pine (*Pinus monticola*) are considered generalists, i.e., adaptations are not well correlated with climatic or geographic variables, yet others, such as Douglas-fir (*Pseudotsuga menziesii*), are much more tightly adapted; hence, movement of seed in this species needs to be restricted. A few species, such as some of the *Thuja* species, have genetic variation substantially lower than most other conifers, and at the extreme, *Pinus resinosa* shows almost no genetic variation.

Sampling strategies for breeding programs have sometimes been designed to take advantage of natural levels of variation among populations. In some cases, usually where exotic species are used, 'provenance effects' may be available to use, or a well-developed 'landrace,' if present, may also be an effective base population. Several large industries have been established from such introductions of materials, as with Monterey pine in New Zealand, Douglas-fir in France, Sitka spruce (*Picea sitchensis*) in the United Kingdom, and *Eucalyptus* spp. in many tropical and semitropical countries.

Genetic Testing

Genetic testing techniques developed over the last several decades have made it possible for much more rapid genetic improvement. However, the underlying reason for genetic gains is the same: most traits have genetic variation, and these differences can be transferred to offspring or progeny (i.e., they are heritable). Overall, most tree improvement programs have focused on improving growth potential, so selection on individual phenotypes has generally not been very effective because growth is typically a lower-heritability trait. However, a few other traits have been successfully improved by phenotypic selection, such as straightness, form characteristics, some disease resistance traits, and wood properties.

Field Test Designs

As in animal breeding, the past 30 years have seen tree breeders increasingly use techniques that more accurately identify and predict the genetic value or worth of selected parent trees. The use of a mother tree's offspring, whether vegetative (clonal) or seedling offspring, is a powerful technique for examining the genetic value of any parent tree. With many offspring trees per parent, planted across several test sites, some trees will sample better than average (i.e., microenvironments), and some worse, but on average the statistical average or mean of the family will reflect closely the true genetic mean of the family. It is a widespread practice to use about 20–30 offspring per family per site, as including more observations per family tends to be inefficient with respect to our interest in being able to compare more families.

The types of designs briefly discussed above, i.e., all genetic entries in the study are replicated in each replication or block, with multiple blocks, are referred to as randomized complete block designs (RCBs). In the field, blocks or replications are laid out with the hope of 'blocking' out patches of similar microsites, but the weakness with the design has typically been that the blocks are too large and fail to partition off much of the environmental variation that occurs within recognizable patches. With fewer numbers of trees per family in each block, and therefore more blocks on the test site, the efficiency of the design becomes greater.

A typical and relatively robust single-tree plot experiment would be one with 25–30 progeny per genetic entry (which means 25–30 blocks or replicates). It is important to note that if there were no environmental patches or gradients on a test site (which is usually never the case), no test site designs would be necessary. Forest tree test sites are normally quite patchy, with large gradients, even if this is not visible at the time of establishing the test sites. Of late, many breeding programs are considering new designs, such as incomplete block designs (ICB).

One significant problem with progeny testing to identify superior parent trees is that when competitive effects among trees take place, it is effectively no longer useful as a genetic trial to compare all genotypes. Slower-growing families will continually be outcompeted and among-family growth differences inflated. Hence, predicting genetic gain from older progeny tests is biased, as the trees are not in a true plantation situation. In recent decades, many genetic-gain trials in many programs have been established to help verify estimates from replicated progeny trials to volume yields on a per-hectare basis. Many institutions working with fast-growing species, such as Douglas-fir and radiata pine, now have very good measures of yield per hectare, with commercially well-known clones or families.

The Problem of Early Selection

In forestry, it is rare (except with some fast-growing hybrid poplars or *Eucalyptus* spp.) for selection ages to approach the final harvest age. This is particularly true for most conifer tree species bred for timber production, where rotation ages can be 25–80 years, depending upon the species and site productivity. In this situation, if the genes that affect the expression of a trait at an early age change their expression, then errors in selection accuracy and prediction in gain will be made. Family selection ages in forest tree breeding have usually been shown to be optimal (based on growth data) at ages 6–12 years. Tree breeders, then, face the issue of making adjustments to the predictions of genetic gain at rotation, to accommodate the juvenile to mature-age genetic correlation being imperfect. It will take several more decades for forest geneticists to understand the magnitudes of age–age genetic correlations in forest trees, so this is an inherent risk in tree breeding – little else can be done at this stage.

Genotype × Environment Interactions

It is also known that a particular genotype may perform differently, relative to others, in different environments. Thus genetic differences can be expressed differently in different environments. This is usually referred to as genotype × environment interaction (G × E) and has been a very important issue for geneticists to consider for many decades. Most conifer breeding programs use several test sites to look for stability in performance. For the most part, conifer genotypes exhibit reasonable performance across many variable sites, except in extreme conditions (e.g., such as low-elevation selections being tested at high elevations). Therefore, it is important that in initial testing schemes, multiple-site field-testing be used in order to establish the magnitude of G × E in the population and identify specific families of interest.

It is generally accepted now that any satisfactory method of analysis of G × E must allow the breeder the ability to differentiate between true changes in rank among genotypes in different environments, and that of statistical artifact (e.g., scale effects caused by different means and variances among different sites). The quality of the genetic tests, measured by heritability, is one of the factors that must be considered, along with the similarity in averages and variances.

Advanced-Generation Breeding and Testing

If it proves to be economically and biologically feasible to carry on with a genetic improvement program, the best parents identified through the first round of progeny testing (P_1 selection) need to be mated together. With recurrent selection continuing on this basis, the breeders are essentially creating new allelic combinations from which to change the frequency of genes for the trait of interest by selection. The most advanced conifer programs in the world, e.g., *Pinus taeda*, *P. radiata*, *Pseudotsuga menzesii*, and a few others, are at the filial third (F_3) or filial fourth (F_4) generations.

Traits of Economic Interest

Besides the improvements in growth performance, wood density has been studied and has been found to have higher heritabilities than growth rate, typically twice that of growth rate. However, there are often lower coefficients of phenotypic variation so gains are not large in most wood quality traits particularly when growth rate is also selected. As well, there are typically adverse genetic associations between these two traits. Many other traits are also important in conifer breeding and genetics, such as pest and disease resistance, tree form as it would affect log and timber quality, and many other wood properties. Whether these are being directly selected for economic reasons or not, conifer breeders have investigated these traits to establish the genetic and phenotypic relationships that could affect selection on other main traits (i.e., typically growth).

Mating Designs

There are several ways in which conifer breeders have been making controlled crosses (i.e., mating designs) for advanced-generation breeding. Complete matings of all possible desirable crosses is an ideal, but generally not practical and not economically or biologically necessary. Balanced mating designs are preferred in that estimates of general combining ability (GCA) and specific combining ability (SCA) are unbiased, but this has generally been shown not to be overly important. Making as many crosses as possible in the shortest period of time (as long as each parent is crossed a few times) tends to be a more cost-effective approach, as genetic gain per unit of time is generally the most important measure of long-term achievement in forest tree breeding.

A mating design that has been used often is the factorial design. This is where a tree can serve exclusively as a male or a female in some small mating group. This is one distinct advantage of the factorial design; e.g., if the breeder chooses a breeding group of eight unrelated trees, and mates them in the factorial design, four parents only need to provide pollen, and the other four only need to provide female cones for isolation and breeding. The total number of crosses in this situation is therefore 16. In the most commonly used mating design, the diallel, trees are used both as males or females. Complete diallel mating designs are generally not necessary, and the partial half-diallel scheme is usually employed by most tree breeding programs. However, after three to five crosses per tree it has been shown that there is little added benefit for the purposes of family and within-family selection.

Although there has been substantial debate about which approaches are best for advanced-generation field tests and selections (i.e., 'forward' selections), the most effective method will likely be determined by local operational and practical matters more than by theoretical ones. For instance, large homogenous single-family blocks (e.g., 100 full-sibling trees in each block with no replication) have been established, which allow the breeder a much better visual comparison of all cohorts in that family. With homogeneous test environments, this method can be very effective. On the other hand, breeders are usually still interested in applying selection at the family level, before selecting a few individual trees within families. In such cases, the designs, such as those discussed above (i.e., RCB designs), need to be used. Selecting individual trees for the next generation from single-tree plot or incomplete block designs is still possible with these designs (relative to the use of RCBs, or large single-family plots). However, it is likely that more reliance must be put on the family level of selection and therefore the use of more statistical assumptions and methodologies.

Breeding Population Structure

It has been shown that high short-term gains are possible with a relatively small breeding population, without losing much genetic variability (sometimes it may actually increase) even over several generations. If, for example, an aggressive program is considered appropriate, an elite breeding population of about 30 parents could be crossed together for the second generation population. In this situation, however, many of the lower-frequency genes, which may not have strong effects on the trait of interest, will be lost by genetic sampling effects. But including dozens more, or even a hundred, will only slightly reduce the chance of these loses. Moreover, these low-frequency genes do not have much affect on the genetic variation under selection. So other approaches should be developed to accommodate these kinds of genes (i.e., gene conservation programs). Most conifer breeding programs around the world now work with relatively small population sizes in the F_2 and F_3 generations, but maintain larger genetic reserves by other means.

Once this issue of population size has been resolved, it would be important to consider issues of relatedness that will be built up over time in the breeding population. This is inevitable in any breeding program, so tree breeders have to design methods to minimize the effects of accumulated inbreeding as best as possible. Subdividing the breeding population into groups that remain separate from intercrossing, sometimes referred to as sublines, allows the breeder to make matings among trees within sublines over generations but never crossing trees among sublines. This approach is now common in most tree breeding programs, as it allows the breeder the option of making selections among unrelated groups, which will be important for commercial seed production, usually in seed orchards.

Inbreeding Depression

As discussed above, it is inevitable that there will be relatedness among future-generation selections. Inbreeding is generally undesirable, because when related individuals are intermated, the deleterious genes (typically present even in highly selected parents) will be become homozygous at frequencies higher than expected by chance. If too few individuals are selected, or selection is not strong enough to eliminate these homozygous individuals, some deleterious alleles can become fixed in the selected population and overall performance or fitness will be lowered in the population.

Most tree species simply grow too slowly and are too difficult to work with to develop inbred lines, as has been done in some crop species. In forest tree seed orchards, or production populations of trees, as mentioned earlier, a breeder can take one or a small number of trees from each breeding group (subline) and inbreeding is effectively zero and production is maximized.

In the breeding population, mating decisions that minimize crosses among close relatives over time, and generate a large number of offspring per generation, will reduce the risks and hazards of inbreeding depression. With other experimental organisms (e.g., mice, maize) adequate population sizes with strong selection, has, over time, offset these effects and made genetic improvement a long-term possibility.

Genetic Diversity and Risk in Forestry

There are essentially two types of risks that foresters and forest genetic resource managers need to consider:

1. Is there a threat from a currently known pest that may be able to overcome current levels of natural resistance in the species and inflict unacceptable losses in planted forests?

   There are several ways in which this can be addressed, but all will depend upon a good understanding of the genetic basis of the resistance. For instance, several types of resistance mechanisms could be deployed in mixtures to make it difficult for the insect or pest to mutate to overcome all resistance genes at once. Another approach could be to deploy some susceptible genotypes along with resistant genotypes that rely on a single resistance gene or mechanism. The hope is that there is less pressure on the insect to evolve virulence to the resistant gene, while allowing for a commercially viable crop.
2. The geneticist must consider that there may be some future risk of a currently unknown threat (e.g., the introduction of an exotic pest). This is likely the case in which some natural resistance, controlled by genetic variations present in the population, is lost by mismanagement of genetic diversity in the deployment population. Responsible genetic management policy needs to be founded on this basic premise.

   Several research approaches have been considered with respect to this problem. As a general rule it has been shown that a very large number of genotypes, say much greater than 30–40, do not add any additional levels of 'genetic safety' over what natural forest regeneration might be able to provide. In fact, a relatively safe range can be between 10 and 30 unrelated genotypes. This is due to the following: genes at low frequency in the original wild population, which may be able to provide some resistance or increase fitness of the tree, will not be at frequencies high enough to protect even these natural stands. In other words, there would not be enough surviving and unrelated individuals in the wild stand with the resistant gene to serve as parents to regenerate the stand.

In summary, the deployment of genetic variation across the landscape for timber production must balance several factors, but a linear increase in some measure of diversity does not, in itself, provide a linear decrease in risk.

Gene Conservation

Basic measures in most tree breeding and conservation programs are to outline, document, and establish where and how certain classes of genes and genetic variation are best maintained over time and space, in case they are needed. Gene conservation should be viewed as a type of genetic 'insurance,' but the breeding populations, if present, should maintain most of the variation needed for the short and medium term future.

The loss of additive genetic variation in a population can be approximated by the formula $1/(2N_e)$, where N_e is the effective population size, so a sample of 30 trees from an infinitely large population will contain over 98% of the original genetic variation in the population. However, what will not be present in relatively small breeding populations are most of the genes that were at relatively low frequency in the original population. Conservation of these genes, either singly or in some complex of frequencies, is why gene conservation programs are needed and have to be designed to achieve over time. Breeding populations, clone banks, provenance trials, progeny tests, can all be linked, along with *in situ* populations (protected areas, such as parks, or managed forests with natural regeneration) to form the base of material for a conservation strategy.

Climate Change and Tree Breeding

Tree breeders may need to develop breeds today, for climates several decades from now. Assuming climates do change as predicted from global circulation models, it is largely up to the genetic resource manager, with an understanding of genetic variations and patterns of adaptation that the species exhibits, to respond now and generate material that will continue to produce the products we desire. Climate change models, and predictions of changes in biotypes around the world, can only tell us where the problems will be, but do nothing in themselves to offer solutions. The management and movement of the appropriate populations, largely developed and understood by researchers and tree breeders, will be the viable approach for forest managers to consider. Most wild populations of conifers, indeed most tree species, will not be able to migrate enough to maintain much resemblance to current forest ecosystem types. In this respect, climate change research in forest management is first and foremost a problem of genetic resource management.

Biotechnology and its Role in Conifer Breeding

There has been much technical development over the last decade with respect to cloning forest trees and changing the genetics of plants with transgene technologies. Cloning techniques, such as simple grafting, go back as far as the first grape varieties, but with current tissue culture techniques in conifers, such as somatic embryogenesis, genetic transformation using recombinant DNA technology is possible. Still uncertain, however, are the economics and social acceptance of genetically modified trees.

Molecular genetic markers are also becoming more important tools in forest genetics research and breeding, especially as genomes are becoming better understood with more complete molecular analysis. The use of marker technology for marker-assisted selection in applied breeding programs is also possible, but has not yet been applied widely in forestry tree breeding, primarily because of costs. Nevertheless, the information from molecular genetics research is uncovering many interesting aspects of gene evolution and function.

Conclusions

Tree breeding techniques (e.g., modern selection, breeding, and testing methods) are of course of paramount importance in pursuing improved quality of commercial conifers for traits of interest. Important techniques in tree breeding that have developed over recent years mainly revolve around field-test designs, mating designs for advanced-generation breeding, and many specialized procedures to assess traits of interest. New areas of research and program management are required in the areas of conservation of genetic variation, deployment patterns for improved varieties, special traits that require innovative assessment and selection systems, molecular genetics and genomics, multiple population breeding, and genetic management information systems. Of utmost importance, however, is that tree breeding programs consider the simplest and most effective methods that can be handled by the organization in realistic time frames.

See also: **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change; Genetic Systems of Forest Trees; Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics. **Tree Breeding, Practices**: A Historical Overview of Forest Tree Improvement; Breeding and Genetic Resources of Scots Pine; Breeding for Disease and Insect Resistance; Breeding Theory and Genetic Testing; Economic Returns from Tree Breeding; Genetics and Improvement of Wood Properties; *Pinus Radiata* Genetics. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources.

Further Reading

Clausen J, Keck DD, and Hiesey WW (1940) *Experimental Studies on the Nature of Species*. Washington, DC: Carnegie Institute.

Falconer DS and Mackay TFC (1995) *Introduction to Quantitative Genetics*, 4th edn. Harlow, UK: Longman.

Lambeth CC (1980) Juvenile–mature correlations in Pinaceae and implications for early selection. *Forest Science* 26: 571–580.

Morgenstern EK (1996) *Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture*. Vancouver, BC: University of British Columbia Press.

Muller-Starck G and Schubert R (eds) (2001) Genetic Responses of Forest Systems to Changing Environmental Conditions. Dordrecht, The Netherlands: Kluwer.

Namkoong G, Kang HC, and Brouard JS (1988) *Tree Breeding: Principles and Strategies*. New York: Springer-Verlag.

White TL and Hodge GR (1989) *Predicting Breeding Values, with Applications in Forest Tree Improvement*. Boston, MA: Kluwer.

Young A, Boshier DH, and Boyle T (2000) *Forest Conservation Genetics: Principles and Practices*. Collingwood, Australia: CSIRO.

Zobel BJ and Talbert J (1984) *Applied Forest Tree Improvement*. New York: John Wiley.

Zobel BJ and van Buijtenen JP (1989) *Wood Variation: Its Causes and Control*. Berlin: Springer-Verlag.

Breeding Theory and Genetic Testing

T L White, University of Florida, Gainesville, FL, USA

Introduction

Tree breeding programs, also called tree improvement programs, create genetically improved varieties for reforestation and afforestation. As with breeding programs of agricultural crops and animals, these programs aim to change allele frequencies for a few key traits of a given species through repeated cycles of activities such as selection, breeding, and genetic testing. Today, tree improvement is an integral component of most plantation programs in the world with the ultimate goal being to increase the economic and social value of the planted forest. Unlike annual crops, trees are long-lived and difficult to work with due to their size. This means that, while the concepts of tree breeding and crop breeding are similar, the details differ greatly.

Owing to differences in species' biology, silviculture, product goals and economic considerations, tree improvement programs for distinct species differ dramatically in both design and intensity. Nevertheless, there are basic concepts and activities common to most programs. The aim here is to describe these common activities and the underlying theory on which they are based.

Principles of Recurrent Selection

Recurrent selection means repeated cycles of selection and breeding aimed at gradual genetic improvement of a few key traits in a single species. The benefits of breeding are cumulative in that each cycle or generation of improvement builds upon advances made in prior generations. Genetic gain in selected traits results from changes in frequencies of alleles at loci controlling expression of those traits, with favorable alleles increasing in frequency. Since most commercially important traits are polygenic (i.e., controlled by many loci), gene frequencies change slowly at any single locus and these changes are generally unknown to breeders. Rather, progress is measured by mean performance for target traits (e.g., greater harvest yield, reduction in disease incidence, or increased wood density). Performance for non-target traits should change little, if at all, as long as those traits are controlled by different loci than the target traits.

With the rare exception of programs involving radiation or chemical mutagenesis, tree breeding programs do not create new genetic variation; rather, they utilize naturally occurring variation in starting populations of the species of interest. Then, through recurrent selection and breeding, the existing variation is repackaged into individuals containing higher frequencies of favorable alleles for target traits. Some crop breeding programs began over 10 000 years ago and today's domesticated varieties do not even resemble their original progenitors, thus demonstrating the power of recurrent selection. Tree breeding programs are much less advanced. In fact, for most forest tree species, there have been three or fewer generations or cycles of recurrent selection and breeding. This means that today's genetically improved varieties of forest trees are essentially the native species, and the only changes might be faster growth rate, better disease resistance, straighter stems, higher wood density, or other small quantitative changes in a few key traits.

The oldest form of recurrent selection is called simple recurrent selection (SRS) and each cycle of breeding involves only two steps: (1) mass selection of individuals based solely on their outward, phenotypic appearance; and (2) intermating these selections to produce the offspring for the next generation. This was the method used over 10 000 years ago by ancient farmers to improve their field crops; seed from selected plants was retained for next year's crop. SRS is rarely used in tree breeding programs today, because it is less efficient at achieving genetic gains than forms of recurrent selection that incorporate genetic testing and pedigree control.

Almost all tree breeding programs employ recurrent selection for general combining ability (RS-GCA) in which genetic testing follows selection. This entails planting identified offspring from all the selections in randomized, replicated experiments. Selections with high GCA values for any trait are those that produce top-performing offspring. After genetic testing, selections with low GCA values are discarded, while those with high GCAs (or offspring of high GCA parents) are included in future cycles of breeding. Genetic testing greatly increases the genetic gain above that from mass selection and is especially effective for traits with low heritabilities (as for most traits of trees).

Nearly all tree breeding programs rely on RS-GCA involving recurrent cycles of selection, breeding, and genetic testing. In these breeding programs, only additive effects of alleles (whereby offspring tend to be intermediate to their parents) accumulate in the breeding population, meaning that genetic effects due to dominance and epistasis do not contribute to the cumulative genetic progress in the breeding population. In the early cycles (say the first 10), genetic variability for the selected traits changes little from that in the initial founding population, and genetic gain is similar in each successive cycle given similar selection intensities and breeding practices. That is, it takes many cycles of recurrent selection to lead to a plateau after which selection is ineffective (through fixation of favorable alleles or other causes). Beginning with larger founding populations and infusing unrelated material into the population extend the number of cycles before a selection plateau is reached.

Activities and Populations of a Typical Breeding Cycle

The activities and population types of tree improvement programs are summarized using a model called the breeding cycle (**Figure 1**). The activities of selection (to choose the selected population of genotypes) and breeding (to form the offspring that comprise the next generation's base population) are core activities that must occur each cycle or generation of breeding. The other activities and population types may or may not occur. Programs differ widely in how these activities are implemented, in the size and occurrence of the various types of populations, and in program intensity. Further, the cycles of breeding may not be discrete but rather overlapping with several staggered sets of activities all occurring simultaneously. Here, to stress the concepts, we explain each population type as if it were physically distinct and occurred each cycle of improvement.

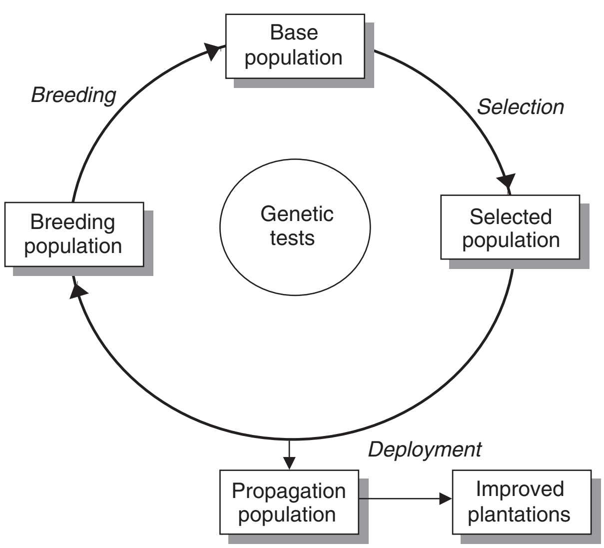


Figure 1 Schematic diagram of the breeding cycle of tree improvement programs showing the population types of genotypes that are formed (inside boxes) and the activities that are conducted (in italics) in a single cycle of improvement. Selection and breeding must be conducted each cycle, while the other activities may or may not occur. Starting at the top, the cycle turns a single revolution for each cycle or generation of selection and breeding in a recurrent improvement program. Adapted with permission from White TL (1987) *New Forests* 4: 325–342.

Base Populations

The base population of a given cycle of improvement consists of all available candidate trees that could be selected. The base population is very large consisting of many thousands of genetically distinct individuals. At the beginning of a program, the base population consists of all trees available for selection growing in natural stands and possibly plantations within the defined breeding zone (i.e., the geographical area for which an improved variety is being developed).

Determining breeding zone boundaries is a critical decision in tree improvement programs, because each breeding zone has a separate improvement program with its own distinct base, selected, breeding and propagation populations. For example, the program for Douglas-fir (*Pseudotsuga menziesii*) in the northwestern USA defined 80 first-cycle breeding zones each with an average size of 40 000 ha of native forests. Thus, there were 80 distinct first-generation improvement programs, each with its own breeding cycle, different set of population types, and improved variety being developed. In contrast, the program for *Pinus elliottii* (slash pine) in the southeastern USA defined one breeding zone consisting of the entire natural range of the species (approximately 4 000 000 ha of timberlands). The differences in size and number of breeding zones between these two programs reflect both the more homogeneous climate in the southeastern USA and differences in breeding philosophy.

Advanced-generation base populations (i.e., after the first complete breeding cycle) consist of genetically improved trees formed by intermating members of the breeding population and planting their offspring in genetic test plantations. All trees in these genetic tests are available to be chosen for advanced-generation selected populations.

Selection and Breeding

Selection and breeding are applied sequentially during each cycle of improvement (**Figure 1**). For most tree improvement programs the selected population in any given cycle contains between 100 and 1000 selected trees for a single breeding zone. In the first cycle of improvement, trees are selected from natural stands and plantations based solely on their superior phenotypic appearance, and this is called mass selection (**Figure 2a**). Advanced-generation selections are made from pedigreed populations growing in genetic tests, and selection effectiveness is increased by using all information available about a candidate's progeny, relatives, and ancestors (**Figure 2b**).

Figure 2 Forming the selected population means choosing superior individuals from the base population. (a) First-generation selection of *Pinus taeda* growing in the base population consisting of natural forests in Arkansas, USA. (Photograph courtesy of E.J. Jokela.) (b) Advanced-generation selection of *Eucalyptus grandis* growing in a base population consisting of pedigreed, randomized, replicated genetic tests of Cartón de Colombia.

Genetic gain in a given trait is achieved only if the selected population has a higher frequency of favorable alleles than the base population from which the selections were made. Genetic gain is greater if the selection is very intensive (only the very best individuals are selected) and if the trait is under strong genetic control (i.e., has a high heritability) with appreciable genetic variation. Allele frequencies differ between the base and selected populations both by intent and by chance. The breeder selects superior individuals and therefore intentionally alters allele frequencies for the target traits. In addition, allele frequencies for all traits (not just those included in the selection criteria) may change by chance due to sampling (i.e., choosing a subset of trees from a larger population). Some very rare alleles present in the base population can be absent from the selected population; however, with hundreds of individuals in the selected population, allele loss or large random changes in allele frequencies are unlikely.

After selection, some or all of the selections are included in that cycle's breeding population and are intermated to regenerate genetic variability through recombination of alleles during sexual reproduction. Intermating to produce full-sib families involves controlled pollination among selections. Female flowers on some selections are bagged (and emasculated if needed) to prevent contaminant pollination, and then pollen from other parents is injected into the bags (**Figure 3**). When two superior parents are mated, not all their offspring are superior, because some offspring in a family receive more favorable alleles from their parents than others. Intermating results in a large amount of genetic variation both among and within the families planted in the genetic tests that form the new base population. Selection of superior trees from among these newly created progeny is the basis for making continuing genetic progress from recurrent cycles of selection and intermating.

Deployment of Genetically Improved Varieties

The ultimate goal of all tree improvement programs is to create improved varieties of trees to use for reforestation and afforestation of new plantations. This represents a tangible economic and social gain: higher-yielding, healthier planted forests. In each cycle of improvement, the propagation population (also called the production population or deployment population) is formed from some or all of the members of the selected population. Usually only a small subset of the very best selections is chosen to produce a sufficient quantity of genetically improved plants to meet the annual needs of the operational forestation program. The trees used for reforestation are a genetically improved variety (also called a breed), and the activity of mass propagation and planting of an improved variety is deployment.

The propagation population is distinguished from the central core of the breeding cycle in **Figure 1**, because core activities focus on maintaining a broad genetic base and achieving genetic gains over many generations of improvement. In contrast, the propagation population produces a commercial variety to maximize genetic gain in operational plantations in the short term. Seed orchards, a common type of propagation population, are often formed by grafting the very best members of the selected population into a single location that is managed intensively for the production of seed (**Figure 4**). The genetically improved seed from open pollination among the grafted trees is then grown by the nursery manager and the seedlings used for forestation.

There are other options for forming the propagation population. For example, clonal forestry can be achieved for some tree species either through rooted cuttings or somatic embryogenesis. With this option, the top performing clones are identified through genetic testing and comprise the propagation population. These 20 or so clones are mass propagated to create enough trees to meet the annual forestation demand. The clones deployed to operational plantations are the improved variety.

It is common to include only the very best selections in the propagation population; for example, the selected population might contain several hundred genotypes, while the propagation population

Figure 3 *Pinus taeda* is monoecious meaning that pollen catkins (a) and female strobili (b) are borne in different structures on the same tree. Controlled pollination of two parents for breeding takes 18 months and entails: (1) collecting catkins and drying them to extract pollen from the male parent; (2) bagging (c) the female strobili in the spring of year 1 to prevent wind pollination by other males; (3) injecting the pollen from the male parent into the bags covering the strobili of the female parent; (4) allowing pollen tubes (d) to begin growing in the first year and effect fertilization in spring of the second year; and (5) collecting full-sib seed in the fall of year 2, some 18 months after pollination.

might consist of the best 20 to 50. This increases the genetic gain expected from the operational variety that is planted, but also reduces its genetic diversity. It is also common to continually upgrade the genetic quality of the propagation population even during a single cycle of improvement. As information becomes available from genetic tests, genetically inferior selections can be removed from the propagation population, while superior selections not originally included can be added. This means that the improved variety being planted may change in its genetic composition and expected gain within a single cycle of improvement. This dynamic, rolling-front nature of improved varieties in forestry may be the reason why varieties are not given names as are cultivars in crops and breeds in animals.

Infusions from External Populations

Most tree improvement programs take advantage of opportunities to acquire new genetic material and infuse it into the breeding population. The infusions can be aimed at improving a specific trait. For example, the *Pinus elliottii* program in the southeastern USA selected nearly 500 disease-free trees in stands highly infected with fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*) to increase the frequency of resistance alleles in the breeding population. Another reason to include infusions is to broaden the genetic diversity existing in the program. For example, the *P. taeda* (loblolly pine) program in the southeastern USA made 3300 new selections to broaden the genetic diversity of several breeding populations spanning multiple breeding zones. In advanced-generation programs, it is often desirable to obtain infusions as proven selections from other programs working on the same species. Breeding programs for *Eucalyptus grandis* in many different countries sometimes exchange material for this purpose.

With infusions, the new material should be evaluated for target traits and adaptability through genetic tests to ensure that gains are not made in some traits with inadvertent losses in others. Tested infusions of sufficient merit are then intermated in the breeding population as part of the regular

Figure 4 Aerial view of a 12-year-old grafted seed orchard of *Pinus elliottii* showing the wide spacing and intensive management (mowing and weed control in the rows) aimed at maximizing seed production. The 50 or so superior selections grafted into this orchard are each represented by many grafted trees (called ramets) and together these ramets from the same selection form a clone (i.e., have the same genotype). Ramets from the same clone are separated from each other and the 50 superior clones are allowed to wind pollinate to produce seed for operational reforestation. This seed is a genetically improved variety with the amount of genetic gain depending directly on the genetic superiority of the clones grafted into the seed orchard.

breeding program. This maintains broad genetic diversity in the breeding population.

Advanced-Generation Tree Breeding Programs

Many tree breeding programs are entering the second or third cycle of breeding. These programs differ widely in breeding strategy, program design, and program intensity; yet, all programs face common challenges and sets of issues. In particular, all programs seek to achieve near-optimal short-term genetic gains in a few traits, while maintaining sufficient genetic diversity in the breeding population to ensure near-optimal long-term genetic gains, flexibility to changing conditions, and gene conservation. Common issues facing all programs addressing these goals are conveniently grouped for discussion below according to the population types of the breeding cycle.

Breeding Zones, Base Populations, and Selected Populations

Most advanced-generation tree breeding programs are opting for relatively large breeding zones encompassing sizeable portions of their plantation estate. Even if there is moderate genotype × environment interaction present within a breeding zone, many programs are choosing to breed for broad adaptability by making selections that perform well across all edaphoclimatic conditions within the zone. Minimizing the number of breeding zones has two distinct advantages: (1) the breeding and testing programs in each zone can be larger and more intensive, thereby achieving larger gains; and (2) costs are reduced, because there are fewer breeding populations and testing programs to manage.

Tree breeding programs with multiple breeding zones for the same species sometimes opt for overlapping zones that share selections among neighboring zones to reduce costs and increase gains. For example, the second-cycle *P. taeda* program in the southeastern USA defined multiple overlapping breeding zones, and each zone recruits new selections from zones on both sides. That is, excellent selections made in one zone are included in the selected populations of the neighboring zones. It is also possible to recruit material from other breeding programs of the same species in other regions or countries. Thus, advanced-generation breeding programs can capitalize on top genetic material from many sources provided the material is well adapted to the breeding zone.

With breeding zones defined, the next steps are to decide on how many selections to make (i.e., the size of the selected population), which traits to select for, and how to make the selections to achieve both genetic gain and diversity. Many advanced-generation tree breeding programs include 300 to 400 selections in the selected population for a given breeding zone in a single cycle. This number is sufficient to sustain near-maximum long-term gains over several cycles of recurrent breeding, even when there are several traits and when intensive efforts are used to achieve large gains in the first few generations. However, quite large populations (1000 or so) are required to ensure that almost all rare alleles are maintained in the population for many generations if the breeding population is also serving a gene-conservation role.

In all tree breeding, it is important to focus on very few traits. Inclusion of too many traits (say more than five) seriously dilutes the gains made on any one trait. Volume growth is almost always one of the important traits because it transcends product goals and technologies. Other important traits often include resistance to important edaphoclimatic stresses or fungal diseases. Finally, wood quality traits have become more important in recent years. When considering the candidate suite of traits, priority should go to those that:

- have high economic importance under a wide variety of future ownership, market, and technological scenarios
- are under moderate to strong genetic control

- are expressed at young tree ages and easily measured
- do not have unfavorable genetic correlations with other target traits.

The next step is to make selections and in advanced-generation programs these usually come from pedigreed genetic tests planted in randomized, replicated designs established on multiple sites in the breeding zone. Very often, data from the genetic tests are highly unbalanced, with not all families planted on all sites, varying test quality among sites and, sometimes, varying mating and field designs. The first step is to analyze the data properly using an analytical technique, called best linear unbiased prediction (BLUP), which incorporates all data from all sources to produce a unified set of predicted genetic values for each trait.

Next, a selection index is developed to weight each trait according to economic or other criteria, such that a single genetic worth is predicted for each pedigreed tree (which aggregates the BLUP predictions for each trait into a single weighted average for each tree). If there are say 50 000 pedigreed trees in genetic tests, and the breeder aims for a selected population with 300 individuals, the process is: (1) all 50 000 candidates are ranked according to their predicted genetic worth; and (2) the breeder begins at the top of list and selects winners subject to penalties for, or constraints on, relatedness. Normally, the penalty for relatedness means that only a certain number of selections can be made within a given family, and more are allowed from better families. Many programs include top performing selections from multiple generations, such as grandparents, parents, and offspring.

Use of a selection index often identifies candidates that are above average for all traits in the index but not outstanding for any single trait. In other words, the index-identified trees are most suitable for maximizing genetic worth of the aggregate index but do not maximize gain for each trait. Therefore, breeders usually include additional selections that are outstanding for each of the target traits.

Breeding Populations

After selection, the chosen trees are usually grafted into a convenient location for breeding (**Figure 3**). If all, say 300 to 400, selections are grafted and bred upon, then the breeding and selected populations are identical. Unlike most first-generation tree breeding programs that employed unstructured breeding populations in which all selections were bred in similar mating designs, advanced-generation programs structure the breeding population for at least three reasons.

First, many programs stratify the breeding population into two or more levels according to predicted genetic value with the top stratum being called the elite population. The elite population might contain the top 10% of the selections in the breeding population (e.g., the top 30 selections if the breeding population has 300 selections). The goal is to make more rapid and larger genetic gains in this small subset of the breeding population through accelerated breeding and more intensive genetic testing. The rest of the breeding population is allocated to the larger main population which is bred and tested less intensively to minimize costs, maintain genetic diversity, and achieve long-term genetic gains. As new selections are made in subsequent generations of breeding, they can be allocated to the elite, main, or both. This gene flow between the elite and main breeding populations increases genetic gain and diversity in the elite population.

Second, when the breeding population is subdivided for the purpose of applying different selection criteria to different segments, the subdivisions are called multiple populations or breeds. For example, the breeding population might be divided into three breeds with one being bred mainly for disease resistance for deployment to high-hazard sites, one as a multipurpose breed for general use, and the third for solidwood, high-value products. There might be some traits in common to all three breeds (such as rapid growth), but others that are only important in one breed or another (such as lumber quality in the solidwood population). The goal is to make more rapid gains for each of the breeds by minimizing the number of traits being improved. There can be few or many breeds, and there is no specific control on relatedness among them. Top selections and their relatives that possess many desirable traits may occur in more than one of the breeds.

The third and final type of structure to the breeding population aims to control the pattern of relatedness in the breeding population and produce noninbred offspring for operational deployment. Use of a single, unified breeding population eventually builds up relatedness among members of the breeding population and, if related parents are crossed to produce offspring for operational plantations, the plantations suffer from inbreeding depression. To avoid this problem, the breeding population is divided into sublines (sometimes called breeding groups). All breeding is conducted among selections in the same subline, and each subsequent generation's selections are assigned to the same subline as their progenitors. There is no breeding or relatedness among groups. All sublines are bred for the same objectives using the same selection criteria. Over generations of breeding, relatedness builds up within each subline; however, members from different sublines are always unrelated, even after many generations of breeding. Therefore, any mating between members from different sublines always results in outcrossed progeny, precluding inbreeding depression. So, by choosing selections from different sublines to form the propagation population, outcrossed offspring are guaranteed for operational plantations.

In real tree breeding programs all three types of structure described above are used simultaneously. In addition, mating designs and field designs vary. This makes for a wide variety of breeding strategies, population structures, and program intensities in advanced generations.

Propagation Populations and Deployment

Most advanced-generation programs still employ open-pollinated (OP) seed orchards, as previously described, in which 15 to 40 top, unrelated selections are grafted into a single location to interpollinate and produce improved seed for operational forestation. Seed is often collected and deployed by OP family; this is called family forestry. For example, if there are 20 to 50 ramets of each of 30 clones in the orchard, then seed from all ramets of each clone is bulked together to produce 30 seedlots, one for each clone. Each seedlot is kept separate for storage, nursery production, and plantation establishment. This approach reduces genetic diversity only slightly, and allows families to be deployed to sites to which they are most suited based on genetic testing information of the maternal parent (e.g., disease-resistant families to high-hazard sites).

Family forestry is sometimes based on full-sib families created by controlled pollination (CP) (**Figure 3**). Top performing parents, based on performance of their offspring in genetic tests, are crossed together. If the CP process is efficient enough, the CP seed can be delivered directly to the nursery for growing seedlings for operational forestation. More commonly, the CP seed is too expensive for this option, and the seed is used to create hedges or stool beds in the nursery. Shoot tips from such plants are then rooted in either greenhouses or outdoor nurseries, and the resulting rooted cuttings from top full-sib families are planted operationally. This technique is being widely used for radiata pine (*Pinus radiata*) in Australia, New Zealand, and Chile.

In addition to family forestry, some intensive tree improvement programs are employing clonal forestry in which 10 to 30 well-tested clones are planted operationally. Clonal forestry means that a single genotype may be planted across many hectares (**Figure 5**). This achieves maximum genetic gain if top performing clones are planted, but eliminates genetic diversity within a single plantation. Several clones are often planted in patches (also called monoclonal mosaics) across the landscape, and most organizations limit the area of land that can be planted with a single clone. Clonal forestry is completely operational in intensive programs planting various species of *Eucalyptus*, *Salix*, and *Populus* that can be propagated easily as rooted cuttings. Conifers have proven more challenging since it is not possible, in general, to produce rooted cuttings from selection-age trees. Tissue culture techniques hold promise for achieving clonal forestry in conifers.

Figure 5 Nine-year-old clonal plantation of *Eucalyptus grandis* belonging to Mondi Forests in South Africa. All trees are a single genotype, a clone, and hence there is no genetic diversity within this plantation. Genetic diversity on a landscape scale is achieved by planting several clones in a patchwork in any one year and limiting the total area in which a given clone can be planted commercially.

Genetic Testing

Genetic tests consist of pedigreed, labeled offspring, or clonal propagules (ramets) usually established in randomized, replicated experiments in field locations on forest sites. Genetic tests are fundamental to all tree improvement programs and a single series of tests can serve any or all of the following objectives:

1. Evaluate relative genetic quality of selections to allow better selections to be favored in breeding and deployment.
2. Estimate genetic parameters such as heritabilities, genetic correlations, and genotype × environment interactions to facilitate programmatic decisions and development of breeding strategies.
3. Plant offspring from breeding to create a base population of new genotypes from which to make the next cycle of selections.
4. Quantify or demonstrate genetic gains made by the program.

Mating designs and field designs, specifying how the genetic material is created and arranged in the experiment, are discussed below for this range of objectives.

Mating Designs for Genetic Tests

Incomplete-pedigree mating designs When many parents are allowed to intermate with no control on pedigree and a single bulk lot of seed is collected, then there is no knowledge of maternal or paternal identity. Bulk collections are most useful for comparing means of different populations such as in realized gains trials (objective 4 mentioned above). For example, consider 200 selections in a selected population with the top 20 being used in the propagation population to produce seed for operational plantations. Two genetic entries (a bulk seed collection from the 200 and one from the 20) could be planted in randomized, replicated designs across several test locations to compare genetic gain differences between the two populations. Unpedigreed, bulk collections are not used for any of the other three objectives of genetic tests.

In OP mating designs, seed is collected from each of the parents in the population and kept separate by parent for planting as OP families. For each tree planted, the female parent is known but the male parent is unknown. If there are 200 parents in the selected population, a test of all parents would involve planting 200 genetic entries or treatments (i.e., 200 OP families). OP mating designs are widely used for a variety of angiosperm and gymnosperm species, and are especially useful when many different male parents pollinate each family (i.e., when the OP families are highly outcrossed). When this occurs, OP families can be used very effectively for ranking selections and estimating most genetic parameters (objectives 1 and 2), and these designs are efficient and cost-effective.

Use of OP mating designs for creating a base population from which to make selections has been criticized on the basis that the male parentage is unknown meaning that two selections from different OP families could have the same male parent. Subsequent intermating of these selections in a propagation population (e.g., if both selections were grafted in the same seed orchard) could lead to inbreeding depression and hence reduced gain in the operational plantations. However, more recently, OP mating designs have been recommended for creating the base population based on theoretical gains calculations, empirical evidence of substantial genetic gains, and logistical ease coupled with low cost. Thus, OP mating designs have a role in some advanced-generation programs. For example, a program could opt to breed the elite portion of the breeding population using full-sib, complete pedigree designs (see next section), but use OP mating for rapid, repeated cycling of the main portion of the breeding population.

In pollen mix (PM) or polymix mating designs, controlled pollination is used to pollinate each female parent with a mixture of pollen from a number of male parents (**Figure 3**). As with OP designs, there is one family for each parent being tested (i.e., 200 PM families for 200 parents in a selected population), and progeny trees from each PM family are labeled according to their female parent. PM designs are very cost-effective for estimating most genetic parameters and for ranking selections based on performance of their offspring but not for making fully pedigreed selections. Disadvantages of PM compared to OP designs are increased cost and time associated with controlled pollination.

Complete pedigree (full-sib family) designs There are various mating designs that employ full-sib (FS) families and hence maintain complete pedigree of all progeny planted. These designs share the following characteristics: (1) controlled pollination is used to create the seedling offspring; (2) identification of progeny trees in the field requires naming both parents; (3) the maximum number of unrelated forward selections is one-half the number of parents assuming parents are unrelated; and (4) each parent should be mated with four or more other parents to assure precise parental rankings.

Some FS designs can be prohibitive to implement owing to the large number of controlled crosses. For example, for a selected population of 200 parents, there are 19 900 possible pairs of matings ($200 \times 199/2$) in what is called a half-diallel without selfs. Even large tree improvement programs limit the number of total crosses for a given breeding zone to no more than several hundred FS families per cycle. The discussion below does not describe the variety of designs available, but rather focuses on one design that is feasible, cost-effective, and efficient for all four objectives of genetic tests listed above.

In a partial diallel mating design only some of the possible pairs of crosses are made, and there are many variants of partial diallels that make more or fewer crosses. More crosses per parent mean more precision for estimating genetic parameters (objective 2), for ranking the parents (objective 1), and for achieving more gain from making selections from the offspring planted (objective 3). Four or five crosses per parent seem optimal for most purposes, if all crosses are successful. For example, if there are 200 parents in the selected population and each parent is crossed with four other parents, there would be a total of 400 full-sib families to establish in genetic tests.

In partial diallels and other mating designs, it is best to create the full-sib families such that there is a genetic linkage, called connectedness, among all parents. Even if two parents are never mated together directly, they can still be connected indirectly (e.g., crosses A × B, B × C, and C × D connect A with C and D). In this way, all crosses provide information about all parents. Disconnected designs with small groups of parents separated from others are less efficient for ranking parents.

Full-sib families are sometimes generated and planted over a period of years in what is called a rolling-front approach. As trees in the breeding population begin to flower, they are crossed with others that are flowering. Instead of waiting for all crosses to be completed and planted in a single series of genetic tests, the crosses are planted as seed becomes available. There are several series of genetic tests planted over a series of years. This creates unbalanced data, since each series contains only a partial set of the full-sib families; however, the data can be analyzed with BLUP if proper connectedness among the series is maintained.

Field Designs for Genetic Tests

Defining the field design of any series of genetic tests means specifying: (1) plot shape and number of trees per plot; (2) statistical design at each location including randomization scheme and number of replicates; (3) number and location of field sites; and (4) inclusion of other seedlings or clones as checklots, borders, and fillers. Specification of an optimal field design involves statistical, genetic, logistical, and economic issues. Most important are the objectives of the tests and, just as for mating designs, some field designs achieve certain objectives better than others. Here two extreme field designs are discussed, one appropriate for simultaneously achieving objectives 1 to 3 and the other suitable for estimating realized gains (objective 4).

Field design for breeding and base population genetic tests Often in advanced-generation breeding programs, a single series of full-sib tests is aimed at estimating genetic parameters (e.g., heritability and genotype × environment interaction for key traits), ranking the parents in the breeding population and making the next-generation selections from the progeny planted (objectives 1 to 3). Nearly always, there are numerous families (50 to 400) to accommodate, and an appropriate field design is: (1) single-tree plots (STP) meaning that each full-sib family is represented by a single progeny tree as its own plot within each complete replicate; (2) an incomplete block design in which each complete replicate is further subdivided into smaller units called incomplete blocks; (3) fifteen to 20 complete replicates at each location (meaning 15 to 20 offspring per family planted at each location); and (4) four to eight field sites (each with this same design) that span the range of edaphoclimatic conditions in the breeding zone. For a test series with 200 full-sib families, 15 replicates per site and five sites, there would be 15 000 progeny trees planted (200 × 15 = 3000 per site) and each family would be represented by 75 trees (15 replicates × 5 sites × 1 tree per replicate).

STPs assure higher statistical precision (i.e., better genetic parameter estimates and better rankings of parents, families, and progeny trees) than do experiments with row plots or rectangular plots that contain multiple trees per family. This is for two reasons: (1) STPs allow more replicates for a given effort, so each family samples more of the microsite variability on a site instead of being clumped together in multiple-tree plots on fewer microsites; and (2) STPs mean that the size of each replicate is smaller for a given number of entries, so replicates are more homogeneous. STPs facilitate testing large numbers of families or clones in many replicates.

Even with STPs, each replicate can occupy a large area. For example, with a typical planting density of 1200 trees per hectare, a test with 200 families in STPs means that each replicate is 0.17 ha (200/1200). In most places, replicates smaller than 0.1 ha are advisable. This is the reason to further subdivide each complete replicate into incomplete blocks. Each incomplete block might contain 15 to 30 trees planted in a more uniform microenvironment than families in the rest of the same complete replicate. The incomplete blocks add another blocking factor used to adjust entry means for microsite differences among incomplete blocks. This reduces the experimental error and increases the precision of the rankings of genetic entries by removing sources of environmental noise from comparisons of genetic entries. Use of incomplete block designs requires special computer programs to design the layout and analyze the data; however, these designs increase precision with no additional costs of test implementation, maintenance, or measurement.

There is a trade-off between the number of complete replicates per test site and number of sites in a test series. The total number of progeny needed per full-sib family across all sites ranges from 50 to 150 depending on several factors. So, with more replicates per site, fewer sites are needed. However, enough sites are needed to adequately sample the edaphoclimatic zones within the breeding zone. For example, a less intensive breeding program with relatively uniform conditions across a small planting zone might opt to plant a test series on three different site locations with 20 complete replicates per site (60 total trees per family), while a more intensive program with a large breeding zone spanning several soil types and climates might opt to establish a test series on eight sites with 15 replicates per site (120 trees per family). These numbers of sites are inflated if the risk of catastrophic loss of entire test sites is appreciable.

Field design for quantifying realized gains Estimating progress from a tree breeding program involves field tests of material of distinct levels of genetic improvement that reflect different stages of program development over time. For example, a single test series might aim to estimate the genetic means of the following nine entries for a few key traits: (1) an unimproved bulk seedlot that represents the operational plantations established before tree breeding began; (2) two bulk seedlots collected from a first-generation seed orchard before and after roguing of inferior clones; (3) three single-family seedlots of families planted operationally; and (4) three operational clones. Tests might also compare first-, second- and third-generation commercial breeds to quantify progress.

Usually, the mating and field designs of realized gains tests (also called yield trials) simulate genetic and stand-level growing conditions of operational plantations so that the estimates of gain are appropriate for subsequent harvest scheduling and economic analysis (e.g., to justify the expenditures on the breeding program). For these reasons, common features of tests to estimate realized gain include:

1. The tested materials simulate operational varieties or breeds from the past, present or future.
2. Unimproved seedlots or unimproved clones are included to have a baseline for comparing newer varieties.
3. Rectangular plots of each genetic entry are used to approximate competitive conditions existing in operational plantations.
4. Tests are of long duration (half to full rotation length) to quantify gains in harvest yield and product quality.

Points 3 and 4 argue for using plots large enough to permit normal silvicultural activities (fertilization, weed control, and thinning) for an entire rotation period. Therefore, square or rectangular plots, each plot containing 25 to 100 trees of the same genetic entry (e.g., same seedlot, family, or clone) are recommended for realized-gains tests. Rectangular plots are preferred because they simulate stand conditions in operational plantations, and so produce unbiased estimates of yield on a per unit area basis. Inter-tree competition intensifies as trees age, and genotypes that start slowly may be disadvantaged. Therefore, means from small plots (e.g., STPs described above) may be biased with results favoring genetic entries that are strong competitors, especially at early ages. Rectangular plots avoid these biases since inter-tree competition is among trees of the same genetic entry (same bulk mix, family, or clone).

The disadvantage of rectangular plots is that replicate sizes are large, so only a small number of different genetic entries can be included (normally fewer than 10 different entries in a given test series) and the number of replicates is limited on a given site. A test series is normally established on several site locations both to accumulate enough replicates to produce sufficient precision for comparing the genetic entries and to ensure that inferences about genetic gains and program progress truly apply to the entire program. Incomplete block designs are very useful to increase precision of comparing the genetic entries, but still the number of entries needs to be small.

Conclusions

Tree breeding programs develop genetically improved varieties for forestation through repeated cycles of activities such as selection, breeding, and genetic testing. Selection aims to increase the frequency of favorable alleles of a few important traits, while breeding re-creates and repackages genetic variation so that still better selections can be made in the next cycle of selection. Nearly all programs rely on a breeding strategy involving recurrent selection for general combining ability, which means that genetic tests are used during each cycle of breeding to rank the parents in the breeding population and increase gains from selection. Thus, designing, implementing, and analyzing genetic tests are critical aspects of tree breeding programs that must be done well to maximize genetic gain per unit time at minimum cost. Tree breeding programs vary widely in design, breeding strategy, and intensity owing to differences in species' biology, breeding objectives, and economic considerations. Nevertheless, tree breeding is an integral part of operational silviculture for most plantation forestry programs in the world. New technologies such as tissue culture to achieve operational planting of tested clones, marker-assisted breeding to increase gain from selection, and genetic modification to insert novel genes all have promise to enhance gains from tree breeding, but must be tested for effectiveness, safety, and public acceptance.

See also: **Genetics and Genetic Resources**: Genecology and Adaptation of Forest Trees; Genetic Systems of Forest Trees; Propagation Technology for Forest Trees; Quantitative Genetic Principles. **Tree Breeding, Practices**: A Historical Overview of Forest Tree Improvement; Breeding for Disease and Insect Resistance; Economic Returns from Tree Breeding; Forest Genetics and Tree Breeding; Current and Future Signposts; *Pinus Radiata* Genetics.

Further Reading

Ahuja MR and Libby WJ (1993) *Genetics and Biotechnology*, vol. 1, *Clonal Forestry*. New York: Springer-Verlag.

Eldridge K, Davidson J, Harwood C, and Van Wyk G (1994) *Eucalypt Domestication and Breeding*. Oxford, UK: Clarendon Press.

Lindgren D and Mullin TJ (1997) Balancing gain and relatedness in selection. *Silvae Genetica* 46: 124–129.

Mandal AK and Gibson GI (1998) *Forest Genetics and Tree Breeding*. Daryaganj, New Delhi, India: CBS Publishing.

Namkoong G, Kang HC, and Brouard JS (1988) *Tree Breeding: Principles and Strategies*. New York: Springer-Verlag.

Williams ER, Matheson AC, and Harwood CE (2002) *Experimental Design and Analysis for Tree Improvement*. Collingwood, Australia: CSIRO.

White TL (1987) A conceptual framework for tree improvement programs. *New Forests* 4: 325–342.

White TL (1992) Advanced-generation breeding populations: size and structure. In *Proceedings of the IUFRO Resolving Tropical Forestry. Resource Concerns through Tree Improvement, Gene Conservation, and Domestication of New Species*, October 9–18, Cali, Colombia, pp. 208–222.

White TL, Neale DB, and Adams WT (2003) *Forest Genetics*. Wallingford, UK: CAB International.

Young A, Boshier D, and Boyle T (eds) (2000) *Forest Conservation Genetics*. Collingwood, Australia: CSIRO.

Zobel BJ and Talbert J (1984) *Applied Forest Tree Improvement*. New York: John Wiley.

Economic Returns from Tree Breeding

P J Kanowski, Australian National University, Canberra, Australia
N M G Borralho, Forest and Paper Research Institute (RAIZ), Alcoentre, Portugal

Introduction

The economic returns from tree breeding can be estimated over time-frames ranging from the short to the long term, on scales varying from that of an individual enterprise to the entire extent of a species' use, in terms of each individual strategic and technical decision or of their cumulative effect, and in purely financial or in wider economic terms. The gains realized by particular stages or elements of tree breeding can be so dramatic that only the most cursory economic evaluation is necessary to substantiate them; conversely, strategic and technological options may be so complex, and realization of benefits so contingent on particular assumptions, that sophisticated economic analyses are necessary to inform investment decisions.

As for many forestry activities, economic analyses of tree breeding investments are variously complicated by long investment and rotation cycles, uncertainties about costs and benefits over these long time horizons, and by the challenges of accounting for nonmarket benefits and costs. However, there is both a long history of, and an increasing focus on, economic analyses of tree breeding investment decisions, which have contributed significantly to the design and development of tree breeding strategies and programs.

Economic returns from tree breeding are determined by species- and program-specific combinations of the following key parameters:

- the genetic characteristics of the population subject to breeding–reflecting inherent levels of genetic variation in a species, the extent to which that variation has been sampled in the population subject to breeding, and the stage of breeding of the population
- the breeding strategies and technologies employed, and the breeding objectives specified
- the value of the products and services, and the scale of deployment, of improved populations
- the institutional arrangements for breeding and benefit sharing.

Our discussion of the topic is structured around these parameters. In general, they are better characterized for longer-established, advanced industrial tree breeding programs, such as those for loblolly pine (*Pinus taeda*) in the southeast USA, radiata pine (*P. radiata*) in the southern hemisphere, or *Eucalyptus* species in continents other than North America. Industrial tree breeding programs are typically more advanced and data-rich, and have markets and benefit regimes that are generally better defined, than are programs for the breeding of trees for nonindustrial uses. Consequently, while the latter also have the demonstrated potential to make very significant economic contributions to people's livelihoods and to environmental services, they are not necessarily easily evaluated by conventional economic analyses applied to investment decisions.

Realization of returns from any tree breeding is dependent on appropriate silviculture and management of genetically improved trees, and appropriate processing of their products. There are many cases where predicted or potential gains from tree breeding have not been realized because one or more of these technologies has not been optimized or implemented for genetically improved trees or products. An example of the profound impact of silviculture on the capture of economic returns from breeding is illustrated by **Figure 1**.

Figure 1 Economically significant differences due to silviculture in first-generation Caribbean pine (*Pinus caribaea* var. *hondurensis*) performance in coastal central Queensland, Australia. Trial age is about 20 years; the researcher stands in an experimental plot which received neither preplanting site preparation nor postplanting fertilizer application; a plot of the same genotypes, which received both site preparation and fertilizer, is in the background. The experiment was established by the Queensland Department of Forestry. Photograph by Peter Kanowski.

Evaluating Economic Returns from Tree Breeding

Like evaluation of many other forestry investments, the relatively long time intervals between investment and returns both dominate and complicate economic analyses of returns from tree breeding. Historically, most industrial tree growing rotations have been more than 25 years, complicating direct comparisons of more-improved and less-improved material. While many industrial plantations and nonindustrial species are now managed on much shorter rotations, significant practical problems remain in making accurate comparisons. Improved genotypes seldom grow in an environment identical to that of earlier tree crops, as both environments and management practices change. Technological changes in all aspects of tree growing – in the nursery, in silviculture, and in product processing – have profound and interconnected impacts on tree performance and on product recovery, value and economic returns.

Economic returns from breeding may also be evaluated from perspectives of different interests, as follows.

1. Those who have invested, or are considering investment, in tree breeding activities. Typical investment criteria are those such as the internal rate of return, present net worth, or benefit–cost ratio of funds invested, or the minimum scale of deployment of bred material required to break even. These assessments may be applied to whole breeding programs, or to particular separable aspects of them, such as the decision to invest in a new seed orchard or in vegetative rather than seedling propagation.
2. Tree growers, who vary in scale from corporations or public sector agencies with annual planting programs on the order of millions of plants, to small-scale resource-poor farmers who, at the extreme, may be making decisions about individual trees. In both cases, however, decision criteria are likely to reflect an assessment of likely net gain, perhaps including nonmarket values, over the investment period. Criteria may include implicit or explicit assessment of the risks of not investing – for example, in terms of poor adaptation of unimproved material or potential loss of market share – as well as the anticipated direct financial gains from the investment. For those with limited access to financial resources, such as poor farmers, the immediate cost may be a more significant determinant of the investment decision than the ultimate returns on investment.
3. Purchasers of forest products and services, ranging from governments or communities willing to pay for environmental services, to large-scale industrial wood-processing enterprises, to individuals

purchasing individual products (e.g., fruit or poles) at a local market. Ultimately, their decisions provide the market signals on which the decisions of the preceding two groups stand or fall. Their decisions may be expressed through a price differential, or simply through giving preference to particular genotypes, leaving those without such genotypes as residual suppliers with more limited market access.

For these reasons, there is no single economic criterion against which tree breeding investments are or should be judged. The balance of benefits between private interests and public good may also change over time, necessitating evaluation against different criteria. As in other areas of innovation, there is often a phase in which the benefits of tree breeding are captured principally by a few breeders, tree growers, or product processors who have access to new material or technologies. As these materials or technologies become more widely adopted, there is no longer a comparative advantage for the innovators, and the economic benefits from tree breeding will accrue to society more generally rather than to those leading the innovation.

The Genetic Characteristics of Tree Populations

Forests and woodlands are the most biologically diverse terrestrial ecosystems. With some notable exceptions, the tree species which are the defining feature of these ecosystems have been little domesticated relative to the crop plants or animals upon which agricultural production is based. Although their gene pools have been altered, sometimes profoundly, by a wide range of human activities, the genetic resources of most tree species remain rich, a consequence of the longevity of individual trees, their outcrossing breeding system, the extensive geographic distribution of many species, and the high proportion of genes common across most populations in most species. Even for those species that have been the subject of informal domestication or of organized breeding, tree breeders still have – in general – relatively easy access to extensive gene pools which are highly diverse compared to those of other plant species, although some of these genetic resources are now threatened by the unprecedented global rate and scale of forest loss and degradation over the nineteenth and twentieth centuries.

Consequently, there are few tree species for which levels of genetic variation are insufficient to expect significant genetic gains from breeding, although the extent to which these genetic gains translate to economic gains depends on the factors discussed below. *Pinus torreyana* is one such example, as a consequence of a genetic bottleneck in its evolutionary history. Another example is the Australian Gondwanan relic species Wollemi pine (*Wollemia nobilis*), represented by only a few individuals in the wild. Even in such cases, where the species has a commercial value, significant economic returns may be possible simply from propagation. This is the case for Wollemi pine which, although discovered only in 1994, is now being vegetatively propagated on a scale sufficient for large-scale commercial release as an ornamental in 2005, using propagation technologies developed for the related Australian industrial plantation species *Araucaria cunninghamii*. The economic returns from this venture are anticipated to be both commercially attractive and sufficient to contribute significant funds towards conservation efforts for the species.

Stages of Tree Domestication and Breeding

Some tree species have a long history, often of millennia, of informal domestication. These are species important for food and in traditional land use systems: e.g., those of the genera *Artocarpus*, the jakfruits and breadfruits of Asia, or *Mangifera*, the tropically widely distributed mangoes; the leguminous genera *Faidherbia* and *Leucaena* of, respectively, Africa and the New World; or *Fraxinus* and *Quercus*, the European ashes and oaks. The situation of these species, subject to many generations of informal selection and often to induced or spontaneous hybridization, parallels that of other long but extensively domesticated crops, with an often imprecise distinction between natural and naturalized populations. Consequently, the genetic resources available for breeding comprise a highly heterogenous mixture, ranging from highly selected individuals with significant immediate economic value to wild relatives whose value has yet to be established and which may take many cycles of breeding to realize.

Relatively few tree species (around 500 of the presumed more than 50 000) have been subjected to any level of deliberate selection or breeding. The breeding histories of these species are quite contrasting, with contrasting implications for breeding options and associated economic returns.

1. A small group of tree species is of high significance in cultivation in horticultural or estate systems, or in arboriculture. Examples include apple (*Malus* spp.), coffee (*Coffea* spp.), coconut (*Cocos nucifera*), rubber (*Hevea brasiliensis*), and numerous ornamentals. While the principles of assessment of economic returns from these species do not differ

from those for other trees, and tree breeders have much to learn from these industries, the associated body of literature is sufficiently distinct and well addressed elsewhere to not be the subject of this review.

2. Around 200 species have been subject to at least one cycle of breeding (i.e., selection, mating, and testing); a similar number have simply been included in genetic tests. Those subject to the most intensive breeding efforts are the 60 or so species, principally of the genera *Acacia*, *Eucalyptus*, *Picea*, *Pinus*, *Pseudotsuga*, *Populus*, *Larix*, and *Tectona*, that have been improved for industrial wood production (i.e., for solid or reconstituted wood and for pulp) over typically not longer than some fraction of the past 50 years. These populations provide the bulk of our experience and information about the tree breeding and its economic returns, and a few of them provide our only experience of returns associated with advanced generations.
3. Another 60 or so more taxonomically disparate species, amongst them some of the long-domesticated species, have become the subject of breeding for nonindustrial objectives in the past few decades. Examples include species of the tropical and subtropical *Acacia*, *Azadirachta*, *Calliandra*, *Calycophyllum*, *Casuarina*, *Dalbergia*, *Faidherbia*, *Gliricidia*, *Grevillea*, *Irvingia*, *Leucaena*, and *Prosopis*, and the temperate *Acacia*, *Alnus*, and *Salix*. Breeding objectives and strategies, and management regimes, for these species are typically more diverse than for those bred for industrial wood production, and most of the economic returns realized to date are associated with the early stages of breeding.

Figure 2 Economically significant variation in a Douglas-fir (*Pseudotsuga menziesii*) provenance trial, Limousin region, France. Trial age is about 10 years; the student stands between blocks representing an Oregon (background left) and northern British Columbia (foreground and right) provenances. The experiment was established by Office National des Fôrets. Photograph by Peter Kanowski.

Economic Returns from Early Stages of Breeding

The early stages of tree breeding typically involve species and provenance selection, the selection of individual trees within these populations, and the establishment of seed orchards to provide improved material for both production and for further breeding. Given the undomesticated or little-domesticated status and genetic richness of most tree species, substantial genetic gains are possible from the basic first step of species and provenance selection; further substantial gains can be achieved from subsequent individual tree selection and the establishment of seed orchards. The economic gains associated with these genetic gains depend on both the cost of undertaking the breeding activities and on the economic value of the improved material.

The genetic gains achieved at these stages in most tree breeding programs have, almost invariably, been large and cost-effective; they are typified by **Figure 2** which, for a striking but not atypical case, illustrates the extent to which simple provenance selection influences the viability of a species for economic use. Selection on this fundamental basis, for both immediate gain and as the foundation for subsequent breeding, remains the basis of economic returns for new programs, exotic environments, or new breeding objectives. The gains from these early stages of selection can be enhanced by judicious use of any a priori knowledge of patterns of variation and environmental adaptation over a species' range in both natural and exotic environments.

Almost all quantitative data describing genetic and economic gains from this stage of breeding originate from industrial tree improvement programs, many programs now have sophisticated systems for updating breeding and genetic values for individuals, such as Australia's 'Treeplan' or New Zealand's 'GF-Plus' scheme. The gains realized in commercially utilizable stem volume, the initial focus for most industrial programs, from provenance and the first generation of individual tree selection have typically been at least 10% (where provenance differences are small), and often up to 30–50% (where provenance differences are great), over unimproved population means. Gains realized have reflected, to varying extents, selection of well-adapted provenance(s), effective within-provenance selection, and in some cases the release from inbreeding depression associated with natural or small populations. In the most straightforward and historically typical case, where growers' returns for a particular industrial species were dependent simply on the value of wood produced in large-scale afforestation, these genetic gains corresponded to very favorable returns on investment; benefit–cost ratios greater than 5, and internal rates of return of 10–15%, are commonly reported.

Data for nonindustrial species are scarce, reflecting the more recent origins of formal improvement programs. However, nonindustrial tree species appear to be no less genetically variable than industrial species, suggesting that expectations of realized gains should be comparable. The attribution of costs and benefits does, however, differ significantly between many industrial and nonindustrial species; in the former case, benefits typically accrue to an industrial-scale enterprise, whereas in the latter, the intended beneficiaries are typically resource-poor small-scale farmers. The increasing scale of 'outgrower' schemes, under which small-scale farmers grow industrial tree crops under contract to forest products enterprises, blurs this distinction and provides another perspective on the evaluation of economic returns. Where outgrower schemes are well established and offer the option of access to genetically improved material at additional cost, such as for some eucalypts in South Africa, high levels of uptake of advanced material suggest that growers judge the additional cost per plant to be a good investment.

Economic Returns from Advanced Cycles of Tree Breeding

Economic returns from advanced (i.e., later) cycles of tree breeding are founded on the populations established and selections made in the initial stages. As breeding advances from initial stages to subsequent cycles, strategic objectives and breeding options have generally become more focused–for example, through the clearer definition of breeding objectives, more efficient approaches to genetic testing and selection, the better use of genetic information and advanced statistical methods, and sharper analysis of the options amongst various mating designs and multiplication options. Each of these has implications for economic returns, as we discuss below.

In general, the evidence from 'advanced' generations of tree breeding, represented by only a small number of species to date, suggests that it is possible to continue to achieve high rates of economic return over at least a few generations. The capacity to deliver continuing genetic gains and economic returns depends on:

- the clearer definition of breeding objectives and their relation to economic returns
- the better understanding, as a result of accumulating species-specific genetic information over generations, of the genetic structure and parameters of populations
- the efficient design and conduct of breeding activities, to optimize investments amongst alternative breeding strategies, and amongst the elements of tree breeding activities such as selection, mating, and multiplication
- advances in technologies, ranging from simple propagation methods to advanced biotechnologies, and including forest management and product processing technologies
- the optimization of forest and tree management regimes and product processing systems.

Each of these advances helps the breeder, grower, and processor improve the efficiency of and return from their efforts. Economic analyses of returns on investment for various individual elements of advanced generation breeding are encouraging, but analyses of actual gains realized from the overall package of advanced breeding activities await the further progress of these programs.

Breeding Strategies, Technologies, and Objectives

From the 1990s, tree breeders began to follow the lead of their animal-breeding colleagues in defining breeding strategies and objectives more explicitly and formally. Increasing sophistication and competition in markets for forest products and services, and in those for growing trees, have encouraged breeders to focus more sharply on maximizing value gain and optimizing investments – a process that requires both explicit definition of the breeding objectives and assessment of strategic options to achieve them. Technological advances in many aspects of the biological sciences and breeding operations have allowed options that were not previously possible, or enhanced the efficiency of existing options. At the same time, the large scale of deployment in some plantation forestry systems has allowed levels of investment in breeding that would otherwise not be possible, and has helped develop and prove new technologies with wider relevance, such as those for cuttings production of species previously propagated only by seed, or the many applications of molecular genetics.

Breeding Strategies and Technologies

Breeding strategies provide both the conceptual and operational frameworks for tree breeding activities, and comprise both an overall plan and its particular elements – principally selection methods, mating and testing designs, and multiplication processes. They are enabled, and constrained, by technologies relevant to breeding activities. Breeding strategy options are determined principally by the breeding objectives specified, the species' biological and genetic characteristics, the available technologies, and the human and financial resources invested. These factors depend at least in part on the value of products and services, and the likely scale of deployment, of improved populations. Strategies and technologies that deliver outcomes more quickly, by reducing the time associated with breeding activities, are generally most appealing in terms of economic criteria.

An array of breeding strategies, from simple to sophisticated, is available to the breeder. Experience in tree breeding demonstrates the economic importance of designing and implementing strategies appropriate to the species, its scale of deployment, and the production system. In general, simple strategies and technologies, such as those based on mass selection and seedling seed orchards, can be very cost-effective for species for which only limited resources can be found or justified. As the level of available investment increases, reflecting the relative economic importance of a species or judgements about its potential, more sophisticated strategies and technologies become economically accessible and justified.

Decisions to adopt, or not adopt, particular strategic options and technologies reflect an economic assessment of their benefits relative to their costs; there are many examples of how such decisions, ranging from the use of biotechnologies to the choice of propagation system or the decision to incorporate a particular trait in a breeding objective, have been informed by various forms of economic analysis. Estimation of break-even thresholds, in terms of the extent of deployment or level of gain required to justify an investment, or of the investment's likely internal rate of return, are common means of economic analysis of strategic and technological breeding decisions.

Specification of Breeding Objectives

A breeding objective is the specific combination of traits that a breeder seeks to improve, weighted according to their relative economic worth. In the first phase of tree breeding, breeding objectives were typically defined (often necessarily) subjectively and imprecisely. However, both theoretical and empirical evidence demonstrate that, as in plant and animal breeding more generally, progressing to less subjective and more accurate definition of breeding objectives is one of the most significant means of enhancing economic returns from tree breeding. Even preliminary economic information about particular production systems can considerably clarify breeding objectives, which also depend on genetic information generated by a breeding program. Consequently, the refinement of breeding objectives usually proceeds in conjunction with the progress of breeding into advanced generations.

Definition of breeding objectives has to consider both costs and income associated with the production system under consideration, which may vary for example from that for multipurpose trees grown on small-scale farms for fodder, fuelwood, and fruit to that for industrial-scale pulpwood plantations. In terms of the breeding objective, economic returns can be maximized by increasing income (e.g., from achieving higher growth rates without prejudicing wood quality), decreasing costs (e.g., reducing processing costs by altering wood properties), or both. Retirement of the breeding objective for eucalypt pulp production in Portugal offers a typical example; two generations of selection were expected to increase income by 1.5% and decrease production costs by 16%, saving $US7.2 million per annum for a 250,000 tonne pulp mill.

The economic returns associated with clearer definition of breeding objectives are dependent on the characteristics of the species being bred, the costs and income associated with particular production system and suite of products, and the scale of deployment. Notwithstanding this heterogeneity, empirical results over the past decade suggest that investment in the clearer definition of breeding objectives generates substantial economic returns to both the breeder and grower of forest products.

The Value and Scale of Deployment of Improved Populations

The economic returns from tree breeding are ultimately dependent on the value of the products and services, and the scale of deployment, of improved populations. As each of these increases, so do the capacity for investing and the potential for generating returns from investments in breeding. The value of improved populations has historically depended only on their physical wood and/or non-wood products. However, value might also be reflected in terms of the opportunity costs avoided, and expanded by the services as well as the products of trees. Breeding for disease resistance exemplifies the former, and has been demonstrated to generate very favorable benefit–cost ratios; an example is that of fusiform rust resistance in southern pines in the USA, which is expected to return benefits at least four times greater than costs. The emergence of environmental services markets, such as those for carbon or ecosystem restoration, offers additional opportunities for the definition and delivery of breeding objectives, and consequent income generation.

The scale of deployment of improved populations is a significant determinant of the income stream against which the fixed costs of breeding will be offset. For these reasons, assessment of threshold levels of deployment or uptake are a common means of economic evaluation of breeding options. The role that many governments assume, of helping to foster new industries, is one reason why many tree breeding programs worldwide began with significant public-sector involvement, often transferring progressively to the private sector as industries became established on a scale sufficient to support commercial ventures. It is also one of the reasons that the public sector retains a substantial role in breeding of many nonindustrial species.

Institutional Arrangements for Breeding and Benefit Sharing

Institutional arrangements for breeding and benefit sharing impact on the distribution of costs and benefits associated with tree breeding. Historically, access to genetic resources of tree species has seldom been restricted; more usually, access has been facilitated by strong cooperation between countries and between public and private sectors. For reasons outlined above, most tree breeding programs began, and many remain, in the public domain, and have been judged against broader economic, rather than narrower financial, criteria. However, tree genetic resources and breeding activities are becoming increasingly proprietary, mirroring more general trade and intellectual property regimes. These changes challenge some of the important assumptions on which public investments in tree breeding have been made, and are likely to make breeding of some species more economically attractive and that of others less so.

Public-sector entities investing in breeding are likely to have different performance criteria than private investors, leading to different forms of economic evaluation. They may, for example, be willing to incorporate consideration of externalities, such as the potential for industry development or employment generation, the maintenance of rural livelihoods, or the delivery of environmental services, into evaluations; they are also likely to have access to lower-cost capital, and have a longer time horizon, than private sector investors. Where the investment is part of a development assistance program, as has been the case for both industrial and nonindustrial tree species, economic criteria may be very broadly defined, for example, the potential to contribute to sustainable livelihoods, or to address environmental degradation. However, in such cases, it is likely that investment in tree breeding will still need to be justified against alternative investment options.

Conclusions

Prudent investments in tree breeding offer the prospect of good economic returns, frequently greater than those from alternative forestry investments. Their realization is, however, contingent on good silviculture and management and appropriate product processing, which themselves also demand astute investments. High returns can be achieved most easily in the early stages of breeding, but evidence suggests that they can be sustained over subsequent generations through more focused, informed, and efficient breeding. Simple breeding strategies can yield relatively good returns, and may have advantages over more sophisticated strategies in terms of lesser risk and opportunity cost. However, more sophisticated strategies are likely to be necessary to optimize returns from advanced generations of breeding. The value of forest products and services, and the scale of deployment, of improved populations have significant influence on the magnitude of economic returns from tree breeding. The institutional arrangements for breeding and benefit sharing impact on the distribution of costs and benefits associated with tree breeding, and thus on the economic returns to different parties. The criteria against which the economic returns from tree breeding are assessed are also likely to depend on whether the evaluation is undertaken from the perspective of the breeder, the tree grower, or the purchaser of forest products and services.

See also: **Genetics and Genetic Resources**: Propagation Technology for Forest Trees; Quantitative Genetic Principles. **Tree Breeding, Practices**: Breeding and Genetic Resources of Scots Pine; Breeding for Disease and Insect Resistance; Genetic Improvement of Eucalypts; Genetics and Improvement of Wood Properties; Nitrogen-fixing Tree Improvement and Culture; *Pinus*

Radiata Genetics; Southern Pine Breeding and Genetic Resources; Tropical Hardwoods Breeding and Genetic Resources. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Breeding Theory and Genetic Testing; Conifer Breeding Principles and Processes; Forest Genetics and Tree Breeding; Current and Future Signposts. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources.

Further Reading

Borralho NMG, Cotterill PP, and Kanowski PJ (1993) Breeding objectives for pulp production of *Eucalyptus globulus* under different industrial cost structures. *Canadian Journal of Forest Research* 23: 648–656.

CSIRO Australia (1999) *Benefits from CSIRO Research for the Forestry, Wood and Paper Industries Sector: Impact Analysis and Evaluation*. Canberra: CSIRO Forestry and Forest Products.

Cubbage FW, Pye JM, and Holmes TP (2000) An economic evaluation of fusiform rust protection research. *Southern Journal of Applied Forestry* 24: 77–85.

Heisey P, Srinivasan CS, and Thirtle C (2001) *Public Sector Plant Breeding in a Privatizing World*. Agriculture Information Bulletin no. 772. Washington, DC: US Department of Agriculture.

Johnson GR, Wheeler NC, and Strauss SH (2000) Financial feasibility of marker-aided selection in Douglas-fir. *Canadian Journal of Forest Research* 30: 1942–1952.

Last FT (ed.) (2001) *Tree Crop Ecosystems*. Amsterdam: Elsevier.

Löfgren K-G (1988) On the economic value of genetic progress in forestry. *Forest Science* 34: 708–723.

McKenney D, Fox G, and van Vuuren W (1992) An economic comparison of black spruce and jack pine tree improvement. *Forest Ecology and Management* 50: 85–101.

Simons AJ (1996) Delivery of improvement for agroforestry trees. In: Dieters MJ, Matheson AC, Nikles DG, Harwood CE, and Walker SM (eds) *Tree Improvement for Sustainable Tropical Forestry*, pp. 391–400. Gympie, Australia: Queensland Forestry Research Institute.

TREE PHYSIOLOGY

Contents

Physiology and Silviculture

C Beadle, CSIRO Forestry and Forest Products, Hobart, Tasmania, Australia
R Sands, University of Canterbury, Christchurch, New Zealand

Published by Elsevier Ltd., 2004

Introduction

Physiology is the study of how plants function. Ecophysiology is the study of how a community of plants, animals, and microorganisms function together. Environmental ecophysiology is the study of how factors such as light, temperature, atmospheric carbon dioxide concentration, wind, relative humidity, soil water, and nutrients affect community function. Silviculture is the science and art of using environmental ecophysiology, wittingly or unwittingly, to manage forests.

The physiological processes observed in trees are common to most plants. As with other species in the plant kingdom, trees are found across a range of environments and therefore display a very wide range of adaptation to environment. In this article we examine the basic physiological processes that govern tree function and indicate how this information can be applied to silviculture.

Silvicultural practices are directed towards a management objective. These include ensuring adequate regeneration, promoting some species over others, making trees grow faster, improving the quality of wood, protecting the trees from pests and diseases, sustaining water supply and soil chemical and physical properties, and conserving biodiversity. Many traditional silvicultural practices were developed before there was little physiological awareness of how trees grow. However, there is ample evidence that an understanding of environmental ecophysiology can assist in improving current, and developing new, silvicultural practices.

For convenience we consider the relationships between physiology and silviculture in the context of (a) the aboveground (aerial) environment and (b) the belowground (soil) environment.

The Aboveground Environment

The leaves, their structural properties and display, and their interaction with environmental variables determine photosynthesis, the process that drives all plant growth and therefore all biological systems. The environmental variables include quantity and quality of light intercepted by the foliage, atmospheric carbon dioxide concentration, air temperature, vapor pressure deficit, and wind. Based on an understanding of the relationships between photosynthesis and environment, silviculturalists manipulate the forest to achieve a particular management objective.

Leaves

The leaves of trees vary considerably in their size and shape. There are well-defined differences in the period of time that they remain functional. This is in part related to the architecture of the tree including whether the species is evergreen or deciduous. Size and longevity of leaves are affected by environmental stress. These properties are concerned with leaf expansion, retention, and senescence, and determine the size and extent of the canopy. Leaf structure and angle vary with depth in the canopy. These properties are dynamic and driven by the immediate light environment, and related to the physiological activity of the leaves (*see* **Tree Physiology:** Canopy Processes).

Leaf growth Leaves grow by expanding their surface area and increasing their mass. Their potential for expansion is determined by the extent of cell division and their size by the capacity of those cells to expand. In the absence of stress, rates of growth and leaf size at maturity are primarily determined by temperature and nutrition. Cell expansion is a function of leaf turgor (see Water relations below) and quite sensitive to water stress. Cell division and the rate of emergence of leaves are less sensitive to stress but have a large demand for the products of photosynthesis (assimilates). Growth requires an irreversible increase in cell volume that occurs above a threshold or critical value of turgor. Foliar nitrogen (N) has a large effect on final leaf size.

The period as well as the rate of expansion of leaves can vary considerably within and between species. In tropical species, rates of leaf extension can be as high as 18 mm day^{-1} and growth can be completed in 2 weeks. In conifers, needle extension can continue for several months. In eucalypts, a genus with a naked bud habit that allows continuous growth if conditions remain favorable, leaf size will be reduced while water stress develops or at the end of the growing season where low temperatures limit growth.

Leaf longevity Leaf longevity is the period that a leaf remains functional between initiation and fall. The period can vary up to three orders of magnitude between species. Longevity is often related to patterns of growth and levels of stress experienced by species in their native habitats. In the very slow-growing and long-lived bristlecone pine (*Pinus longaeva*), leaves have a lifespan of up to 45 years; in early-successional rainforest species lifespan may be just 50 days. Coniferous leaves have a longer lifespan than evergreen broadleaves while that of deciduous species is largely dictated by the length of the growing season. In tropical deciduous species, leaf longevity is strongly seasonal and largely determined by the levels and intensity of water stress that induce earlier leaf senescence and leaf fall.

Leaf longevity affects fluctuations in the extent of the canopy. However, the physiological activity of leaves across a range of species is closely related to their longevity. For example, a coniferous needle over a 5-year lifespan can fix two to three times the amount of CO_2 in photosynthesis than a deciduous leaf in one growing season, but at a lower rate of photosynthesis per unit leaf area. Leaf longevity is associated also with adaptation to stress. Plants that have leaves with a long lifespan minimize investment in new foliage but the leaves are suited to survival, for example through being structurally and chemically more robust in order to deter herbivory.

Photosynthesis

Photosynthesis converts solar (light) energy into dry mass and occurs in the leaves. The biophysical and biochemical processes that constitute photosynthesis are located in the mesophyll tissue, layers of cells that contain chlorophyll and other pigments, and enzymes. These processes involve both light and dark reactions. In the light reactions, solar energy in the spectrum between 400 and 700 nm is absorbed by chlorophyll and converted to chemical energy which is stored as phosphorylation potential (ATP) and as reducing power (NADPH). The dark reactions then lead to the reduction of carbon dioxide (CO_2) and its conversion to simple carbohydrates (CH_2O, sugars). The biochemical cycle that drives photosynthesis is the Calvin or photosynthetic carbon reduction cycle. Trees use this cycle only for photosynthesis and are C_3 plants. The enzyme (that catalyzes a reaction between two substrates, ribulose 1,6-*bis*phosphate and CO_2; see **Figure 1b**) involved in the first reducing step is ribulose 1,6-*bis*phosphate carboxylase, commonly referred to as Rubisco. It is present in leaves at high concentrations but these vary widely according to incident levels of light on the leaf, and the availability of nutrients (as Rubisco, a protein, has a high demand for nitrogen-based resources) and water. Photosynthesis is commonly measured as the amount of CO_2 fixed per unit leaf area per unit time. The photosynthetic capacity or maximum rate of photosynthesis varies widely between tree species, from <5 to around 25–30 μmol $CO_2\,m^{-2}\,s^{-1}$. Species with higher photosynthetic capacity are usually associated with higher rates of growth. Leaf photosynthesis is commonly measured using gas-exchange analysis; micrometeorological techniques are used over whole canopies (*see* **Tree Physiology**: Canopy Processes).

Gas exchange In order to absorb CO_2 for photosynthesis, leaves expose a wet surface to a drier atmosphere. The evaporative loss of water that occurs results in cooling that assists maintaining equable temperatures for photosynthesis. To prevent dehydration, the epidermis has a relatively impermeable cuticle and turgor-operated valves called stomata. Changes in turgor lead to the opening and closing of the stomata. This regulates the diffusion of water vapor out of, and of CO_2 into, the leaf in a process referred to as gas exchange. The driving force in gas exchange is the concentration difference between the external atmosphere and, for CO_2, the concentration within the leaf; for water it is the saturated vapor pressure at the leaf temperature. The (stomatal) conductance is a measure of the degree of opening of the stomata.

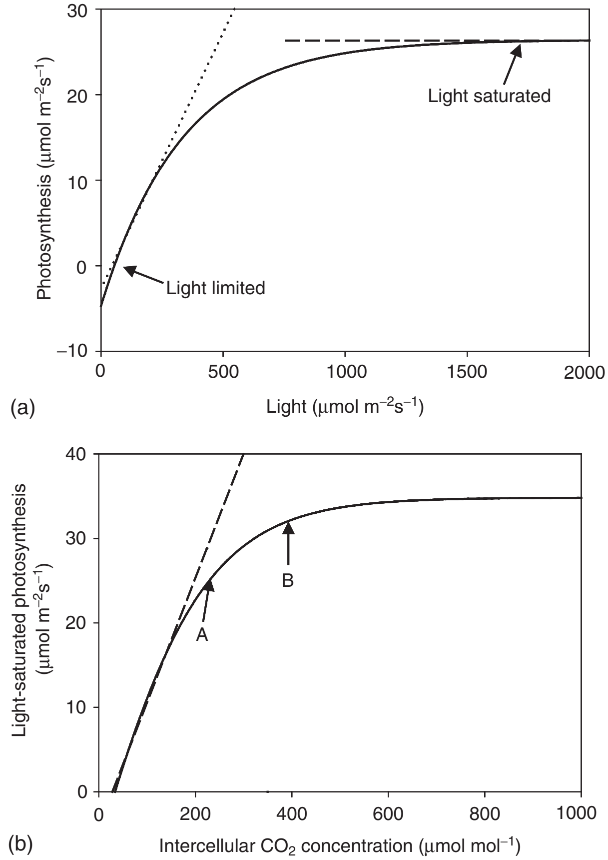


Figure 1 (a) The response of photosynthesis to increasing levels of light. At very low light levels, photosynthesis is negative as the rate of dark respiration (which results in the release of CO_2) is greater than the rate of photosynthesis. Photosynthesis then increases rapidly, the dotted line representing the initial slope of the response or quantum yield (μmol CO_2 fixed per μmol incident or absorbed light). At high light levels, photosynthesis becomes light saturated (broken line). Full sunlight varies with season but is approximately 2000 (μmol $m^{-2}\,s^{-1}$). (b) The response of light-saturated photosynthesis to intracellular CO_2 concentration, a measure of the concentration in the internal spaces of the leaf that is available to be fixed in the mesophyll cells. The broken line measures the carboxylation efficiency and indicates that photosynthesis is RuBP (ribulose 1,6-*bis*phosphate) saturated. As CO_2 concentration increases, photosynthesis becomes limited by the regeneration of RuBP in the Calvin cycle. Point A represents the rate of photosynthesis that occurs at atmospheric CO_2 concentration; point B the rate if there was no stomatal limitation.

Environment and photosynthesis Light and CO_2 are essential to photosynthesis as explained above. Light varies both diurnally and seasonally, and in a tree canopy the levels of light incident on a leaf will vary with position and orientation of the leaf. Leaves adapt to their incident light environment but have a characteristic light-response curve (**Figure 1a**). When light levels are low, photosynthesis is limited by light. When light levels are high in C_3 plants, photosynthesis is light-saturated.

Carbon dioxide and water (see below) are the essential substrates of photosynthesis. Photosynthesis is CO_2 limited at low levels of CO_2 concentration but the process becomes saturated at high concentrations (**Figure 1b**). The average atmospheric CO_2 concentration today (in 2004) is approximately 370 μmol mol^{-1}. Thus rates of photosynthesis will continue to increase if anthropogenic release of CO_2 into the atmosphere continues at current rates. This will lead to further increases in photosynthesis assuming no change in other factors that affect the rate of photosynthesis, for example temperature. As trees are the major terrestrial global sink for CO_2, this has environmental as well as biological significance.

Temperature is closely associated with photosynthesis as we are dealing with a biochemical process where rates of reaction increase with temperature, approximately doubling with each 10°C increase in temperature. Thus photosynthesis varies both diurnally and seasonally. However, as pointed out above, leaf initiation and shedding are also driven by the availability of water. Thus photosynthesis tends to be most active over the middle range of temperatures, that is the response curve is parabolic, and decreases at very low and very high temperatures that are often associated with stress. Extremes of temperature are often associated with photoinhibition and photorespiration (see below). Seasonal shifts in temperature result in adaptive changes that are defined by the slope of the line relating the optimum temperature for photosynthesis and the acclimation or ambient temperature. Species from a continental climate and a more variable diurnal temperature range tend to have a broad temperature maximum to maximize uptake of CO_2 in photosynthesis whereas in species from a coastal environment, where diurnal changes in temperature are moderate, uptake of CO_2 has a more dynamic response to changes in temperature.

Rates of photosynthesis are also limited by nutrient and water stress (see below). Given that nitrogen and phosphorus are essential components of the photosynthetic process (Rubisco, ATP, and NADPH) positive associations between photosynthetic capacity and leaf nitrogen and leaf phosphorus are observed. However the effects of atmospheric and soil water stress on photosynthesis are primarily caused by changes in response to leaf water status and vapor pressure deficit on stomatal conductance.

Stomatal conductance Stomata are powerful regulators of gas exchange and linear relationships between rate of photosynthesis and stomatal conductance are often observed in trees. This relationship may become nonlinear at high conductance as the rate limitation may no longer be diffusion of CO_2 into the leaf but reside in the activity of photosynthetic processes in the mesophyll. As with rates of photosynthesis, there is a considerable variation in maximum stomatal conductance between species where low conductance is often associated with low photosynthetic capacity and vice versa.

Stomata open and close as a result of increases and decreases in turgor, respectively, of guard cells that surround the stomatal pore. However these changes in turgor are driven by active mechanisms that involve the transport of ions, in particular potassium. The regulation of stomata is complex but in general they open in response to light, have a parabolic response to temperature and close in response to atmospheric (vapor pressure) and leaf (soil) water deficits (**Figure 2**). The sensitivity of stomata to these variables varies between species, and as with photosynthesis, there is adaptation of stomatal conductance to the ambient environment. Trees are tall crops and the leaves are closely coupled to the atmosphere (*see* **Tree Physiology**: Canopy Processes). As a result, stomatal conductance of trees is often observed to be quite sensitive to vapor pressure deficit.

Effects of age The photosynthetic capacity and maximum stomatal conductance of leaves changes during their development, maturation, and senescence. On tree species that have several cohorts of leaves, for example conifers, there may be considerable stratification of physiological activity, the lowest being associated with the oldest leaves. Trees are perennial crops and some are very long-lived. There is evidence that tree aging is associated with a decline in photosynthetic capacity though this is linked to changes in other areas of physiological activity.

Photoinhibition Photoinhibition is associated with the absorption of light by plants in excess of that required for photosynthesis and is manifest in a reduced photosynthetic capacity. Photoinhibition occurs when leaves are under stress, for example during conditions of low temperature or water stress, such that the rate at which enzymes function in the Calvin cycle is limited. Sustained decreases in the efficiency of photosynthesis and quantum yield, a measure of the efficiency of conversion of light to biomass, are observed that can be detected by chlorophyll fluorescence and are associated with prevention of damage to the photosynthetic system. If light is absorbed in excess but not dissipated, oxidative damage occurs. Prevention of damage is associated with the xanthophyll cycle, an interconversion of carotenoid pigments that results in the harmless dissipation of light as heat energy, and a range of other potential mechanisms, some unproven.

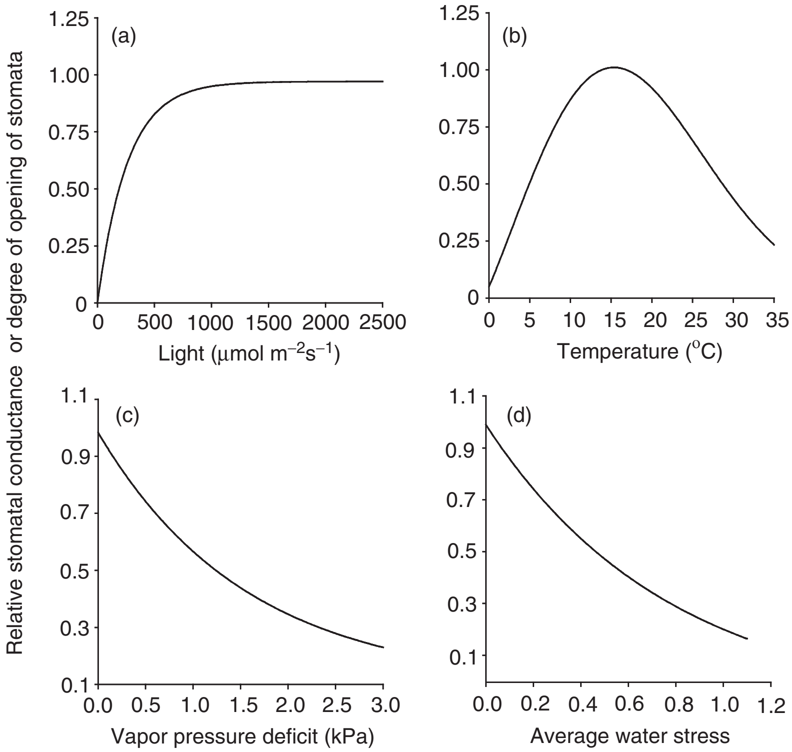


Figure 2 Stomatal respond to their environment. Stomata open rapidly in response to increasing light levels (a). Stomata also open in response to increasing temperature but are observed to close at high temperatures (b). However this is often because the stomata are sensitive to increasing vapor pressure deficit (the difference between the saturated vapor pressure at the air temperature and the actual vapor pressure) (c) and vapor pressure deficit increases with temperature. Stomata are also responsive to the water status of the leaf (d); this is measured by considering the water stress history (measured as the pre-dawn water potential) that the leaf has experienced. The stomata of tree species differ in their response to these environmental variables.

Respiration Respiration is a process that consumes oxygen and releases CO_2, water, and energy. Most respiration is independent of light and produces energy to support growth. However, photorespiration occurs only in the light and competes directly with photosynthesis in a process where both oxygen and CO_2 compete for ribulose 1,6-*bis*phosphate and Rubisco. This reduces the efficiency of utilization of CO_2 in the Calvin cycle and causes photosynthesis of C_3 plants to saturate at lower values of light and photosynthesis than in C_4 plants. (C_4 plants can largely overcome the negative effects of photorespiration by using anatomical and biochemical mechanisms to deny access of oxygen to Rubisco.) Photorespiration is most active at high light intensities and temperatures and acts, along with photoinhibition, to reduce photosynthesis.

Silviculture

Several tools are available to silviculturalists to manipulate the aboveground environment. Choice of species, stocking density, the use of monocultural or mixed-species plantings, shelter belts, pruning, and thinning are some. Application of fertilizer and irrigation, although altering the belowground environment in the first instance, change growth rates and canopy size, thereby altering also the aboveground environment. Some of the ways these actions affect physiological activity will now be explored.

Light The classical silvicultural systems in natural forests are single-tree selection, group selection, shelterwood, and clear-cut. This series represents a progressive increase in the amount of light reaching the forest floor to promote regeneration. The appropriate system is determined to a large extent by the photosynthetic properties of the trees. Although clear-cuts are considered by many to be environmentally unfriendly, there are circumstances in which this system is the most appropriate. In native forest, many 'clear-cuts' that arise from natural disturbance (e.g., by fire) are essential for regeneration and replacement of the same forest type. For example, *Eucalyptus regnans* is a major forest type in southeastern Australia which often occurs as a single species of the same age. This age is determined by the timing of the fire event that destroyed the previous forest and provided a large seedbed out in the open. Physiologists call *E. regnans* a 'sun' or 'shade-intolerant' plant. Conversely, in the rainforests of northeastern Australia, *Alocasia macrorrhiza* grows as an understory species and regenerates and persists under low light. *A. macrorrhiza* is a popular indoor plant. Physiologists call it a 'shade' or 'shade-tolerant' plant. The photosynthetic properties of sun plants and shade plants are shown in **Figure 3**.

It can be seen that sun plants (e.g., *E. regnans*) typically grow faster than shade plants (e.g., *A. macrorrhiza*) but only if there is plenty of light reaching the leaves. *Eucalyptus regnans* grows very poorly under shade and indeed will only regenerate and grow satisfactorily in the open. *Alocasia macrorrhiza* grows much slower than *E. regnans* but it can establish and persist at lower light levels. The light compensation point (the light level at which net photosynthesis is zero) is considerably less in *A. macrorrhiza* than in *E. regnans*. Thus use of a silvicultural regime that shades *E. regnans* regeneration is likely to fail. Pioneer species that are intolerant of shade (like *E. regnans*) are usually very productive and readily establish on bare sites. Successful plantation trees are often pioneer species that occur naturally as even-aged monocultures. By contrast species with photosynthetic properties adapted to growth under shade are not suited to being regenerated in the open and attempts to use these species in plantations often fail.

The manipulation of light in forest plantations through stocking density at planting and thinning during the rotation are used to optimize the amount of light intercepted by an individual tree and therefore its size, at the same time maximizing the quantity of wood produced per unit area, and the quality of the wood required for a particular end-use. High initial stockings in all types of forest promote height growth, straight and single-stemmed trees, and prevent the development of large branches. Thinning reduces between-tree competition and allows increased growth of remaining trees. Pruning reduces the size of the knotty core and allows the development of knot-free clear wood by removing the lower branches, often in a series of progressive lifts.

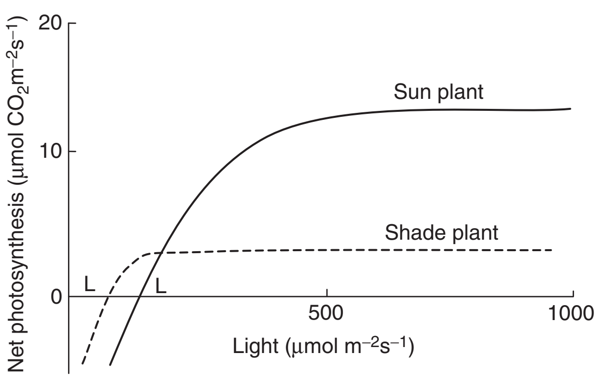


Figure 3 A typical relationship between net photosynthesis and light for single unshaded leaves of sun plants and shade plants. L is the light compensation point.

Pruning and thinning are associated with changes in the photosynthetic activity of leaves. Green pruning that removes live branches reduces the total number of leaves per tree; thinning changes the distribution of light incident on the leaves of the retained trees. A quantitative understanding of the physiological responses to both practices is used as a basis for management. The reduction in canopy size with green pruning significantly increases the rate of photosynthesis of the residual leaves throughout the crown. There is also an increase in the rate of leaf development and delayed senescence of existing leaves. The magnitude and duration of these responses is related to the severity of pruning. Thus an increasing capacity for photosynthesis at tree level is offset by an increasing reduction in crown size. The balance point is the pruning severity beyond which reduction in growth is observed. The enhanced levels of light-saturated leaf level photosynthesis observed following thinning are related to the increase in the fraction of incident light penetrating to the middle and lower parts of the canopy compared to that in unthinned stands. The magnitude of this response increases with time from thinning and is associated with increased levels of leaf nitrogen concentration and changes in its distribution commensurate with its allocation according to the prevailing light environment. Thinning is also associated with increases in tree-growth efficiency, the amount of stemwood produced per unit leaf area.

Carbon dioxide As CO_2 is a primary reactant of photosynthesis, increases in its concentration in the atmosphere have the potential to increase growth rates. Indeed, artificial enrichment of CO_2 concentrations in nurseries has been used to that effect. The concentration of CO_2 in the atmosphere has been increasing exponentially for over 100 years, mainly from burning fossil fuels but also from the clearing and burning of vegetation, including forests which historically have been very large sinks for CO_2. If not already occurring, it is expected that climates will change as a result of increased CO_2 concentrations in the atmosphere and that the consequences of this will be largely negative for human welfare. Forests, however, all other things being equal, may be more productive, though any increase in average temperatures and the distribution and quantity of rainfall will change species boundaries.

While changes in atmospheric CO_2 concentration are beyond their control silviculturalists can manipulate CO_2 to their advantage by increasing the stomatal conductance of CO_2 from the atmosphere into the leaves through the stomata. Silviculture is used in a broad sense to maximize photosynthesis in this way. For example weed control, the removal of competition for resources, i.e., light, nutrients, and water, ensures that these are used to support uptake of CO_2 by the tree crop only. This is particularly important when any one resource is a major factor limiting plant growth.

Air temperature Very low temperatures can 'damage' the physiological integrity of plant tissue. This is, in particular, a silvicultural issue in nurseries where seedlings are raised under conditions that are mild compared to those at the planting site. Two types of damage may occur. Physical frost damage is caused by the freezing and expansion of intracellular fluid that result in cell breakage. Photodamage associated with photoinhibition is caused when more light is absorbed than can be dissipated harmlessly. This leads to reactions that destroy cell membranes. Silviculturalists impose 'hardening' in the nursery to make the seedlings physiologically more resistant to frost and low temperature after transplanting. These include progressive exposure to lower temperatures that leads to improved resistance because the seedlings increase the osmotic concentration of cell contents, thereby decreasing their freezing point. Low temperature and nutrient starvation increase resistance to photodamage by stimulating the activity of physiological processes that dissipate light energy. In addition, shadecloth is used to reduce the levels of incident light on seedlings. The pattern of regeneration of tree seedlings in native forest is affected by the degree of cold-induced photoinhibition and greater exposure increases the intensity of a frost event. Shelterwood systems reduce exposure and increase average minimum temperature, thereby supporting seedling survival.

Wind A boundary layer of relatively still air at the leaf surface contributes to the resistance to transfer of CO_2 into, and water vapor out of, the leaf. However forests with high canopies are aerodynamically rough and the atmospheric climate comes very close to the leaf surface. Consequently boundary-layer conductance is very high and reinforced by wind mixing up the air close to the leaf surface. Photosynthesis is increased in gentle to moderate winds but severe winds can accelerate water loss, promoting stomatal closure and a reduction in photosynthesis. Strong winds can also cause mechanical damage to trees. Planting patterns are used to promote shelter within a stand, and belts of trees planted strategically to reduce wind speed across the stand.

The Belowground Environment

Plants require water and nutrients for growth and these are obtained in the main by absorption through roots. Thus the physiological condition of the aboveground parts of the plant are reliant on soil properties, and processes that control root development and the exploration of the soil (*see* **Tree Physiology**: Root System Physiology) and the acquisition, translocation, and storage of nutrients (*see* **Tree Physiology**: Nutritional Physiology of Trees). Conversely root systems are reliant on the translocation of assimilates from leaves for their growth and energy requirements. Changes in soil water content can have a profound effect on physiological activity and are associated with reductions in water potential and water content throughout the plant.

Water Relations

The amount of water used directly in the biochemical reactions of photosynthesis is very small compared to that transpired by leaves. Changes in water status strongly influence tree growth through their effect on leaf expansion and shoot and root extension. As water status decreases, turgor is reduced, stomata close, and direct effects of water stress on chloroplast processes reduce the rate of photosynthesis. There is evidence that hormonal signals transmitted between the root surface and leaves can trigger changes in stomatal conductance in response to the current level of water supply.

Water content, water potential, and water transport Water status can be measured gravimetrically as tissue water content, most often relative to its saturated or turgid weight. Water moves along gradients of water potential (that has units of pressure) which is defined as the potential energy per unit volume of water with reference to pure water at zero potential. Water in most biological systems and in soil has less potential energy than pure water. Consequently values of water potential are negative and water moves along negative potential (pressure) gradients. A key measurement of leaf water potential is made pre-dawn to determine the minimum level of water stress. This value is taken when there is little or no net flux of water through the tree and therefore estimates the water potential at the soil–root interface.

The water potential of a leaf (shoot or root) is the sum of two components, a negative osmotic potential arising from the presence of dissolved solutes in the cell and a positive turgor potential arising from the pressure exerted on the cells by their walls. These variables, and a measure of the elasticity of the cell walls, can be derived from the relationship, referred to as the pressure–volume curve, between water potential and water content.

In response to the demand for water at the evaporating surface, leaf water potential becomes more negative to increase the potential gradient. As the soil dries and soil water potential becomes more negative, a strategy for maintaining the same flux of water through the plant is to further lower leaf water potential to maintain the potential gradient. Trees are observed to adopt a range of strategies to deal with water stress including an inherently low osmotic potential, lowering of leaf osmotic potential that is referred to as osmotic adjustment, and elastic tissues that allow the maintenance of turgor over a wider range of tissue water contents. Trees with high osmotic potentials and inelastic tissues that promote rapid loss of turgor are associated with a high stomatal sensitivity to leaf water status and drought avoidance. Conversely, trees with low osmotic potential and elastic tissues are associated with a low stomatal sensitivity and drought tolerance.

Sapwood The major conducting pathway for water between the roots and the leaves is the stem sapwood. The sapwood consists of a network of interconnecting pipes which in trees is made up of xylem vessels or tracheids. This 'pipe model' link between sapwood and leaves implies a causal relationship although the direction of causation remains unclear. Thus stem sapwood area can be an accurate scalar for estimating leaf area due to its role in supplying water to the transpiring foliage (*see* **Tree Physiology**: A Whole Tree Perspective).

Silviculture

The growth and function of roots is influenced by soil water, soil nutrients, soil air, soil strength, soil temperature, soil salinity, soil acidity, soil sodicity, and soil toxicity. Silviculturalists can manipulate these environmental factors to their advantage, using techniques such as cultivation, including mounding and deep ripping, or by species selection. A soil environment that promotes root development does not necessarily mean that the growth of roots will be greater than that of the stem, branches, and foliage. Indeed it is usually the opposite. Thus if the soil has plenty of water and nutrients but the aboveground environment is in some way deficient, e.g., there are low levels of incident light, then the tree will partition more assimilates to aboveground growth in a bid to capture more light.

When dealing with an interface between soils and roots, there is a knowledge boundary and exploitation of a physiological understanding of root behavior requires close cooperation with soil scientists as well as silviculturalists.

Water Irrigation is not usually an option for the silviculturalist, except in nurseries or in disposal of treated sewage effluent (*see* **Soil Development and Properties**: Waste Treatment and Recycling). However there are silvicultural strategies that can conserve scarce soil water and ensure that it is used most efficiently in growth. The most fundamental is avoidance of dry sites but as these are often unsuitable for activities other than forestry, an option is a tree species that will grow and survive at such a site. Trees vary in their response and ability to adapt to soil water stress. They also vary in their ability to close their stomata in response to the dryness of the atmosphere (measured as the vapor pressure deficit). Water-use efficiency, a term that measures biomass produced per unit of water transpired varies a limited amount and is not commonly used as a selection tool in forestry. In environments that have higher levels of water supply but where water stress is still the major factor limiting tree growth, one strategy is to deliver the soil water to the crop trees only. This can be achieved by reducing the evaporation of water directly from the soil by using mulches or retaining litter. In addition, spacing and thinning the tree crop reduces the total transpiring area. Besides increasing tree survival, this option can be used to maximize the growth of the retained trees and provides a basis for the sustainable use of available soil water across rotations. As pointed out above, weed control is an essential part of management on dry sites.

Eucalypts provide an example of where insufficient knowledge of tree physiology has resulted in poor silviculture and created a potential environmental weed. Australia is a large and predominantly dry country dominated by genus *Eucalyptus*. This genus includes some very fast-growing species and the inference was made that some of these species might be successful on sites with low rainfall. However the fast-growing species are native to wetter sites and are not physiologically well adapted to severe water stress. Thus many early plantings of eucalypts outside of Australia on dry sites failed because of inappropriate species selection. When these same species escaped to sites with higher water supply, they became aggressive weeds and suppressed the growth of more desirable species. An understanding of the physiology of water use would have foreseen these eventualities. A general strategy among plants for conserving soil water is to close stomata, but this will also reduce growth rates because photosynthesis will also be reduced. However several eucalypt species tolerate drought and do not close their stomata so much as the soil dries or as the vapor pressure deficit increases (**Figure 4**). This means that when eucalypts are grown in competition with more conservative and slower-growing species, they transpire more water and exhaust the soil water supply faster. Eucalypts often survive by dropping their leaves and then regenerating their foliage from dormant buds when the conditions are again favorable for growth, a strategy that also makes them highly competitive species in some exotic environments.

Nutrients The elements essential for growth were established by physiologists in the early twentieth century and mineral nutrition is now relatively well understood in the context of the processes that drive plant growth. Application of fertilizer to forests is an established silvicultural practice. For example rates of canopy development and canopy size are strongly dependent on the supply of nitrogen. Fertilizers are also used to correct nutrient imbalances which can impair the functioning of processes that are crucial to acceptable growth and form. However, there are other ways of managing forest nutrition. Cultivation, residue retention, elimination of burning, organic matter maintenance, prevention of erosion, use of legumes, application of treated municipal wastes, and the promotion of mycorrhizal infection of roots are all forms of management of nutrition, and in all of these cases a knowledge of the underlying physiological processes helps in defining the most appropriate regimes.

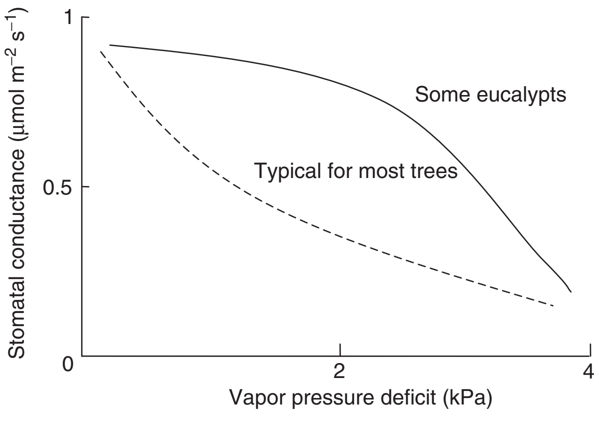


Figure 4 The typical relationship between stomatal conductance and vapor pressure deficit for most trees compared to that of some eucalypts.

Small amounts of nutrients can also enter foliage and soil through atmospheric deposition and this can be critical to the welfare of certain ecosystems. However, nutrient inputs from air pollution can be significant. Soils in southern Sweden have been estimated to receive approximately 30 kg ha^{-1} of free nitrogen from the combustion of coal and other fossil fuels in Germany. This, combined with increased CO_2 concentrations in the atmosphere, has resulted in higher growth rates. However, air pollution is not recommended as an acceptable silvicultural practice!

Soil air and soil strength Roots need oxygen for respiration and growth. Oxygen can be reduced to critical limits in situations where the air-filled pore space in the soil is reduced, such as in clay soils, in waterlogged soils, and in compacted soils. Reduced soil air will impair membrane function and therefore can reduce the uptake of water across the root endodermis. This means that a soil with too much water can actually cause water stress in the tree. Waterlogged soils can be mounded and compacted soils can be ripped.

In order for roots to grow they need to overcome the mechanical resistance offered by the soil. This mechanical resistance or impedance is related to the strength of the soil. Root growth rates decrease exponentially with increasing soil strength (**Figure 5**). Ripping the soil can reduce soil strength but it is better to have soil management regimes that do not cause soil compaction in the first place. The strength of a particular soil increases with soil bulk density (a measure of soil compaction) and decreases with soil water content. This means that root growth in a drying soil will be reduced because of both the lower water potential in the soil and the increased soil strength. Thus soil cultivation can alleviate water stress in plants in compacted soils to some extent.

Cultivation Soils are cultivated (by plowing, mounding, ripping) as part of plantation establishment to control weeds, to release nitrogen, to improve access to soil water and drainage, and to reduce soil strength. Cultivation regimes are usually based on empirical trials. Silvicultural practices informed by empirical trials or trial and error must by their very nature be blunt tools. The tendency has been to assume a worst-case scenario and

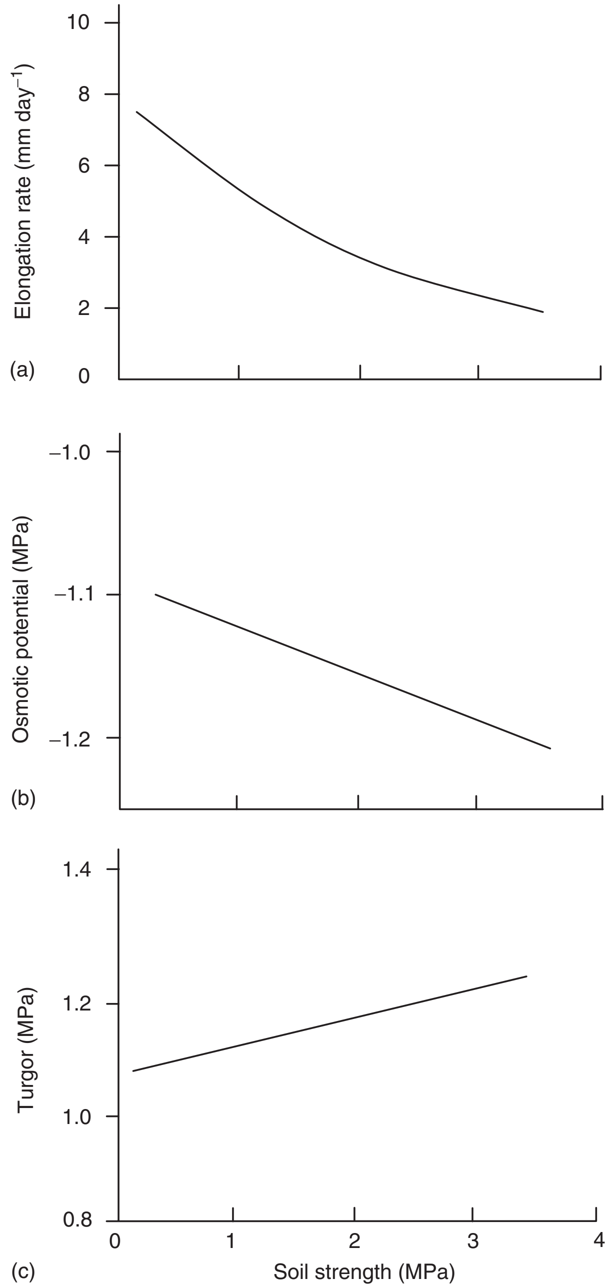


Figure 5 The effect of soil strength on (a) the rate of elongation of roots of radiata pine, (b) the osmotic potential of the cells in the root elongation zone, and (c) the turgor of the cells in the root elongation zone. Part (a) shows that the rate of root elongation decreases exponentially with increasing soil strength; (b) demonstrates that elongating cells reduce their osmotic potential (osmoregulation) in response to increasing soil strength which results in an increase in turgor (c) which can compensate in part for the increasing mechanical impedance of the soil. Adapted with permission from Zou C, Sands R, and Sun O (2000) *Tree Physiology* 20: 1205–1207.

consequently to overcultivate in order to be sure that an effect is realized. Thus knowledge of root physiology can assist the silviculturalist in making a more informed decision.

Process-Based Models: A Synthesis and Conclusion

There has been considerable effort in recent years to inform silviculture through process-based models. These are complementing and extending the use of empirical models. Empirical models can only be used to predict growth for the sites, environments, and conditions on which they are based, i.e., they are site specific.

Physiological relationships of the type described in this article form the basis of process-based models that can describe forest growth. These models are ‘process-based’ because growth is predicted from a knowledge of how physiological processes respond to environment and to silviculture. The advantage of these models is that they can be used across a range of environments where a species is grown although the parameters of the model, for example light-saturated photosynthesis or resistance to uptake of water by roots, may change with species. These models are becoming very sophisticated and dynamic such that they can now be used for predicting responses to silviculture and growth in future rotations based on an understanding of the resources used to support the current rotation.

The lines of communication between physiologists and silviculturalists have been improved but there is still a long way to go. It is essential that Schools of Forestry teach tree physiology in order for silviculturalists to be able to communicate with physiologists. It is perhaps equally important that silviculture be taught as applied environmental ecophysiology in an economic and social context.

Further Reading

Atwell B, Kriedemann P, and Turnbull C (eds) (1999) *Plants in Action*. South Yarra, Australia: Macmillan Education Australia.

Grossnickle SC (2000) *Ecophysiology of Northern Spruce Species: The Performance of Planted Seedlings*. Ottawa, Canada: NRC Research Press.

Hall DO, Scurlock JMO, Bolhàr-Nordenkampf H, Leegood RC, Long SP (eds) (1993) *Photosynthesis and Production in a Changing Environment: A Field and Laboratory Manual*. London: Chapman & Hall.

Kramer PJ and Boyer JS (1995) *Water Relations of Plants and Soils*. London: Academic Press.

Lambers H, Chapin FS III (1998) *Plant Physiological Ecology*. New York: Springer-Verlag.

Nambiar EKS and Brown AG (eds) (1997) *Management of Soil, Nutrients and Water in Tropical Plantation Forests*. ACIAR Monograph no. 43. Canberra, Australia: ACIAR.

Schulze ED and Caldwell MM (eds) (1993) *Ecophysiology of Photosynthesis*. New York: Springer-Verlag.

Taiz L and Zieger E (1998) *Plant Physiology*. Sunderland, MA: Sinauer Associates.

A Whole Tree Perspective

T M Hinckley, University of Washington, Seattle, WA, USA

Introduction

Trees are spectacular organisms (**Figure 1**); they can accumulate an incredible amount of biomass, they can live for long times, they can grow in extraordinarily stressful environments, they are globally important because of their historic roles in providing fuel and fiber and their more recent and emerging roles in providing chemicals including pharmaceuticals, providing habitat for a diverse array of organisms, and sequestering carbon. Although any organism is the sum of its parts, changes in the function of a part (e.g., leaf herbivory as the result of an insect outbreak) are not always reflected in changes in the whole organism (i.e., a scaling issue). As a consequence, knowledge about the growth, development, functioning, and morphology of the parts enables one to understand the mechanisms behind how a tree grows, develops, functions, and, ultimately, appears, but this knowledge alone often fails to predict accurately the response of the whole organism (i.e., issues of scaling and context). Therefore, an article focusing on the integrated whole organism has merit. Other articles in this Encyclopedia have either viewed a part of the whole tree or a particular process or property of the tree. In contrast, this article will take an integrated approach and focus on the entire tree.

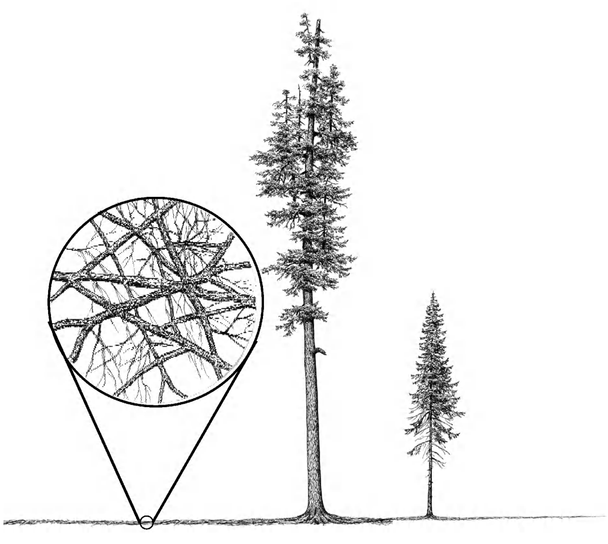


Figure 1 Two *Pseudotsuga menziesii* trees, one an old-growth, the other 80 years old, are shown with their 'root' systems. Emphasized in this drawing is the change in crown complexity, as well as size, with age and the horizontal and interconnected extent of the root systems. Drawn by Dr Robert Van Pelt.

Five topics will be developed here. First, the nature and definition of the individual organism will be explored. Second, the current status of understanding at the whole organism level about one of several key physiological processes associated with carbon, water, and nutrient acquisition and their use will be presented. Third, 'perception' of internal and external changes, and then the transmission and 'interpretation' of this 'perception' are critical for tree survival. The whole area of biophysical and biochemical signaling has become a major topic and research area at the tissue and cell levels of biological organization – what is known at higher levels? Fourth, there are a number of scaling issues that need additional discussion; for example, over the last 10 to 15 years, branches have been defined as an appropriate, intermediate scale of biological organization for the study of large, complex trees – there may be significant weaknesses in this assumption. Fifth and finally, major human social and cultural development was set in motion between 8000 and 10 000 years ago by the domestication of a few critical crop species and now we are totally dependent upon these. Over this same period of time, comparatively little genetic selection has occurred with forest trees. Because of advances in molecular biology and genetics, opportunities to domesticate trees over vastly shorter time scales are now possible.

Definition of the Whole Tree

The whole tree (i.e., the organism) might be defined as a system of relatively fine organs (i.e., foliage and fine roots) acquiring resources (i.e., carbon, nutrients, and water) then linked via a coarser system of roots, stems, and branches to create a particular form. Architectural form, trade-offs between structure and function, and optimization of carbon 'investment' in the construction and maintenance of support and transport tissue vs. tissue involved in resource acquisition are widely discussed in the literature. Therefore, the visible form that a tree takes is the result of architectural and process rules (i.e., the hardwired or genetic component) and their interplay over time with the combined abiotic and biotic environment. This interplay has been examined in a number of ways: (1) efforts to seek general rules of form and function, (2) documentation under natural and experimental conditions of changes in form and function with abrupt changes in the environment, (3) common garden studies involving many different genotypes and at least two very different 'gardens,' and (4), most recently, the use of a wide range of molecular tools. Emerging from these studies are a number of generalizations. First, trees, within a prescribed genetic framework, respond to a set of environmental conditions and this response can be described morphologically (e.g., sun–shade), physiologically (e.g., quantum efficiency), and allometrically (e.g., root:shoot ratio). Second, trees, in contrast to most plants and animals, may harbor tremendous genetic variation (however, it is not certain whether this translates to higher levels of adaptive genetic variation). Third, the individual tree often has a very large capacity to acclimate to new or different environmental conditions. Fourth, large differences in morphology or function between one genotype and another may be due to only a few genes; unfortunately, there is insufficient evidence at present for this to be unequivocal.

Trees are large, sessile organisms capable of long life and capable of living in extraordinarily diverse environments. These attributes place special restrictions on the form and function of trees. The desiccation properties of woody angiosperms and gymnosperms versus other photosynthesizing plants have been compared and a major difference in the two groups' ability to tolerate or function at low water potentials was noted. The inability of woody angiosperms and gymnosperms to tolerate low water potentials means that water loss must be strongly (and rapidly) regulated. How then do stomata 80 m from the root system perceive decreases in soil water potential (or cessation of root growth)? In addition, competition for resources, particularly light, has favored two very different life history traits and these are often found together in the same organism. Height growth, whether to gain competitive advantages for light or reproduction or both, means that transporting resources becomes increasingly difficult and, as trees become taller and bigger, potentially carbon maintenance costs increase. Finally, as a result of increases in tree height, foliage is always being added at the top (i.e., in relatively high light environments) and lost at the bottom (i.e., in low light environments). In sum, a tree's response to competition is carbon-costly and mechanically risky and, therefore, establishes one of the first goals of domestication; that is the elimination of continuous height growth (discussed below).

Although the aboveground portion of one tree can be readily and visually separated from another tree, where one organism stops belowground and another begins is not clear. Root grafts, known for a long time, represent one means by which one organism and another may be connected positively (resources) and negatively (disease). However, belowground connections may be far more complex and extensive – evidence suggests that mycorrhizal roots of an individual of one species are connected with other individuals of the same species. In fact, mycorrhizal roots of one species may be connected to another species. For example, in 1997, Simard and others found that stable ^{13}C moves from the deciduous hardwood *Betula papyrifera* to the evergreen conifer *Pseudotsuga menziesii* and vice versa via a common, interconnected ecto-mycorrhizal species. These experiments indicated that belowground carbon sharing is of sufficient magnitude that it may help ensure the coexistence of these two species in mixed communities.

More recent work using radioactive ^{14}C demonstrated bidirectional carbon exchange, depending upon phenological state, between the spring ephemeral *Erythronium americanum* and sugar maple (*Acer saccharum)* saplings via the mycelium of arbuscular mycorrhizal (AM) fungi. It was also noted that the exchange via the AM fungi was specific because there was no uptake of ^{14}C in associated yellow birches (*Betula alleghaniensis*) (an ecto-mycorrhizal tree species). Such studies illustrate how, via interconnected AM or ecto-mycorrhizae, individuals of the same species and of different species can positively influence each other. Implied then is that the absence of this connection could negatively affect the remaining organism – this suggests that the individual's performance is more than the combination of its genetic background and the environment or that the definition of either the 'individual' or the 'environment' must be made more comprehensive.

Fungal endophytes are fungi growing asymptomatically on stems and leaves. They have been found in every species of plant examined to date, including marine macroalgae, mosses, ferns, 'gymnosperms,' and herbaceous and woody angiosperms. Research more than two decades old on species-specific endophytes and the 'extended phenotype' in grasses has demonstrated the close relatedness of this mutualism where the endophytic fungi lives on the host species and, as a consequence, deters herbivores and enhances the physiology of the host. For several species of grass, the endophytic relationship may be necessary for survival. In a 2002 study of *Dichanthelium lanuginosum* plants from geothermal soils in Lassen Volcanic and Yellowstone National Parks, Redman and others noted that the beneficial effect of a fungal symbiosis increased with soil temperatures. In contrast to grasses, the newly discovered relationship between endophytes and trees is different – many endophytic species coexist on leaves and stems, they are highly diverse within and among host, they are transmitted horizontally (vs. within the seed or clonally) and they may not defend the host against herbivores. However in spite of the uncertainty about whether tree endophytes provide benefits to the host or not, a number of researchers are beginning to examine both natural and genetically engineered endophytic relationships with host trees (e.g., white pine blister rust and *Pinus monticola* and *P. albicaulis*). If fungal diversity mimics the noted enormous diversity of prokaryotic organisms both above and below ground, then there could be several important consequences to our consideration of the organism (and, therefore, groups of organisms in stands, communities, or ecosystems). First, it may be, except under experimental conditions, difficult to study the individual organism separated from its associated microflora. As a consequence, we have an 'extended phenotype' to consider. Second, because evolutionary change occurs rather slowly in long-lived organisms, evolutionary changes in the associated microflora may play a significant role in 'assisting' the host organism to deal with, for example, historical and projected climate change. Third, any consideration of domestication must also consider opportunities with the associated or introduced microflora. As this section concludes, our definition of the whole organism has been greatly extended. In addition, we have seen how trees, perhaps because of their size and longevity, may have temporally and spatially a vastly more diverse and complex relationship with other organisms.

Key Structural–Functional Relationships

A number of important structural–functional relationships might be presented (e.g., carbon allocation, crown and root architecture, and hydraulic architecture). It is important to note that these can be treated as separate topics; however, they must be ultimately integrated when considering the whole organism. Although all three of these have been extensively covered elsewhere (*see* **Tree Physiology**: Canopy Processes; Nutritional Physiology of Trees; Shoot Growth and Canopy Development), I have chosen plant hydraulic architecture both because of personal interest, but also because it provides clear evidence of structural–functional integration that spans from fractions of a minute to the lifetime of the tree and because it is a subject that supports and links well with subsequent sections.

Plant Hydraulic Architecture

Hydraulic architecture has been for the last 25 years and is still a dominant theme in plant and tree water relations. In a recent comparison of leaf-specific hydraulic conductance to transpiration or whole-plant hydraulic conductance to plant leaf area over vastly different life-forms, strong support was found for function–structure integration. Further, it was suggested that there is considerable flexibility in these relationships depending upon the availability of resources. In a very careful analysis of the water conducting system in *Laurus azorica* trees, it was found that there was a strong relationship between petiole hydraulic conductivity and whole tree or stand transpiration; however, it was noted that stem hydraulic capacity exceeded actual water movement by almost a factor of 45. This could perhaps be a safety feature where the stem can transport all the water needed using only a small fraction of its vessels – the remaining vessels may serve in a capacitance role. Somewhat similar results were found when the hydraulic conductances of fine and coarse roots of *Prunus* were compared: coarse root capacity was not the limiting factor.

Hydraulic redistribution of water within the root system is now well documented. Perhaps even more noteworthy have been the recent observations on giant, coastal *Sequoia sempervirens* trees. Unlike work published on large, old-growth *P. menziesii* that demonstrated a considerable lag between xylem water movement at 50 m vs. 2 m, the new observations indicate no lags and even reverse flow where the source of water is either from dew on the foliage or from pools of water in large branch crotches. The presence of roots in these pools means that the hydraulic gradient to the foliage should be thought of in terms of meters vs. tens of meters. Clear, general structural–functional relationships with regard to tree hydraulic properties may exist, but considerable variability appears also to occur. Although the quantitative nature of science tends to focus on means and patterns, variation and outliers may be equally important to understand and document.

Integration also implies that the water system within a tree forms an integrated network; however, a number of investigations of insect activity and herbivory within the crown of trees suggest otherwise. In addition to clear within-plant heterogeneity in growth, morphology, and chemistry, due to differences in tissue age, light availability, or previous damage by herbivores, some of these studies indicated that heterogeneity originated in the soil environment (experimentally demonstrated via split-root studies) and can be modulated or accentuated by the pattern of water transport (e.g., sectoral vs. nonsectoral). Hydraulic architecture provides a wonderful framework to understand tree function and structure; however, large gaps in our understanding of how the entire system might be integrated (e.g., reconciling the segmentation theory to the limiting role that root xylem hydraulic conductivity plays or cavitation as an early warning system vs. a source of water or refilling as a diurnal vs. seasonal process) still exist.

Signaling

Because of the massive size of trees and the lack of a central nervous system, long-distance communication would seem to be both critical and mechanistically interesting. For example, sudden damage to the root system or rapid changes in soil oxygen, temperature, or moisture could have a profound effect on water supply. Because water loss is only regulated at the stomatal-leaf level, until stomata were to close, a 5-m or 65-m tree would continue to lose water and would soon reach critical leaf and xylem water potentials. During a typical day, leaf water potentials decline to near critical, but rarely less than critical levels. That is, a tree functions near the point of catastrophic xylem failure (i.e., runaway cavitation). Critical leaf water potentials have long been known to cause stomatal closure; however, this might be a case of 'too little – too late.' Without adequate short- and long-distance 'communication,' xylem water potential could easily exceed this critical point.

For a long time, plant growth substances (or regulators or hormones) have been recognized as important controls over plant growth and function, including stomatal control. The timing of the onset and cessation of growth and dormancy, for example, appears to be under a number of different controls. Changes from juvenile to mature, the onset of reproductive activity, and reproductive activity itself are under strong control. Plant form, as manifested by apical dominance and apical control, is controlled by plant growth substances. Watching the initiation and spread of vegetative growth in the crown of a tree would certainly suggest that various chemicals, transported in the xylem or phloem, could be largely responsible. Herbaceous plants, tree seedlings, and tree saplings have all been shown to transport various substances (e.g., K^+, Ca^{++}, abscisic acid (ABA), and zeatin riboside (i.e., a cytokinin)) from the root to the shoot in response to changes in the rhizosphere. Flooding, root damage, and cessation of root growth due to temperature or compaction have all been shown to elicit a group of growth inhibitors (e.g., increases in ABA) and suppress growth promoters (e.g., cytokinins) – these then result in stomatal closure and cessation of leaf growth. The response of trees to wounding suggests that wound-induced (win) mRNAs are transmitted in the same manner and direction as currently produced photosynthates (e.g., acropetally in leaves and branches near the apex of the tree, both acropetally and basipetally in leaves and branches found in mid positions, and largely basipetally in lower leaves or branches). Clearly, biochemical messages or signals can be moved in both the phloem and xylem; however, their movement, except in ring-porous species, will be relatively slow (less than 8 m and $1\,\mathrm{m\,h^{-1}}$ for diffuse-porous and gymnosperms, respectively).

Present opinion is that long-distance transport of a biochemical message would be too slow to provide timely stomatal closure in *Pinus sylvestris*. There is limited (controversial and shaky) evidence that small changes in water potential, due to a few cavitation events, may be propagated close to the speed of sound within the microfibrils of the cell wall – this biophysical message then results in the release of Ca^{++} or ABA at the stomata. Even studies of herbaceous plants such as *Ricinus communis* have suggested that initial changes in stomatal conductance were not due to ABA transport from the roots to the foliage, but due to changes in root hydraulic conductivity. Unfortunately for large trees, the transmission of gradual changes in root hydraulic conductivity is likely not fast enough to cause stomatal closure and avoidance of runaway cavitation. Evidence, albeit again controversial, has been provided for very rapid responses in large (35 m plus) *Nothofagus* trees in New Zealand. Therefore, there is limited evidence for a mechanism for rapid signaling within a large tree; however, as attractive as this might be, there is still too little evidence.

Over relatively short distances (i.e., within a cell, between cells, and even within a tissue), there has been a recent explosion in information on signaling. Whether one is reviewing an organ or a whole organism level study of plant growth substances and their role, one is impressed with the difficulty of elucidating mechanism and particular an integrated, *in situ* view of biophysical and biochemical mechanisms responsible for signaling. What is needed is an understanding of rapid, long-distance signaling in very large trees.

Scaling

The ecological and physiological literature is filled with studies from 0.1-ha plots or from chloroplasts or leaves and then extrapolated and discussed at much larger scales. The process of scaling has been discussed, reviewed and used extensively. Because of this article's focus on the organism and the comments under the section on the definition of the organism, it is worth reviewing an important point and presenting some current aspects of scaling that might be useful to take from this article. For me, what continues to be an important lesson of scaling is the following observation. One should always be concerned with three scales in any study. The scale below that of the study provides an understanding of mechanism and the scale above that of the study provides the context – for our present purpose, the parts of the tree are critical for mechanism and the stand (or population), community, and ecosystem are critical for context.

Scaling in physiological ecology appears to focus on a number of specific issues. First, can one scale one's readings at, for example, the leaf level to the whole tree. Second, scaling from a seedling to a tree involves understanding how morphology and process change with stage of development. Finally, for large, complex organisms, is it possible to use an intermediate scale (i.e., between the leaf and the tree) for study and, therefore, scaling? The branch has become a favorite example of this latter issue. Recent research has highlighted ways in which branch autonomy may fail and, therefore, the reliance on branches as an intermediate step in scaling may also fail.

Of the diversity of different invasive and noninvasive techniques that have emerged over the last two decades, perhaps the use of stable isotopes has proven the most useful for whole plant studies of (1) carbon allocation and movement within an individual, from parent to offspring via seed, between individuals, and within ecosystem(s), and (2) water movement. Techniques to measure water flow, especially those that can be used to develop depth profiles and can detect both zero flow and flow in either direction, have also been invaluable in an understanding of the parts and the whole.

Domestication

Around 10 000 years ago, people living in the Fertile Crescent (in what is now the Middle East) began to rely increasingly on domesticated grains such as rye. Domesticated corn appeared about 9000 years ago in Mexico and rice in China around 8000 years ago. These events had a profound influence on humans. As an increasing number of crops (and animals) became domesticated, there was a transformation from hunting and gathering to agricultural cultivation and associated settlements. In terms of social evolution, this was extraordinary. Today, we recognize the absolute dependence of most human societies (and all developed societies) on domesticated crops and animals. For plants, we also understand the genetic changes linked to domestication. There appear to have been three features associated with the domestication of most crop plants: (1) there was a radical transformation of the wild plant in terms of structure and function (often the domesticated plant shows little or no resemblance to the original progenitor), (2) this transformation typically involved a few key mutations and these had huge effects, and (3) the initial transformations occurred very soon in the process, that is, they were rapid. It is important to note that the first mutation(s) associated with domestication were likely very rare and were probably noted because of either intensive observation (via gathering) or early cultivation. Since these first large steps, refinements using conventional breeding methods have come much more slowly, have represented much more subtle changes in structure and function, and have involved a greater number of genes.

Over this same period of time, why were trees not domesticated? A number of reasons may exist for this and they include: the relatively long generation cycle in trees, the lack of edible products from most trees, the high inherent genetic and phenotypic variability within populations and between populations of trees, and the difficulty of both observing and capturing useful mutations. Clearly some selection and partial domestication has occurred (e.g., *Olea europea* and *Pinus caribaea*); however, in comparison to say the domestication of corn, trees are still analogous to the original teosinte.

Having this background and now having the platform provided by molecular biology and genetics, it should be possible to domesticate trees. What specific attributes might one seek? The following is a potential list:

1. A high rate of biomass accumulation.
2. Strong apical control (i.e., a single axis).
3. A narrow, confined crown with minimal branching.
4. Maximum light interception by the foliage and high quantum use efficiencies.
5. Apical meristems, buds, or shoots insensitive to the presence of neighboring trees (i.e., competition insensitive).
6. Reduced height growth after some initial, rapid minimal gain in height (i.e., a platform on which biomass is added).
7. Greater carbon allocation to the stem.
8. No reproductive activity (unless elicited).
9. Low cell lignin content.
10. No 'juvenile' stemwood (assumes the stem is the site of biomass accumulation).
11. More efficient resource acquisition especially by roots and associated microflora.

Many of these, as happened with crop domestication, represent dramatic changes in the structure of a tree and how that structure functions. Our ability to visualize this 'new' tree is extraordinarily difficult as we are so used to incremental changes. Modeling, including the use of 'virtual plants,' offers one approach. However, there are large segments of society who, for one reason or another, will find such a transformation of a tree unacceptable. Relying on either conventional silviculture or further increases in a CO_2 fertilizing effect to meet future fiber and fuel needs may not be realistic. Given continued population growth, increased consumption, the relatively low carbon costs of using wood and wood products (vs. other products for construction, for heating, for chemicals), it would seem unwise not to explore this opportunity. Had the same constraints been placed on the original progenitors for our current agricultural crops, I would not be writing and you would not be reading.

Summary and Conclusions

Understanding how the whole organism functions, and that it is not merely the sum of its parts, that it can be represented as an 'extended phenotype,' and that an untapped potential for change in its phenotype exists are the key messages developed within this article. It is also clear that there are very large unknowns: what are the controls on age- and size-related declines in productivity, how is 'information' transmitted through an organism, and how is transport in the phloem and the xylem controlled and integrated? Finally, what changes in structure and function would accompany domestication and how does our current understanding of whole tree physiology aid or impede domestication?

See also: **Ecology**: Forest Canopies. **Environment**: Carbon Cycle. **Hydrology**: Hydrological Cycle. **Soil Biology and Tree Growth**: Tree Roots and their Interaction with Soil. **Tree Physiology**: Canopy Processes; Mycorrhizae; Nutritional Physiology of Trees; Physiology and Silviculture; Root System Physiology; Shoot Growth and Canopy Development; Stress; Tropical Tree Seed Physiology; Xylem Physiology.

Further Reading

Cermák J, Jiménez MS, González-Rodríguez AM, and Morales D (2002) Laurel forests in Tenerife, Canary Islands: II. Efficiency of the water conducting system in *Laurus azonica* trees. *Trees* 16: 538–546.

Dawson TE, Mambelli S, Plamboeck AH, Templer PH, and Tu KP (2002) Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33: 507–559.

Jackson MB (2002) Long-distance signaling from roots to shoots assessed: the flooding story. *Journal of Experimental Botany* 53L: 175–181.

Köstner BMM, Schulze E-D, Kelliher FM, *et al.* (1992) Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy-correlation measurements. *Oecologia* 91: 350–359.

Lerat S, Gauci R, Catford JG, *et al.* (2002) C-14 transfer between the spring ephemeral *Erythronium americanum* and sugar maple saplings via arbuscular mycorrhizal fungi in natural stands. *Oecologia* 132: 181–187.

Mencuccini M (2003) The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. *Plant, Cell and Environment* 26: 163–182.

Mitton JB (2003) The union of ecology and evolution: extended phenotypes and community genetics. *BioScience* 53: 208–209.

Perks MP, Irvine J, and Grace J (2002) Canopy stomatal conductance and xylem sap abscisic acid (ABA) in mature Scots pine during a gradually imposed drought. *Tree Physiology* 22: 877–883.

Redman RS, Sheehan KB, Stout RG, *et al.* (2002) Thermotolerance generated by plant/fungal symbiosis. *Science* 298: 1581.

Simard SW, Perry DA, Jones MD, *et al.* (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388: 579–582.

Sprugel DG (2002) When branch autonomy fails: Milton's Law of resource availability and allocation. *Tree Physiology* 22: 1119–1124.

Tyree MT and Zimmermann MH (2003) *Xylem Structure and the Ascent of Sap*. Berlin, Germany: Springer-Verlag.

Xylem Physiology

J R Barnett, University of Reading, Reading, UK

Introduction

Secondary xylem, or wood, is a product of the activity of a secondary meristem, the vascular cambium. Those plants which possess one can be very long-lived, their life span being only limited by catastrophic events such as gales and lightning strikes or disease. More wood is added each season, with the result that it is the most abundant natural product on earth. The cambium and xylem differentiation have been the subjects of a number of monographs and it is not the purpose of this chapter to précis these works. Rather, some important aspects of the way the structure of wood is related to its behavior and properties postdifferentiation will be considered. Only a brief overview can be presented here and the reader is recommended to the list of further reading for more comprehensive reviews.

The structure of wood differs between tree species as a result of local evolutionary pressures and each has its own wood properties. This was exploited intuitively early in human history and is one of the factors that make wood such a variable and useful raw material. The long life span and generation times of trees meant that many also developed the ability to survive the significant changes in environmental conditions which occur from time to time. This is evidenced by the fact that arboreta, botanic and private gardens, city parks, and streets are furnished with tree species which evolved in regions whose climate and range of day lengths were markedly different from those in which they are now growing successfully. Sometimes the trees are more successful in terms of growth in an alien environment than in their native home. *Pinus radiata*, a native of the Monterey peninsula, where it is slow-growing and of poor form (from a forester's viewpoint), has become the linchpin of the New Zealand forest industry, where it is fast-growing and of good form (*see* **Tree Breeding, Practices**: *Pinus radiata* Genetics).

The evolutionary process has thus resulted in selection of trees which may be considered overdesigned for survival in their environment as it is today. A 500-year-old oak tree growing in the UK will have experienced the mini ice ages of the seventeenth and nineteenth centuries, and periods of global warming in between. It is often only when trees are growing at the limits of their geographical range where environmental conditions are limiting that the value of some morphological and anatomical adaptations can be understood.

The Biological Functions of Wood

Wood has two major functions: firstly, to support the crown of the tree, enabling the leaves to compete for light, and secondly, to provide a conduit for water and nutrients between the roots and the crown. It also incidentally supports the phloem which comprises the inner bark and conducts nutrients from the leaves to other parts of the tree. As the crown moves higher and enlarges, the stem must thicken to support the extra mass. Eventually the wood at the base of the stem may support hundreds of tonnes. The wood must also be able to maintain the tree stem in a vertical posture, and the branches at appropriate angles, while being able to absorb any physical stresses imposed by the environment without breaking.

Wood also has to conduct water efficiently and safely in conditions which may vary from extreme drought to flooding or freezing. In some cases, different species have adopted different anatomical strategies to cope with similar environmental conditions. Scots pine and silver birch live side by side in the boreal forests of Scandinavia and northern Europe, yet their wood anatomies are quite different. However, their strategies for coping with winter drought and freezing conditions are equally successful.

If wood were simply dead material it would be unable to deal with many of the stresses encountered by the tree during its life. In fact, the wood of young trees and the outer or sapwood of older trees may contain as much as 50% of living parenchyma cells. These cells have been regarded as being mainly for storage and, in the case of rays, for radial transport of water and raw materials. As will be described below, however, they are also involved in defense and in controlling water movement. Wood is thus far more active in its own interests than appears at first sight.

The Cellular Structure of Wood

The anatomy of wood has been amply documented in the literature. It is made up of two cellular systems, the axial system, responsible for structural support and vertical water movement, and the ray system, which provides a pathway for radial movement of water, nutrients, and other materials. A few woody species, for example, members of the genus *Hebe*, lack rays, but this is comparatively unusual. The wood anatomy of coniferous trees (gymnosperms) is fundamentally different from that of broadleaved trees (angiosperms) in that the axial system comprises a single cell type, the tracheid, which is responsible for both support and water conduction (**Figures 1** and **2**). Angiosperms have evolved a system in which the water-conducting elements are aligned to form tubes (vessels). These are interspersed among other cell types, predominantly fibers and parenchyma cells (**Figures 3** and **4**). There are a few exceptions to this in primitive families such as the Winteraceae, Pseudowinteraceae, and Trochodendraceae, which have an anatomical structure superficially similar to that of gymnosperms.

Vessel Distribution and Function

The wood of angiosperms is commonly classified into two types based on the distribution of vessels. In the diffuse-porous type, vessels have a more or less uniform diameter across an annual ring and are dispersed more or less evenly throughout the wood (**Figure 3**). In the ring-porous type, large-diameter

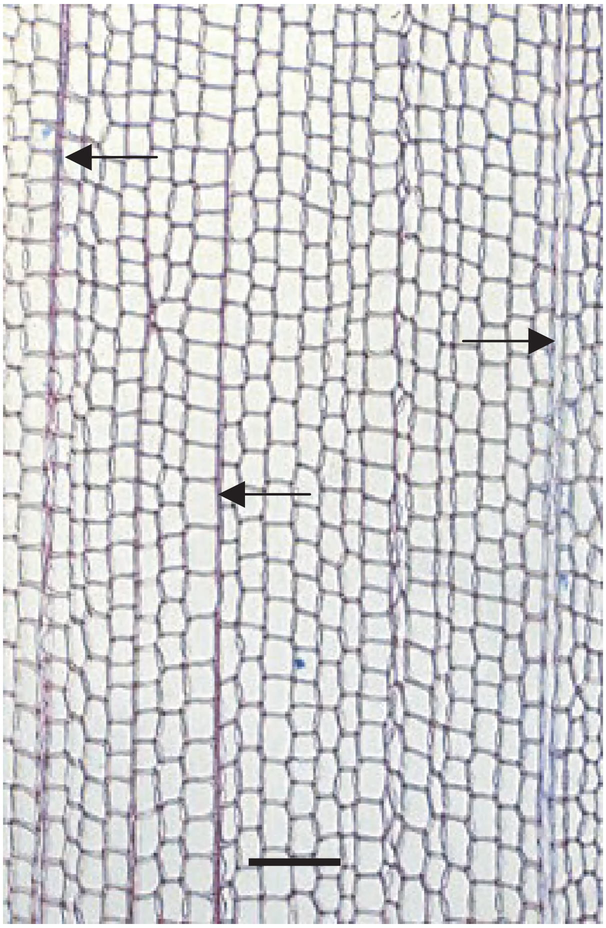


Figure 1 Transverse section through earlywood of *Pinus sylvestris*. The axial elements are all of one type (tracheids), giving the wood a homogeneous appearance. Rays are visible running at right angles to the long axis of the tracheids (arrows). Scale bar = 100 μm.

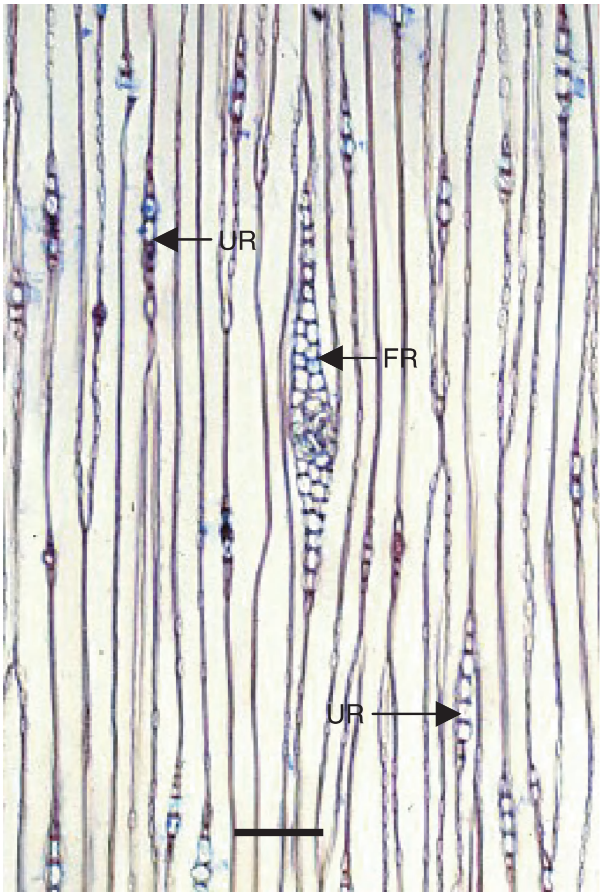


Figure 2 Tangential longitudinal section through earlywood of *Pinus sylvestris*. The tracheids are longer than the section, although a few ends may be seen. The cut ends of uniseriate rays (UR) and a large fusiform ray (FR) can also be seen. Scale bar = 100 μm.

vessels, often visible to the naked eye, are formed in spring at the beginning of the growing season while smaller vessels are formed during the main period of growth (**Figures 5** and **6**).

Hydraulic Conductivity and Safety

The size and arrangement of vessel elements have evolved to optimize hydraulic conductivity. Ring-porous species conduct water in sufficient quantities to supply the needs of the crown through their outermost growth ring. They are able to do this because the diameter of their springwood vessels is large. Since the conductivity of a tube is proportional to the fourth power of its radius (Poiseuille's law), a ring-porous species such as *Quercus robur* in which earlywood vessels typically have a diameter of 400–500 μm is theoretically 625 times more efficient than a vessel in a diffuse-porous species like *Liquidambar styraciflua*, in which vessel diameter is 80–100 μm, and 10 000 times more efficient than a tracheid in a conifer with a diameter of 40–50 μm. Diffuse-porous species and gymnosperms therefore require far more actively conducting elements than ring-porous species and conduct water through several of their outer growth rings. The situation is more complex than this, however. While oak vessels can be considered as relatively unobstructed pipes whose simple perforation plates hardly obtrude into the lumen of the vessel, they have finite length and closed ends. This means that water has to move to adjoining and overlapping vessels through the membranes of the numerous pits between them. Conductivity may also be restricted in some species by the presence of scalariform, reticulate or foraminate perforation plates between the cells which make up the vessels. Measurements have shown that in vessels of *Betula pubescens* axial conductivity is about a third of that in an unobstructed capillary.

In gaining an advantage in terms of efficiency, ring-porous trees have compromised their hydraulic

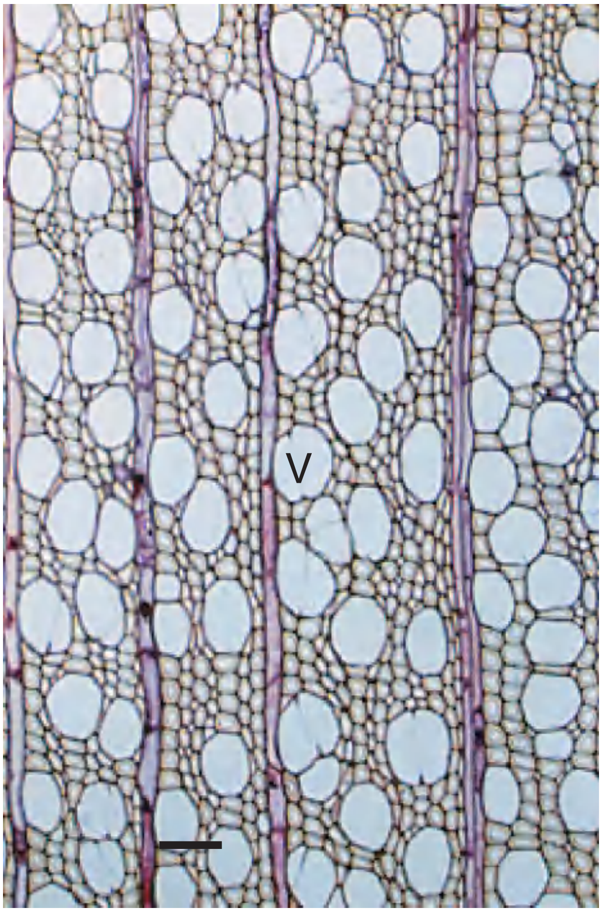


Figure 3 Transverse section through wood of *Liquidambar styraciflua*. Water-conducting vessels (V) are interspersed among smaller-diameter fibres and parenchyma. Scale bar = 100 μm.

Figure 4 Tangential longitudinal section through wood of *Liquidambar styraciflua*. The cut ends of rays are seen interspersed among the fibers and vessels (arrows). The vessels (V) contain some tyloses (T). Scale bar = 100 μm.

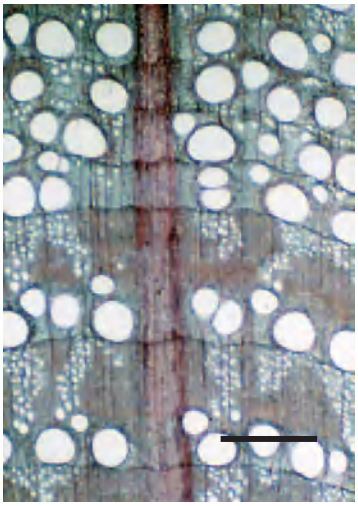


Figure 5 Low magnification of a transverse section through wood of *Quercus robur*. The ring-porous nature of the wood is clearly seen in the two growth rings at the bottom of the figure. At the top, the ring width in four successive years has been reduced by adverse growing conditions. Although the large springwood vessels have been produced in each year, the summer wood is much reduced. Scale bar = 1 mm.

safety. Damage to a single vessel is much more serious than damage to a single vessel in a diffuse-porous species. This was clearly demonstrated in the case of Dutch elm disease, in which the tree responded to a toxin secreted by the fungal pathogen *Ceratocystis ulmi* by forming tyloses in its vessels, blocking them and starving the crown of water.

In diffuse-porous species, the diameter of vessels increases markedly from juvenile to mature wood and from the top of the tree towards the base in any growth ring. As vessel diameter increases, their number per unit area of cross-section decreases (**Figure** 7). An explanation for this lies in the fact that, as the tree grows, there is a need for a larger proportion of fibers for support. To accommodate this while maintaining water flow to the larger crown, the tree produces fewer vessels of larger diameter.

Calculations using Poiseuille's relationship and compensating for the reduced area occupied by vessel elements suggest that the wood in outer growth rings in *Betula* has a conductivity three to

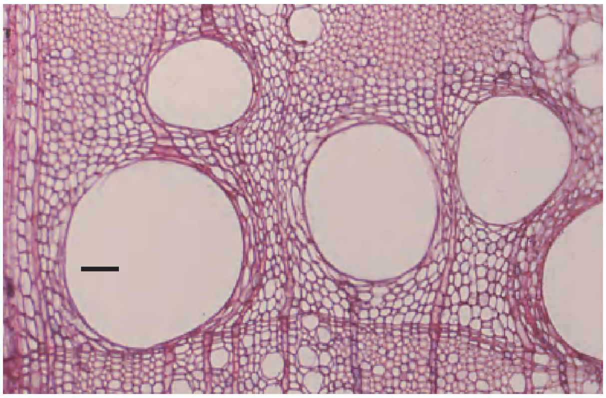


Figure 6 Greater magnification of springwood in *Quercus robur* showing the large diameter of earlywood vessels. Small-diameter latewood vessels are visible at the end of the previous year's growth (bottom of the micrograph) and at the beginning of the summerwood (top of the micrograph). Scale bar = 100 μm.

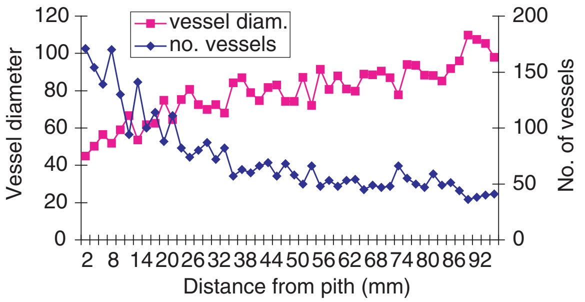


Figure 7 Number of vessels per mm^2 and vessel diameter in *Betula pendula* plotted against distance from the pith. There is a clear inverse relationship between vessel number and diameter.

five times greater than that in the innermost growth rings. The real difference is probably less than this owing to the restrictions on movement imposed by scalariform perforation plates and pit membranes, although the effect of this would be the same for all vessels, regardless of diameter.

Freezing

Trees in boreal regions must be adapted to cope with low winter temperatures which may freeze the water in their conducting elements. During freezing, air comes out of solution and forms small bubbles which in vessels or tracheids of trees will necessarily be small, and provided the water thaws before the sapstream goes into tension in spring, will be redissolved. If allowed to coalesce with other bubbles before redissolving, however, there is a possibility that embolisms could form. Scalariform perforation plates in the vessels of boreal angiosperms preclude this by preventing movement of small bubbles between vessel elements, while bordered pits do the same for conifer tracheids.

It has been suggested that, since conifers show almost no loss in xylem conductivity following freezing, the vesselless condition of the Winteraceae may in fact represent an evolution from a form possessing vessels. The loss of vessels and the return to a system of tracheids for water conduction enabled the retention of leaves and photosynthesis under freezing conditions.

Xylem Parenchyma

Students are often taught that wood is a dead structure resulting from terminal differentiation of cambial derivatives. As far as the sapwood is concerned, nothing could be further from the truth. In some species 50% or more may comprise living parenchyma. As parenchyma contributes little to the physical strength of wood, and is to some extent undesirable as fines in pulp, its functions in the wood have not been thoroughly investigated. It is, however, certain that it provides storage for materials such as starch and proteins, and secondary compounds such as tannins. It is also certain that it forms the pathway for transport of raw materials from the phloem to the cambium, its differentiating derivatives and developing heartwood. In the latter case they may also be involved in synthesis of the secondary compounds deposited in heartwood.

In addition to the axial parenchyma cells, the ray system is made up entirely of parenchyma cells in all but a few members of the Pinaceae, which also have ray tracheids. Individual parenchyma cells do not exist in isolation but all are interconnected by plasmodesmata, their protoplasts thus forming part of a great symplasm running throughout the living tissues of the tree. Recent work has shown that a system of microtubules and microfilaments, which is continuous with the system present in the axial parenchyma cells of the xylem and parenchyma cells and companion cells of the phloem, runs through the ray system via the plasmodesmata. In view of the known transport functions of these cytoskeletal components it is likely that they provide the system for moving materials around the developing and mature secondary tissues in the stem.

Parenchyma cells actively assist water movement, particularly when transpiration is not possible. Deciduous trees need to build up internal turgor to swell their buds and developing leaves in the spring. They do this by breaking down starch in their parenchyma cells and transferring the sugars to the lumens of adjacent vessels. This creates an osmotic potential, increasing internal pressure and providing turgor for growth. Humans have exploited this phenomenon in the collection of maple syrup and birch sap, both of which are collected in late winter before budbreak. It is a common misconception that the sugary solution is produced by the phloem, when in fact it is the wood which is tapped to obtain the liquid. Trees in cloud forest, where relative humidity may approach 100%, appear to use the same technique to move water when significant transpiration is not occurring, switching back to transpiration for this purpose and restoring starch levels when the relative humidity falls.

In addition to these functions, the parenchyma system plays a key part in protecting the tree from pathogen attack. Its role can range from blocking damaged vessels by producing tyloses to repairing small cavities caused by the activity of insect pathogens such as cambium miners or by removing bark by accidental damage or herbivore activity. It is also involved in creating barrier zones to resist the spread of decay fungi through the wood.

Tyloses

Tyloses form in some ring and diffuse porous species when embolisms arise in vessels either during drought or in response to wounding (**Figure 8a–d**). In normally conducting sapwood, the tendency for net water movement from vessels through pit membranes into adjoining living parenchyma cells by osmosis is countered by the tension in the sapstream. When the sapstream is broken, this balance is destroyed and there is a net osmotic flow of water into the parenchyma cells. The resulting pressure increase causes the pit membranes to swell into the vessel lumen (**Figure 8a**). To prevent rupture of the membrane, the protoplast actively consolidates the membrane and may even move into the tylosis thus formed. An individual tylosis takes on the appearance of a balloon blown into the vessel lumen (**Figure 8c**). More usually, however, numerous tyloses arise simultaneously from all or most of the vessel/parenchyma pit membranes in the vicinity (**Figure 8b**), resulting in a network of cell wall material which may become lignified, blocking the vessel (**Figure 8d**). The blocking of vessels in this way, while locally useful in preventing water loss and pathogen entry, may have fatal consequences for the tree, as in the case of Dutch elm disease.

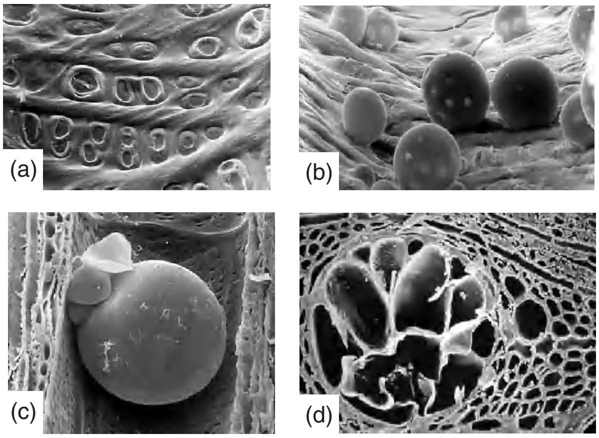


Figure 8 Stages in the formation of tyloses in *Quercus robur*. (a) Pit membranes beginning to bulge into the vessel lumen ($\times$350). (b) Young tyloses ($\times$250). (c) Older tyloses almost filling the cell lumen ($\times$80). (d) Multiple tyloses completely blocking the vessel ($\times$80).

Tylosis-like structures have been described as forming in *Fraxinus*, although these structures are not true tyloses. They are in fact formed by extrusion of material into the vessel lumen through the pit membrane from adjacent parenchyma cells. The membrane itself does not grow and bulge into the lumen as in the case of tyloses.

Callus Formation

It is only by having living parenchyma cells that the sapwood can respond to damage caused by phenomena such as branches breaking and removal of bark by herbivores. On release of the constraining pressures by which they are normally surrounded, parenchyma cells dedifferentiate to form callus which eventually differentiates, forming new periderm or meristematic tissues. The role of parenchyma in repairing the damage caused by mining insects is illustrated by the case of *Phytobia betulae* which lays its eggs below the bark on young shoots of *Betula pendula*. The larva tunnels downwards through the layer of cambium and young, differentiating xylem cells. The tunnels are repaired and blocked by the production of callus from xylem ray parenchyma and eventually the cambium itself is restored in the wounded region.

Defense Against Fungal Pathogens

In the case of fungal penetration into the xylem by wood-rotting fungi, the response to infection is the production of a discolored zone of sapwood known as a barrier zone in an attempt to restrict further penetration of the pathogen. Microscopy has shown that vessels in the sapwood in the discolored areas are blocked either by tyloses or by vessel plugs made up of fibrillar material and so-called accessory compounds. In *B. pendula*, the protective layer disintegrates following wounding and it is possible that it is incorporated into the fibrillar deposits extruded into the vessel lumen. These changes, however, are not a specific response to fungal invasion; they can also be induced by simple wounding and are a normal response in branch and stem tissue close to pruning wounds.

Some tree species defend themselves by exuding resins or gums, produced by and stored in parenchyma cells associated with resin canals or gum ducts. Wounding stimulates activity of parenchymatous cells which form the epithelium of these canals and ducts and large quantities of resin or gums are moved to the wounded surface. This prevents or inhibits the penetration of pathogens into the wood through the wound.

The Role of Fibers and Tracheids

The fibers of angiosperm wood and the tracheids of gymnosperm wood are the load-bearing cells in the tree, and are thus the main determinants of the properties of timber in use. In angiosperms the morphology of fibers shows a gradation from cells which are superficially similar to the tracheids of conifers (and which are consequently referred to as tracheids), to libriform fibers, which are shorter and have very little pitting. Intermediate cell types are usually referred to as fiber tracheids. Although these cells are normally dead, the conditions being experienced by the tree when they are formed affect the way the cell wall is laid down, adapting them to their role in helping the tree to survive.

Remarkably, but perhaps unsurprisingly, the structure of the secondary cell wall (apart from some variation in pit size and form) is similar in all of these cell types. The cellulose of secondary walls is laid down as lamellae of parallel cellulose microfibrils. In fibers and tracheids these are clearly arranged into three layers known as the S_1, S_2, and S_3 layers, with the suffixed numbers referring to the sequence in which the layers are laid down, the S_1 being the first-formed and therefore outermost layer, the S_3 being the last-formed and innermost layer. The S_1 and S_3 layers have microfibrils arranged at a large angle to the cell axis, while the S_2 microfibrils are arranged at a smaller angle. This structure explains the ability of the cell to withstand, without collapsing, vertical and lateral compressive forces, and in the case of tracheids which are conducting water, the internal tension, to which it is subjected. The angle of microfibrils in the S_2 layer is responsible for many of the physical properties of fibers and tracheids. In the center of a tree where the wood was formed when the cambium was young (juvenile or corewood), the microfibril angle is large (45° or more is not uncommon in conifers). In later-formed wood (mature or outerwood), the microfibril angle is small, typically less than 10°.

A large microfibril angle confers flexibility on the young stem, enabling it to withstand high winds without breaking, while the small microfibril angle in mature wood confers the stiffness needed by an older tree to support large weights. This has survival advantages for the living tree but creates problems in utilization, where juvenile wood is insufficiently stiff to be used for high-value purposes such as construction. This was of little consequence when old trees were harvested and the majority of the wood in the tree was mature. As demand for timber products and pulp has increased, so has pressure for short-rotation cropping of fast-growing trees. Harvesting trees at 35 years of age, for example, means that 50% or more of the tree may comprise juvenile wood and be of low commercial value. This has led to an upsurge of interest in microfibril angle and whether it can be reduced in juvenile wood. The consequences of reducing the juvenile wood microfibril angle for the living tree, where it may make it susceptible to breaking in the wind, will have to be borne in mind by breeders and molecular biologists in deciding how far it is possible to go along this route.

Most interest in microfibril angle has centered on coniferous trees. Measurements on silver birch, however, have suggested that in this species the large microfibril angles associated with corewood in pines are not present. In fact, the angle rarely exceeds 20° in any part of the trunk. Those results that have been reported for hardwood species such as eucalypts and *Liriodendron tulipifera* suggest that microfibril angle in hardwood fibers is lower than that in conifer tracheids. It may be that the presence of vessels interspersed among fibers in a hardwood confers flexibility on the young stem that has to be countered by a smaller microfibril angle in the fibers.

In addition to cellulose, lignin has a major role in increasing the compressive strength of fibers and tracheids, typically comprising some 20% of the walls of fibers in angiosperms and 35% of the walls of tracheids in gymnosperms. It is laid down between the cellulose microfibrils to which it is bound by hemicelluloses. Without the evolution of lignification, trees could not have evolved as tall, massive organisms. Lignin is, however, a major problem for the paper industry where its removal in order to separate fibers and enable production of bright, white paper is expensive. Disposal of the extracted lignin also poses major problems. Genetic modification has been explored as a way of solving these problems, although the essential role of lignin in the successful life of trees means that improvement will have to be limited to producing trees whose lignin is easier to remove, rather than trees without lignin.

Reaction Wood

Trees can modify the structure of the walls of tracheids and fibers during their differentiation to deal with imposed stress. In gymnosperms, the tracheids formed under a compressive load on the lower side of branches and leaning stems, or the leeward side of the tree with respect to the prevailing wind, have a larger than normal microfibril angle and extra lignification. In this case the wood is known as compression wood. In angiosperms, fibers formed under tension on the upper side of branches and leaning stems and the windward side of the tree develop a special wall layer, the gelatinous layer, which comprises almost pure cellulose with a very small microfibril angle. Wood containing these fibers is known as tension wood. Collectively these two types are known as reaction wood and they are essential to the tree to maintain an upright main stem, correct branch angles, and prevent branches drooping under their own weight. However, reaction wood is a serious problem for the timber and pulp industries and has been the subject of intensive research. As with microfibril angle, however, any attempts to modify reaction wood production must also consider the consequences of doing so for the tree.

See also: **Hydrology**: Hydrological Cycle. **Tree Physiology**: A Whole Tree Perspective; Physiology and Silviculture. **Wood Formation and Properties**: Formation and Structure of Wood; Wood Quality.

Further Reading

Barnett JR (1981) *Xylem Cell Development*. Tunbridge Wells: Castle House Publications.
Barnett JR and Jeronimidis G (2003) *Wood Quality and its Biological Basis*. Oxford: Blackwell.
Braun HJ (1984) The significance of the accessory tissues of the hydrosystem for osmotic water shifting as the second principle of water ascent, with some thoughts concerning the evolution of trees. *IAWA Bulletin* 5: 275–294.
Butterfield BG (1998) *Microfibril Angle in Wood*. International Association of Wood Anatomists/International Union of Forestry Research Organizations. Canterbury, New Zealand: University of Canterbury.
Butterfield BG and Meylan BA (1980) *Three Dimensional Structure of Wood: An Ultrastructural Approach*. London: Chapman & Hall.
Carlquist S (1975) *Ecological Strategies of Xylem Evolution*. Berkeley: University of California Press.
Iqbal M (1995) *The Cambial Derivatives. Handbuch der Planzenanatomie*, Vol. 9(4). Berlin: Gebrüder Borntraeger.
Larson PR (1994) *The Vascular Cambium: Development and Structure*. Berlin: Springer-Verlag.
Savidge RA, Barnett JR, and Napier R (2000) *Cell and Molecular Biology of Wood Formation*. Oxford: BIOS Scientific.
Timell TE (1986) *Compression Wood in Gymnosperms*. Berlin: Springer-Verlag.
Wilson K and White DJB (1986) *The Anatomy of Wood, its Diversity and Variability*. London: Stobart.
Zimmermann MH (1964) *The Formation of Wood in Forest Trees*. New York: Academic Press.
Zimmermann MH (1983) *Xylem Structure and the Ascent of Sap*. Berlin: Springer-Verlag.

Tropical Tree Seed Physiology

E M Flores and J A Vozzo, US Department of Agriculture Forest Service, Starkville, MS, USA

Introduction

Forest trees are a renewable natural resource. Understanding forest dynamics, trees, seeds, and seedlings as indisputable factors and basic units of regeneration has become important in developing effective techniques to promote conservation, management, and rational use of remaining forests. These are significant rudiments to implement successful reforestation programs.

The Angiosperm Seed

Seed Development

The fruit is the structure containing the seed. It develops from the gynoecium of the flower, which is frequently associated with other floral organs. The ovary wall forms the pericarp (fruit wall), and the fertilized ovule forms the seed. Fruit ripening is followed by senescence and, sometimes, dehiscence and abscission.

The process of seed development has three functional phases:

1. Cell divisions to produce the seedcoat, the endosperm, and the embryo (embryogenesis); this stage is characterized by an enhanced increase in fresh weight. Embryo development includes establishing a precise spatial organization of cells derived from the zygote (pattern of formation) and the generation of cell diversity inside the developing embryo (cytodifferentiation). These processes are coordinated to develop a recognizable morphological structure, regulated by the embryogenic pattern of the species (**Figure 1**).
2. Storage of reserves leading to an increase in dry weight.
3. Maturation drying leading to a stage of metabolic quiescence, interpolated between the end of seed development and the beginning of germination.

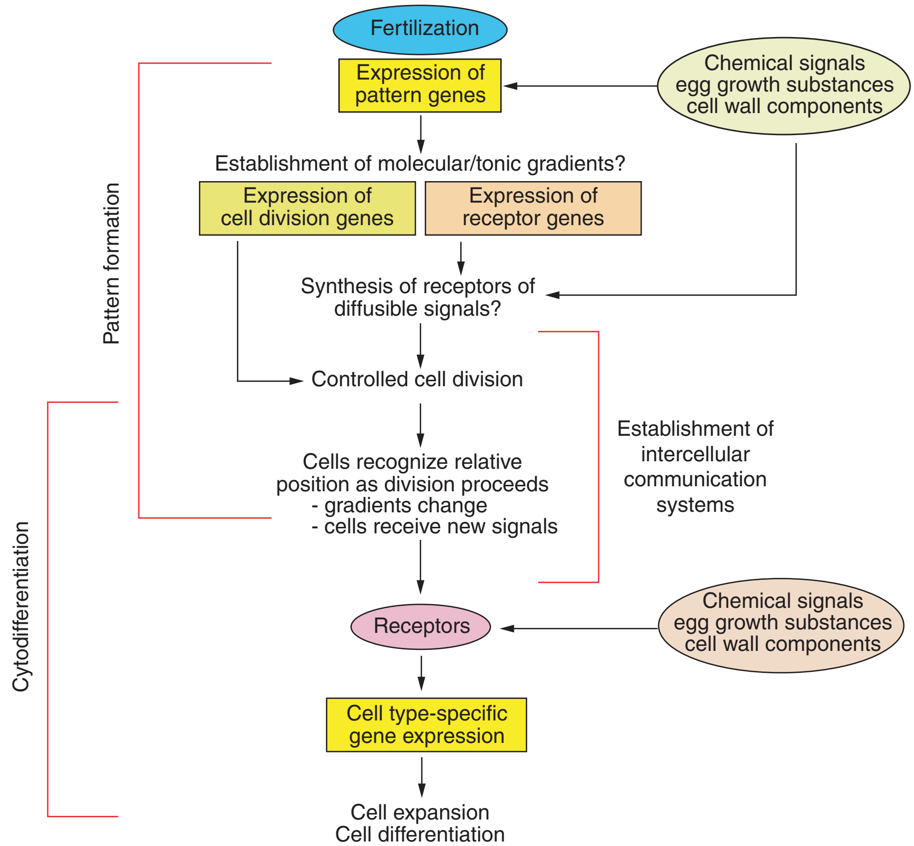


Figure 1 Gene expression during embryo development. Redrawn with permission from Lindsey K and Topping JF (1993) Embryogenesis: a question of pattern. *Journal of Experimental Botany* 44: 359–374.

> Seed inactivity is promoted by reduction of water content in the tissues, seedcoat impermeability, and inhibitors. Seed drying also reduces the synthesis of storage proteins.

Ovule, embryo, and endosperm development are coordinated and have contributions from both sporophytic and male and female gametophytic genes. Growth regulators present in the tissues of developing seeds (indol acetic acid, gibberellins, cytokinins, and abscisic acid) are active in seed development; accumulation of the storage reserves; development of the extra seminal tissues; and physiological changes of tissues and organs surrounding the developing fruit.

Many tropical and temperate seeds do not undergo drying, do not experience reduced cellular metabolism, and do not exhibit a clear end to seed development. During fruit dehiscence and dispersal, seed development is followed by germination-seed development without interruption. In some species, the seedling develops when the seed is still inside the fruit and is attached to the parent tree. These seeds are called viviparous (**Figure 2**). Mangroves growing on protected tropical coasts are the best-known examples of viviparous seeds. Overgrown seeds, which have a continuous embryo development limited by a hard and indehiscent pericarp or a late dehiscence pericarp (e.g., *Dipteryx*, *Prioria*) (**Figure 3**) may represent an intermediate type.

Figure 2 Viviparous seed of *Inga paterno*. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

Embryo development in seeds without maturation drying is similar in its early stages to that of seeds with maturation drying; however, variations

Figure 3 *Prioria copaifera* fruit (pod) enclosing an overgrown seed. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

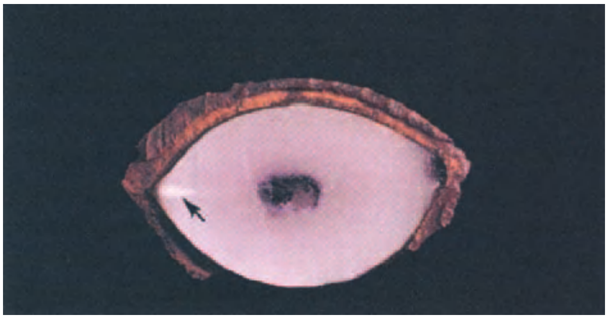


Figure 4 *Calatola costaricensis* drupe showing small, rudimentary embryo within a large seed. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

appear in late embryogenesis. Many seeds without maturation drying are large, with well-developed embryos (e.g., *Aesculus*, *Calophyllum*, *Dipterocarpus*, *Hevea*, *Quercus*, and *Sclerocarya*). Other seeds are large but have a small, rudimentary embryo (e.g., *Calatola*) (**Figure 4**). All these seeds increase in dry weight until fruit dehiscence, with insignificant loss in fresh weight. Embryo growth may continue (increasing in dry weight) after dehiscence in the absence of enough water to promote germination. However, in the tropical forest with very high rainfall the seeds or fruits (diaspores) fall down on very humid soils, sometimes inundated, and continue hydrating.

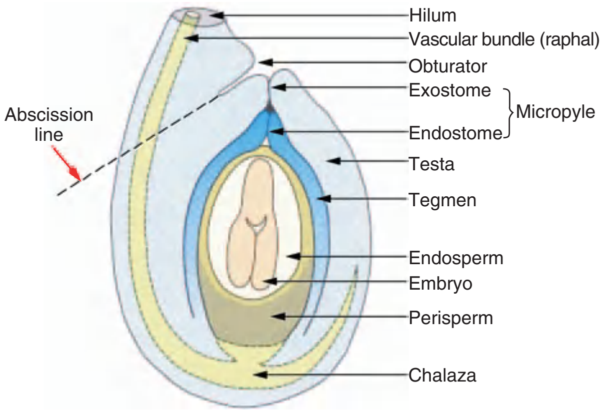


Figure 5 Diagram of typical mature seed. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

Some embryos have a suspensor. It seems to accomplish an active and dynamic role in nutrient absorption from the surrounding somatic tissues and transportation to the developing embryo as well as a source of nutrients and growth regulators for the developing embryo. The suspensor contains gibberellic acid, auxins, and cytokinins; the concentrations of these substances follow a fluctuation pattern.

The Mature Seed

The mature seed generally has a seed coat (product of one or both ovule integuments), an endosperm, and an embryo (**Figure 5**). Some mature seeds retain a remnant of nucellar tissue called a perisperm. The degree to which these structures continue their development, are reduced or reabsorbed, or disappear during the late stages of seed development leads to distinct structural patterns associated with physiological differences.

Storage of reserves Seeds store lipids, carbohydrates, and proteins to nourish the embryo (before and after germination) and to develop the early stages of seedling development. They are a source of precursors for carbon skeletons and provide energy when assembling precursors. Reserves may be stored in cell walls of different tissues, perisperm, endosperm, cotyledons, hypocotyl, and chalaza. The endosperm does not have a significant role at the proembryo stage, but it is important during embryo development and seed germination. The formation of the endosperm, its reabsorption, and the transference of reserves to the embryo are controlled genetically.

Lipids, which appear as lipidic bodies in the endosperm and the embryo, are a greater source of nourishment than the carbohydrates. The seeds without maturation drying are rich in lipids (e.g., *Virola koschnyi* ≥41%, *Calophyllum brasiliense*

38–39%). Carbohydrates are stored as starch or in thick cell walls rich in hemicelluloses.

Nearly all seeds contain proteins as reserve. They are found as aleurone grains and supply the nitrogen in early stages of plant development. In addition to the homogeneous protein matrix, aleurone grains contain crystals of proteins, minerals, and calcium oxalate. Several cations (K, Mg, Ca, Fe, Ba, Mn) are also found as globoid crystals. Seeds with maturation drying accumulate disaccharides, such as the saccharose and oligosaccharides, in the form of stachyose and raffinose. It has been suggested that these sugars are associated with tolerance to desiccation; however, some seeds sensitive to desiccation also accumulate sugars and saccharose (e.g., *Avicennia marina*) or saccharose and raffinose (e.g., *Quercus robur*).

Relationships between Seed Structure and Storage Behavior

Seeds losing water during maturation drying gradually acquire tolerance to desiccation; others maintain a high water content, do not reduce cellular metabolism, and are sensitive to desiccation and temperature decreases. The tolerance/intolerance to desiccation shown by these seeds in their natural environment is also seen in their storage.

Sensitivity to desiccation limits seed storage potential, genetic conservation, and use in trade. Two types of seeds based on sensitivity to desiccation are recognized: orthodox seeds (those that undergo maturation drying) and recalcitrant seeds (those that do not undergo maturation drying).

The ability to tolerate desiccation by orthodox seeds is associated with metabolic changes such as respiration decrease, increase of some carbohydrates or oligosaccharides, and accumulation of dehydrines (late embryogenesis abundant (LEA) proteins). During germination, seeds lose this tolerance several hours after radicle protrusion. Dehydration at this stage leads to irreversible damage, in which the peroxidation of lipids and free radicals has an important role. However, mature orthodox seeds can be dehydrated without damage to very low levels of moisture (1–5%) and in a variety of conditions. Bound water (structural) is less easily frozen than free water. Bound water seems to be a crucial component to tolerating desiccation, and in the orthodox seeds all water is bound. In storage, the longevity of seeds increases with a reduction of the water content in a predictable and quantifiable manner. These seeds may be subdivided into (1) true orthodox, which can be stored for long periods at seed moisture contents of 5–10% and subfreezing temperatures, and (2) suborthodox, which can be stored under the same conditions, but for shorter periods due to high lipid content or thin seed coats.

Recalcitrant seeds are rich in free water and neither tolerate nor survive desiccation. The dehydration of tissues provokes membrane deterioration (plasma membrane and mitochondria), protein denaturation, and reduction of both the respiratory rate and the adenosine triphosphate (ATP) level. The oxidative processes and the free radical seem to be involved in cellular and molecular deterioration. Seeds show a strong resistance to rehydration and the loss of cellular integrity leads to a loss of viability. Recalcitrant seeds are present in at least 70% of tropical trees. Their sensitivity to a low temperature is due to the high water content.

Because some seeds do not fit readily into either orthodox or recalcitrant categories, they have been clustered in a third category: the intermediate seeds. These seeds survive desiccation at intermediate moisture levels but not to the degree of orthodox seeds. This last category can be considered arbitrary, and the existence of a recalcitrance gradient throughout the different species has been suggested.

Variations in the sites of water storage and the gradual damage observed in the seed tissues when it dehydrates can be illustrated by the seeds of the following species: *Calophyllum brasiliense*, *Otoba novogranatensis*, *Minquartia guianensis*, *Caryocar costaricense*, and *Lecythis ampla* (**Figures 6–10**) (**Table 1**).

How does dehydration affect seeds? In *Calophyllum brasiliense* the hard seed coat resists desiccation; water loss is slow. Once the seed coat dehydrates, the water loss directly affects the embryo, with the exposed radicle being the most rapidly affected. The small plumule enclosed by thick cotyledons dehydrates last. *Otoba novogranatensis* and *Minquartia guianensis* have minute rudimentary embryos. The sequence of dehydration is seedcoat → peripheral endosperm and radicle → remaining embryo → inner endosperm.

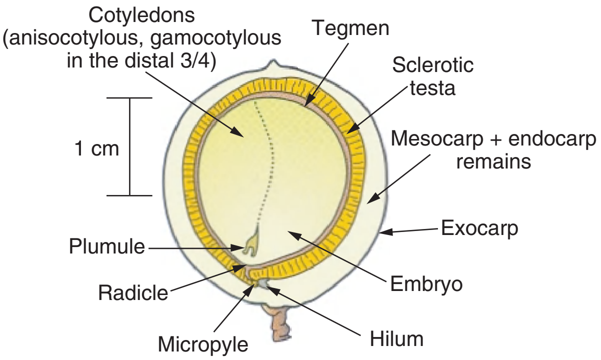


Figure 6 *Calophyllum brasiliense* berry (longitudinal section). Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

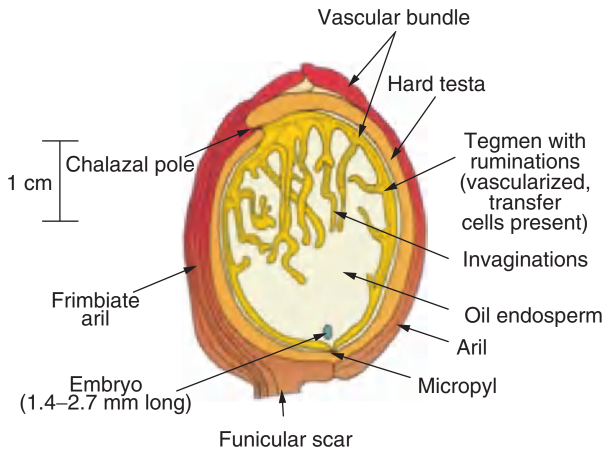


Figure 7 *Otoba novogranatensis* seed (longitudinal section). Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

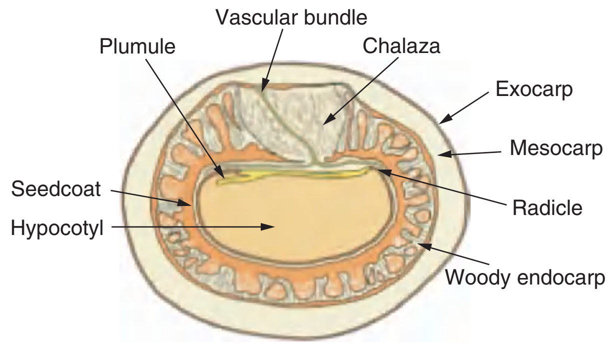


Figure 9 *Caryocar costaricense* drupe (longitudinal section). Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

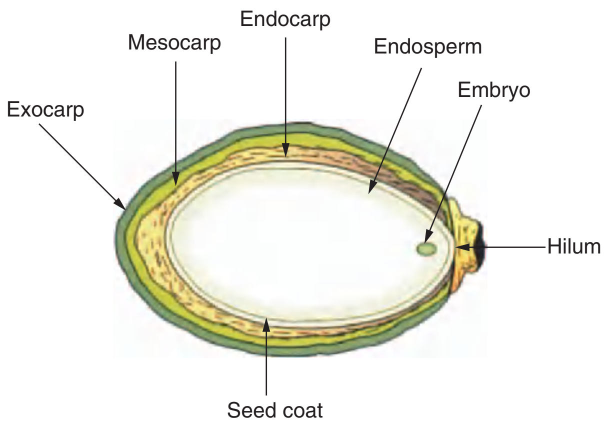


Figure 8 *Minquartia guianensis* drupe (longitudinal section). Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

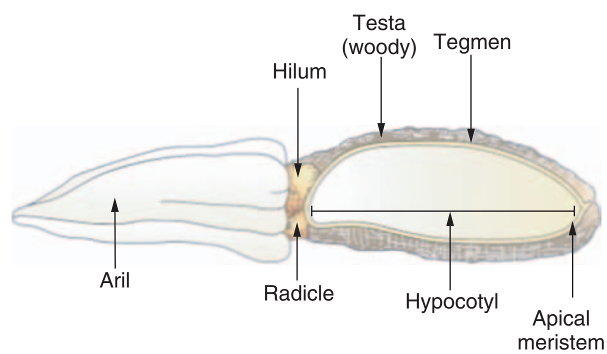


Figure 10 *Lecythis ampla* seed (longitudinal section).

Otoba novogranatensis is more sensitive to desiccation than *Minquartia guianensis,* due to endosperm rumination and tegmen vascularization. *Caryocar costaricense* has a curved, accumbent embryo and the plumule and radicle dehydrate immediately after endocarp dehydration. The dehydration of *Lecythis ampla* seeds first affects the seed coat and then the meristematic poles (radical and apical); they die instantly after seed coat dehydration.

The seeds enclosed in berries (*Calophyllum brasiliense*) or drupes (*Caryocar costaricense*, *M. guianensis*) are protected by the pericarp tissues, which help maintain seed moisture. In these cases, the functional unit is the fruit and dehydration is slower.

The moisture level below which a seed loses its viability varies from one seed to another. Variations are found among seeds collected from the same tree as well as from different trees, zones, seasons, or years. The recalcitrant behavior seems to be genetically determined and its genetic base is still not well understood. The variations found can be explained if the seed history from flower inception to seed dispersal and germination is analyzed carefully.

The difference found between temperate and tropical recalcitrant seeds must be added to the gradient found in recalcitrance manifestation. The first cannot be dried but can be stored for 3–5 years at near-freezing temperatures; the latter cannot be dried and will not survive temperatures below 10–15°C, depending on the species.

Data for tissue, cell, and biochemical alterations produced by dehydration in the recalcitrant seeds are limited, and no appropriate strategies and mechanisms to manage them under storage conditions have been found. The morphological diversity found in these seeds and the variations in the sequence and speed of seed dehydration further complicate the issue. The problem of cellular desiccation is complex; it seems to involve genetic components that lead to mechanisms of cellular protection. These mechanisms limit the cell damage produced by seed dehydration and promote cellular repair, reversing the changes induced by water loss. The accumulation of protecting substances in the tolerant tissues is

Table 1 Structural variation of recalcitrant seeds from five neotropical species during seed dispersal. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service

Structure	Calophyllum brasiliense	Otoba novogranatensis	Minquartia guianensis	Caryocar costaricense	Lecythis ampla
Fruit	Berry	Septicidal capsule	Drupe	Drupe	Pyxidium
Type of diaspores	Fruit	Seed	Fruit	Fruit	Seed
Endocarp surrounding the mature seed	Soft, thin, crushed	Absent	Drupe, hard endocarp	Drupe, hard endocarp	Absent
Seed coat	Hard	Hard	Soft	Papyraceous	Hard
Testa	Hard	Hard	Soft	Soft	Hard
Tegmen	Thin, soft	Thin, ruminate	Soft, fragmentary	Thin, soft	Remnants
Endosperm	Absent in the mature seed	Massive, nuclear–cellular	Massive, cellular	Absent in the mature seed	Absent in the mature seed
Embryo	Massive, complete	Minute, rudimentary	Minute, rudimentary	Massive, complete	Massive, undifferentiated
Cotyledons	Massive, fused	Differentiates and develops during germination	Differentiates and develops during germination	Small, scaly	Differentiates and develops during germination, small, scaly
Hypocotyl	Thick, massive	Differentiates and develops during germination	Differentiates and develops during germination	Thick, massive	Thick, massive
Epicotyl	Very small	Differentiates and develops during germination	Differentiates and develops during germination	Very small	Differentiates and develops during germination
Radicle	Thick, small	Differentiates and develops during germination	Differentiates and develops during germination	Thick, small	Rudimentary
Reserves location	Cotyledons, hypocotyl	Endosperm	Endosperm	Hypocotyl	Hypocotyl
Water storage	Whole embryo	Mainly endosperm	Mainly endosperm	Hypocotyl	Hypocotyl

quite possible. Disaccharides (saccharose) and oligosaccharides (raffinose and stachyose) may have an important role in the stabilization and maintenance of the membrane system and other sensitive systems.

The Gymnosperm Seed

Gymnosperm seeds are not enclosed within a gynoecium. They are exposed on scales or similar structures clustered in gynostrobiles (female strobiles). The zygote forms the embryo (2*n*), which remains immersed in the nutritious tissue (endosperm) of the megagametophyte (*n*). The integument gives rise to the seed coat (2*n*, part of the tissues of the maternal tree) (**Figure 11**).

The seed matures in two to three seasons. The content, behavior, and fluctuation of growth regulators are similar to those of the angiosperms. The lipid content in the seeds is high, although carbohydrates and proteins are also present.

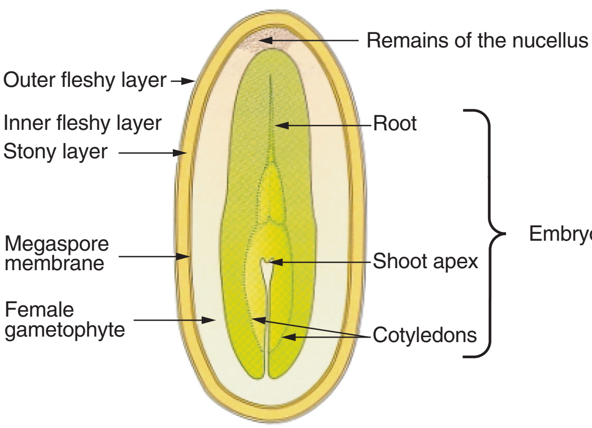


Figure 11 *Pinus* seed. From *Comparative Morphology of Vascular Plants*, 2edn. by Foster and Gifford © 1974, 1989 by WH Freeman and Company. Used with permission.

Fruit and Seed Dispersal

Seed dispersal is a critical stage in the life cycle of the species. It transports physiologically independent individuals to the habitat occupied by their parents or to new suitable territories, where the seeds may colonize if environmental conditions are favorable. The unit of dispersal (diaspore, propagule, or diseminule) is determined by the embryo, the seed, the fruit, or the fruit and associated parts of the modified perianth, the receptacle, or combinations.

Diaspores can be dispersed in space and time. Dispersal in space is the transport from one site to another, usually far from the parent tree. Dispersal in time is the quiescence or inactivity of diaspores for a variable period of time. Later, they can activate by environmental stimuli and resume the germination process.

The dispersal of diaspores can be biotic (zoochorous) or abiotic (azoochorous) and their morphology is related to the method of dispersal. In biotic dispersal the vectors are numerous: invertebrates (flies, dung insects, ants (myrmecochory), earthworms, and snails), herbivorous fish (ichthyochory), marine turtles, lizards and desert iguanas (saurochory), birds (ornithochory), and mammals including human beings (mammaliochory). Abiotic dispersal is by wind (anemochory), water (hydrochory) or the tree itself (autochory). The last is achieved by active ballistics (tension generated by the dehydration of hygroscopic tissues), passive ballistics (movements of the seeds enclosed in the fruit), creeping diaspores, and barochory (dispersal by weight).

Biotic dispersal could be epizoochorous if the transport of diaspores is passive, external, and occurs through diaspore adhesion to animal skin (hairs) or feathers. It is synzoochorous when animals, eating part of the seeds but not ingesting them, actively transport the diaspores, and it is endozoochorous if the diaspore containing the seed or the seed itself, is ingested and eventually regurgitated or defecated intact. Zoochorous dispersal requires nutritious tissues in the diaspore, chemical attractants, mimetism, or adhesive structures.

In tropical forests, most dispersal is achieved by vertebrates, which obtain food from the seeds and other edible parts of the fruit. Zoochorous dispersal ($\geq 80\%$) is dominant in the tropics. In primary forests, zoochory may increase to 87–90%. Most diaspores dispersed by water come from riparian species and are typical in marshes or mangrove vegetation, while those dispersed by wind grow at forest edges.

The specificity of disperser or dispersers is uncommon. Most fruits and seeds are used and dispersed by several or many vectors, which may include consumers, commensals, predators, commensals and dispersers, or predators and dispersers.

Germination

The process of germination involves the transition of cells from a dehydrating stage and low metabolic activity to a hydrated and metabolically active stage. Water is absorbed in a triphasic way: imbibition, germination *sensu stricto*, and embryo development. Imbibition is the rapid absorption of water leading to a regular increment in the respiratory activity. Germination *sensu stricto* is the process of embryo activation, not accompanied by any apparent morphological change. Embryo development is marked by radicle elongation and a significant change in the physiology of the embryo. This phase is crucial, because seedling development depends on it. In most cases, the seed germinates only if the respiration and production of ATP are adequate, creating an oxygen requirement.

Germination culminates with radicle protrusion into the adjacent tissues. In recalcitrant seeds with minute, rudimentary embryos or large embryos with a rudimentary radicle (reduced to a radical meristem), the development of the radicle implies cell division and elongation.

Environmental Influences

The external environmental factors regulating the activity of the maternal tree during seed maturation include temperature, light, photoperiod and thermoperiod, relative air moisture, and water potential in the soil. The internal parameters are the water potential of the maternal tree, its nutritional and hormonal state, and the position of the seed on the tree. The environmental factors involved directly in the process of germination are temperature, light, and gas.

Water

In orthodox seeds, water imbibition allows metabolic reactivation and restoration of membranes and organelles, activation of the enzymatic system, respiration, and synthesis of RNA and proteins. The water imbibing the seed is equivalent to two or three times the dry weight of the seed. The net diffusion occurs in a descendent gradient of water potential (or energetic state of the water); in other words, from pure water to water containing solutes). The potential of a cell inside a seed is determined by the osmotic potential (ψ_p), by the concentration of solutes (more solutes = less osmotic potential), the matric component (ψ_c), by the hydration of matrices (cell walls, starch, protein bodies), and the pressure potential (ψ_p), permitting water intake and putting pressure on the cell wall. In the water potential of the soil, only ψ_c has an important function. Water absorption has three phases:

1. A rapid initial imbibition that is strongly influenced by the matric forces.
2. A phase of slow water intake in which metabolic activity begins. The length of this phase is correlated with the intensity of the dormancy.
3. A rapid phase intensified by metabolism activation occurring only in nondormant seeds involved in active germination. In many cases, it coincides with seed coat breaking and radicle protrusion.

Reserve mobilization and enzymatic activation depend on hydration; the best germination occurs with a low moisture tension (0.005–0.500 bars). If the tension is zero, the water pellicle around the seed inhibits the absorption of oxygen.

Temperature

Under natural conditions, temperature determines the capacity and rate of germination, removing the primary and inducing secondary dormancy. For germination, the upper limit is about 45°C and the lower 3–5°C. Many species germinate at about 40°C, but the seedlings are abnormal; others can germinate near the lower temperature limit but they rarely produce normal seedlings. The regimes of alternating temperature (20°C at night and 30°C during the day) seem optimal for species from temperate zones, although similar results are obtained with constant temperatures of 25°C. In tropical species the best range is usually 25–30°C.

Light

Light stimulates germination, but it is not strictly necessary for most seeds; however, some pioneer tropical species (*Cecropia*, *Heliocarpus*) typical of areas in early succession, have photoblastic seeds. A pigment called phytochrome is involved in the photo control of the germination; it exists in two reversible forms (**Figure 12**).

Light sensitivity is influenced by pretreatment with temperature. With an increment of cold pretreatment, seed germination can be increased in darkness and the sensitivity to far-red light decreased. The requirement of light for germination varies with the amount of imbibed water.

Genetic Influence

The genome received by the diaspore controls germination (**Figure 13**) (**Table 2**) and a network of genes regulates ovule morphogenesis. Several parts of the diaspore differ in genotype; the tissues of the fruit, other tissues surrounding the seed, and the seed coat have the maternal genotype. The endosperm is one-third paternal and two-thirds maternal in the most common type of seed. The embryo is one-half paternal and one-half maternal. In general, the genotype of one or both parents affects the structure and composition of the various parts of the diaspore. For example, the genes expressed in the megagametophyte play a role in the induction of seed development, primarily in embryo and endosperm development. The expression of some maternal genes is required for normal endosperm development. The endogenous annual rhythm of the germinability of the seed and the internal mechanisms regulating it are not well known.

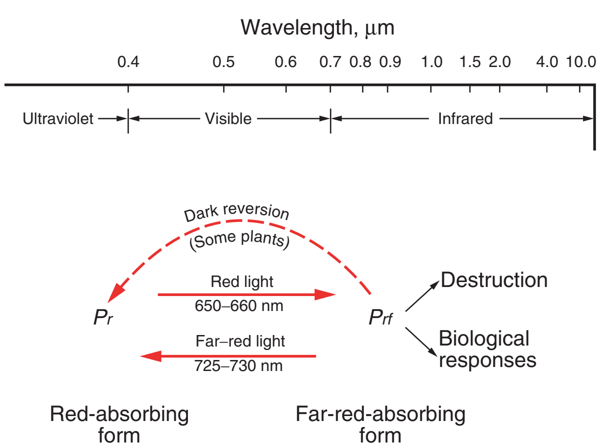


Figure 12 Diagram of reaction for spectral-driven phytochrome reversibility. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

Seed Respiration

Respiration permits the acquisition of energy. It requires oxygen and the removal of CO_2. High levels of CO_2 can inhibit germination, and a lack of oxygen has the same effect although some species can germinate in anaerobic conditions.

The inhibited seed has three active routes of respiration: glycolysis, pentose-phosphate, and the citric acid cycle (Krebs cycle). Glycolysis – catalyzed by cytoplasmic enzymes – and the Krebs cycle (inside the mitochondria) are essential for the production of ATP. The respiratory process in the orthodox seed involves three or four stages:

1. High oxygen (O_2) consumption and a linear increment in respiration during tissue hydration (hydration and activation of mitochondrial enzymes in the Krebs cycle and the electron chain).
2. Decrease in the respiration proportional to the stabilization of O_2 intake. The seed is hydrated and the enzymatic system is active. Between stages (2) and (3), the radicle protrudes (it coincides with phases (2) and (3) of the imbibition process). The seed coat (or seed coat + endocarp or pericarp) can be a physical barrier limiting O_2 intake.
3. Respiratory reactivation due to activation of the embryo axis and meristems and mobilization of stored reserves. The breaking of the seed coat may contribute to increasing the intake of O_2.
4. Respiration restricted to storage tissues whose reserves are being degraded and removed.

Longevity, Viability, and Dormancy

The period of time in which the seed remains viable in the ground is called longevity. Viability is the germinative capacity; its loss is the final stage of

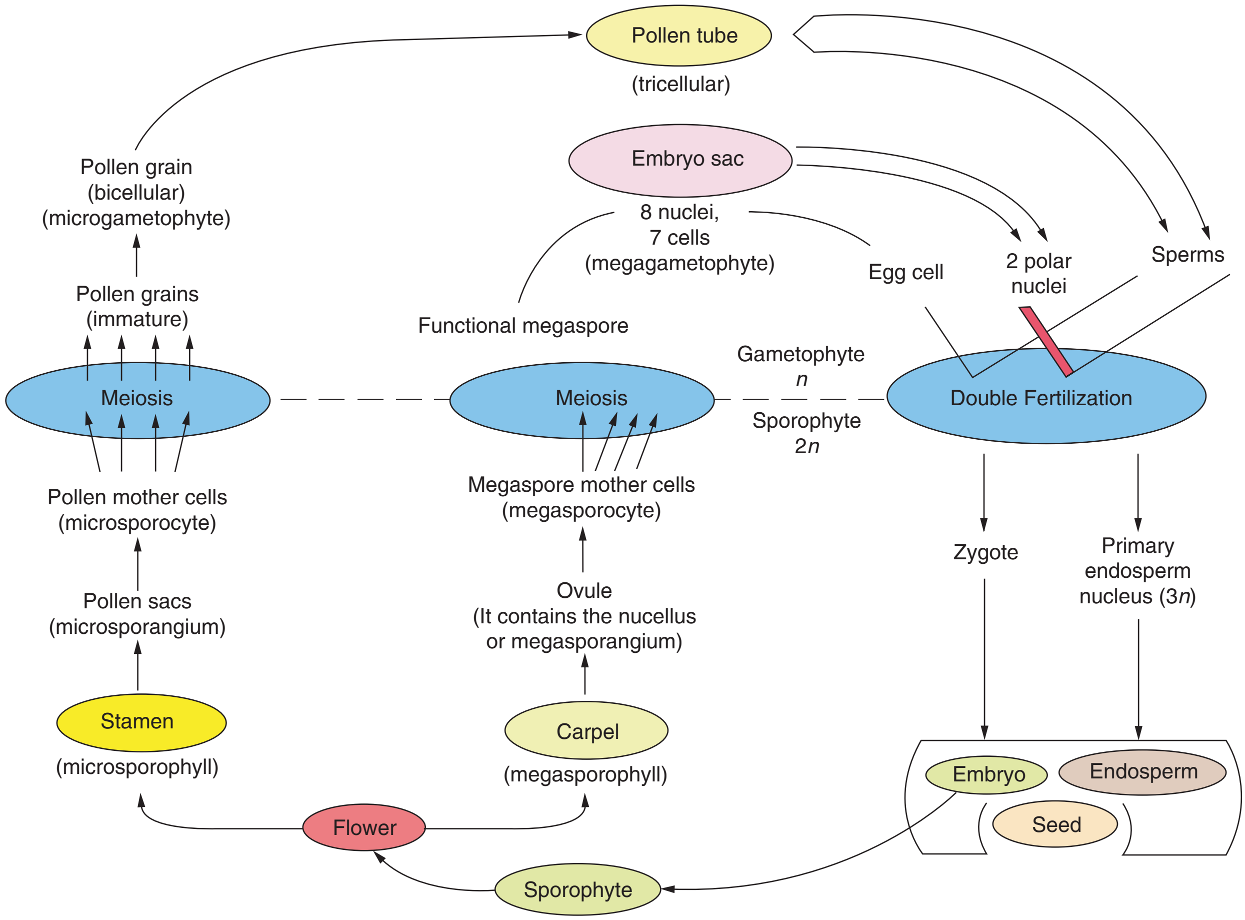


Figure 13 Angiosperm reproductive cycle. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

seed deterioration. Species from wet tropical forests tend to lose viability rapidly; perhaps 60% to 70% lose it in 3–6 months. Some species lose viability in days or weeks.

To survive in the ground, seeds must maintain viability during the time in which germination is inhibited by dormancy or quiescence. Dormancy is the suppression of germination under favorable environmental conditions. Approximately 10% of tropical species show dormancy. Several conditions cause dormancy: rudimentary or physiologically immature embryos, hard or impermeable seed coats, endogenous growth regulators inhibiting germination, or inadequate storage; some dormancies are the product of multifactorial interactions. Soaking in running water, hot water, hydrogen peroxide, and physical scarification are treatments used to break seed coat dormancy.

Dormancy can be innate or induced. Innate dormancy (primary) prevents the germination of seeds during their development and maturation in the maternal tree and usually some time after dispersal or collection. Dormancy is innate external (primary external) when the seed coat, the endocarp or the pericarp are hard or woody, impermeable to gases or water, or mechanically resistant (e.g., *Enterolobium*, *Samanea*). The environment can reinforce the quiescence. When the embryo contains inhibitory substances or it is physiologically immature, the dormancy is innate internal or primary internal (e.g., *Juniperus virginiana*).

The innate dormancy declines before or after dehiscence. This period is called postmaturation dormancy. The heritability of dormancy is complex because the distinct parts of the seed are genetically different.

Induced dormancy (secondary) develops after the dispersal or collection of nondormant seeds or seeds emerging with partial or total primary dormancy. Essentially, it reflects no sensitivity to germination inductors, internal or external.

Germination can be inhibited by exposing the seeds to long periods of white light, especially to densities of high radiant flows or far-red light. Dormancy can also be prevented, delayed, or reduced by intermittent light of low intensity. Innate dormancy is absent in the recalcitrant seeds of the tropics.

Table 2 Levels of genetic variation, events and facts

Levels of genetic variation		*Events and facts*
Gamete production	Microsporogenesis and microgametogenesis	• The microsporocyte or pollen mother cell (2*n*) has two chromosome sets (maternal and paternal). • Meiosis gives rise to four haploid microspores. They are not genetically equivalent. • Each microspore undergoes asymmetric division and finally produces a pollen grain with a vegetative cell and two sperm cells (frequently dimorphic).
	Megasporogenesis and Megagametogenesis	• The megasporocyte or megaspore mother cell (2*n*) has two chromosome sets (maternal and paternal). • Meiosis gives rise to four haploid megaspores. They are not genetically equivalent. • Three megaspores degenerate, one survives (chalazal) and is functional. • Megaspore divisions originate the embryo sac (megagametophyte). It contains the egg cell (*n*). • The megagametophyte is regulated by its genes and those of neighboring cells and tissues. • The megagametophyte regulates seed development after fertilization.
Gamete level		• The egg cell and the sperms have nuclear and cytoplasmic DNA (mitochondria and plastids). • Plastid DNA (plastome) interacts strongly with nuclear DNA. • In most species, plastids are inherited by maternal line (includes plastid DNA). • Plastids reproduce by binary fission. Some mutants are unable to reproduce; the mutation is lethal. • Mitochondrial DNA is usually inherited by maternal line (egg cell). • Sperm cells (two per pollen tube) are frequently dimorphic. One may have mitochondria; the other may have plastids. Probably different patterns of male cytoplasmic DNA transmission. • Is sperm behavior in double fertilization predetermined or at random?
Parent trees		• Self-sterility (homogamy) and separation of sexes in space or time to favor cross-pollination • Female parent tree: ○ The egg cell (embryo sac) in the ovule of each flower could be genetically different to that of the neighboring flowers. ○ In flowers with several ovules per gynoecium (ovary), the egg cell (embryo sac) of each ovule could be genetically different to that of the neighboring ovules. ○ Pollen received by egg cells (embryo sacs of different ovules) in an ovary with several fruits could be genetically different and provided by several sources. ○ Seeds are not genetically equivalent. • Male parent tree: ○ Pollen grains are not genetically equivalent. • Multiple parent trees: ○ Mixture of pollen grains genetically different
Incompatibility systems		• They maintain a high degree of genetic heterozygosis in the species population. • They operate at the stigma or style level. • Incompatibility could be sporophytic or gametophytic.
Gametophytic mutations		• They are lethal if the megagametophyte (embryo sac) is affected. • If the pollen is affected fertilization could fail or seed abortion takes place at different stages of development. • If both gametophytes are affected there is not fertilization, seed is empty (no embryo) or the embryo is not viable. • Endosperm: If endospermic DNA is aberrant seeds fail to develop.
Diaspore genome		• Several parts of the diaspore differ in genotype; the tissues of the fruit, other tissues surrounding the seed, and the seed coat have the maternal genotype. The endosperm is one-third paternal and two-thirds maternal in the most common type of seed. The embryo is one-half paternal and one-half maternal. In general, the genotype of one or both parents affects the structure and composition of the various parts of the diaspore.
Pollination and seed dispersal		• In cross-pollination species, the paternal genes move twice (pollination and seed dispersal) in each generation; the maternal genes move once (in autopollination or cross-pollination). Therefore, in cross-pollinated species the paternal genes move farther in each generation. • Pollination is at random. One or several donors provide pollen to the same flower or different flowers in the tree. • The pattern of dispersal contributes to structure population, to potential genetic drift, and to natural selection.

The emergence from dormancy is frequently regulated by a promoter–inhibitor system, where the principal promoter is gibberellic acid (GA_3) and the main inhibitor is abscisic acid (ABA). Low levels of inhibitor and high levels of promoter induce germination. According to some studies, it is not possible at present to determine the precise function of ABA in the induction of dormancy.

See also: **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species. **Tree Physiology**: Physiology of Sexual Reproduction in Trees.

Further Reading

Allen PS and Meyer SE (1998) Ecological aspects of seed dormancy loss. *Seed Science Research* 8: 183–191.
Bewley JD and Black M (1994) Seeds: physiology of development and germination. *Plant Cell* 9: 1055–1066.
Chaudhury AM, Koltunow A, Payne T, *et al*. (2001) Control of early seed development. *Annual Reviews of Cell and Development Biology* 17: 677–699.
Foster ANS and Gifford EM (1974) *Comparative Morphology of Vascular Plants*. San Francisco, CA: WH Freeman.
Hilhorst HWM (1998) The regulation of secondary dormancy: the membrane hypothesis revisited. *Seed Science Research* 8: 77–90.
Koornneef M, Bentsink L, and Hilhorst H (2002) Seed dormancy and germination. *Current Opinion in Plant Biology* 5(1): 33–36.
Lindsey K and Topping JF (1993) Embryogenesis: a question of pattern. *Journal of Experimental Botany* 44: 359–374.
Ray A (1997) Three's company: regulatory cross-talk during seed development. *Plant Cell* 9: 665–667.
Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.
Welbaum GE, Bradford KJ, Yim KO, Booth DT, and Oluoch MO (1998) Biophysical, physiological and biochemical processes regulating seed germination. *Seed Science Research* 8: 161–172.

Shoot Growth and Canopy Development

S W Hallgren, Oklahoma State University, Stillwater, OK, USA

Introduction

As shoots grow and become numerous a canopy develops. The mass and surface area of the leaves in the canopy reach a maximum amount relatively early in the life of a stand. Subsequent growth of the trunk and branches serves to lift the canopy higher and higher above the ground. The form and arrangement of the branches and leaves in the canopy are an important reflection of the architectural type. Tree architecture is difficult to study and describe because trees are very large, very long-lived, and have a complex hierarchy of components. Much of tree architecture is inherited. Trees look different because they have evolved in different climates – tropical palms (e.g., *Corypha elata*) versus alpine firs (e.g., *Abies alba*), coastal mangroves (e.g., *Rhizophora mangle*) versus savanna baobabs (e.g., *Adansonia digitata*) and niches (overstory Douglas-firs (*Pseudotsuga menziesii*) versus understory Pacific yews (*Taxus brevifolia*), overstory oaks (e.g., *Quercus alba*) versus understory dogwoods (e.g., *Cornus florida*). In addition to variation in the inherited types, there is tremendous genetic variation in response to the local environmental variables of solar radiation, competition, and availability of nutrients and water. The phytochrome-mediated response to plant shade is strongly inherited. Trees appear to grow toward the light, but are really growing away from shade. The intensity of competition determines the tree size and shape. Some species can grow larger than others under extreme competition. The xylem is well suited to support the tree and conduct water, but the hydraulic limits of the xylem to transport large volumes of water from the soil to the distant transpiring leaves also sets limits to tree size and form.

Tree Growth

Plant growth is defined as the increase in size by cell production and enlargement. Apical meristems at the tips of stems are responsible for primary growth to increase stem length and for the production of initials for the lateral appendages to the stem. The lateral meristem or cambium at the periphery of the stem between the xylem and phloem provides secondary growth to maintain vascular connections and increase mechanical support through increased diameter. Stems carry the leaves responsible for photosynthesis and the flowers responsible for reproduction. Although plant growth may appear simple from this description, when the entire scope of species is considered, growth provides an enormous variety of patterns in time and space that produce a bewildering array of architectures. Extensive studies of tree architecture have shown the existence of predictable types that reflect adaptation to environmental factors and competition.

The tree phenotype is the manifestation of the genetic information in the genotype acting through developmental processes under the constraints of the environment to produce an adapted type. There is a huge genetic diversity of trees because they have become adapted to such a wide range of terrestrial environments from rain forests to arid deserts and from warm tropics to cold boreal regions. Because trees are long-lived sessile organisms and cannot move in space to escape environmental stresses that change through time, they have very high phenotypic plasticity that allows them to acclimatize to long- and short-term environmental changes. A site that provided plenty of light may become strongly shaded by competition. A site that was once adequately supplied with moisture may become too wet or too dry.

Almost all trees begin life near or at the soil surface. Because it is the primary site of energy exchange, plants at the bare soil surface experience the greatest extremes and the most rapid environmental changes. Small young trees experience a single soil and shoot environment. There are qualitative and quantitative changes in tree–environment interactions as the tree becomes larger.

Rapid early growth allows the tree to become established and escape the harsh conditions at the soil surface. The roots and shoots grow farther and farther away from the soil surface and the single plant begins to experience many different environments at the same time. The environmental extremes and rapid changes are not experienced by the large tree in the same way as the small tree, because most of the tree is far above or below the soil surface and the large tree shades the environment near its base. Consequently, there are quantitative and qualitative changes in shoot growth as a tree ages and becomes larger.

Tree Architecture

The growth and proliferation of individual shoots lead to development of the tree and canopy architecture. Trees can be viewed as an assemblage of components or modules that are repeated and follow a hierarchy of types. Each component type more or less serves the same purpose, responds the same way to the environment, and is autonomous at its own level. The above-ground components of a tree in order of increasing size are: (1) apical meristem; (2) leaf; (3) shoot unit or metamere (node with its lateral appendage, usually a leaf, and structure in the axil of the lateral appendage and the proximal internode); (4) extension unit for a growth period; and (5) crown. The greatest diversity of tree architecture is found in the tropics where there are stable equable climates, a great diversity of climates, large areas of forest, and relatively little environmental change over thousands of years.

There are over 20 distinct architectural models among the tropical trees. Major functional characteristics determining models are the life span of the apical meristem and how the vegetative apical meristems differentiate. The apical meristem is of central importance, as it produces elongation growth and is the origin of the secondary or lateral meristem. In addition, many types of trees such as palms, palm-like trees, and tree ferns do not have a secondary meristem.

Apical meristems produce either a sexual or vegetative axis in an irreversible developmental process. The production of a sexual axis ends the life span of the apical meristem while the life span of the vegetative axis may continue indefinitely. Apical meristems show continuous or rhythmic growth. Continuous growth produces an axis with essentially equivalent internodes, leaves, and lateral branches. In contrast, rhythmic growth with alternating periods of growth and rest produces an axis with alternating long and short internodes and leaves and lateral branches that differ with internode length. Whether a species shows continuous or rhythmic growth has a substantial influence on its response to the environment and its form. Continuous growth is associated with unchanging environment and even when there are changes the tree responds by increasing or decreasing growth, but it does not produce resting buds. Examples include members of the family Palmae, the mangrove *Rhizophora mangle*, and species in the genera *Juniperus*, *Thuja*, and *Chamaecyparis*. Rhythmic growth is associated with a climate with substantially different seasons of growth and rest and the production of a resting bud. The genus *Pinus* is widespread and shows a lot of variation in growth pattern. Northern species such as *P. resinosa* often have a very rigid pattern of rhythmic growth that produces one shoot flush each year in the spring and is under strong genetic control. It shows little capacity to take advantage of prolonged favorable weather by producing more than one shoot in a year. In contrast, southern species such as *P. taeda* may show rhythmic production of one to several flushes depending on the weather.

Apical meristems produce either orthotropic or plagiotropic shoots. Orthotropic axes are erect, show radial symmetry, may have a spiral leaf arrangement, and are produced most often by the leading shoot. They are associated with vigorous young growth and tend to decrease in very old and severely stressed plants. Plagiotropic axes are horizontal, show dorsiventral symmetry, have a distichous leaf arrangement, and are produced most often by lateral shoots. They are associated with slow weak growth and tend to increase in very old trees and severely stressed plants. These architectural characteristics are genetically controlled and constrain the ultimate tree form.

The majority of trees develop the form of a large central trunk with side branches while a relatively small number of trees, mainly those mentioned above with no secondary meristem, develop a single nonbranched axis. The excurrent or conical tree form is associated with conifers and cold climates with abundant snow and ice. The form obviously facilitates the shedding of ice and snow which could damage the crown if allowed to accumulate. The deliquescent tree form is associated with angiosperms and warm climates lacking snow and ice. This form may be an advantage where competition for light is extreme.

Shade Avoidance

The radiation environment is the most important factor determining shoot growth and canopy development. The leaves of trees are displayed to capture light energy, because plants need light energy for photosynthesis. Leaves and their stems have two options when subjected to shade: (1) adapt to functioning in the shade and (2) grow toward the unaltered light to increase photosynthesis. Shade leaves have greater photosynthetic efficiency in the low light because they develop greater surface area for light interception and they are thinner with less pubescence and less dense mesophyll cells for better light penetration and reduced reflection. In addition, shade leaves are oriented horizontally to intercept more light than the vertically oriented sun leaves. Shade plants increase the ratio of photosynthesizing machinery to respiring structural support material. Although plants can adapt to shade, those growing in the shade are usually not as vigorous as plants in full sun. Current research findings indicate that plants actually grow away from shade cast by competing plants. Competing plants change the quality of the light and this change is a signal that induces a growth increase response in internodes. The capacity to avoid plant shade was not important and probably did not evolve until plants became large enough to cast shade on their neighbors.

The shade signal is read by phytochrome in plants. Phytochrome has two interconvertible forms. One form (Pr) absorbs mainly red photons (maximum absorption 665 nm) and the other (Pfr) absorbs mainly far-red photons (maximum absorption 730 nm). The absorption by either form causes it to convert to the other form. Light in this range of the spectrum is little affected by clouds or rain but can be changed significantly by vegetation. Plants strongly absorb red (R) and reflect far-red (FR) light; consequently, the R:FR ratio (ratio of photon flux at 660 nm and 730 nm) tends to be reduced by canopy shade. The R:FR ratio varies significantly with degree of shade (0.05–1.15 in canopy shade to 1.05–1.25 in full sun) and elicits large changes in the proportion of phytochrome in the Pfr form (Pfr/P ranges from 0.65 in full sun to 0.20 in deep shade). A wide variety of plant processes are known to respond to the R:FR ratio, including meristem activity, tissue differentiation (e.g., flowering versus vegetative), senescence, abscission, assimilate distribution, and chloroplast development (**Table 1**). Logarithmic stem elongation has been shown to have a strong inverse linear relation to the Pfr/P value. It has been shown that the strength of the elongation response to Pfr/P is genetically controlled and is very low in shade-tolerant plants and very high in shade-intolerant plants (**Figure 1**). It would be very interesting to learn whether the other plant responses to the R:FR ratio are similarly related to genetic variation in shade tolerance.

It appears that much of the plant response to shade is mediated by phytochrome. The very plastic response of trees to the radiation environment provides the capability to fine-tune tree architecture to achieve the greatest fitness. Even the germination of seeds is regulated by the light environment in some species. This capacity is under genetic control and plants adapt to a wide range of shade environments. The trees producing a canopy that creates the greatest change in the radiation environment (greatest change in R:FR ratio) generally show the smallest

Table 1 Shade avoidance responses

Plant physiological process	*Shade avoidance response*
Extension growth	Accelerated
Internode extension	Rapidly increased
Petiole extension	Rapidly increased
Leaf development	Retarded
Leaf area growth	Slightly reduced
Leaf thickness	Reduced
Apical dominance	Strengthened
Branching	Inhibited
Flowering	Accelerated
Rate of flowering	Greatly increased
Seed set	Severely reduced
Fruit development	Truncated
Senescence	Accelerated
Leaf senescence	Advanced
Leaf abscission	Advanced
Assimilate distribution	Marked change
Deposition in storage organ	Severe reduction

Reproduced with permission from Smith H (2000) Plant architecture and light signals. In: Marshall B and Roberts JA (eds) *Leaf Development and Canopy Growth* pp. 118–144. Oxford, UK: Blackwell.

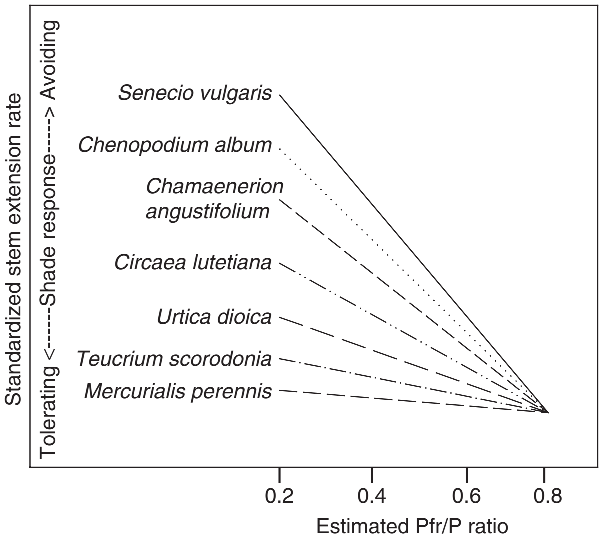


Figure 1 The elongation response to change in the Pfr/P ratio is much greater in plants that avoid shade than in those that tolerate shade. Reproduced with permission from Smith H (2000) Plant architecture and light signals. In: Marshall B and Roberts JA (eds) *Leaf Development and Canopy Growth*, pp. 118–144. Oxford, UK: Blackwell.

response to changes in shade. In contrast, trees producing a canopy that creates the smallest change in the radiation environment generally show the greatest response to shade.

Recent advances in phytochrome research have provided significant knowledge of plant response to shade. It has been common knowledge for a long time that tree stem and leaf growth are affected by light and for the most part there was a sense that intensity of light was the main signal. It has become clear that light quality as it is altered by vegetation is a major signal in photomorphogenesis. Shoot growth and canopy development are guided by the radiation environment. Genes encoding for several phytochromes responsible for very different processes, including seed germination, flowering, elongation, and tuberization, have been found in *Arabidopsis*.

Current research activity seeks to determine how to manipulate the shade avoidance response mediated by phytochrome through genetic means. There are many mutants that have provided new information. A transgenic crop has been produced that appears to have reduced shade avoidance. It has reduced stem elongation which presumably allows greater energy investment in the part of the plant to be harvested, the fruit. In the case of trees, it may be more productive to search for ways to increase the shade avoidance response to produce more stemwood. The large number of phytochromes and their interactions will make the genetic engineering of shade avoidance a long and meticulous process. But it will certainly proceed faster than traditional breeding for the same trait.

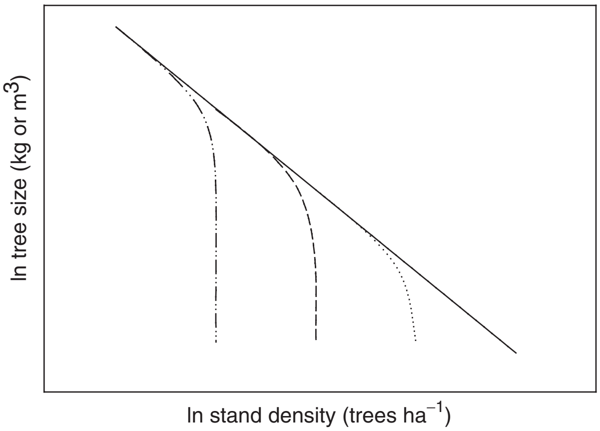


Figure 2 The maximum size–density relation for even-aged single species stands has a slope close to $-3/2$ when ln (tree size) is plotted against ln (density). Trees in low-density stands increase in size until they reach the maximum attainable for the given density. Further increase in size will only occur when density decreases through mortality.

The Maximum Size–Density Relation

The maximum size–density relation depends on the assumptions that trees of a certain species all have the same allometric growth and that trees on a fully occupied site will experience self-thinning. Trees growing in even-aged single-species stands will grow to a certain size that depends on density and they can not grow larger unless density is reduced by mortality (**Figure 2**). This appears to be consistent with the concept of a maximum biological productivity. Furthermore, the size–density relation is independent of site quality and stand age. The relationship between average plant size and stand density is bounded asymptotically by the $-3/2$ power rule:

$$s = a\rho^{-3/2}$$

where s = plant weight or volume, a = a constant, and ρ = stand density. This can also be written as:

$$\ln s = \ln a - 3/2 \ln \rho$$

The relation is common to all species studied to date and, although the slope varies somewhat, it is usually close to $-3/2$. The height of the line does vary considerably by species. At a stand density of 2470 trees ha^{-1} *Abies magnifica* and *Sequoia sempervirens* will attain a maximum average stand diameter of 25.4 cm; density must be reduced to 2050 for *A. concolor* and *Pinus ponderosa*, 1470 for *Pseudotsuga menziesii*, 1110 for *Pinus taeda* and 990 for *P. palustris* to achieve the same diameter. Apparently, the efficiency with which each species occupies space varies considerably among species. The maximum size–density relation is a powerful tool for determining tree size and shape.

Hydraulic Architecture

The leaves displayed by branches in the canopy to capture light energy and fix carbon also transpire large amounts of water. Transpiration is a consequence of opening stomata to exchange CO_2. In addition, it serves at least three other purposes: (1) it moderates leaf temperature variation by evaporative cooling; (2) it transports mineral ions from the soil to leaves and ends of branches; and (3) it transports information about the environment from the roots to the leaves and branches. The necessity to transport large amounts of water from the soil to the leaves requires a special architecture of stems and leaves dictated by the properties of water, the physical environment, and the plant.

As soon as the stomata open, water evaporates from the inside of the leaf, causing a drop in water potential. Water moves into the roots from the soil and up the xylem from the roots to replace the transpired water. It moves along xylem conduits down a water potential gradient. The water is under tension and resists cavitation due to cohesive forces. The xylem provides a rigid conducting system of tubes where the secondary cell walls are the tubes and the lumens are the conducting voids filled with water. Gymnosperm xylem is composed mainly of very small closed tracheids, and in angiosperms the conducting elements are mainly vessels, thousands of times larger than tracheids, composed of stacked vessel elements with perforated end-walls. Water moves between conducting elements through pits along the sides and ends.

Flow through the xylem is proportional to its conductance and the driving force. Conductance depends on diameter of the lumens, conduit number, roughness of the interior walls, and restrictions of the pits. The driving force is a pressure difference in water potential set up by transpiration from the leaves. To maintain water flow the xylem must be constructed to have a conductance sufficient to transport water under a driving force that can be created and sustained in the conduits. The average driving force across the entire plant is essentially the water potential difference between the root tip and the leaf tip per unit of length ($MPa\,m^{-1}$). The driving force may not be of the same magnitude throughout the plant. If the water potential gradient is too small anywhere along the xylem the water will not move.

Water flow occurs when the water potential difference is adequate to create a flow. The greatest potential differences and greatest water flows occur when soil water is plentiful and the water potential is high. As soil water declines the water potential in the plant also declines to maintain water flow. Eventually, water potential in the plant will decline to a level that increases the risk for cavitation, a break in the water column filled with air or water vapor. Water flow in a conduit ends when a cavitation occurs and does not resume until it is refilled. If cavitations become numerous and transpiration continues, water potential must drop further to maintain flow in the remaining flow channels. The decreasing water potential may provoke runaway cavitation, a vicious cycle of increasing cavitation and decreasing water potential that can continue and eventually result in total failure of the xylem to conduct water. There is a lot of evidence that trees often approach low water potentials close to the threshold for catastrophic cavitation at midday on sunny days. Stomata close just in time to prevent disaster. In fact, some persons wonder if that is not the main purpose for stomata.

There is a potential for xylem characteristics that promote high conductivity and those that protect against cavitations to have conflicting effects. Conductivity can be increased by producing larger-diameter conducting elements with few flow constrictions between them; however, there is some evidence these qualities may increase the vulnerability to cavitation. Although it seems that high conductivity and low vulnerability to cavitation would be beneficial traits, the research results concerning a possible trade-off between these two traits are not conclusive. On the other hand, high vulnerability of certain plant parts could turn them into expendable parts that cavitate to protect the rest of the plant from excessively low water potentials.

Canopy architecture must meet the requirement that the xylem conduct sufficient water to meet transpiration demands. The capacity to absorb and transport water to the transpiring leaves depends on conductivity and vulnerability to cavitation of the xylem and rhizosphere. For a given root area/leaf area ratio this capacity is determined by hydraulic properties of the xylem and soil (**Figure 3**).

Stem length and leaf area will be determined by the hydraulic properties of the xylem in addition to root absorbing capacity and the capacity of the soil to provide water.

Recent research findings have pointed to the possibility that plants can fine-tune water use through signaling soil water availability and controlling xylem conductivity. Roots may be sending a

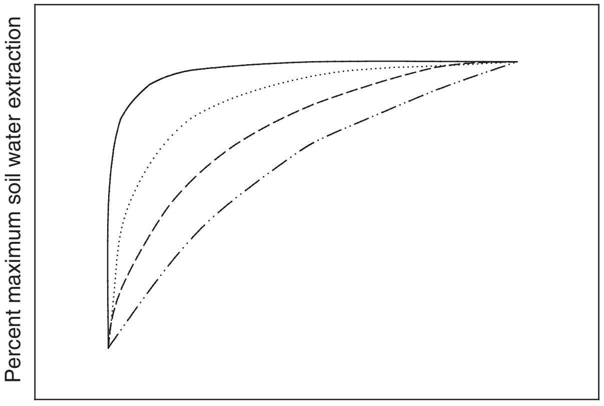


Figure 3 The maximum soil water extraction potential before cavitation causes failure to conduct somewhere in the soil–plant system occurs at the highest attainable root area/leaf area ratio. Decreasing soil water extraction potential occurs with declining root area/leaf area ratio due to loss of conductivity first in the xylem and later in the rhizosphere. Each curve represents the relation between extraction potential and root area/leaf area ratio for a different soil and xylem type. The upper curve could be a loam soil and drought-resistant species highly resistant to cavitation and the lower curves a sandy soil and drought-susceptible species not resistant to cavitation. Modified with permission from Hacke UG, Sperry JS, Ewers BE, *et al.* (2000) Influence of soil porosity on water use in *Pinus taeda. Oecologia* 124: 494–505.

signal in the water flow to the leaves to regulate stomatal opening depending on soil water status. Research has indicated that the ion content in the xylem sap influences hydrogels and xylem conductivity. Hydrogels in the pit membranes between xylem elements may open and close pit pores to increase and decrease conductivity to different parts of the canopy. The question is whether the phloem or some other mechanism adjusts xylem conductivity depending on canopy demands. Both mechanisms of fine-tuning water use would mean the tree would be less subject to low water potentials and water stress. Tree architecture could be more closely tuned to environmental demands without heavy overbuilding to produce xylem with excess conductivity or excess protection against cavitation.

Conclusions

Tree growth is started by linear primary growth of the apical meristem which is followed by volume growth of the secondary lateral meristem. Although this constrains the plant form, trees have evolved a startling variety of architectural types. The shoot is elaborated and multiplied to produce a canopy which serves the purpose of capturing light energy and facilitating the reproduction of adapted types through flowering. Inherited architectural types have been identified and described. They range from the steeply conical forms that shed snow and ice in cold climates to the deliquescent crowns that dominate the forest and capture a good share of the solar radiation in dense tropical forests. The greatest variety of inherited architectural types is found in tropical forests.

The main environmental factor shaping canopy development is the radiation environment. Phytochrome is the substance in plants that interprets the radiation environment and elicits a light response in almost all growth activities. Although plants appear to grow to the light, the elongation response to light is a mechanism to avoid shade. Increased understanding of the shade response improves the interpretation of canopy development and produces better management of stand density. Despite genetic engineering being tedious and complicated because of interactions among the different phytochromes and a potential for negative effects of genetic transformations, it appears to show a lot of promise for increasing harvest yield in trees. It is easy to imagine there may be economic value for an increased shade avoidance response that produces trees that grow faster in height, straighter, and with fewer branches. The size and shape of trees in dense stands follow a trajectory defined by the maximum size–density relation. An interesting question is whether phytochrome plays a role in the effects of competition described by this relation.

Trees must transport large amounts of water to transpiring leaves. Recent research suggests that the conducting system from the roots, through the xylem to the leaves is far more than just passive tubes responding to physical laws. Xylem morphology and anatomy balance conductivity with protection against cavitation. Cavitation in some plant parts may protect others against low water potential. Signaling within the plant and variable xylem conductivity may permit fine-tuning of water use by the tree. These mechanisms may allow tree architecture that is not excessively expensive and overbuilt to protect against water stress.

See also: **Ecology**: Forest Canopies. **Tree Physiology**: A Whole Tree Perspective; Canopy Processes; Xylem Physiology.

Further Reading

Cannell MGR, Thompson S, and Lines R (1976) An analysis of inherent differences in shoot growth within some north temperate conifers. In: Cannell MGR and Last FT (eds) *Tree Physiology and Yield Improvement*, pp. 173–205. New York: Academic Press.

Drew TJ and Flewelling JW (1977) Some recent Japanese theories of yield–density relationships and their application to Monterey pine plantations. *Forest Science* 23: 517–534.
Hacke UG, Sperry JS, Ewers BE, *et al.* (2000) Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124: 495–505.
Hallé F, Oldeman RAA, and Tomlinson PB (1978) *Tropical Trees and Forests*. Berlin, Germany: Springer-Verlag.
Horn HS (1971) *Adaptive Geometry of Trees*. Princeton, NJ: Princeton University Press.
Landsberg JJ and Gower ST (1997) Canopy architecture and microclimate. In: Landsberg JJ and Gower ST (eds) *Applications of Physiological Ecology to Forest Management*, pp. 53–91. New York: Academic Press.
Lanner RM (1976) Patterns of shoot development in *Pinus* and their relationship to growth potential. In: Cannell MGR and Last FT (eds) *Tree Physiology and Yield Improvement*, pp. 173–205. New York: Academic Press.
Prusinkiewicz P (1998) Modeling of spatial structure and development of plants: a review. *Scientia Horticulturae* 74: 113–149.
Reineke LH (1933) Perfecting a stand–density index for even-aged forests. *Journal of Agricultural Research* 46: 627–638.
Romberger JA (1963) *Meristems, Growth, and Development in Woody Plants*. Technical bulletin no. 1293. Washington, DC: US Department of Agriculture Forest Service.
Smith H (2000) Plant architecture and light signals. In: Marshall B and Roberts JA (eds) *Leaf Development and Canopy Growth*, pp. 118–144. Oxford, UK: Blackwell.
Sperry JS, Adler FR, Campbell GS, and Comstock JP (1998) Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant Cell and Environment* 21: 347–359.
Tyree MT and Ewers FW (1991) The hydraulic architecture of trees and other woody plants. *New Phytologist* 119: 345–360.
Tyree MT, Davis SD, and Cochard H (1994) Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability of dysfunction? *IAWA Journal* 15: 335–360.
Zwieniecki MA, Melcher PJ, and Holbrook NM (2001) Hydrogel control of xylem hydraulic resistance in plants. *Science* 291: 1059–1062.

Root System Physiology

M A Topa, Boyce Thompson Institute for Plant Research, Ithaca, NY, USA

Introduction

The biotic and abiotic interactions that occur between tree roots and the soil rhizosphere environment are easily the most complex and least understood interactions in plants. Questions concerning the 'missing' carbon sink in terrestrial ecosystems under various global climate change scenarios have increased our interest in elucidating the role below-ground systems play in carbon sequestration and carbon/nutrient cycling. Fine root systems (roots ≤ 2 mm diameter + associated rhizosphere biota), in particular, play a critical role in forest ecosystem function, with more than 50% of annual net primary productivity allocated below ground in many forests. Similar to their aboveground ephemeral counterparts (leaves), fine roots are relatively short-lived, but are the principal tissues for below ground resource acquisition. Yet fine root system demography (i.e., annual production, lifespan, and timing of root initiation and mortality) and function remain one of the most difficult and least understood areas of study because of its complex biodiversity and dynamic nature. The opacity of the soil and complex nature of the root/rhizosphere biotic system pose unique challenges to tree biologists studying root system function and belowground biodiversity.

Because of these challenges, our understanding of root system structure and function in trees is based largely on highly controlled seedling and mesocosm studies. However, to scale from seedlings to mature trees, root system biologists must consider how root function (much of it driven by carbon and nutrient source–sink relationships) and root ontogeny change as seedlings mature (**Table 1**), and how the biodiversity of rhizosphere microorganisms in the field alters root system function. As trees age, whole-plant source–sink relationships change, and nutrient demands are buffered by stored reserves and internal recycling of N and P. Storage carbon plays a critical role in buffering day-to-day or seasonal fluctuations in the carbohydrate supply to roots. Balanced partitioning of recently fixed carbon between immediate use and storage is essential for plant growth and for survival during stress. If an environmental stress decreases the photosynthetic capacity of a tree, then the demand on carbon reserves increases. Because of their low buffering capacity, seedlings are more dependent upon recently acquired nutrients and recently fixed carbon than mature trees, exhibiting a more immediate response and greater susceptibility to environmental stresses than observed in older trees. Consequently, the biggest challenge facing root system biologists is finding new technologies that will allow us to examine *in situ* root system function and demography on trees of variable age or size, with an increased emphasis on mature trees.

As seedlings mature into saplings and trees, their perennial roots will modify the physical, chemical,

Table 1 Comparison of some structural and functional characteristics of seedlings and mature trees that will alter shoot/root relationships and root function

Structure/function	*Seedling*	*Mature tree*
Carbohydrate storage	Low	High
Carbon allocation	None to reproduction, higher to foliage than roots	Higher proportion to reproduction, roots, storage
Drought resistance	Low	High
Leaf conductance	High	Low
Dependence upon recently acquired nutrients	High	Low; buffered by stores
Nutrient retranslocation	Insignificant	High
Proportion of fine roots in secondary:primary growth	Low	High
Proportion of fine roots to total root biomass	High	Low
Proportion of photosynthetic tissues to total biomass	High	Low
Rate of net photosynthesis	High	Low
Root system growth and metabolism	Greater dependence on recently assimilated carbon	More buffered by storage carbon

Modified from Vogt KA, Publicover DA, Bloomfield J, *et al.* (1993) Belowground responses as indicators of environmental change. *Enviromental and Experimental Botany* 1: 189–205.

and microbiological characteristics of their soil environment. Rhizosphere microorganisms such as mycorrhizae, *Rhizobium*, rhizobacteria, and mycorrhizal helper bacteria can stimulate tree growth through enhanced mineralization and nutrient acquisition, biological control of pathogens, and production of plant growth regulators. Tree roots in the field are generally colonized by a high diversity of mycorrhizal species, with the degree and rate of colonization by individual fungal species changing temporally, spatially, with tree or stand age, and with soil and climatic environments. Functioning of the mycorrhizal root and its overall effect on tree growth are mediated by a hierarchy of biotic and abiotic factors at the rhizosphere (soil chemistry, texture, moisture, temperature, and biota), community (plant competitors, animal associates, and tree pathogens) and ecosystem (precipitation patterns, temperature dynamics, and atmospheric chemistry) levels. Since over 90% of the world's land plants belong to families that are commonly mycorrhizal, root function of most trees cannot be examined without considering how mycorrhizas modify the soil environment and host growth. Mycorrhizal associations are discussed in greater detail elsewhere (*see* **Tree Physiology**: Mycorrhizae), but a limited discussion on how they alter tree root function is presented here. Although an entire book could be written on the subject of tree root physiology, I focus on the following aspects of tree root structure and function: root architecture and development, fine root system turnover, and fine root system function. For a more in-depth discussion of these and additional topics, I refer the reader to the list of further reading at the end of this article.

Root Architecture and Development

Root systems of higher plants show considerable architectural variation between species, within a species, and within an individual root system. This variability suggests that any genetic predisposition in root architecture is modified by the external soil environment. In long-lived perennial species, the degree of root plasticity is probably an adaptive response to spatially and temporally heterogeneous soil environments, enhancing a tree's ability to compete for limiting soil resources. Root systems of trees are often described as one of two types: those with taproots that grow rapidly downward, with taproot and lateral roots penetrating lower soil horizons, and those with more shallow, slower-growing primary roots and extensive, rapidly growing lateral roots. However, intraspecific variation in root growth is so great because of soil environmental modifications that interspecific comparisons can be difficult, and generalizations about species rooting depth and spatial deployment are misleading for many species. Certain species are more plastic than others with regard to environmental control of root architecture and spatial deployment in soils. For example, red maple (*Acer rubrum*) develops shallow, lateral roots in swamps and deep taproots in drier, upland soils, whereas some *Eucalyptus* species in dry areas develop a long taproot, but form a shallow root system on better sites.

In general, tree roots will grow in that portion of the soil where moisture, aeration, mechanical properties, and fertility are most favorable. A deep taproot system with a substantial number of lateral roots penetrating the lower soil horizons is typical of easily penetrable, often droughty soils. In contrast, shallow, platelike rooting is a response to edaphic limitations that restrict root growth to upper soil horizons, such as mechanical impedance of lower soil horizons or high water tables found in flooded soil environments. In more easily penetrable soils, the highest density of fine roots is often found in upper 0–10 cm soil horizons because these horizons are generally more aerated, have a higher organic matter content (with higher pools of organic N and P), are more fertile than deeper soils, and are well watered by summer precipitation. This is especially true in tropical and many temperate zone forests. In coniferous forests, rooting density in upper soil horizons tends to increase with stand age, presumably because canopy closure reduces understory competition and the litter layer becomes deeper and well established.

One of the common complaints among tree root biologists is the lack of standardization of root classification systems, making interstudy comparisons difficult and confusing. The problem is not a recent one, reflecting the complex and highly plastic nature of tree root systems growing in a dynamic environment. Studies dating from the early twentieth century used various classification systems that were intertwined with very elaborate, descriptive elements of form, often personalized by the various researchers. Lateral roots were described as: growth roots; long, main, and pioneer roots; surface roots, pioneers, seekers, and searchers; leaders; runners and pioneers; extension roots; primary laterals; or simply laterals or long laterals. More recent ecological, physiological, and silvicultural studies often select a classification system (**Table 2**) based on the ease of use with their particular system (e.g., seedling versus mature tree, greenhouse versus field-grown plants) or experimental design (soil cores, ingrowth cores, minirhizotron observations, etc.). Unfortunately, most of these classification systems do not emphasize differences in morphology or root function, often lumping together roots that may have very different lifespans and function. This is particularly true for smaller-diameter roots ≤ 1.0 mm. Consequently, many researchers use a combination of classification systems to describe their roots. In those species such as *Pinus* that are strongly mycorrhizal, more emphasis needs to be placed on discriminating between mycorrhizal and nonmycorrhizal roots because of differences in lifespan, morphology, and function.

The heterorhizic root system is perhaps one of the most function-oriented classification systems that has withstood the test of time, in part because of its distinction between mycorrhizal and nonmycorrhizal roots. A heterorhizic root system is composed of long lateral and short roots, and is best typified in *Betula*, *Fagus*, and *Pinus*. Long laterals are first- and second-order roots (using developmental terminology) that generally originate in the root collar region, are considered permanent, and increase in diameter by undergoing secondary growth via a cambial layer. Individual long roots exhibit cyclic growth activity independent of each other, with pauses in growth often marked by metacutization. Metacutization is a process of lignification and suberization, resulting in

Table 2 Tree root classification systems

Developmental	Based on the order in which roots arise from primary root or taproot. First-order root arises from primary root or taproot; second-order root arises from first-order root; third-order root arises from second-order root. Often used in seedling studies when entire root is harvested since order of development is easily discernible
Architectural	Based on relationship to smallest root. The ordering system is the complete opposite of the developmental system, with smallest roots labeled first-order. Used in seedling or field studies
Heterorhizy	Long- and short-root habit exemplified by Betulaceae, Fagaceae, and Pinaceae. Long lateral roots are long-lived (many as old as the tree), are subdivided into various types depending upon diameter and point of origin, exhibit cyclic growth with pauses marked by metacutization, and are the framework of the root system. Classes of long roots, based on decreasing diameter, include: pioneer $>$ mother $>$ subordinate mother. Short roots are short-lived, typically ≤ 5 mm in length, do not undergo secondary growth, and are commonly mycorrhizal. Applicable to field studies
Woody/nonwoody roots	Used for some angiosperms not readily classified by long and short roots (e.g., red maple). Framework of permanent woody roots bearing many fans of relatively short-lived nonwoody roots. Nonwoody root fans consist of second- and higher-order nonwoody roots emerging from a first-order nonwoody root (developmental classification terminology)
Coarse/fine roots	Nonstandardized classification system based on root diameter only. The various root diameter classes vary with different studies, but fine roots are often defined as ≤ 2 mm. However, upper-diameter size limits for fine roots vary from 0.5 to 10 mm. Most often used in field ecosystem studies

a resting root that is protected against significant fluctuations in soil environmental conditions such as drought. Short roots are more ephemeral and arise from root primordia similar to those giving rise to long lateral roots, but are characterized by rounded tips with no true root cap, slow rates of cell division, short length, and no secondary growth. Short roots are considered important sites of water and nutrient uptake, and are commonly mycorrhizal, particularly in *Pinus*.

When considering the functional implications of root architecture in trees, it is important to recognize that tree root systems contain various classes of roots that differ functionally and morphologically. Large woody roots are long-lived and are functionally important for carbohydrate and nutrient storage, for structural stability and anchorage, and as transport conduits between fine roots and stems. Since nonmycorrhizal and mycorrhizal fine roots function primarily in water and nutrient acquisition and are often short-lived, enhanced plasticity of the fine root system response versus larger woody roots may be more critical for capturing a heterogeneous supply of soil resources. Accumulating evidence from minirhizotron and other studies suggests that plasticity in fine root initiation, proliferation, and lifespan responses to changes in soil moisture, temperature, and fertilization are important for water and nutrient acquisition in heterogeneous soil environments. Fine root initiation from long-lived deep or other favorably located lateral roots is a competitive advantage for trees when competing with herbaceous understory species for limiting soil resources.

From a carbon standpoint, it may be more cost-effective to shed roots in an unfavorable soil location or during unfavorable times during the year and to construct new roots in potentially more favorable microsites, rather than maintaining existing roots that are less capable of acquiring water and nutrients. However, if the nutrient supply in the new location is short-lived, or a competitor occupies the site more effectively, then root proliferation would not be cost-effective; consequently, there is a certain amount of risk involved in this strategy. In forested ecosystems experiencing a seasonal drought typical of Mediterranean climates, upper soil horizons dry out during the long drought periods. Fine root systems often proliferate in these upper horizons during the wet periods (most likely because of the higher organic matter and nutrient content of soil in this layer), but experience high mortality during the drought. Trees become more dependent upon deep, more stable sources of water during these dry periods, and it is not unusual for fine roots to proliferate from preexisting woody roots in deeper soil horizons. It has been suggested that functional specialization may occur in trees that have two distinct layers of fine root growth in the soil, with the upper layer of roots primarily responsible for nutrient uptake and the lower layer meeting the bulk of the tree's water demands.

Because of the technical difficulty in monitoring root growth *in situ*, most available experimental data on the functional implications of tree root growth and architecture are from destructive harvests or a continuous monitoring via minirhizotron technology of only a portion of the root system. Magnetic resonance imaging (MRI) is an innovative, nondestructive technique in which functional roots can be visualized as a three-dimensional image set within a potting container or intact soil core, and changes in root growth and architecture can be monitored *in situ* over time. The application of this technique to study roots in soil was initially explored over a decade ago. The technique is especially powerful because it provides not only spatial information describing the geometry of root extension through the soil, but it has the ability to distinguish functional from nonfunctional roots *in situ*, as well as the development of water depletion zones in the rhizosphere. The ability of MRI to distinguish functional roots within an undisturbed soil volume provides a unique and powerful tool for examining *in situ* functional implications of root growth and architecture in seedlings over time. New technologies used in combination, such as ground-penetrating radar and stable isotope technology, may provide a better understanding of functional implications of lateral root architecture and distribution of trees in the field.

Fine Root System Turnover: Carbon Costs

The larger woody supportive roots extending from the base of a tree are long-lived (often as old as the tree) and comprise most of the lateral root biomass. However, woody supportive roots account for little of the tree's total root length and metabolic carbon demand. In contrast, fine roots comprise only 5–10% of total root biomass, yet can account for up to 90% of the tree's total root length. In many forests, the annual carbon cost for fine root system production and maintenance may account for 30–75% of net primary productivity, indicating that fine root system carbon demands may represent one of the largest carbon sinks in forested ecosystems. However, estimates for both annual production and lifespan are biased by the methodology and calculations used, making cross-study comparisons difficult. Consequently, we have a poor understanding not only of what controls root lifespan, but how much annual carbon is used to support fine root system (roots + mycorrhizal tips + extramatrical hyphae) growth, respiration, maintenance, nutrient uptake, carbon exudation, and storage reserves. Of these, root system respiration is probably the biggest carbon sink, accounting for up to half of the carbon that is allocated below ground. The high percentage of net primary productivity (NPP) allocated to tree root systems suggests that, although roots may be the most distant carbon sinks from source leaves, they are not the 'poor relations,' having more control over the amount of fixed carbon that is allocated to them than previously thought.

Recent studies using minirhizotron (**Figure 1**) and soil core methodologies suggest that fine root system lifespan is a function of stand characteristics, climate or latitude, tree or stand age, species and ecotype, soil environmental variables such as fertility, water availability, temperature, and soil depth at both stand and microsite levels, carbon status of the tree, timing of root birth, root diameter, root class or type, root order, mycorrhizal colonization, root pathogens, and herbivory. The high variability in fine root system demography (timing of birth and death, and overall lifespan) at the soil microsite level suggests that soil environmental characteristics, in particular, modify stand, seasonal, and genetic controls, and that plasticity is an opportunistic response to a variable resource environment. The lifespan of fine roots in conifers is generally longer than in deciduous trees, ranging from less than 1 to over 20 years, depending upon root order and diameter, with lifespan generally increasing with root diameter.

In contrast to their aboveground ephemeral counterparts (leaves), fine roots of most trees do not appear to have any active separation from the parent in the form of abscission layer. Although lateral branch 'scars' have been observed on parent

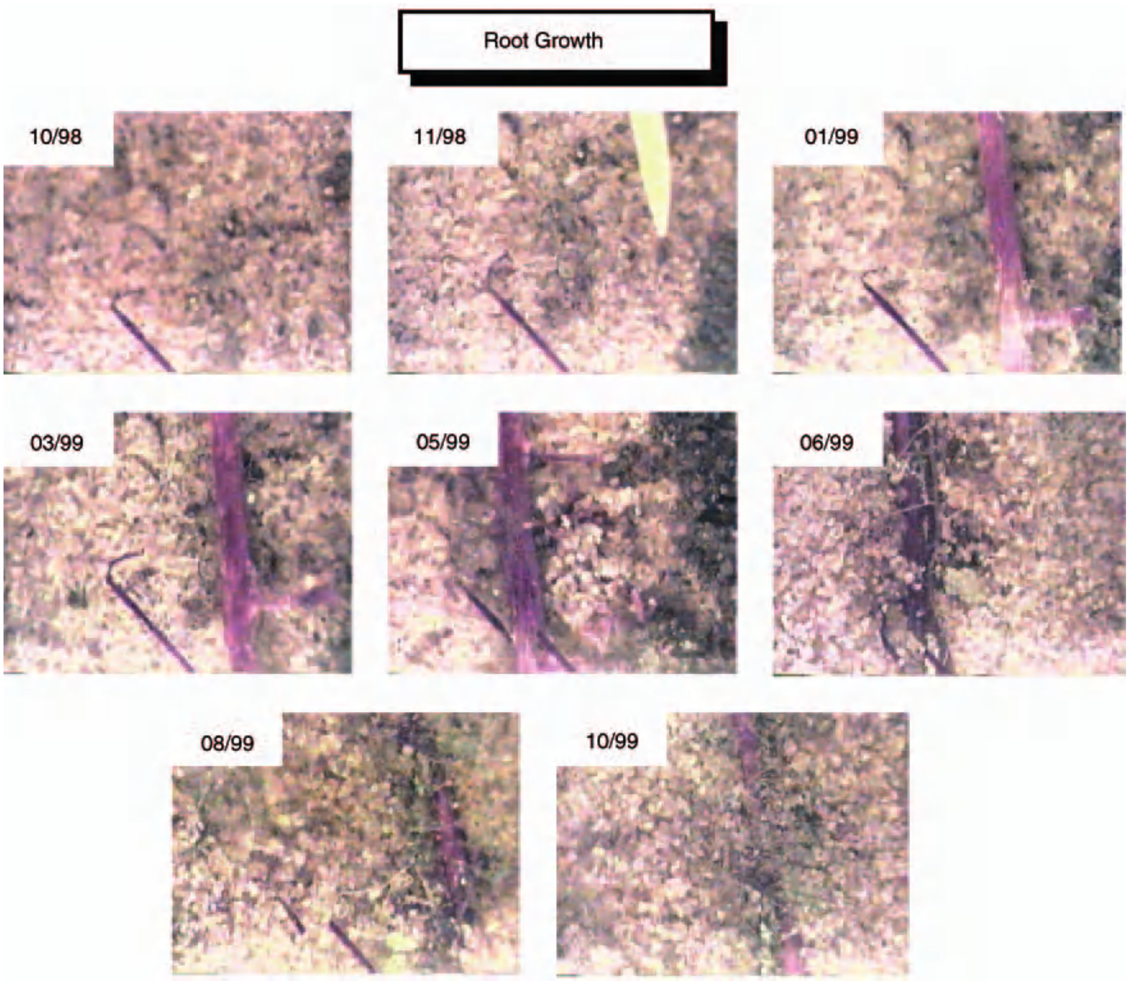


Figure 1 Example of how *in situ* root growth is followed over time using minirhizotron technology. A clear plastic tube is inserted in the ground at a 45° angle, and a camera is inserted into the tube at weekly or monthly intervals, recording images of the same root cohorts growing next to the tube. In the example, a new white root tip appears in 11/98, undergoes browning and secondary growth with bark development, and starts to degrade and disappear by 10/99.

roots in the field, the mechanism causing the mortality of branches is unknown. The development and morphology of the 'scars' have not been examined – the phellogen (bark cambium) of the parent root may simply seal the tissue off once the lateral root branch has started to senesce, as in a wounding response. In trees, suspension of root growth does not necessarily imply that the root is dying. The factors leading to growth suspension (a process called metacutization) may or may not be the same as those that result in root shedding. The mechanism by which roots are shed is poorly understood. It was once thought that roots have a predetermined lifespan and died when their finite supply of carbon was exhausted. However, experimental evidence indicates that root carbohydrate stores are dynamic, varying with season, on a diurnal basis, with age, environmental stress, and tree physiology, and can be replenished throughout the lifespan of the root. Experimental manipulation of the carbon supply has shown that root longevity is strongly influenced by the carbon status of the plant. The internal mechanism is probably one that ultimately restricts carbohydrate transport to the roots and, once root storage reserves have become exhausted, the affected roots will die.

Fine roots appear to have an indeterminate lifespan and die when environmental conditions become unfavorable (e.g., during a long drought), and/or the carbon cost of maintaining roots becomes too great relative to other carbon sinks in the tree. The high root mortality associated with heavy fruiting in *Prunus* and *Citrus*, or with stresses (e.g., defoliation) that can result in carbon shortages in trees may be necessary to maintain whole-tree carbon balance. Atmospheric pollutants such as ozone can affect root growth in trees by reducing the supply of photosynthate available for transport to roots due to inhibitory effects on photosynthesis and leaf growth, and increased leaf carbohydrate demands resulting from accelerated leaf turnover, membrane repair processes, and synthesis of antioxidants. Since most tree–fungal interactions are mediated through a carbon/nutrient exchange within the association, the extent of mycorrhizal formation is particularly sensitive to the availability of carbohydrate from the shoot, and thus, any environmental stress that alters this availability.

Because most forest soils are N- and/or P-deficient, many tree species have coevolved a high dependence on mycorrhizal associations. Mycorrhizae account for 5–80% of total fine root system biomass in conifers, and up to an additional 5–20% of net primary productivity. Hyphae of mycorrhizal fungi have a smaller diameter than roots and cost roughly 10% more to construct, but vastly increase the exploitation potential of tree roots because of their high surface area. In ectomycorrhizae, short roots are covered with a mantle of hyphae from which extramatrical hyphae extend into the soil (**Figure 2**). Over 200 individual hyphae have been observed emerging from a single mycorrhizal tip. An individual hypha may extend more than 2 m and form more than 100 lateral branches. Mycorrhizal associations come at a considerable carbon cost to the tree, but they offer protective benefits against root pathogens, increase the exploitation potential of a root system for immobile nutrients such as phosphate, ammonium, copper, and zinc, protect trees from heavy metals, and help maintain the tree's water status during dry periods.

Although construction costs of mycorrhizal root tips are higher than nonmycorrhizal roots, there is some evidence suggesting that mycorrhizal roots live longer than uncolonized roots on the same tree. This may be due in part to their protective effect against root pathogens, or to the mycorrhizal root's efficient ability to exploit limiting resources from the soil, ultimately increasing carbon flow into mycorrhizal roots. Endomycorrhizal and ectomycorrhizal fungi protect roots from pathogenic organisms possibly by: (1) producing antibiotics and antifungal chemicals (such as phenolic compounds); (2) encouraging the growth of beneficial microorganisms in the rhizosphere; and/or (3) physically protecting the root tips. Unlike woody and fine lateral roots, mycorrhizal roots do not undergo secondary growth, and are more susceptible to pathogenic invasion. Consequently, protecting the root from pathogens is in the mycorrhizal fungi's best interest. Roots of trees brown as they age and undergo secondary growth. In the region immediately proximal to an uncolonized white tip, browning occurs as epidermal and cortical

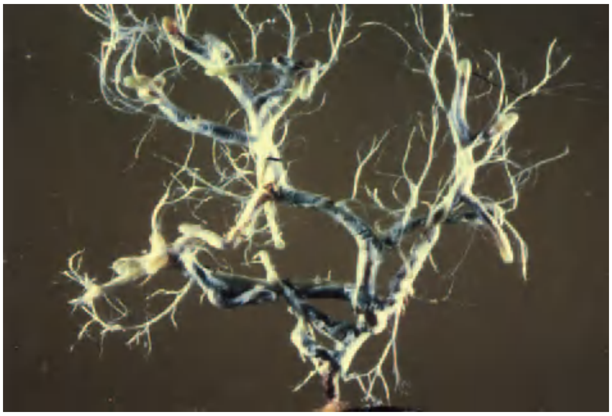


Figure 2 Ectomycorrhizal root of *Pinus* spp. Note extramatrical hyphae emanating from bifurcated root tip. Courtesy of Dr. Larry Peterson.

tissues break down and fill with condensed tannins. The tannin and suberin deposits are believed to serve a protective function against both pathogenic and mutualist fungi in this tannin zone and in tissue that has undergone secondary growth with a well-developed periderm.

Fine Root System Function: Nutrient Uptake

Supplying trees with nutrients is one of the major functions of their root systems. Perennial root systems of trees can modify rhizosphere soil over time, often enhancing the soil chemical environment by increasing its organic matter content and nutrient and water retention capacities, and making it a more hospitable place for beneficial rhizosphere microbes. Although the soil solution is the immediate source of nutrients for plants, it is in equilibrium with nutrients in the solid soil phase. When depleted by roots, the soil solution can be replenished by desorption and ion-exchange reactions. Whether energy is expended in uptake (traditionally referred to as active uptake) and if uptake is under metabolic control are in part determined by whether uptake is with or against the electrochemical gradient and if the ion is transported across the plasma membrane from the root apoplast into the symplasm.

The radial pathways for ion and water movement are extracellular (apoplastic) and intracellular (symplastic). The apoplastic pathway is a system of pores and wall surfaces outside the plasma membranes of epidermal, cortical, and stelar parenchyma cells, with the Casparian band in the endodermis blocking apoplastic passage of ions into the stele. In the symplastic pathway, plasmodesmata provide continuity or passage between the cytoplasm of living cells, offering a pathway of low resistance. In trees, nutrient uptake along the root axis varies with the nutrient. Uptake of some nutrients, such as calcium and iron, appear to be restricted to apical zones, while uptake of others (such as phosphate and nitrate) occur in older tissues of roots, even those undergoing secondary growth. How nutrients are transported across the periderm of fine roots is unknown, but field and greenhouse studies suggest that it does occur.

The ability of tree roots to acquire nutrients from a given volume of soil may vary with species, genotype, degree of mycorrhizal colonization, and rhizosphere microbial populations. Many plant nutritionists prefer to use the term 'acquisition' when referring to nutrient uptake by roots because it emphasizes that more is involved in getting inorganic nutrients into plants than ion transport across cell walls. Nutrient acquisition is the dynamic interaction between plant, soil, and rhizosphere microbial properties, and is a function of root growth and development, overall plant growth, nutritional status of the plant, uptake (kinetic) properties of the root transporter, concentration of nutrient at the root surface, transport properties from the soil to root (including mass flow and diffusion), mobilization of ions by roots (including desorption, dissolution, and hydrolysis of organic compounds), and mobilization by associated rhizosphere microorganisms (including mycorrhizal and bacterial associates). In mobilization, root exudates (H^+, HCO_3^-, reducing agents, chelating agents, and organic anions) are released into the rhizosphere to alter rhizosphere pH, to balance the electrochemical gradient resulting from anion and cation uptake, and to make some ions more available for plant uptake while excluding others (e.g., heavy metals). In addition, enzymes such as phosphatase are released by rhizosphere microorganisms and roots of some tree species, mobilizing organic sources of P that would otherwise be unavailable for uptake.

The nutritional characteristics of seedlings and mature trees, in particular, the nutrient transport systems, and what regulates these systems, are poorly understood. Although genotypic variation in nutrient uptake has been observed in many species, whether the differences are a result of genetically controlled differences in the transport system (e.g., maximum rate of uptake capacity ($V_{\max}$) or affinity of the transporter for the ion (K_m)), or are simply a consequence of differences in growth, is less clear. Studies addressing how growth controls nutrient uptake at the root plasma membrane are scarce. Many studies with herbaceous and woody species (the latter, seedling studies only) have found a positive correlation between nutrient uptake rates and relative growth, suggesting that plant 'demand' is an important determinant of nutrient uptake rate. However, in trees, nutrient storage may be as strong a nutrient sink as growth. Thus, any relationship between growth and nutrient uptake will be confounded by a tree's inherent capacity for storage and nutrient retranslocation from other plant tissues.

The stimulation of physiological uptake capacity and root growth in nutrient-rich zones and their suppression in nutrient-poor zones are well-documented responses to a spatially heterogeneous supply of nutrients in herbaceous species, and more recently, in some woody species. These compensatory responses may enable trees to grow in naturally heterogeneous soil environments by allocating limiting resources in ways that maximize nutrient absorption. Although the stimulation of uptake capacity in nutrient-rich patches is a well-documented response, the mechanism regulating uptake is not fully understood. Split-root experiments with herbaceous species have suggested that, when roots encounter a P-rich zone, uptake capacity not only increases but is maintained, despite high internal P concentrations in those roots. Accumulating evidence with herbaceous plants suggests that shoot 'demand' regulates N and P uptake and loading into the xylem, possibly via cycling of that nutrient in the phloem. Regulation of nutrient uptake in trees is complicated by their perennial long-lived habits, high storage capacities, and seasonal remobilization of certain nutrients, in particular, N and P. Recent studies suggest that organic forms of N and P in trees are more important storage forms of those nutrients than inorganic forms. In roots, immediate assimilation of N and P into an organic form would keep cytoplasmic concentrations of the inorganic form low, maintaining or stimulating continued uptake of that nutrient.

For nutrients that are highly mobile in the soil (e.g., NO_3^-), a high uptake capacity (a physiological response) is an important component of root competition where depletion zones of adjacent roots overlap. However, for immobile ions such as inorganic phosphate (P_i), stimulation of root growth in a nutrient-rich zone might be more critical than an increase in physiological uptake capacity. Phosphate concentrations of most soils are seldom higher than $10\,\mu mol^{-1}$ P. Diffusion of P to the root may limit P_i uptake more than any kinetic parameter controlling influx, i.e., V_{max} and even K_m. In soil-grown plants, higher uptake rates by roots growing in a P-rich zone will soon become limited by low P_i concentrations in the rhizosphere. Highly branched root systems are believed to be more efficient at exploiting soil for immobile ions such as NH_4^+ and phosphate. Consequently, for immobile nutrients, nutrient acquisition is probably most enhanced by increasing the surface area available for absorption via root proliferation, an alteration of root architecture, root hair initiation, or mycorrhizal colonization. In general, the finer the root, the greater the return per unit investment of carbon.

Spatial and temporal nutrient heterogeneity occurs in soils from both natural and managed ecosystems at scales relevant to individual plants; consequently, a plastic response in root physiology and/or in growth would be an important competitive trait. Temporal pulses of nutrients become available to plants during spring snow melt, during autumnal leaf fall, with seasonal rains, etc. Spatial patchiness of supply is common in most soils and greatest for immobile nutrients such as P_i. Soil tillage may increase the size of the patch, but not eliminate it. Fine root proliferation in a nutrient-rich patch is not necessarily cost-effective if the ion is highly mobile, the patch is short-lived, or a competitor occupies the patch more effectively. The degree of root proliferation is influenced by soil concentration and whole-plant demand for that nutrient, and may be species-specific. Root system response to patches may differ among species from different successional stages or nutrient status. For example, fast-growing species from nutrient-rich habitats may exhibit higher plasticity in physiological rates of uptake and root morphology, while slow-growing species from nutrient-poor habitats may conserve carbon by depending upon long-lived root systems, and respond to soil heterogeneity primarily by increasing uptake rates. However, this latter strategy would be less effective for acquiring immobile ions such as P_i and ammonium.

Because of their extensive hyphal network, mycorrhizal associations increase the exploitation potential of a root system for immobile nutrients such as phosphate, ammonium, copper, and zinc. Nutritional benefits of mycorrhizae are most significant in N- and P-deficient soils. Except in the most productive forests, N and/or often P concentrations in the soil generally limit growth of most trees, especially during periods when nutrient demands are high. Consequently, it is not surprising that many tree species, particularly coniferous species, have coevolved a mutualistic dependence on mycorrhizal associations, with development most pronounced in infertile than fertile soils, or where nutrients become available in seasonal flushes. It has been estimated that, when root growth is restricted, external hyphae of endomycorrhizae can deliver up to 80% and 25% of the plant's P and N requirements, respectively, with greater nutritional benefits possible in ectomycorrhizal associations.

Ectomycorrhizae improve host N and P nutrition in deficient soils by accessing organic pools that would otherwise be inaccessible to roots – this is particularly critical in forest ecosystems, where the largest pools of N (and P) are the organic pools. Proteins and other organic N compounds are bound in recalcitrant forms of organic matter or are chemically fixed in clays, which protect them from rapid microbial breakdown. Thus, even though soil N greatly exceeds plant N, many forested ecosystems are N-limited because only a small fraction of total N is available in an inorganic form to plants. However, mycorrhizae allow woody plants to compete with soil microorganisms for organic forms of both N and P. The ability of ericoid and ectomycorrhizae to use protein as a growth substrate is correlated with the production of extracellular acid proteinases in external hyphae, whereas extracellular acid phosphatases and phytase catalyze the release of P_i from organic complexes in the soil. Some tree species, particularly those that are adapted to highly organic, nutrient-deficient soils, appear to have proteinase, phosphatase, and phytase activity in nonmycorrhizal roots. However, because nonmycorrhizal roots are at a spatial disadvantage in competition with microorganisms, activity levels in nonmycorrhizal roots in the field are probably low compared with mycorrhizal roots. It is important to note that, although mycorrhizae increase the supply of N and P available to the host root apoplast, further uptake and transport of these nutrients across the root plasmamembrane into the symplast and ultimately xylem are dependent upon characteristics of the tree's transport system.

In the process of cation and anion uptake, roots of plants excrete protons, bicarbonate ions, and organic acids to their rhizospheres to maintain an electrical charge balance. However, in doing so, rhizosphere pH can be altered. Since the solubility of many nutrients in the soil is pH-dependent, plant roots can enhance solubility of a limiting nutrient (such as P) or decrease the solubility of potentially toxic elements (e.g., Al) simply by altering their rhizosphere pH. Other forms of root exudates associated with nutrient uptake include sugars, amino acids, acid proteinases, phosphatases, and phytases. The efflux of organic substrates from roots such as exudates, mucilages, lysates, and water-insoluble components associated with growth (sloughing of root cap cells and cell wall debris) are a significant source of carbon for microbial and mycorrhizal associates because they are easily assimilated. Colonization by mycorrhizal fungi is generally higher in roots with high (sugar) exudation rates. Microbial use of rhizodeposited carbon substrates has a major influence of nutrient availability in the rhizosphere, with the overall benefits to the tree (and forest) most likely justifying the carbon cost. Unfortunately, our understanding of root exudation, both benefits and costs, is limited by the technological difficulty in measuring this process *in situ*, particularly since any disturbance to the root will alter exudation and respiratory losses.

Fine Root System Function: Water Uptake

Plant water deficit has been implicated more than any other environmental stress as the most important soil parameter limiting carbon fixation, growth, and net primary production on a global scale. Up to 80–90% of the variation in diameter growth in trees can be attributed to variations in rainfall and plant water stress. Excellent reviews on the importance of water on tree growth, the absorption of water and the ascent of sap are provided in the further reading section. This section will focus instead on how tree roots respond to water stress. In dry soils, trees with large canopies and/or poor stomatal control are particularly susceptible to water stress. If water loss via leaf transpiration exceeds water absorption by roots, a tree must regulate its water use, find additional water sources, or find other means of conserving water while meeting metabolic and growth requirements to avoid hydraulic failure. Some hydraulic models have suggested that in the soil → root → leaf → atmosphere hydraulic pathway, xylem of fine roots may be the weak link and act as hydraulic 'fuses' analogous to the protective function of electrical fuses. By localizing any break or cavitation in the hydraulic pathway to the more vulnerable but ephemeral fine roots, trees can minimize root replacement and xylem-refilling costs. The tree can get rid of fine roots that no longer have access to a reliable water supply and allocate more carbon to root growth in soil microsites or horizons with a more abundant and stable supply of water.

Trees are capable of growing in a wide range of soils that differ greatly in their hydraulic characteristics, presenting different challenges to roots trying to extract water from them. For example, coarse soils lose more moisture and conductivity at higher water potentials than fine soils because of weaker capillary forces retaining water in the larger pore spaces. Consequently, plants growing in sandy soils may become water-stressed at relatively high soil water potentials compared to plants in fine soils. Trees can differ considerably in their potential for water extraction, depending upon root-to-leaf ratio, rooting depth and density, degree of mycorrhizal colonization, and their resistance to cavitation. Since water is absorbed via roots and lost via transpiration in leaves, the ratio of fine root area to leaf area must be high enough to avoid hydraulic failure in the rhizosphere (i.e., loss of hydraulic contact between the root and soil), while approaching maximum extraction potential. Not unexpectedly, both nutrient and water deficits in the soil generally lead to similar shifts in whole-tree carbon allocation, i.e., more carbon is generally allocated to root growth to enhance the exploitation potential of fine root systems. However, in coarse soils with high soil porosity, a tree's response to fertilization amendments could compromise its drought tolerance because fertilization generally decreases the fine root-to-leaf area ratio.

In arid environments and in forests that are subjected to seasonal drought, deep taproots and lateral roots growing in lower soil horizons (with a more stable water supply) may support much of the tree's water demands during times of water stress. Upper soil horizons are more subject to large fluctuations in water content than deeper soil horizons because of evaporation and plant water uptake, whereas deeper soil horizons are likely to be buffered by ground water recharge. In arid and semiarid environments, it is not uncommon for taproots to extend 10–20 m into the soil to tap into a more stable water source. Using stable hydrogen isotopic analysis of source water, several researchers have found that even riparian trees in arid and semiarid regions utilize ground water instead of less reliable surface water sources (i.e., stream water and precipitation). This utilization strategy may in part be due to the large fluctuations in stream discharge rates that generally occur during the lifetime of most trees in riparian habitats, helping the trees to survive periods of low discharge during extreme droughts.

Although deep roots provide access to a stable water source, trees are generally more dependent upon fine root growth in the more nutrient-rich upper soil horizons to meet the bulk of their nutrient requirements. Consequently, trees in forests experiencing seasonal drought often experience fine root proliferation in upper soil horizons during the wetter periods to maximize nutrient exploitation of these horizons, but high mortality during the seasonal drought. In less arid environments, this ability to switch among different water sources could increase a plant's ability to compete for limiting water resources when upper soil horizons dry out. Whether nutrient uptake by surface roots in the drier upper horizons continues to occur during this switch to deeper water sources is most likely a function of plant nutrient demands, soil moisture in these upper horizons, soil porosity, the degree of fine root system production, and whether hydraulic lift may be rewetting these drier horizons. In hydraulic lift, water absorbed by deep roots of trees or shrubs passes through roots in the drier, upper soil horizons, and rewets rhizosphere soil during periods when transpiration ceases (generally at night). The process is believed to be primarily passive, driven by root and soil water potential gradients. The 'lifted' rhizosphere water in these upper soil horizons is then reabsorbed the next day and transpired. Hydraulic lift has been demonstrated in tree species occurring in arid, semiarid, and even in some mesic forest environments. The persistence of hydraulic lift over long periods in otherwise dry upper horizon soils could prolong the lifespan and activities of fine root systems in upper soil horizons, improve ion mobility in rhizosphere soil, and maintain nutrient uptake in the more nutrient-rich upper horizon soils.

The root–soil interface, or rhizosphere, is a dynamic environment between the tree root, rhizosphere biota (both microbes and mycorrhizas), and soil environment. With the exception of nitrogen-fixing organisms and mycorrhizae, we know very little about how rhizosphere microbes (including those microbes associated with mycorrhizae) may alter root function and tree growth. It is impossible to study tree root physiology and forest (belowground) ecosystem function without considering rhizosphere biota. With increasing demands for shorter rotations and faster-growing trees in plantations, existing fertility of forest soils must be improved. A greater consideration of how forest management practices alter soil biology and root function could ultimately lead to more efficient tree root systems.

See also: **Tree Physiology**: A Whole Tree Perspective; Mycorrhizae; Nutritional Physiology of Trees.

Further Reading

Augé RM (2001) Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11: 3–42.
Chalot M and Brun A (1998) Physiology of organic nitrogen acquisition by ectomycorrhizal fungi and ectomycorrhizas. *FEMS Microbiology Reviews* 22: 21–44.
Eissenstat D and Yanai RD (1996) The ecology of root lifespan. *Advances in Ecological Research* 27: 1–60.
Esau K (1977) *Anatomy of Seed Plants*. New York: John Wiley.
Farrar JF and Jones DL (2002) The control of carbon acquisition by roots. *New Phytologist* 147: 43–53.
Johnston JM (2002) Forest ecosystem recovery in the southeast US: soil ecology as an essential component of ecosystem management. *Forest Ecology and Management* 155: 187–203.
Jungk AO (1996) Dynamics of nutrient movement at the soil–root interface. In: Waisel Y, Eshel A, and Kafkafi U (eds) *Plant Roots: The Hidden Half*, pp. 455–481. New York: Marcel Dekker.
Kozlowski TT and Pallardy SG (1997a) *Physiology of Woody Plants*. San Diego, CA: Academic Press.
Kozlowski TT and Pallardy SG (1997b) *Growth Control in Woody Plants*. San Diego, CA: Academic Press.
Smith SE and Read DJ (1997) *Mycorrhizal Symbiosis*. San Diego, CA: Academic Press.
Smith SE and Smith FA (1990) Tansley review no. 20. Structure and function of the interfaces in biotrophic symbioses as they relate to nutrient transport. *New Phytologist* 114: 1–38.
Sutton RF (1969) *Form and Development of Conifer Root Systems*. Technical communication no. 7. Oxford, UK: Commonwealth Forestry Bureau.
Vogt KA, Publicover DA, Bloomfield J, *et al.* (1993) Belowground responses as indicators of environmental change. *Environmental and Experimental Botany* 1: 189–205.
Waisel Y, Eshel A, and Kafkafi U (2002) *Plant Roots: The Hidden Half*. New York: Marcel Dekker.

Nutritional Physiology of Trees

P Smethurst, CSIRO Forestry and Forest Products and Cooperative Research Centre for Sustainable Production, Hobart, Tasmania, Australia

Published by Elsevier Ltd., 2004

Introduction

Healthy trees require balanced nutrition to support metabolism and growth. Nutritional physiology is the field of knowledge pertaining to the uptake, utilization, storage, and internal transport and recycling of mineral nutrients. Here, nutritional physiology is described where possible with particular reference to trees and forests. First, a brief historical perspective of major developments in this field is followed by a description of essential nutrients. Finally, some aspects that pertain more to trees than other plant forms are outlined, i.e., nutrient pools and cycling. Trees have somewhat unique nutritional aspects related to their longevity, size and, in common with some other plant forms, the generally heterogeneous and low-nutrient-availability conditions to which some trees are adapted.

History and Key Contributors

The early history of tree physiology is that of plant physiology in general (**Table 1**). As long ago as 2500 BC, writings mentioned the fertility of the land, e.g., in Mesopotamia. Since those times, and up until about the end of the sixteenth century, interest developed in the effect of soil amendments on plant growth. By the end of this period, it was recognized that each soil type provided a different sort of nourishment and that it was affected by amendments and related to the ash content of plants. The next century and a half was characterized by the search for this nourishment, which was referred to as the 'principle vegetation.' This period was accompanied by advances in chemistry that enabled analysis of plant and animal materials. It was not until 1775 that Francis Home's analyses and experiments indicated that there was more than one 'principle.' Field plot experimentation commenced in the nineteenth century around the period when Liebig and Sprengel arrived at the law of minimum, i.e., yield was in direct relation to the single most limiting nutrient and unrelated to the level of others. With further advances in chemical analysis and experimental techniques, the importance of nutrients present in ever lower concentrations became evident from about the midnineteenth century. During the twentieth century, much work was done on the precise role played by each nutrient using ever more sophisticated techniques, e.g., histology, microscopy, chemical purifications and analysis, and isotopic tracers.

Trees were included in some of these earlier studies, e.g., van Helmont studied the growth of a small willow, but specific studies of trees as distinct from other plant forms were not initiated until much later. During the twentieth century, some unique aspects of trees were elucidated, i.e., physiology of woody tissues, nutrient retranslocation, hydraulic properties, and nutrient budgets.

In recent decades, notable developments have occurred in understanding: (1) the processes delivering nutrients to roots; (2) the transport processes across plant membranes (e.g., during uptake by cells in roots and leaves); (3) the detailed biochemistry of nutrients; (4) the genetic and hormonal controls of a plant's response to its nutritional environment; and (5) nutritional effects on photosynthesis and assimilate partitioning.

Nutritional physiology has now reached the stage where individual or small numbers of genes have been identified that control specific nutritional process, e.g., nutrient transport across membranes. There is a remarkable degree of similarity in genetic make-up across the plant kingdom. Hence, processes studied in plants in general are also likely to be applicable to trees, but it appears that subtle differences in the control of genetic expression lead to the main differences in nutritional physiology between trees and other forms of plants.

Nutrients and Their Functional Roles

Carbon, hydrogen, and oxygen are essential for plant growth and are taken up as either CO_2 or water. Other elements essential or beneficial to growth are called mineral nutrients. Each mineral nutrient has one or more specific functions (**Table 2**). Essential nutrients are generally divided into groups based on concentration; macronutrients have concentrations greater than about $10\,\mu mol\,g^{-1}$ dry weight, and micronutrients less than this concentration. Other nutrients considered essential or beneficial for some higher plants are sodium (Na), silicon (Si), and cobalt (Co). There is also interest in selenium (Se), aluminum (Al), iodine (I), and vanadium (V), but further research is needed to clarify their status.

The concentration of ions in cytoplasm is maintained within limits imposed by the conditions required to maintain the integrity of organelles and cellular processes. An abundance of any particular ion will cause more of that ion to be stored at high concentrations in vacuoles or in other relatively nonreactive forms or locations. The distribution of

Table 1 Significant events in the development of tree nutritional physiology

Date or period	*Author(s)*[a]	*Significance*
2500 BC	Various	Fertility of land recognized
900–0 BC	Various	Amendments promoted fertility
1563	Palissy	Ash content of plants represented material removed from soil
1561–1624	Bacon	Unique nourishment in soil
1577–1644	von Helmont	Water was the only nourishment
1627–1691	Boyle	Chemical analysis indicated that plants contained salts, spirits, earth, and oil, which were all formed from water
1604–1668	Glauber	Saltpeter (KNO_3), not water, was the main component of vegetation
1643–1679	Mayow	Seasonal niter variations in soil implied uptake by plants
1700	Woodward	Growth dependent on impurities in water
1741–1820	Young	Pot experiments showed that substances added to soil could promote or retard growth
1775	Home	More than one principle in vegetation
	de Saussaure	O_2 uptake and CO_2 released by plants, but the opposite occurred under light and CO_2 was essential for growth; soil supplied ash and N; roots were selectively permeable to water and salts; plant composition varied with soil and age
1802–1882	Boussingault	Field plot experimentation
1787–1873	Sprengel and von Liebig	C came from the atmosphere, and H from water; alkaline metals needed to neutralize acids formed by plants as a result of metabolic activities; P necessary for seed production; toxicities related to excessive uptake and inadequate excretion; plant analysis led to fertilizer recommendations; law of the minimum
1843–*c.* 1890	Laws and Gilbert	N needed to be added to nonlegumes; soil fertility could be maintained by chemical fertilizers
1860–present	Various	Identification of essential and beneficial nutrients required in very low concentrations
1920	Hoagland	Composition of soil solution related to plant growth
1970–1991	Asher, Ingestad	Concepts and methods linking relative rates of growth, nutrient supply, and uptake
1977, 1984	Nye and Tinker, Barber	Mass-flow and diffusion theory in relation to nutrient supply and uptake
1950–1980	Passiourra	Soil–plant water relations
1970–1990	Jarvis	Forest water relations
1970–1992	Marschner, Mengel and Kirkby	Plant mineral nutrition
1960–1990	Various	Nutrient budgets of forest ecosystems; descriptions of tree root systems
1970–1993	Epstein, Clarkson	Kinetics of nutrient uptake
1991	Nambiar and Fife	Nutrient retranslocation in trees
1990s	Various	Genetic control of nutrition in several simple or agriculturally important plants

[a] Since 1900, it has been increasingly difficult to attribute significant advances to individuals, but some key examples are indicated; significant advances tend now to be marked more by key syntheses of an accumulation of many incremental advances than by major new discoveries.

nutrients within a cell is therefore not uniform but localized into zones of either storage or use. Forms, utilization, and storage of the essential nutrients are summarized as follows.

Nitrogen

Because of the importance of N in plant metabolism, leaf area development, greenness (chlorophyll amount and function), and overall plant growth and yield are strongly dependent on an adequate N supply. Most forest tree species grow well with either NH_4^+ or NO_3^- as their main N source, but a few have a preference for one or the other form. Nitrate is usually reduced to ammonia in the roots, but, with high levels of supply, reduction can be delayed until it reaches the leaves. Ammonia, which damages cellular processes, is rapidly incorporated into amino acids and its equilibrium with NH_4^+ is highly pH-dependent. In leaves, a complex and incompletely understood set of interactions between vacuolar, cytoplasmic, and apoplastic NH_3 and NH_4^+ concentrations occurs such that acceptable concentrations of NH_3 are maintained in the cytoplasm and these processes are mediated by ion-transporters in the membranes between these compartments.

Potassium

Potassium does not bond with C and is present in plant tissues (organic matter) as inorganic K^+. The main role of K is in water relations (turgor control) and in the neutralization of weak acids in the cytosol and chloroplast; enzyme activation is another

Table 2 Mineral nutrients essential for healthy growth of higher plants, including trees

Nutrient	*Adequate foliar concentration for many species (μmol g^{-1} DW)*	*Function*
Nitrogen (N)	1000	Amino acids, proteins, nucleotides, nucleic acids, chlorophyll, and coenzymes
Potassium (K)	250	Osmosis and ionic balance; stomata control; activates many enzymes; phloem loading; plant movement
Calcium (Ca)	125	Cell walls; enzyme cofactor; membrane permeability; regulates membrane and enzyme activities; secondary messenger
Magnesium (Mg)	80	Chlorophyll; activates many enzymes
Phosphorus (P)	60	Energy transport; nucleic acids, several coenzymes, phospholipids
Sulfur (S)	30	Some amino acids and proteins; coenzyme A
Chlorine (Cl)	3	Osmosis and ionic balance; probably photosynthesis reactions producing O
Iron (Fe)	2	Chlorophyll synthesis; cytochromes and nitrogenase
Boron (B)	2	Ca utilization; nucleic acid synthesis; membrane integrity
Manganese (Mn)	1	Some enzymes; chloroplast membrane integrity; O release during photosynthesis
Zinc (Zn)	0.3	Many enzymes
Copper (Cu)	0.1	Enzymatic oxidation and reduction
Nickel (Ni)	0.001	Enzyme function in N metabolism
Molybdenum (Mo)	0.001	N fixation and N reduction

important role. To some extent K can be substituted by other cations (Na, Mg, and Ca) or organic solutes.

Calcium

Calcium in plants is mostly in vacuoles and in cell walls; there is very little in cytoplasm. In vacuoles, Ca is commonly precipitated as insoluble crystals of oxalates, and in some species as insoluble carbonate, phosphate, or sulfate. Apart from storage, and by interaction with cytosolic Ca across vacuolar membranes, vacuolar Ca serves in osmoregulation and as a secondary messenger. In cell walls, Ca is bound to pectate polysaccharides. Very low concentrations of free Ca^{2+} (*c.* 100 nmol L^{-1}) are maintained in cytoplasm, apparently to avoid precipitation with organic phosphates such as adenosine triphosphate (ATP), and to avoid inhibition of many enzyme systems. The role of Ca in enzyme activation seems to be regulated through reversible binding to small proteins such as calmodulin. Ca is also very important to membrane stability, thereby regulating the leakage of cytoplasmic solutes and maintaining compartmentation of cells.

Magnesium

Magnesium is an essential part of chlorophyll, and up to half of total Mg may be in this form. It also combines with ATP to allow it to function in many reactions, and it activates many enzymes needed in photosynthesis, respiration, and nucleic acid synthesis. A substantial proportion of Mg is also involved in the regulation of cellular pH and the cation–anion balance. The concentration of Mg in the cytoplasm is strictly controlled so as not to inhibit photosynthesis and storage is mainly in vacuoles.

Phosphorus

Phosphorus is taken up largely as inorganic phosphate (P_i). The form of P_i, in both the plant and soil, is highly pH-dependent such that the degree of protonation ranges from none (PO_4^{3-}) in alkaline solutions to three (H_3PO_4) in strongly acid solutions. Inorganic P is rapidly incorporated into organic compounds, e.g., sugar phosphates, phospholipids, nucleic acids, and phosphate esters. As P supply increases beyond sufficiency, P_i accumulates in vacuoles and as polyphosphate and phytate.

Sulfur

Sulfur is taken up by roots as SO_4^{2-}, which either accumulates or is reduced to $-S_2$ or –SH forms. Sulfur is an essential component of many metabolic compounds, e.g., some amino acids, enzymes, coenzymes, and cofactors, and the S–S bond is responsible for maintaining many of the folds in proteins. Sulfur is particularly important for photosynthesis and oil production.

Chlorine

Chlorine seems to be important in charge-balance and osmotic functions, and it is concentrated in chloroplasts but does not occur as a metabolite.

Iron

Iron acts as a structural component and cofactor for enzymatic reactions, and it is absorbed and utilized in the Fe^{2+} form.

Boron

Boron uptake is mainly passive as boric acid (H_3BO_3). Boron is involved in development and growth of meristems, but it is poorly retranslocated from older shoots to more actively growing shoots. Boron has a strong affinity for OH^- groups and is thereby mainly involved in cell walls, sugar translocation, membrane transport, carbohydrate metabolism, RNA metabolism, and photohormonal activity. Boron can accumulate in the ends of needles of conifers to very high concentrations, which reflects unidirectional transport during transpiration.

Other Micronutrients

Further details of Mn, Zn, Cu, Ni, and Mo are given in the further reading list; although these nutrients occur at very low concentrations, they are essential for plant growth.

Nutrient Supply

Nutrient uptake by roots accounts for nearly all nutrient uptake under natural and cultivated conditions, but foliar uptake is important under some circumstances, e.g., in densely populated areas where NH_3 gas and other nutrients in dust are significant, in nurseries where nutrients are applied as foliar sprays, and in forest plantations where foliar sprays are used to correct some micronutrient deficiencies.

Nutrients are taken up by roots mainly as inorganic ions from soil solution. The rate of uptake depends primarily on the concentration in the soil solution immediately adjacent to the root. The rate of nutrient uptake is independent of the rate of water uptake, but the concentrations of nutrients at root surfaces depend strongly on soil water content. Soil water content is important because it affects root growth and nutrient transport to the root surface in both the water flux created by transpiration (called mass flow), and the diffusive flux towards or away from the root. The forms of ions taken up by roots differ somewhat with plant species and growing conditions, and they are regulated by a combination of soil processes, the importance of which depends on the nutrient in question. These processes include organic matter mineralization/immobilization, mineral dissolution/precipitation, solid/liquid equilibria, oxidation/reduction reactions, and solid, liquid, and gaseous inputs and outputs (*see* **Soil Development and Properties**: Nutrient Cycling).

Uptake and Translocation

Nutrients move passively between, but external to, cells in the root cortex (apoplastic transport). Uptake, i.e., nutrient movement across the plasmalemma of root cells, can be a passive process, but it is more often an active process requiring energy, because the ion movement is usually against a gradient in electrochemical potential. A variety of mechanisms specific and nonspecific to individual ions are involved in uptake, some of which are well understood, but most of which are only postulated or poorly defined. Some of these mechanisms are restricted to certain groups of related plants but most occur widely across the plant kingdom, including trees.

Some nutrients are transformed soon after uptake, e.g., NO_3^- is often reduced to NH_4^+ and incorporated into amino acids in roots prior to transport to the shoot. Nutrients generally diffuse radially inwards in roots from one cell to the next by crossing plasmodesmata (**Figure 1**). Water can also pass from cell to cell via a transcellular path, but this is unlikely to be an important path for nutrients. Via plasmodesmata, nutrients pass the casparian strip, which largely blocks apoplastic transport at the endodermis, and they continue on to the cytoplasm of the xylem parenchyma cells. A mainly active process then releases nutrients into xylem vessels for passive transport towards the shoot. Transport in xylem sap involves exchange with cell walls and surrounding living cells. Coniferous trees lack continuous vessels but instead have tracheids which somewhat impede the flow upwards. However, they allow intensive transfer of solutes between xylem and phloem. Xylem-to-phloem transfer is important because water transport is directed mainly towards zones of high transpiration; these are not the zones of high nutrient demand because their main growth phase has passed. Phloem-to-xylem transfer occurs but its importance is largely unknown. The proportions of xylem and phloem transport depend on the ion of interest and other conditions.

Nutrients diffuse from the xylem into the apoplasm of the target tissue, which is usually a leaf. Transfer into the cytoplasm is analogous to uptake in roots and hence it is usually active. The uptake of foliar-applied nutrients is by the same mechanism if the nutrient has been able to pass the cuticle which is waxy and poorly pervious in some species.

Nutrient Pools and Internal and External Cycling

One key difference between trees and most other plant forms is their lifespan. The oldest trees are

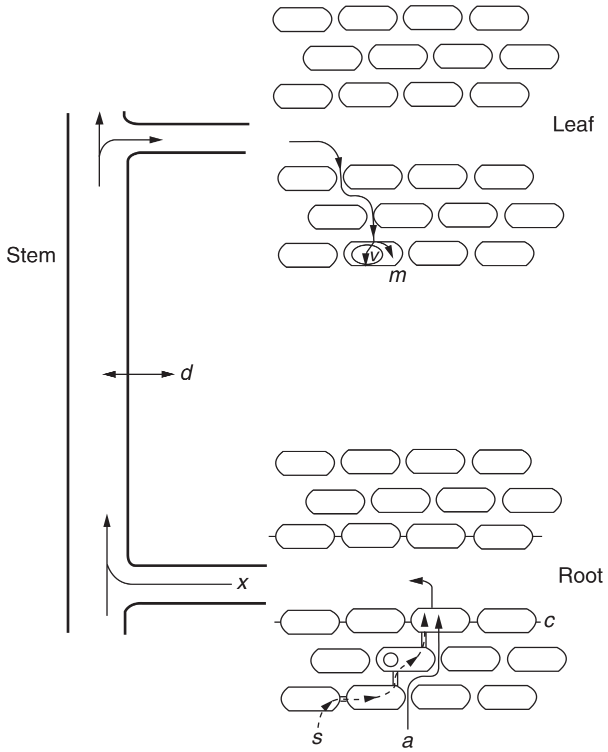


Figure 1 Simplified diagram of the path of nutrients from soil solution to utilization and storage in leaves. Nutrients move through roots external to the plasmalemma of cells, i.e., apoplastic (*a*) pathway, or are taken up across these membranes and transfer to adjacent cells via plasmodesmata, i.e., symplastic (*s*) pathway. Symplastic transport may include transformation and intermediate storage, e.g., in vacuoles (*v*). Apoplastic passage to the xylem is largely blocked by an impermeable casparian band (*c*) and suberized cell walls. Once released to the xylem stream (*x*), nutrients are transported towards the shoot, but during transport they may diffuse (*d*) reversibly into adjacent tissues, e.g., phloem and sapwood. In leaves, nutrients continue to be carried in veins and into cell walls via diffusion and mass flow of the transpiration stream. Uptake into leaf cells then occurs across the plasmalemma, followed by metabolic use (*m*) or storage, e.g., in vacuoles (*v*). Some nutrients are involved in symplastic–apoplastic exchange during the life of a leaf, and withdrawn to other tissues before or during senescence.

several thousand years old, and even most production forests are one or more decades old when harvested. In contrast, most of our knowledge about nutritional physiology has been developed from studies of species that live for only a year or two. Because of the longevity of trees, some aspects of nutrition develop that are not as obvious in ecosystems based on shorter-lived species. Of particular note are the low concentrations of nutrients in wood compared to other tissues, the large pools of nutrients potentially held in trees, the large proportion of annual nutrient supply that can be satisfied by internal nutrient recycling, and the importance of external nutrient cycling in older forests. Some of these points are illustrated by an examination of the budgets of various nutrients for a typical 50-year-old, high-productivity eucalypt forest (**Table 3**) and a typical 16-year-old loblolly pine (*Pinus elliottii*) plantation (**Table 4**), and for K in 10- and 40-year-old black pine (*P. nigra*) plantations (**Figure 2**).

In recent decades, substantial knowledge has accrued on nutrient budgets for a variety of forest ecosystems and the processes controlling the rates of transfer of nutrients between pools has been greatly clarified. For example, it used to be thought that nutrient retranslocation from nonsenescing foliage was a response to low nutrient availability, i.e., under nutrient-stressed conditions the proportion of nutrients retranslocated would be increased, even if the total amount was less when compared to less nutrient-limited conditions. However, in many species, it seems retranslocation is driven by the rate of growth, such that the total amounts and proportions of nutrients (on a whole-tree basis) required for new growth that are met by nutrient retranslocation increases with growth rate, which in turn is often positively correlated with external nutrient supply. Relatively fertile conditions can stimulate growth to such an extent that external nutrient supply cannot meet the demand of an expanding canopy. Nutrients are then withdrawn from leaves or needles lower in the canopy that remain alive and retranslocated to zones of higher demand. Hence, retranslocation is demand-driven. A separate mechanism drives nutrient withdrawal from senescing leaves such that the proportion of nutrients in individual leaves (or needles) withdrawn prior to senescence will depend on genotype, nutrient status, and other environmental factors. This process is most pronounced in deciduous trees, but it is also significant in evergreens. Leaf senescence is triggered by seasonal and microclimatic effects related to reduced light availability or temperature, and in some cases is under hormonal control (e.g., auxins and cytokinins). Leaf senescence and nutrient withdrawal to various degrees can also be triggered by water or nutrient limitations or toxicities (e.g., of salt or Al) or shading.

In contrast to non-woody species, sapwood provides trees with a transient store of some nutrients under some conditions. For example, N can move into sapwood during periods when uptake greatly exceeds the requirement for new growth, and later be withdrawn when nutrient supply–demand conditions are reversed.

Conclusions

Interest in soil fertility and plant nutrition can be traced back several millennia, and several centuries

Table 3 Mass of organic matter and amounts of nutrients in pools and transfers in a typical eucalypt forest of high productivity aged 50 years

	Organic matter ($t\,ha^{-1}$)	*N*	*P*	*Ca ($kg\,ha^{-1}$)*	*Mg*	*K*
Pools						
Above-ground stand	500	500	50	500	250	400
Litter layer	30	150	10	110	30	25
Return from plant to soil per year						
Litterfall	8	60	2	60	20	10
Leaching	0.05	5	<0.1	5	2	15
Inputs and outputs per year						
Rainfall	0.01	5	<0.1	5	5	2
Streamflow		5	0.01	0.2	3	2
Total cycle per year[a]		105	6	75	32	53
Return, plant to soil		65	2	65	22	35
Internal redistribution		30	3	0	5	10
Inputs–outputs		7	<0.1	5	2	0
Net supply from soil reserves per year		10	1	5	3	8
Other inputs per year						
N_2-fixation, asymbiotic + symbiotic		7				
Rock weathering		0	0.1	3	1	8

[a] Total cycle is the sum of all of the fluxes between plant and soil plus that needed for new growth.
Reproduced with permission from Attiwill PM and Adams MA (1993) Nutrient cycling in forests. Tansley Review No. 50. *New Phytologist* 124: 561–582.

Table 4 Transfer rates of nutrients in a typical 16-year-old loblolly pine plantation

Component	*N*	*P*	*K*	Ca	*Mg*
	($kg\,ha^{-1}\,year^{-1}$)				
Requirement of trees					
New needles	55.0	6.3	31.9	8.1	4.8
1-year-old needles	0	0	0	8.1	0
Initiated branches	4.3	0.7	5.2	1.7	0.7
1-year-old branches	2.3	0.3	–0.6	2.5	0.4
Stem	5.3	0.6	4.4	3.0	1.2
Roots < 1 cm in diameter	48.7	12.3	20.0	34.4	9.2
Roots > 1 cm in diameter	1.5	0.4	2.4	0.7	0.7
Total requirements	117.1	20.6	64.5	58.5	17.0
Transfer within trees					
From 2-year-old needles	17.0	0	18.0	0	0
Transfer to forest floor					
Litterfall	58.2	7.8	16.0	29.2	6.9
Throughfall + steamflow	9.6	0.5	12.3	6.0	2.0
Total to forest floor	67.8	8.3	28.3	35.2	8.9
Transfer to mineral soil					
Forest floor to mineral soil	25.2	4.0	20.6	24.1	4.7
Roots <1 cm in diameter to soil	48.7	12.3	20.0	34.4	9.2
Total to mineral soil	73.9	16.3	40.6	58.5	13.9
Additional transfer					
Requirements in excess to transfer to mineral soil	26.2	4.3	4.7	0	3.1
Soil depletion	38	0.34	48	35	10
Loss in ground water	0.70	0.03	1.56	1.26	0.88

Reproduced with permission from Wells CG and Jorgensen JR (1975) Nutrient cycling in loblolly pine plantations. In: Bernier B and Winget CH (eds) *Forest Soils and Forest Land Management*, pp. 137–158. Quebec: Les Presses de l'Université Laval.

for trees *per se*, but the rate of improvement in our scientific understanding of nutritional physiology has increased markedly in recent decades. The growth, maintenance, and reproduction of plants requires 14 nutrients supplied mainly from the soil through a variety of uptake mechanisms in roots. Transport from the roots, via xylem to leaves, involves a variety of passive and active mechanisms to move nutrients between zones of different concentration. Ultimately, nutrients are utilized in specific metabolic roles, or, if in excess, are generally reversibly stored in particular zones of the cell or less

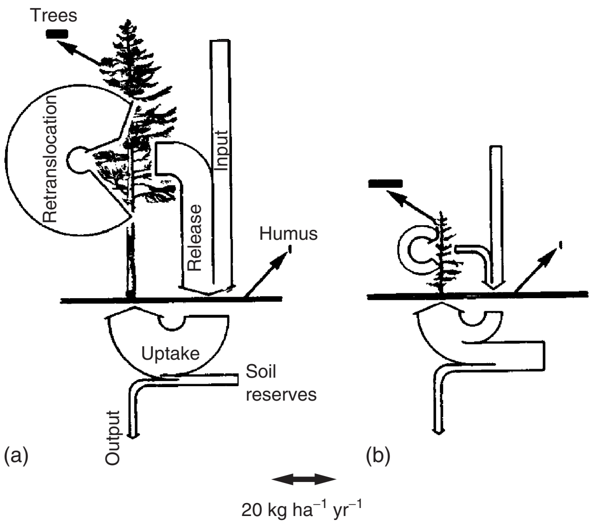


Figure 2 Patterns of *K* cycling in (a) 40-year-old and (b) 10-year-old *Pinus nigra* plantations. This diagram illustrates the change in sources and sinks of nutrients as a tree grows. The older trees here had about half the annual requirement for K as the younger trees. Most of this requirement was met by retranslocation and cycling through the litter layer, in contrast to a younger tree that relied heavily on soil reserves. Reproduced with permission from Miller H (1984) Dynamics of nutrient cycling in plantation ecosystems. In: Bowen GD and Nambiar EKS (eds) *Nutrition of Plantation Forests*, pp. 53–78. London: Academic Press.

reactive forms. Nutrient retranslocation occurs to meet the demands of an expanding canopy and some nutrients are conserved by withdrawal from leaves during senescence; these processes are quite pronounced in trees. Numerous physiological mechanisms are under some degree of genetic control, the elucidation of which will be a major focus of investigation for the next few decades. In contrast to non-woody plants, trees can to some extent store nutrients in sapwood under very high nutrient supply regimes and later withdraw these nutrients during periods of insufficient supply from soil.

See also: **Soil Biology and Tree Growth**: Soil Organic Matter Forms and Functions; Tree Roots and their Interaction with Soil. **Soil Development and Properties**: Nutrient Cycling; Nutrient Limitations and Fertilization. **Tree Physiology**: A Whole Tree Perspective; Physiology and Silviculture; Root System Physiology; Shoot Growth and Canopy Development; Stress; Xylem Physiology.

Further Reading

Asher CJ (1991) Beneficial elements, functional nutrients, and possible new essential elements. In: Mortvedt JJ (ed.) *Micronutrients in Agriculture*, 2nd edn, SSSA Book Series, No. 4, pp. 703–723. Madison, WI: Soil Science Society of America.

Attiwill PM and Adams MA (eds) (1996) *Nutrition of Eucalypts*. Collingwood, Australia: CSIRO Publishing.

Atwell BJ, Kriedemann PE, and Turnbull CGN (eds) (1999) *Plants in Action: Adaptation in Nature, Performance in Cultivation*. South Yarra, Australia: Macmillan Education.

Barber SA (1995) *Soil Nutrient Bioavailability: A Mechanistic Approach*, 2nd edn. New York: John Wiley.

Bowen GD and Nambiar EKS (eds) (1984) *Nutrition of Plantation Forests*. London: Academic Press.

Clarkson DT and Hawkesford MJ (1993) Molecular biological approaches to plant nutrition. *Plant Soil* 155/156: 21–31.

Horst WJ, Schenk MK, Bürkert A, *et al*. (eds) (2001) *Plant Nutrition: Food Security and Sustainability of Agro-Ecosystems Through Basic and Applied Research*. 14th International Plant Nutrition Colloquium, Developments in Plant and Soil Science, vol. 92. Dordrecht, The Netherlands: Kluwer Academic.

Kozlowski TT and Pallardy SG (1997) *Physiology of Woody Plants*, 2nd edn. San Diego, CA: Academic Press.

Marschner H (1995) *Mineral Nutrition of Higher Plants*, 2nd edn. London: Academic Press.

Mengel K and Kirkby EA (1982) *Principles of Plant Nutrition. Potash Institute*, 3rd edn. Bern, Switzerland: International Potash Institute.

Nambiar EKS and Fife DN (1991) Nutrient retranslocation in temperate conifers. *Tree Physiology* 9: 185–207.

Nilsson LO, Hüttl RF, and Johansson UT (eds) (1995) Nutrient uptake and cycling in forest ecosystems. In *Proceedings of CEC/IUFRO Symposium*, *Developments in Plant and Soil Science*, vol. 62. Dordrecht, The Netherlands: Kluwer Academic.

Salisbury FB and Ross CW (1992) *Plant Physiology*, 4th edn. Belkmont, CA: Wadsworth.

Tinker PB and Nye PH (2000) *Solute Movement in the Rhizosphere*. New York: Oxford University Press.

Canopy Processes

R O Teskey, University of Georgia, Athens, GA, USA

Introduction

A forest canopy is the aggregate of the leaves of trees that typically forms a layer overhead. It may also include the leaves of vines, epiphytes, and parasitic plants when they are present. A canopy can have large gaps, allowing plentiful light to reach the forest floor, or be closed and dense, with almost no light penetrating below it. The primary purpose of the forest canopy is to capture solar energy needed for photosynthesis. A number of factors can reduce the potential carbon gain of forests by preventing the achievement of a high leaf surface area in the canopy or by reducing the rate of net photosynthesis of leaves. A forest canopy also releases a large amount of water into the atmosphere in the process of transpiration. The amount of water transpired from a forest is closely associated with the leaf surface area of the canopy.

Canopy Photosynthesis

Within-Canopy Environmental Characteristics

Attributes of the canopy are the sum of the functions of all the leaves that make up the canopy. Through the process of photosynthesis each leaf creates carbohydrates from atmospheric carbon dioxide (CO_2). Leaves within a canopy photosynthesize at different rates, depending on available resources and microclimate at specific canopy positions. The most important rate-controlling factors are solar radiation, temperature, CO_2 concentration, vapor pressure deficit (an index of the dryness of the air calculated from relative humidity and temperature), available soil moisture and acquired nutrients. During the daytime, microclimatic conditions, temperature, humidity and CO_2, can vary within the canopy, with higher temperatures, lower humidity and near-atmospheric CO_2 concentrations occurring near the top of the canopy, and lower temperatures, higher humidity and lower CO_2 concentrations occurring near the bottom of the canopy. These trends tend to reverse at night. If the canopy is open, allowing wind to penetrate throughout, there is little appreciable difference in temperature, humidity, or CO_2 concentration among canopy positions.

Of the environmental factors affecting photosynthesis, the one that varies to the largest extent within the canopy is solar radiation. Only a portion of the solar spectrum is used in photosynthesis, between wavelengths of 400 and 700 nm. This portion of the spectrum is called photosynthetically active radiation (PAR). Most of the radiant energy found in longer wavelengths, i.e., heat, is reflected or transmitted through the leaves, while most of the PAR is absorbed by the leaves. This creates variations in light quality above, within and below the canopy. Often 80–95% of the incoming PAR is absorbed in a well-developed forest canopy, allowing little solar energy to pass through to the plants in the understory. Plants below the canopy respond to this light stress by developing thin leaves that efficiently photosynthesize in low light conditions (high quantum yield) and have growth patterns that are characterized by long internode lengths that minimize mutual shading and shading from competing plants.

The amount of PAR received at different depths within the canopy can be approximated using Beer's law:

$$I_z = I_0 \exp(-kL_z) \tag{1}$$

where I_z is the average solar radiation at height z within the canopy, I_0 is solar radiation above the canopy, k is the light extinction coefficient, and L_z is the leaf area index for that portion of the canopy above height z. The light extinction coefficient varies with species and forest type. Typical values of k for coniferous forest canopies range between 0.4 and 0.65, and between 0.5 and 0.8 for broadleaf deciduous forest canopies. In most cases, in coniferous and deciduous forests the value of k falls between 0.5 and 0.6. The pattern of solar radiation through hypothetical forests with different values of k (**Figure 1**) illustrates the effectiveness of light absorption by the canopy and the reduction in available light with depth within the canopy. It should be noted that the application of Beer's law assumes that the canopy consists of leaves that are randomly distributed throughout the canopy. This is never the case in actual forests because the foliage is always arrayed on branches and often clumped near the end of the branch. Clumping is particularly evident in conifers and this results in more light transmission through the canopy than would be predicted by Beer's law. In coniferous forests, discrepancies of 30% or more in calculated light transmission through the canopy can be attributed to nonrandom spatial variation in the foliage. This error is often lower in deciduous species.

Within-Canopy Foliar Characteristics

Leaf morphology changes dramatically in most tree species as a consequence of changing light conditions from the top to the bottom of the canopy. The most limiting factor to photosynthesis at the bottom of the canopy is solar radiation, and leaves at that level show an acclimation to this limitation by developing a high specific leaf area (SLA, defined as the surface area-to-mass ratio of a leaf) meaning they are very thin, often with only two or three cell layers capable of photosynthesis. This improves their ability to efficiently fix carbon at low light levels, and the photosynthetic light compensation point is lowered, although the maximum light saturated rate of photosynthesis is also reduced. Leaves near the top of the canopy are not light limited, but are often water- and heat-stressed. In this portion of the canopy the leaves have multiple photosynthetic cell layers in the mesophyll, and therefore a lower SLA, are smaller, reducing the boundary layer, and can

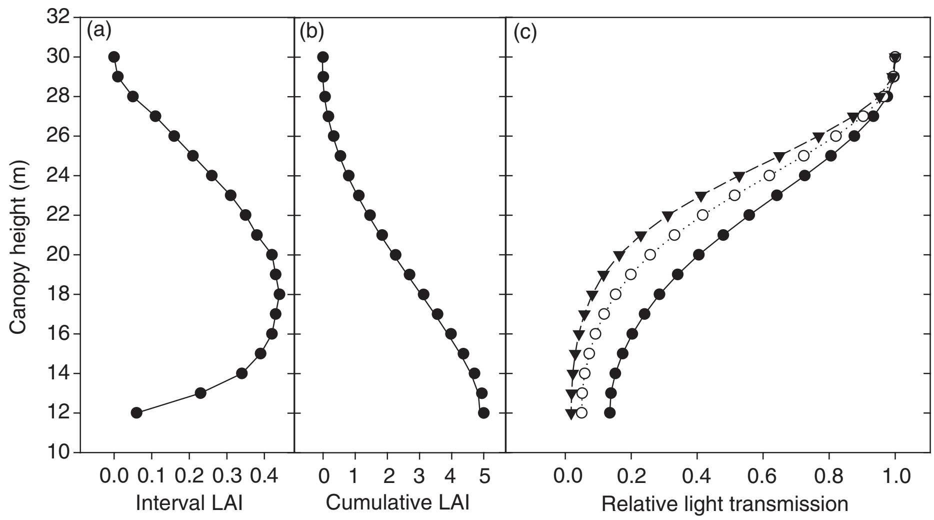


Figure 1 (a) Projected leaf surface area profile by 1-m intervals within a typical (hypothetical) forest canopy with a leaf area index (LAI) of 5 ($m^2 m^{-2}$). (b) Cumulative LAI with canopy depth. (c) Relative light transmission through the canopy calculated from Beer's law (eqn [1]) assuming light extinction coefficients of 0.4 (triangles), 0.6 (open circles), and 0.8 (filled circles).

have lower stomatal density, all attributes that make them more able to conserve water and/or dissipate heat. In broadleaf species, leaf orientation also tends to shift from canopy top to bottom, with leaves in their most horizontal position at the canopy bottom and in their most vertical position at the top. This improves light absorption at the bottom of the canopy and reduces the heat load on the leaves at the top of the canopy.

Between the top and bottom of the canopy a continuous gradient of changing SLA usually can be found as the microenvironment changes. Values of SLA can double from the top to the bottom of a forest canopy. The SLA of a leaf is inversely related to the daily sunlight under which the leaf developed within the canopy. The light saturated rate of net photosynthesis of the leaf is also inversely correlated to its SLA. On the other hand, there is a direct positive relationship between SLA, the nitrogen content of the leaf, and physiological activity. Higher levels of nutrients, in particular nitrogen, are found in regions of the canopy that receive the highest amounts of solar radiation, and also have the highest SLA, i.e., the leaves found at the tops of trees and the upper third of the canopy. Most, if not all, quantifiable aspects of leaf metabolism decrease from top to bottom of the canopy, including maximum rates of photosynthesis and respiration, number of mitochondria and chloroplasts, and chlorophyll, starch, and sugar contents.

Leaf Area Index

A forest canopy consists of thousands of individual leaves arrayed in complex patterns. Leaf shapes, sizes, and longevities as well as branching patterns vary tremendously among tree species. However, there are effective ways of making useful comparisons between forest types at the scale of the canopy by reducing variation in measurements of these attributes. One of the most widely used bases for comparison of canopies is the measurement of leaf area index (LAI). To calculate LAI, the surface area of the leaves is summed and divided by the ground surface area that they occupy. Both areas are measured in the same units, e.g., $m^2 m^{-2}$, so LAI is dimensionless. The 'projected' leaf area of the leaves in the canopy is often used to determine LAI. Projected leaf area is the surface area of a leaf that intercepts a direct beam of light. In the case of a flat leaf of a deciduous broadleaf species, it is simply the area of one side of the leaf. For more complex leaf shapes, such as conifer needles, it is the area of the leaf that intercepts a direct beam of light projected onto a flat surface. Projected leaf area provides a measure of the surface area of leaves that can absorb direct beam solar radiation. The use of projected leaf area as the basis for comparison among species minimizes variation by reducing the myriad complex leaf shapes into the effective absorbing surface area. Occasionally when comparisons of LAI are made, total surface area of leaves (all-sided leaf area) is used instead of projected leaf area. The reader is cautioned that these values of LAI will be two to four times greater than those based on projected leaf area. The difficulty in accurately measuring leaf area in conifers has sometimes led to the substitution of leaf biomass for leaf area. This is suitable for comparisons made within a species, but can introduce unwanted variation when comparisons are made across species with a wide range of SLA.

When maximum LAI values (projected leaf area basis) of forests growing in fertile and moist conditions are compared, they are typically between 5 and 7. Assuming that 95% of the incoming solar radiation is the practical maximum that can be absorbed by a canopy, then with a light extinction coefficient (*k*) of 0.5, using Beer's law (eqn [1]) full interception would occur at LAI = 6. If the value of *k* was 0.4 or 0.8, then the LAI value for full interception would be 7.5 and 3.8, respectively. Although unusual, occasionally LAI values for forests have been reported to be substantially higher, in the range of 10 to 20. One possible explanation is that in these cases the foliage was highly clumped. Clumping has the effect of reducing the effectiveness of interception of solar radiation by individual leaves. In turn, to maximize intercepted radiation the trees would have to produce substantially more leaves than in a less clumped forest canopy.

As a young forest approaches canopy closure, its maximum leaf area will exceed the stable LAI value. In favorable conditions this transient LAI could temporarily exceed 7. This reflects the high degree of competition between trees that occurs at this point of stand development. However, such a high LAI cannot be sustained and the highest long-term average LAI is usually around 5. Lower maximum LAIs are very common, and reflect site resource limitations to tree growth. The LAI of a forest is not constant, and will tend to fluctuate yearly due to differences in seasonal weather patterns, drought, or perturbations that the forest may experience such as fire, insect infestation or disease. If the stress is severe, the LAI will be reduced within the year. Drought and insect defoliation, for example, can have this effect. However, more commonly, a stress or decrease in resource availability will result in a lower leaf area in the subsequent year. Similarly, an increase in resources will increase the LAI in the current year in a forest that contains tree species with recurrent or continuous flushing patterns, and will cause an increase in LAI in the following year in all species. The increase in LAI in the subsequent year is due to the development of more leaf initials within the dormant period bud and the acquisition and storage of resources, particularly carbohydrates and nutrients, to support the additional leaves.

Intercepted Solar Radiation

For a given species, LAI and leaf biomass have strong positive correlations with most measures of stand growth or productivity across sites or treatments. These same relationships, while generally remaining positively correlated, are more variable when comparisons are made among species because LAI does not adequately account for how effectively solar radiation is absorbed by the canopy. Absorption is a function of the total amount of leaves in the canopy and how those leaves are displayed. The latter is determined by canopy and branch architecture, and leaf distribution and orientation. The depth of the canopy, branch pattern and orientation, leaf size, shape and arrangement on the branches, and overlap among leaves and branches within the canopy all affect how much solar radiation a canopy can absorb.

The quantity of solar energy absorbed by the canopy determines to a large extent how much carbon is gained through photosynthesis, and this in turn, defines the productivity of the forest. A generalized relationship between absorbed radiation and forest growth can be seen in **Figure 2**. This diagram illustrates that the general relationship between stand growth and the amount of intercepted solar radiation is usually linear. Over short time periods, for example days or weeks within a single growing season, there could be substantial nonlinear variation in this relationship, but over longer time

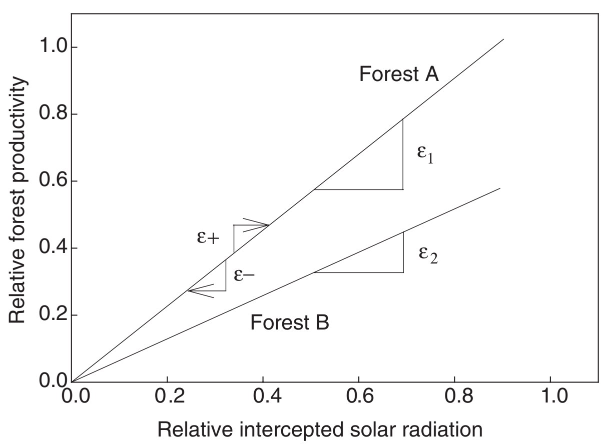


Figure 2 Idealized relationships between intercepted radiation and forest productivity. The two lines represent forest types with a high dry matter : radiation quotient (ε_1, Forest A) and a low dry matter : radiation quotient (ε_2, Forest B). When comparing between forest types, a higher canopy photosynthesis (ε_1 versus ε_2) results in greater carbon gain per unit of intercepted radiation. However, within the same forest type short-term changes in ε caused by increased resource availability ($\varepsilon+$) or environmental stress ($\varepsilon-$) produce adjustments in canopy leaf area, so that over time forest productivity for a given forest type tends to remain linearly related to intercepted radiation. Adapted and modified with permission from Jarvis PG and Leverenz JW (1983) Productivity of temperate, deciduous and evergreen forests. In: Lange OL, Nobel PS, Osmond CB, and Ziegler H (eds) *Physiological Plant Ecology, vol. 4, Encyclopedia of Plant Physiology New Series 12D*, pp. 233–280. Heidelberg, Germany: Springer-Verlag.

periods, such as growing seasons and years, variation is greatly reduced and a linear relationship becomes evident. The linear nature of this relationship holds within and across species, which is an indication that it is a more robust measure of canopy carbon gain than LAI. Different types of forests and species will produce relationships with different slopes due to inherent differences in physiological processes, including photosynthetic capacity of the leaves.

The slope of the relationship, ε, has been termed the dry matter : radiation quotient and is determined by a wide range of factors. It is important to remember that the term ε is an amalgamation of many important physiological attributes that contribute to growth, including photosynthesis, respiration, carbon allocation and plant responses to environmental stresses. The maximum potential value of ε can be estimated based on the following information: (1) a tree requires 20 mole quanta of solar energy to assimilate a mole of CO_2, (2) there are 2.3 mole quanta per MJ of absorbed solar radiation (or 4.6 mole quanta per MJ of PAR), (3) the mass of a mole of CO_2 is 44 g, and (4) an estimated conversion factor from mass of CO_2 to mass of dry matter is 0.5. The maximum potential conversion of solar radiation to dry matter in a plant is $(2.3/20)(44 \times 0.5) = 2.5\,\mathrm{g\,MJ^{-1}}$ (total solar) or $5.0\,\mathrm{g\,MJ^{-1}}$ (PAR). Typical values of ε for crops range from 1.1 to $1.7\,\mathrm{g\,MJ^{-1}}$ (total solar) while for forests values have been reported from 0.2 to $1.4\,\mathrm{g\,MJ^{-1}}$. This range in reported values indicates that the dry matter : radiation quotient of forest canopies of different species or species mixtures can vary greatly. However, the ε for a single species or a group of species, on a single site or on similar sites, will be nearly constant, because, in large part, the pattern of carbon allocation among leaves, roots, and stem is controlled principally by soil resources, especially nitrogen and water availability, and the genetic characteristics of the species. Likewise, the inherent photosynthetic and respiratory capacities of the foliage and woody tissues are fixed.

On a single site, in any given year, conditions that affect photosynthesis of the leaves will vary. When conditions are less favorable, the trees allocate more carbon to roots, and, because there is less carbon remaining for leaves, fewer, or smaller, leaves are produced. When conditions are more favorable for photosynthesis, more, or larger, leaves, are produced, and less carbon is allocated to the root system. In the short term, this produces temporary shifts to higher or lower values of ε. However, over longer time periods, such as a growing season or year, the changes in carbon availability and proportions allocated for root and leaf growth result in a strongly linear relationship between intercepted radiation and aboveground stand growth.

Since we know that many factors affect the rate of photosynthesis of leaves, why is intercepted solar radiation so strongly correlated with forest productivity? While there is still more research needed to fully understand these phenomena, the current explanation is that tree species in general utilize a similar strategy for growth and survival, which is to grow more leaves when more resources are available, rather than increase the photosynthetic capacity of a fixed amount of leaves. For example, on droughty or low-fertility sites, the carbohydrate and nutrient supply is limited, allocation favors roots, and fewer leaves are produced; thus, the amount of solar radiation intercepted is low. On resource-rich sites, available carbohydrates and nutrients are used to create more leaves, which in turn intercept more radiation and produce higher levels of carbohydrates for export to the rest of the tree. An individual species that is naturally occurring or planted across a wide variety of sites can often be defined by a single line (**Figure 2**) that represents its long-term productivity as a function of intercepted radiation. In other words, ε remains relatively constant for a species. On resource-rich sites, more leaves are produced in the canopy and more radiation is absorbed by them, while on the resource-poor sites, fewer leaves can be produced, and growth is proportionately reduced.

Measurement Approaches

Canopy carbon gain has been estimated in a number of ways. It has been inferred from changes in biomass, modeled by integrating the rates of physiological processes over time, and measured by micrometeorological techniques. The recent development of relatively reliable and robust instrumentation for eddy covariance measurements (a micrometeorological technique that measures the CO_2 concentration in eddies of air allowing the calculation of the flux of CO_2 into and out of an ecosystem) has made this an important method for estimating total net CO_2 uptake or release by a forest ecosystem. Usually eddy covariance measurements are only made above the canopy, so this technique cannot discern where within the ecosystem (soil, plants, animals) the CO_2 is being absorbed or released. As a result, unless it is combined with more measurements, it only provides an estimate of net fluxes of all photosynthetic and respiratory activity. However, this is a very useful approach for characterizing whole ecosystem carbon dynamics, and provides insight into canopy processes. One result of these measurements has been to establish that the rate of CO_2 uptake of canopies in response to PAR is very similar to the light response curves of individual leaves.

Transpiration

All plants lose water through their stomata as they absorb CO_2 from the atmosphere. When the stomata are open during the day, a tremendous amount of water can be lost from the forest canopy. Water loss through stomata is linearly related to stomatal aperture, which is estimated by measuring stomatal conductance. The average stomatal conductance of all the leaves in the canopy is called canopy conductance. Light in visible wavelengths is required for the stomata to open. As a result, transpiration occurs mostly during daylight hours. Only about 5–10% of water loss occurs at night. This loss results from stomata that do not always close fully, particularly as leaves age, and a small amount of diffusion through the leaf cuticle.

Canopy water loss depends on soil water availability, canopy leaf area and environmental conditions, especially PAR and vapor pressure deficit. Vapor pressure deficit (VPD) describes the dryness of the air, and more specifically, the potential gradient for water movement from the leaf to the atmosphere. A high VPD indicates that there is a large water vapor gradient from the leaf to the atmosphere that will cause rapid diffusion of water from the leaf when the stomata are open. The rate of transpiration is closely correlated with VPD, especially under conditions of plentiful soil moisture. Mitigating factors that cause the stomata to close, such as leaf water stress, modify the rate of transpiration and its relationship with VPD.

Estimating Evapotranspiration

Evapotranspiration (E_t), i.e., the combined total of transpiration and evaporation, from a forest has been estimated in many ways. Micrometeorological methods such as the Bowen ratio (the ratio of sensible heat flux to latent heat flux computed from vertical gradients of air temperature and water vapor) and eddy covariance, can be used to estimate evapotranspiration from a forest. Physiologically based methods, including sap flux, porometry, and lysimeters, as well as stream flow from catchments and soil water depletion have been used as well. One of the most proven and widely used approaches is the Penman–Monteith equation:

$$E_t = sA + (c_p \rho_a D g_a)/\{\lambda[s + \gamma(1 + g_a/g_c)]\} \qquad (2)$$

where s is the rate of change of saturation vapor pressure with respect to air temperature, c_p is the specific heat of dry air of density ρ_a, D is vapor pressure deficit of the air, g_a is boundary layer conductance for water vapor, λ is the latent heat of vaporization of water, γ is the psychrometric constant, and g_c is canopy conductance.

In the case of aerodynamically rough canopies, such as in coniferous forests and other forests made up of small leaves, g_a is usually large in relation to g_c. The small leaf size and large boundary layer conductance results in close coupling between leaf and air temperatures, allowing the equation to be simplified to:

$$E_t = (c_p \rho_a / \lambda\gamma) D g_c \qquad (3)$$

Particularly in the simplified form, the dependence of E_t on VPD and canopy conductance is clear. For conifer and other narrow-leaf tree canopies, stomata play an important role in controlling the rate of transpiration. In contrast, in broadleaf canopies, transpiration is much more closely related to the input of solar radiation, and less dependent on canopy conductance. However, there is no notable distinction between daily or hourly maximum rates of E_t in canopies of coniferous, deciduous, or mixed species stands.

Daily Evapotranspiration

Estimates of E_t of forests range from less than 1 to as much as 7 mm day^{-1}, although maximum values are usually reported in the range of 5–6 mm day^{-1}. The low values will occur during drought, or conditions of high atmospheric humidity or low solar radiation, or in forests with very low LAI. The high values indicate that forests can be very effective at absorbing solar radiation, and very well coupled to the atmosphere, because these represent values that are at the theoretical maximum for evaporation. In full sunlight a maximum of 380 calories day^{-1} of energy are available at the earth's surface. As 570 calories are required to evaporate 1 cubic centimeter of water, this is equivalent to a maximum of 6.6 mm day^{-1} of evaporation. Although LAI values indicate that leaf surface area is many times larger than the unit ground surface, water loss cannot exceed that of an equal surface area of water receiving the same amount of energy. Values of E_t that exceed the maximum rate are uncommon, but can occur if an additional source of energy is available, for example from advection.

In summary, when considered from a physiological perspective, a forest canopy is a system for harvesting solar energy. Leaves are displayed throughout the canopy for this purpose as efficiently as possible, within the constraints of the morphology and branch architecture of the tree species that contribute to the canopy. If unconstrained by a lack of site resources for growth, the canopy captures a very large proportion of the sun's available energy. Due to the close coupling between resource acquisition and canopy development, LAI and intercepted radiation are excellent indices of forest productivity. This is because improvements in resource acquisition that increase canopy photosynthesis in the short term lead quickly to increased leaf growth. Likewise, when fewer resources are available, decreased canopy carbon gain causes a subsequent reduction in leaf growth. Forest canopies can also lose appreciable amounts of water through the process of transpiration. Canopy transpiration is positively correlated with LAI, canopy conductance, and available energy. At high values of LAI, the rate of transpiration of forest canopies is comparable to that of open water, providing another example of the effectiveness of forest canopies in absorbing solar energy.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Forest Canopies. **Environment**: Carbon Cycle. **Hydrology**: Hydrological Cycle. **Tree Physiology**: Physiology and Silviculture; Stress.

Further Reading

Holbrook NM and Lund CP (1995) Photosynthesis in forest canopies. In: Lowman MD and Nadkarni NM (eds) *Forest Canopies*, pp. 73–108. San Diego, CA: Academic Press.

Jarvis PG and Leverenz JW (1983) Productivity of temperate, deciduous and evergreen forests. In: Lange OL, Nobel PS, Osmond CB, and Ziegler H (eds) *Physiological Plant Ecology, vol. 4, Encyclopedia of Plant Physiology New Series 12D*, pp. 233–280. Heidelberg, Germany: Springer-Verlag.

Kozlowski TT and Pallardy SG (1997) *Physiology of Woody Plants*. San Diego, CA: Academic Press.

Kramer PJ and Boyer JS (1995) *Water Relations of Plants and Soils*. San Diego, CA: Academic Press.

Landsberg JJ (1986) *Physiological Ecology of Forest Production*. London, UK: Academic Press.

Lassoie JP and Hinckley TM (1991) *Techniques and Approaches in Forest Tree Ecophysiology*. Boca Raton, FL: CRC Press.

Parker GG (1995) Structure and microclimates of forest canopies. In: Lowman MD and Nadkarni NM (eds) *Forest Canopies*, pp. 73–108. San Diego, CA: Academic Press.

Russell G, Jarvis PG, and Monteith JL (1989) Absorption of radiation by canopies and stand growth. In: Russell G, Marshall B, and Jarvis PG (eds) *Plant Canopies: Their Growth, Form and Function*, pp. 21–40. Cambridge, UK: Cambridge University Press.

Smith H (2000) Plant architecture and light signals. In: Marshall B and Roberts JA (eds) *Leaf Development and Canopy Growth*, pp. 118–144. Boca Raton, FL: CRC Press.

Squire GR (2000) Plant and canopy diversity. In: Marshall B and Roberts JA (eds) *Leaf Development and Canopy Growth*, pp. 280–309. Boca Raton, FL: CRC Press.

Stenberg P, DeLucia EH, Schoettle AW, and Smolander H (1995) Photosynthetic light capture and processing from cell to canopy. In: Smith WK and Hinckley TM (eds) *Resource Physiology of Conifers*, pp. 3–38. San Diego, CA: Academic Press.

Waring RH and Running SW (1998) *Forest Ecosystems*. San Diego, CA: Academic Press.

Whitehead D and Jarvis PG (1981) *Water Deficits and Plant Growth*, vol. 6. New York: Academic Press.

Stress

R H Waring, Oregon State University, Corvallis, OR, USA

Introduction

Throughout their lives trees are exposed to a range of stressful conditions. If they are to survive, they must adapt by modifying their metabolism (physiology), cellular structure (anatomy), and form (morphology). Adaptation to a wide range of stresses, however, limits growth and the ability to compete in more favorable environments. The trade-offs are important to recognize in selecting trees that might grow best in a particular environment and in modifying the environment to reduce stressful conditions.

The nomenclature for defining physiological stress is derived from physics with the idea that a force upon a body causes a strain in the opposite direction. The strain is elastic if completely reversible following removal of the stress, or plastic if only partly reversible. How long it takes a plant to recover following exposure to a particular stress or whether the stress is fatal are questions that can be answered by careful observation. Survival following exposure to one stress, however, often increases a plant's susceptibility to another. On the other hand, repeated exposure to one kind of stress can lead to adaptations that increase a tree's ability to tolerate or to avoid the stress.

A brief analysis is presented below of the kinds of tolerance and avoidance mechanisms that trees have evolved to withstand specific stresses. To demonstrate how seasonal variation in climatic conditions imposes stresses on common processes, such as photosynthesis, a simulation model is introduced, and the performance of pine and eucalyptus is compared in an environment where neither species is native. Then, some general biochemical and structural indices of tree stress are introduced. These stress indices change not only in response to variation in climate and soil conditions but also in response to competition among trees. The stress indices are useful in assessing tree susceptibility to attack from insects and disease. In the last section, procedures for separating climatically induced stress from other types are discussed that apply at the landscape level.

Tree Adaptations to Specific Stresses

Trees may alter their biochemistry to tolerate a particular stress that occurs infrequently but the metabolic cost is high for such temporary adjustments. Frequent exposure to a particular stress leads to avoidance mechanisms that may permanently change a tree's physiology, anatomy, and morphology. Tolerance and avoidance mechanisms differ depending on the kind of stress but both types of adaptations may reduce the amount of resources available for above-ground growth under more favorable conditions. If an environment is sufficiently harsh, however, trees that can adapt encounter little competition. Examples of tolerance and avoidance mechanisms are presented in this section in relation to radiation, drought, flooding, temperature extremes, mechanical forces, toxic compounds, and nutrient deficiencies.

Radiation

Solar radiation includes a wide spectral range in wavelengths. The sun's ultraviolet (UV) radiation (200–400 nm) can destroy chemical bonds, whereas its visible light (400–700 nm) is essential for photosynthesis, and its infrared radiation (700–2500 nm) heats plant and soil surfaces. Trees produce a series of phenolic compounds that absorb particular parts of the UV spectrum or they may adapt by producing waxes and whitish hairs on leaf and stem surfaces that reflect a large amount of radiation.

Trees growing in shaded environments can increase photosynthetic pigments that absorb light, such as chlorophyll. Leaves in the upper canopy, however, are exposed to varying light intensities, sometimes greater than their photosynthetic capacity. Under such conditions, many species have evolved the ability to generate special pigments that cycle from absorbing to reflecting modes throughout the day. The shapes of leaves exposed to high radiation are generally smaller, more dissected, and less directly oriented to absorb sunlight than leaves adapted to more shaded conditions. Leaf thickness also generally decreases from the top to the bottom of a forest canopy in response to available light.

Drought and Flooding

Drought and flooding represent extremes in water availability. To avoid drought, vascular plants have evolved the ability to grow roots that can extract water from >10 m depth in the soil and transport it through a series of connected, dead, woody (lignified) cells to leaves situated more than 50 m above the ground. Gymnosperms, represented by pines (*Pinus*), spruces (*Picea*), firs (*Abies*), *Araucaria*, and *Ginkgo*, transport water through specialized (bordered) pits on the connected side walls of tracheids, whereas angiosperms, represented by evergreen and deciduous hardwoods such as *Magnolia*, beech (*Fagus*), maple (*Acer*), and ash (*Fraxinus*), have vessels with perforated plates at each end. The bordered pits and perforated plates reduce the possibility of air being introduced into the conduits when under tension and, if air is introduced, they are designed to remove it.

As tension on water columns increases due to high evaporative demand or drought, stomata are induced to close before irreversible damage to the vascular system results. Trees adapted to periods of seasonal water stress also have the ability to increase solute concentrations in living cells, to reduce the size of vessels and tracheids, and the amount of leaf area supported by a unit of vascular tissue, while at the same time increasing their root systems.

To adapt to periodic flooding, water tupelo (*Nyssa aquatica*), black ash (*Fraxinus nigra*), and other swamp hardwood species have developed metabolic systems that permit root growth and photosynthesis to continue under anaerobic conditions. In addition, baldcypress (*Taxodium distichum*) and other species exposed to chronic flooding have adapted anatomically to allow diffusion of air through specialized tissue to their roots.

Temperature Extremes

Plants adapted to high or low temperatures differ in the biochemical composition of their cellular membranes. These differences influence the ease that chemical elements, organic compounds, and water can be absorbed and transferred from roots to shoots. Tropical trees are adapted to high temperatures but withstand little frost, whereas temperate trees can adjust their cellular structure, when in a dormant state, to prevent ice crystal formation down to $-45°C$, and boreal trees can, when fully preconditioned, withstand temperatures approaching absolute zero.

Plants adapted to subfreezing temperatures reduce their photosynthetic activity before conditions become unfavorable in response to shorter day length. If climatic conditions become warmer, low-temperature adaptations are a disadvantage. At the other extreme, some broad-leafed tree species, when exposed to high radiation when their stomata are closed, initiate the production of volatile isoprene compounds, which protect the photosynthetic machinery within the leaf, and create haze that reduces solar radiation.

Mechanical Forces

Snow, ice, and wind exert mechanical stress on leaves, branches, and stems. Trees species have adapted by folding leaves, by developing flexible stems and branches, by increasing the density of their wood, by shortening and altering the orientation of branches, by increasing the taper of stems, and the proportion of growth allocated to large-diameter roots. In unstable soils, the shape of stems and extension of surface roots may be quite asymmetrical, serving to buttress trees against the forces of gravity.

Mechanical stresses are also induced by feeding and other activities of animals that remove leaves, branches, and bark. Adaptations to herbivory vary from the development of thorns, and prickly leaves to biochemical defenses.

Toxic Compounds

Toxic compounds are widely dispersed in the environment in the form of gases, such as ozone, and as heavy metals such as lead, chrome, nickel, and selenium. Ozone diffuses through stomata into the chloroplast and injures the photosynthetic machinery as well as a tree's ability to transport photosynthate from leaves. Species that are conservative in their use of water maintain less open stomata and therefore take up less ozone over a given period. On the other hand, species that shed their foliage annually suffer less damage per leaf than more drought-adapted species that have long-lived evergreen foliage. To repair ozone-damaged cells requires expenditure of photosynthate and other resources that might otherwise go toward growth or defense.

Heavy metals interfere with the enzyme reactions essential for plant growth and development. Some tropical trees can store toxic compounds in vacuoles that do not disturb cell metabolism; others adapt by producing metal-binding peptides that keep heavy metals out of solution. The synthesis of these compounds is metabolically expensive, and again, like other specific adaptations to stress, reduce a species' ability to compete in environments lacking heavy metals.

Nutrient Deficiencies

Nutrient limitations can reduce growth and increase a tree's susceptibility to other stresses. Trees differ in their demands for specific nutrients, but exhibit a similar optimal balance. At slow growth rates, the overall demand for nutrients is low, and optimal balance can be achieved through selective uptake of scarce nutrients by roots and symbiotic (mycorrhizal) fungi. Some trees species also have symbiotic associations of bacteria that can fix atmospheric nitrogen gas (N_2) into ammonium (NH_4^+), a form available to the host tree as well as to other species. The fixation of nitrogen and acquisition of other nutrients via symbiotic bacteria and fungi, or through production of exudates that stimulate free-living microbial activity to release nutrients from decomposing litter, require a high expenditure of metabolic energy, reducing resources that could go into growth and defense. In many areas once limited by nitrogen, atmospheric depositions have increased from <2 to $>50\,\mathrm{kg\,ha^{-1}\,year^{-1}}$. This increased availability of nitrogen favors above-ground growth, even when other nutrients are in less than optimal supply. As a result of imbalanced nutrition, plants expend energy and create tissues less tolerant to a variety of other stresses.

Process Modeling to Integrate Stress Effects

Trees are exposed throughout their lives to a wide range of different stresses. The question arises, which species might grow best? To assess species performance under a wide range of environmental conditions, physiologically based process models have been developed that have a common structure (**Figure 1**). The maximum rate of photosynthesis is determined by the nutritional status of leaves and the amount of light they absorb. Additional environmental constraints are imposed by frost, drought, high evaporative demand, suboptimum temperatures, and nutrition (and by additional stresses if important, e.g., wind stress, insect defoliation, and ozone). The models take account of interactions among stresses as they affect photosynthesis, respiration, and growth.

If *Pinus ponderosa* and *Eucalyptus globulus* were selected for planting in a cold, drought-prone region of Argentina, *P. ponderosa* would be predicted to photosynthesize and grow nearly four times as well as *E. globulus*, largely because of differences in performance at temperatures between 0°C and 10°C (**Figure 2**). Both species have similar responses to humidity deficits but because the pine grows more foliage it extracts more water from the soil and experiences somewhat more drought stress during the late summer than eucalyptus.

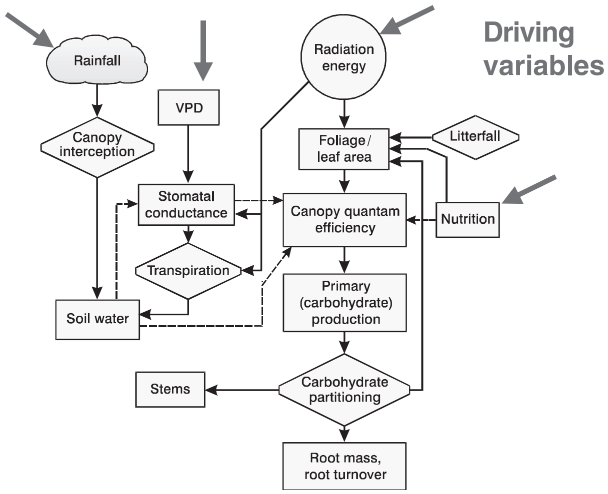


Figure 1 Structure of a physiologically based tree growth model where photosynthesis is constrained by environmental factors that also affect respiration and allocation of resources to growth. VPD, vapor pressure (humidity) deficit. Reproduced with kind permission of Natural Resource Modeling, published by the Rocky Mountain Mathematics Consortium.

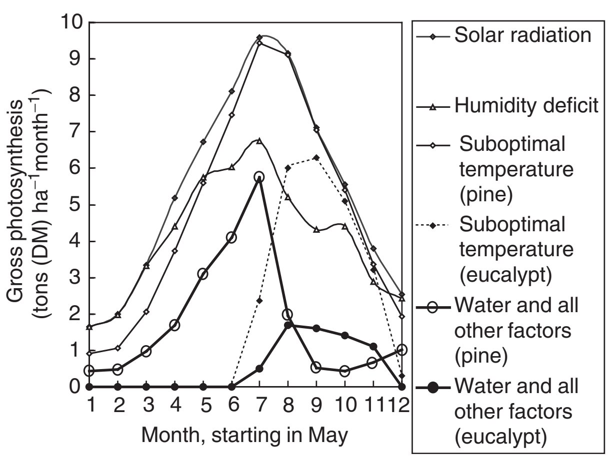


Figure 2 *Eucalyptus globulus* is predicted to grow at less than one-third the rate of *Pinus ponderosa* because it is more poorly adapted to temperatures between 0°C and 10°C that occur frequently at 750 m elevation near Bariloche, Argentina (41° S latitude). Drought and high evaporative demand (humidity deficits) reduce photosynthesis and growth for both species well below limits set by absorbed radiation. DM, dry matter.

The photosynthetic component of process models is well developed and capable of analyzing the impact of rising atmospheric carbon dioxide. Some process models keep track of seasonal changes in storage reserves and predict timing of budbreak, shoot and root elongation, and dormancy. A major challenge remains: to predict competitive relationships in forests composed of many species, some of which fix nitrogen, have roots that access ground water, are tolerant to toxic compounds, or to attack from herbivores and pathogens.

General Indices of Stress

Biochemical Indices

Both biochemical and structural features of trees have been used to assess tree vigor and susceptibility to attack by insects and pathogens. In many cases, specific biochemical compounds have been identified that attract or repel attack. These secondary plant metabolites include alkaloids, nonprotein amino acids, ligans, lipids, phenolic acids, phytoalexins, quinones, terpenes, and steroids.

In a search for general biochemical indicators of stress, physiologists have focused on the storage of starch, an energy source, and amino acids, the building blocks of protein. The seasonal variation in both of these resources can be large so comparisons are generally made during the dormant season. When starch reserves drop below normal, trees become more susceptible to disease. Also, when amino acid concentrations increase with tissue N content, that too is an indication of increased susceptibility. The energy required to store excess amino acids reduces that available for production of defensive compounds. Thus, in Scots pine (*Pinus silvestris*), the concentration of defensive compounds (procyanidins) decreased by 45% while the fraction of arginine in the amino acid pool increased by nearly 400% as foliar N concentrations changed from 1.4% to 2.1%. Expressed as a ratio, a threshold of susceptibility can be identified when leaf N% is in excess of 1.5%. Biochemical ratios of defensive compounds to sugars have also been used to define threshold susceptibility to injury from pathogens (**Figure 3**).

Structural Indices

Wood growth is greatly reduced under stressful conditions but differs with tree size. Physiologists take into account differences in size by calculating partitioning coefficients that express the relative allocation of resources to roots, stems, branches, and foliage. With the knowledge that sapwood cross-sectional area at breast height is correlated with a tree's leaf area, and that stem growth can be related to annual increment in diameter, a general index of tree vigor (growth efficiency) can be defined. Following establishment of a plantation of trees, growth efficiency drops rapidly as the canopy develops and natural mortality (self-thinning) begins. In regions where extensive forests of a particular species exist, outbreaks of insects are

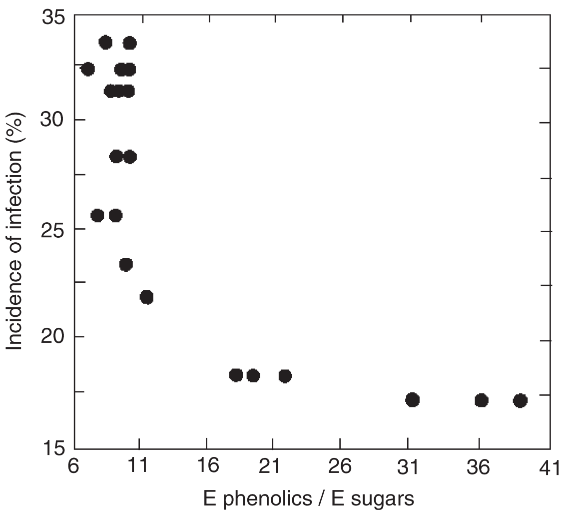


Figure 3 Incidence of infection by a root pathogen, *Armillaria*, on Douglas-fir increased when the ratio of energy (E) required to metabolize defensive compounds (phenolics) in reference to the energy available in sugars drops too low. Reproduced with permission from Waring RH and Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scales*, p. 192. Copyright (1998) Academic Press, San Diego, CA.

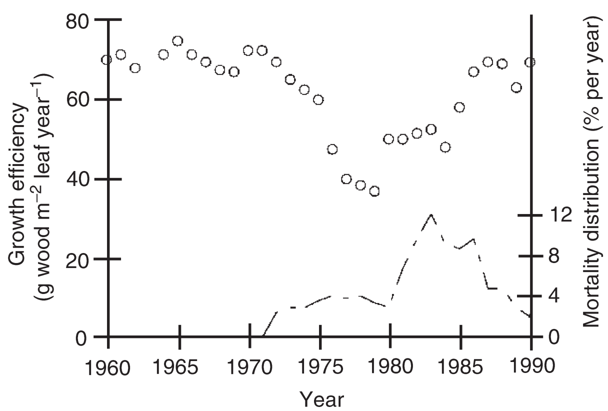


Figure 4 A spruce budworm outbreak in a balsam fir (*Abies balsamea*) stand in Quebec, Canada indicates that tree mortality (dashed line) recorded between 1972 and 1990 restored average tree growth efficiency (circles) to values recorded before the outbreak. Reproduced with permission from Waring RH and Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scales*, p. 192. Copyright (1998) Academic Press, San Diego, CA.

associated with periods when stand growth efficiency drops below normal. The resulting mortality improves the growth efficiency of surviving trees (**Figure 4**). The growth efficiency index, combined with knowledge of the density of bark beetle attack, provides a basis for predicting survival or death of individual trees. Although unusual weather conditions can cause stress, it is often possible to improve tree vigor and biochemical defenses through thinning and application of fertilizer.

Separating Climatic from Other Stresses

Process models, provided with climatic data as well as information on stand structure, can provide monthly and annual estimates of photosynthesis, growth, and growth efficiency. With weather satellites in orbit around the earth, it is possible to obtain estimates of cloud cover and thereby to estimate incoming solar radiation. On clear days, it is also possible to estimate ambient air temperatures, humidity deficits, and periods of drought. With some simplifying assumptions, global variation in terrestrial primary production has been predicted exclusively from weather satellite-derived data. New satellite systems provide 8-day estimates of photosynthesis, and more accurate estimates of changes in canopy leaf area and annual above-ground production. In the future, remote sensing systems already tested from aircraft are being designed to provide improved estimates of changes in forest structure (leaf area and biomass) and canopy biochemistry (lignin and nitrogen concentrations).

With frequent monitoring of the forest condition via remote sensing, it is possible to distinguish disturbances caused by fire, insect outbreaks, logging, and wind storms from those associated with gradual changes in climate and pollutant loads. If conditions shift permanently, trees adapted to the previous environment should experience more stress and eventually be replaced by others better adapted to the new environment.

See also: **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Health and Protection**: Biochemical and Physiological Aspects. **Tree Physiology**: A Whole Tree Perspective; Canopy Processes; Physiology and Silviculture.

Further Reading

Evans J (ed.) (2001) *The Forest Handbook*, vol. 1. Oxford: Blackwell Science.

Franklin SE (2001) *Remote Sensing for Sustainable Forest Management*. New York: Lewis.

Landsberg JJ and Gower ST (1997) *Application of Physiological Ecology to Forest Management*. San Diego, CA: Academic Press.

Levitt J (1980) *Responses of Plants to Environmental Stresses*. vol. 1. New York: Academic Press.

Mitchell CP, Ford-Robertson JB, Hinckley T, and Sennerby-Forsse L (eds) (1992) *Ecophysiology of Short Rotation Forest Crops*. Dordrecht, Netherlands: Kluwer Academic.

Waring RH and Running SW (1998) *Forest Ecosystems: Analysis at Multiple Scales*. San Diego, CA: Academic Press.

Mycorrhizae

D L Godbold, University of Wales, Bangor, UK

Introduction

The term 'mycorrhiza' describes the symbiosis between a plant root and fungal partner. In most cases mycorrhizae are mutualistic symbioses in which both partners benefit from the association. In general, the fungal partner benefits from a supply of photosynthetically fixed carbon from the host plant, whereas plants benefit mainly from greater acquisition of mineral nutrients via fungal structures. Plants may also enjoy several other benefits such as protection against root pathogens and improved water uptake. This article describes the importance of mycorrhizae in forests, the structure of different mycorrhizal types, fungi forming these types, and their global occurrence.

Mycorrhizae can be divided into seven structural types (**Table 1**). With the exceptions of monotropoid and orchid mycorrhizae, all other types can be found on woody plants and trees. Within a single mycorrhizal type there is considerable diversity in structure, development, and function. The identity of the symbionts can have a considerable influence on the structure of mycorrhizae formed. For example, the fungus *Hebeloma crustulinforme* forms ectomycorrhizae with many species of *Picea* and *Pinus*, but arbutoid mycorrhizae with *Arbutus menziesii*. Similarly, fungi forming vesicular-arbuscular mycorrhizae may form mycorrhizae with extensive intracellular coils and few arbuscules in one plant species, and intercellular hyphae and many arbuscules in another plant species.

Ectomycorrhizae

Structure

Ectomycorrhizal roots are characterized by three structural components (**Table 1**, and **Figure 1**): (1) a

Table 1 Characteristics of mycorrhizal types found on woody plants

	Type of mycorrhiza				
	Ecto	*Vesicular-arbuscular*	*Ectoendo*	*Arbutoid*	*Ericoid*
Intracellular colonization	−	+	+	+	+
Fungal mantle	+	−	+	+	−
Hartig net	+	−	+	+	−
Vesicles	−	+	−	−	−
Fungal taxa	Basidiomycete Ascomycete	Zygomycete	Basidiomycete	Basidiomycete	Ascomycete

Modified with permission from Smith SE and Read DJ (1997) *Mycorrhizal Symbiosis*. San Diego, CA: Academic Press.

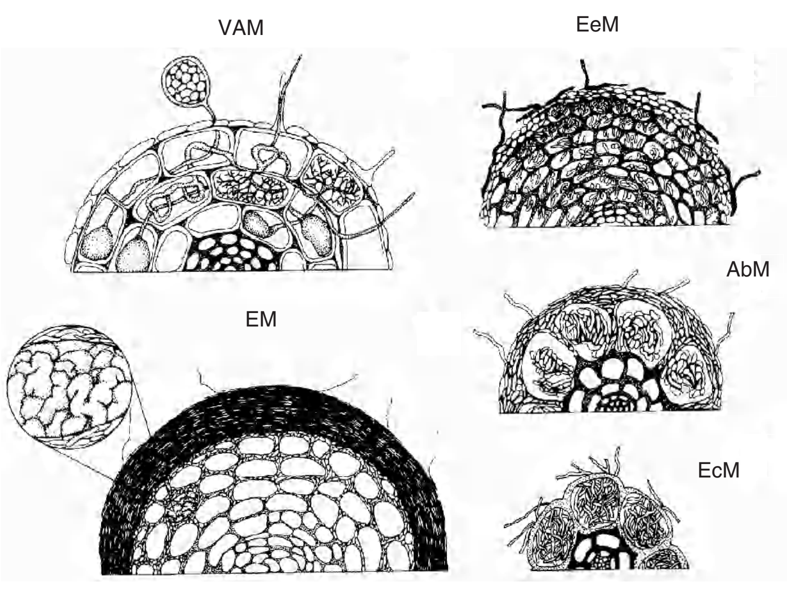


Figure 1 Structures of different mycorrhizal associations. Shown are vesicular–arbuscular mycorrhiza (VAM), ectomycorrhiza (EM), ectendomycorrhiza (EeM), arbutoid mycorrhiza (AbM), and ericoid mycorrhiza (EcM). Redrawn with permission from Allen MF (ed.) (1992) *Mycorrhizal Functioning*. New York: Chapman & Hall.

hyphal sheath or mantle which encloses the root; (2) an inward growth of hyphae between the epidermal or cortical cells forming the Hartig net; and (3) an outward-growing mycelium of hyphae or rhizomorphs forming the extramatrical mycelium. The hyphal mantel constitutes between 20 and 40% of the root dry weight. The cellular structure of the hyphal mantel varies between fungal species and is used to identify species of ectomycorrhizae. The Hartig net forms the contact zone between the cells of the fungal symbiont and host plant. The Hartig net is formed by penetration of hyphae from the inner hyphal mantel. The depth of penetration differs in angiosperms and gymnosperms. In most species of angiosperms penetration is restricted to the outer cortical layer, forming a so-called epidermal Hartig net. Within the epidermal types two forms are found. In the paraepidermal type, the epidermal cells are only partially enclosed by hyphae. In the periepidermal type the epidermal cells are completely encircled by the fungal hyphae. Most species of gymnosperm form a cortical Hartig net, in which several layers of cortical cells extending to the endodermis are enclosed by hyphal layers. Penetration between the root cells is believed to involve fungal enzymes that disrupt the middle lamella, leading to complete fusion of plant and fungal cell walls to form the intercellular matrix or involving layer. Intercellular penetration induces prolific branching of fungal hyphae, producing a fanlike structure that moves across the radial plant cell walls. The prolific branching of hyphae and fusion of the plant and fungal cell walls produce a structure with a high surface area for exchange of mineral elements and metabolites.

The hyphae of the extramatrical mycelium extending from the surface of the hyphal mantel greatly increase the area of contact with the soil. In forest soils, ectomycorrhizal hyphae in the soils have been estimated to have a length of $2000\,\mathrm{km\,m^{-2}}$, several orders of magnitude greater than the length of fine roots. The extramatrical mycelium provides the area of nutrient uptake in the soil and the transport pathway between the soil and the hyphal mantel. Extramatrical hyphae extend from the mantle both as single hyphae and as aggregates forming rhizomorphs. The degree of aggregation and the complexity of the rhizomorph structure vary greatly between fungal species. Six categories of rhizomorph are recognized, the simplest being loose aggregates of hyphae of similar diameter, the most complex having enlarged central hyphae in a highly organized structure. It is assumed that the structural differences in the rhizomorphs are associated with functional differences.

Occurrence

Only about 3% of plant species form ectomycorrhizae but the species that form ectomycorrhizae dominate many ecosystems that occupy a large proportion of the land surface. The majority of economically important timber tree species in temperate regions form ectomycorrhizae. The Pinaceae, from which most species are ectomycorrhizal, dominate the boreal forests of the northern hemisphere. The dominants of the northern temperate forests, Fagaceae, and the southern temperate and subtropical forests, Myrtaceae, are both families of mainly ectomycorrhizal species. Ectomycorrhizal species are also found in the tropics; the Dipterocarpaceae, the most important family in moist and monsoon forests of Southeast Asia, is composed of mainly ectomycorrhiza-forming species.

A number of leguminous tree genera from both the moist tropics and dry miombo woodlands, including *Afzelia*, *Eperua*, and *Intsia*, and *Brachystegia* with *Julbernaldia* respectively, are also known to form ectomycorrhizal associations. However, many of the tree species forming ectomycorrhizae also form vesicular–arbuscular (VA) mycorrhizae. The formation of ectomycorrhizae is linked to accumulation of an organic litter layer in soils.

Fungi forming ectomycorrhizae

A large number of fungi form ectomycorrhizae, the majority being basidiomycetes. Ectomycorrhizae are also formed by a number of ascomycetes and a few species of zygomycetes. It is estimated that between 5000 and 6000 species of fungi form ectomycorrhizae. About 75% of ectomycorrhizae are epigeous, and *c.* 25% hypogeous, including a large number of ascomycetes. Ectomycorrhizal fungi differ in the degree of host specificity. The majority of species have a broad host range colonizing a large number of tree species. However, a number of species have a more restricted range and there are an estimated 250 species that are genus-specific. The root system of an individual tree will normally be colonized by a range of ectomycorrhizal fungal species. The number of fungal species colonizing roots of a tree depends upon both tree species and environmental conditions.

Vesicular–Arbuscular Mycorrhizae

In forestry, VA mycorrhizae are poorly neglected in favor of ectomycorrhizae, yet VA mycorrhizae are found on a large number of temperate tree species and the majority of tropical species.

Structure

The fungal structure of VA mycorrhizae is an internal mycelium growing within the root, intracellular vesicles and arbuscules, and an extraradical mycelium extending into the soil. Whereas all VA mycorrhizae form arbuscules, *Gigaspora* and *Scutellospora* do not form vesicles.

Roots become colonized from hyphae originating from the hyphal mycelium in the soil, spores or old colonized root fragments. The hyphae of the internal mycelium spread from an entry point to form two recognized types of the internal mycelium colonization, the Arum and Paris types. In the Arum type, hyphae proliferate in the cortex by growing longitudinally between host cells. Hyphae grow through longitudinal intercellular air spaces. This type is regarded as the typical VA mycorrhizal type. In the Paris type, hyphae develop intracellular coils and the hyphae spread directly from cell to cell. Arbuscules are formed by repeated dichotomous branching. The width of hyphae decreases from an initial trunk hypha 5–10 μm in diameter to fine branch hyphae less than 1 μm in diameter. In the Arum type arbuscules form from dichotomously branched hyphae that penetrate the cortex cells, whereas in the Paris type arbuscules grow from the intracellular coils. The fungus is always located outside the cytoplasm in an apoplastic compartment. The periarbuscular membrane surrounding the arbuscule is modified functionally. Together with the fungal membrane of the arbuscule, the periarbuscular membrane forms an interfacial zone, important for the transfer of nutrients between the symbionts. Arbuscules are considered the major site of exchange between the fungus and host. Arbuscules start to form approximately 2 days after root penetration, and in fast-growing species arbuscular turnover is about 7 days. However, in slow-growing woodland plants arbuscules are longer-lived and more robustly branched. Compared with the arbuscules the hyphae of the internal mycelium are long-lived and can remain in roots for months.

Vesicles develop to accumulate storage products in many VA mycorrhizal associations. Vesicles are thick-walled hyphal swellings in the root cortex that contain lipids and numerous nuclei. Vesicles vary in shape from ovoid, irregular-lobed to box-like, depending on the fungal species. They are likely to act both as storage organs and as propagules. However little is known about the biology of these structures.

Similar to the extramatrical mycelium of ectomycorrhizal roots, the extraradical mycelium of VA mycorrhizae increases the area of contact with the soil and transport pathway between the soil and the root. The hyphae of the extraradical mycelium are highly branched with species-specific branching patterns.

Occurrence

Most herbaceous plants are colonized by VA mycorrhizae. However, VA mycorrhizae are not restricted to herbaceous plants and are found on a large number of temperate tree species and most tropical trees. The only family of tropical trees that are not typically VA mycorrhizal is the Dipterocarpaceae. Trees of savanna grasslands and semiarid bushlands are also dominated by VA mycorrhiza-forming species. Although, in temperate regions, VA mycorrhiza-forming species are less important in geographical area than ectomycorrhiza-forming species, the majority of temperate tree species form VA mycorrhizae. Whereas the Pinaceae (*Abies*, *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*) are ectomycorrhizal, most other gymnosperms form VA mycorrhizae. This includes the Cupressaceae, Taxaceae, and Taxodiaceae. A number of families of angiosperms also commonly contain VA mycorrhizal-forming species, including the Rosaceae (*Malus* and *Prunus*), Leguminosae, Oleaceae, and Tiliaceae. VA mycorrhizae are reported to be the ecologically most important type in New Zealand forests. However, a large number of species also form both VA mycorrhizae and ectomycorrhizae. The formation of both VA mycorrhizae and ectomycorrhizae is particularly well described on *Eucalyptus*, *Populus*, and *Salix*. In most cases, VA mycorrhizae develop at earlier successional stages than ectomycorrhizae. VA mycorrhizae are more frequent on plants growing on mineral soils.

Fungi Forming Vesicular Arbuscular Mycorrhizae

The fungi of the order Glomales, which form VA mycorrhizae, have been classified into three families containing five genera, *Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus*, and *Scutellospora*. About 150 species have been described. Due to the difficulties involved to identify species colonizing roots, the number of species associated with roots of a single plant in the field is uncertain.

Ectendomycorrhizae

Ectendomycorrhizae are a distinct form of mycorrhiza formed on *Picea* and *Pinus*, mainly on juvenile trees and often in disturbed soils or nurseries.

Structure

Ectendomycorrhizae have some of the structural characteristics of both ectomycorrhizae, and endomycorrhizae. The development of ectendomycorrhizae is similar to that of ectomycorrhizae, resulting in a thin or hyaline hyphal mantel that does not cover the root tip, and a Hartig net that can extend to the inner cortex. However, unlike ectomycorrhizae, ectendomycorrhizae also have intracellular penetrations of hyphae which branch repeatedly once inside the cell.

Occurrence

Ectendomycorrhizae occur primarily on *Picea* and *Pinus*, and are commonly found in pot cultures or nursery trees of several years of age. They occur on a wide range of soil types, but are common on disturbed soils or soils of agricultural origin.

Fungi forming ectendomycorrhizae

Ectendomycorrhizae are formed by a number of fungi but most can be referred to as *Wilcoxina* and assigned to two taxa, *W. mikolae* and *W. rehmii*. *Wilcoxina mikolae* produces chlamydospores and occurs in disturbed mineral soils; *W. rehmii* does not produce chlamydospores and occurs on peaty soils.

Mycorrhizae in the Ericales

Two types of mycorrhizae are formed with woody plants in the Ericales that are important in forest, namely arbutoid and ericoid mycorrhizae.

Arbutoid mycorrhizae are formed on woody plants in the genera *Arbutus* and *Arctostaphylos*, and in genera of the Pyrolaceae including *Chimaphila*, *Moneses*, *Pyrola*, and *Orthilia*. Arbutoid mycorrhizae are characterized by a hyphal mantel and Hartig net similar to that of ectomycorrhizae, but also an intercellular proliferation of mycelia to form dense hyphal complexes. These hyphal complexes can only be revealed by anatomical investigation. The fungi-forming arbutoid mycorrhizae are mainly basidiomycetes that commonly form ectomycorrhizae in other tree species. These include genera of basidiomycetes such as *Laccaria*, *Piloderma*, and *Rhizopogon*, and ascomycetes such as *Cenococcum*.

Ericoid mycorrhizae are formed by most of the genera of plants in the Ericales; these include genera forming important midstory and understory plants such as *Rhododendron* and *Vaccinium*, as well as tree species within the genus *Erica*. The ericoid mycorrhizal root is a delicate structure of only two cortical layers, an outer hypodermis and an inner endodermis, surrounding a stele consisting of only one or two tracheids, a sieve element and a companion cell. Mycorrhizal colonization of the root is restricted to expanded epidermal cells, in which fungal hyphae penetrate the cell walls and form a dense hyphal profusion, fully filling the colonized cell. Examples of fungi-forming ericoid mycorrhizae have been identified as members of the genera *Hymenoscyphus* and *Oidiodendron*. Soils that support ericaceous vegetation are characteristically nutrient-poor.

Species Assemblages Colonizing Trees

Individual trees may be colonized by a large number of species of mycorrhizal fungi. Ectomycorrhizal fungi are divided into broad, intermediate, and narrow-range fungi, reflecting the number of potential host tree species that they colonize. Ectomycorrhizal species are also categorized into early and late successional species, reflecting the appearance of fruiting bodies of the species in developing tree stands. However, species categorized as early successional are also found in mature trees stands, and late successional species often colonize young or juvenile trees growing in mature stands. Little is known about species assemblages in VA colonization of tree species; however, most VA species are believed to be broad-range species. Current knowledge of species assemblages of VA is restricted by problems of *in planta* identification. Species assemblages of trees are influenced by environmental conditions, including, among others, soil fertility, especially nitrogen and soil acidity, elevated atmospheric carbon dioxide, and toxic levels of ozone. The influence of elevated atmospheric carbon dioxide and ozone is thought to be mediated by changes in rates of photosynthesis and hence carbon flow to the mycorrhizae.

Identification of Mycorrhizae

The population structure of arbuscular and ectomycorrhizae can be estimated using fruiting bodies (mushrooms) for ectomycorrhizae or soil spores for arbuscular mycorrhizae. For ectomycorrhizae, fruiting bodies within an area can be collected, identified, and their abundance estimated. However, this depends upon the ectomycorrhizal fungus-forming epigeous fruiting bodies. Fruiting body production often correlates poorly with the below-ground abundance. The spores of arbuscular mycorrhizae must be isolated from the soil and can be identified to genus or species using morphological characteristics.

Ectomycorrhizal fungi colonizing roots can be identified using morphological and molecular biological methods. Morphological identification uses both structural features of the mycorrhizal root tip such as color and ramification, and the cellular patterns of the hyphal mantel. This permits identification to genus or species level. Morphological methods can also be used to identify some arbuscular mycorrhizae. Morphological features that are important include variations in the size, shape, wall thickness, position, and abundance of vesicles, branching patterns, the diameter and structure of hyphae, and the staining intensity of hyphae. However, this method is of limited potential as a single mycorrhizal species may have a different morphology between plant host species. Both ectomycorrhizae and VA mycorrhizae can be identified *in planta* using molecular biological techniques. Ectomycorrhizae are commonly identified by using polymerase chain reaction (PCR) amplification of DNA followed by restriction fragment length polymorphism (RFLP). Target DNA for amplification is often the internal transcribed spacer (ITS) region rDNA. VA mycorrhizae are commonly identified using short arbitrary primers in random amplified polymorphic DNA (RAPD-PCR) techniques. Target regions are often the small subunit (18S) or large subunit (25S) ribosomal gene. These techniques are often used with subsequent RFLP analysis. Family-specific primers allow identification of the major families of VA mycorrhizae.

Tree Benefits of Mycorrhization

Mineral Nutrient Acquisition

The improved mineral nutrition of mycorrhizal plants is well documented, in particular, a role in the uptake of P by ectomycorrhizae or arbuscular mycorrhizae, and N uptake by ectomycorrhizae and to a lesser extent arbuscular mycorrhizae. In *Eucalyptus grandis* and *E. maculata*, inoculation with the ectomycorrhizal fungus *Pisolithus* spp. enabled the seedlings to utilize amino acids as organic N sources, which could not be utilized by nonmycorrhizal seedlings. Ectomycorrhizal colonization facilitates utilization of many organic sources of N, including amino acids, proteins, and leaf litter. *Pinus sylvestris* seedlings colonized with *Suillus bovinus* were able to utilize N from the litter fermentation layer of a forest soil. In addition to the elements P and N, mycorrhizae have been shown to facilitate plant acquisition of Mg, Cu, Zn, and Mn.

Much of the benefit of mycorrhizae in mineral nutrient acquisition is a consequence of the extramatrical or extraradical mycelium. Both ectomycorrhizae and arbuscular mycorrhizae can greatly increase the volume of soil exploited due to the extent and high surface area of the extramatrical mycelium. It has been shown in a number of investigations that the external hyphae of mycorrhizae can absorb P from outside the root depletion zone and transport P to the host plant. In an investigation with Norway spruce (*Picea abies*) and the ectomycorrhizal fungus *Paxillus involutus*, translocation of P by the extramatrical mycelium over a distance of 5 cm was demonstrated. In *Pinus sylvestris* mycorrhizal with *Suillus bovinus*, P was translocated over 30 cm, mainly in rhizomorphs.

The high effectivity of the hyphae of both ectomycorrhizae and arbuscular mycorrhizae in P uptake may also be due to the accumulation of polyphosphates in vacuoles, where they act as both a storage form of P and function in an alternative form of energy storage. In addition to the increase in surface area provided by the extramatrical mycelium, ectomycorrhizae have also been shown to exude organic acids and mobilize sparingly soluble P mineral sources. The ectomycorrhizal fungus *Paxillus involutus* has been shown to exude high amounts of malate and oxalate. *Pinus rigida* ectomycorrhizal with *Pisolithus tinctorius* was able to extract P from insoluble aluminum phosphate. The exudation of organic acids may be a primary factor in the weathering of minerals.

Both ectomycorrhizae and arbuscular mycorrhizae have high levels of phosphatase activity, which are important in the utilization of organic P sources. In forest soils the majority of P in the rooting layer is in the form of organic P. The levels of phosphatase in mycorrhizae are often similar to those of tree fine roots. As an example, in Norway spruce ectomycorrhizal with a number of fungi, similar levels of acid phosphatase were found in mycorrhizal and nonmycorrhizal roots. However, there are differences in the levels of phosphatase activity between different ectomycorrhizal species. In Norway spruce mycorrhizal with *Thelephora terrestris*, a higher phosphomonoesterase activity was found in mycorrhizal roots and rhizomorphs than nonmycorrhizal roots. However, independent of the levels of acid phosphatase activity between mycorrhizae and nonmycorrhizal roots, the large surface area of the extramatrical mycelium will greatly increase the potential to mobilize organic P.

Estimates of the contribution of inorganic P uptake to the total uptake by trees suggest that the contribution may be significant. In Norway spruce ectomycorrhizal with *Paxillus involutus*, 52% of the total P uptake was shown to be via the extramatrical hyphae. It is possible that experimental systems may overestimate the mycorrhizal contribution to P acquisition. However, as the mycorrhizal contribution is so high, it is very likely that under field conditions mycorrhizae play a significant role in P acquisition.

Water relations

Both ectomycorrhizae and arbuscular mycorrhizae can improve the water relations of plants. For example, in two species of *Acacia*, mycorrhizal plants had a higher number of open stomates under drought conditions. However, the mechanisms involved are still controversial. A number of mechanisms of increased host drought tolerance have been suggested, such as increased root hydraulic conductivity, alteration of stomatal regulation due to hormone signals, osmotic adjustment, hyphal water transport, and improved P nutrition. Improved water status has often been associated with improved host P nutrition. That mycorrhization nearly always results in an improved P nutrition of the host plant and/or larger plants often makes interpretation of the mechanisms involved in improved water relationships difficult. However, the rhizomorphs of ectomycorrhizae provide possible conduits for the transport of water. In *Pinus pinaster* inoculated with a number of strains of *Pisolithus tinctorius*, a significant correlation between plant water potential and the extension growth and rhizomorph diameters of the different strains could be shown.

Plant–Pathogen Interactions

Apart from beneficial effects on the nutrition and water supply of host trees, mycorrhizae have been proven to increase the resistance of trees to infection by pathogens of the fine roots. Different species of mycorrhizal fungi vary in their efficiency at preventing root infections, although the mechanisms involved in this process are rather poorly understood. Possible modes of action include the production of antibiotics by the mycorrhizal fungi, stimulation of host defense mechanisms, and the physical barrier presented by the Hartig net in ectomycorrhizae. In casuarina (*Casuarina equisetifolia*) arbuscular mycorrhizal fungi increased the resistance to the root pathogen *Fusarium vesicubesum*. Both ectomycorrhizal and arbuscular mycorrhizal fungi have been shown to produce antibiotics. In addition, ectomycorrhizal fungi produce phenolic substances and oxalic acid that suppress root pathogens.

Amelioration of Metal Toxicity

Ectomycorrhizal fungi have been demonstrated to alleviate growth depressions of tree seedlings due to toxic effects of Al, Ni, Zn, and Cd. For other important heavy metals, for example Hg and Pb, direct evidence of amelioration by ectomycorrhizal fungi is still lacking. Metal tolerance of higher plants may be due to a range of potential processes. These may include: (1) a reduction of metal exposure by excretion of chelating substances; (2) extracellular sequestration (e.g., by mucilage, pH gradients in the rhizosphere); (3) modified uptake systems at the plasmalemma; or (4) intracellular detoxification. Mycorrhizal fungi may also alter metal sensitivity of their hosts by any of the mechanisms outlined. A number of possible mechanisms have been suggested, including: (1) filtering of toxic metals in the hyphal sheath or Hartig net; (2) reduced transfer of metal to the shoot; (3) metal sorption on the extramatrical mycelium; and (4) chelation by organic acids and other substances released by mycorrhizal fungi.

The Costs of Mycorrhization

Production and maintenance of mycorrhizae impose a carbon cost on the host plant in excess of 30% of total photosynthesis. In seedlings growing at adequate nutritional levels, the carbon requirements of the mycorrhizal fungi may result in reduced growth rates of the host plants.

Mycorrhizae in Ecosystems

Boreal and Temperate Forests

In boreal and temperate forests there is good evidence to suggest that ectomycorrhizae play an important role in N recycling and acquisition. Ectomycorrhizal fungi release enzymes such as peroxidase and phenol oxidase that allow them to contribute to decomposer activity. In Ca-deficient forests, ectomycorrhizae have been shown to be involved in the uptake of Ca from mineral weathering. This may be due to the release of organic acids. High release of organic acids, especially oxalate, has also been shown in ectomycorrhizal fungi forming hyphal mats, resulting in bleaching of soil horizons.

The formation of a common hyphal mycelium between different tree species colonized by the same ectomycorrhizal fungus is thought to be involved in the transfer of carbon between species. This has been shown experimentally in a carbon transfer between *Betula papyrifera* and *Pseudotsuga menziesii* sufficient to improve growth. It is believed such carbon transfer may be important for tree seedlings growing in deep shade.

Subtropical and Tropical Forests

In an investigation of the distribution of arbuscular and ectomycorrhizal tree species in savannas, it was shown that ectomycorrhizal trees dominate soils with low levels of N and P, whereas arbuscular mycorrhizal species dominate soil low in P but relatively rich in N. This suggests that ectomycorrhizal trees may have a greater advantage for N acquisition than VA mycorrhizal species. However, in the humid tropics of French Guyana, ectomycorrhizal tree species were found not to dominate the poorest soils. In the moist tropics most tree species are VA mycorrhizal. Many of the soils are acidic and highly leached, with a consequence that the soils have low available P levels due to Al fixation of P. Under these conditions VA mycorrhizae may be important in the rapid cycling and uptake of inorganic P.

Ectomycorrhizal Fungal Fruiting Bodies as Nontimber Forest Products

Fruiting bodies of ectomycorrhizae are commonly collected and sold. In some forest areas the value of the mycorrhizal fungal fruiting body harvest exceeds the value of wood production. Harvesting is mainly restricted to a small number of valuable species such as *Boletus edulis*, *Cantharellus cibarius* (chanterelles), *Tuber magnatum* (white truffles), and *T. melanosporum* (black truffles).

See also: **Health and Protection**: Biochemical and Physiological Aspects. **Tree Physiology**: A Whole Tree Perspective; Nutritional Physiology of Trees; Root System Physiology.

Further Reading

Allen MF (ed.) (1992) *Mycorrhizal Functioning*. New York: Chapman & Hall.
Auge RM (2001) Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11: 3–42.
Jentschke G and Godbold DL (2000) Metal toxicity and ectomycorrhizae. *Physiologia Plantarum* 109: 107–116.
Kapulnik Y and Douds DA (eds) (2000) *Arbuscular Mycorrhizae: Physiology and Function*. Boston, MA: Kluwer.
Smith SE and Read DJ (1997) *Mycorrhizal Symbiosis*. San Diego, CA: Academic Press.
Varma A (ed.) (1998) *Mycorrhiza Manual*. New York: Springer-Verlag.
Varma A and Hock B (eds) (1995) *Mycorrhiza: Structure, Function, Molecular Biology and Biotechnology*. Berlin, Germany: Springer-Verlag.

Physiology of Sexual Reproduction in Trees

J Webber (Retired), Ministry of Forests, Research Branch, Victoria, BC, Canada

Introduction

The physiology of sexual reproduction in forest trees has progressed substantially over the past 20 years. Three previous symposia of the International Union of Forestry Research Organizations (IUFRO) not only summarized current knowledge but also laid out the ground work for future studies. Many of these questions are still valid today but substantial progress has been made in early maturation, flower induction, and pollination biology. Many questions still exist (mechanism of flowering) and new questions are being asked (environmental effects on progeny performance).

New technology, principally molecular techniques, is now available and offers exciting new possibilities for future flowering, pollination, and seed production studies. However, there has been a substantial shift in flowering research. Considerably fewer studies are being published on the mechanism of flowering in conifers but, equally so, the volume of work dealing with hardwoods, especially tropical hardwoods, is growing.

The perspective of this contribution in forest tree seed production has a definite commercial bias. Procuring seed as a mechanism for delivery of tree improvement programs as well as plantation forestry has been the incentive for pursuing both fundamental research and program development. Much of the emphasis has been with seed orchard development simply because it is the most cost-effective tool for delivery of genetic gain.

Developmental biologists may object to my use of the word 'flowering' when referring to conifers. Certainly the use of 'sporangiate strobili' would be more precise but also more awkward. Here 'flowering' is restricted to the general process of sexual reproduction in conifers. The terms 'seed' and 'pollen cones' refer to the mega- and microsporangiate cones, respectively.

Plantation Forestry

According to statistics provided by the Food and Agriculture Organization, global forest plantations have grown from about 18 million hectares in 1980 to 187 million hectares in 2000 (both hardwoods and conifers). This represents about 5% of the total global forest cover. Asia accounts for about 62% of the current plantation area, followed by Europe (17%), North and Central America (9%), South America (6%), Africa (4%), and Oceania (2%). Globally, broadleaved trees make up 40% of the total, of which *Eucalyptus* is the principal genus and conifers make up 31%, of which *Pinus* is the principal genus. Over the past decade, the percentage of these plantations destined for industrial use has increased from 36% to 48%. Tree improvement, as part of plantation forestry, has been a principal driver of flowering research, especially for temperate conifers.

Critical to the success of these programs is a sustainable supply of not only the species but also adapted families/provenances for the designated target areas. Propagules from asexual techniques (rooted cuttings and somatic embryogenesis) will likely increase but for the foreseeable future seed production will supply the bulk of our needs. The single most important source of seed will continue to be natural stands but in many countries, tree improvement and seed orchard programs are beginning to make substantial contributions of seed. In Canada, an estimated 3.9 billion seeds were sown in 1999, of which 0.63 billion (16%) came from seed orchards. The proportion of seed from seed orchards in Canada is expected to rise to about 80% in the next decade.

Seed orchards offer substantial advantages over natural stand production. With the correct choice of sites, flowering is more regular and inducible. Seed yields are higher because pollen supply is not limiting and crop protection measures (insect control) are more readily applied. When seed orchards are based on selected material from genetic improvement programs, the opportunity to take advantage of family-specific traits is available. This will become very important in the near future if forests cannot adapt to global warming. Tropical species will be less affected but north temperate species may not realize predicted gains and, at worst, plantations may fail. In order to respond to these new demands, we must know the reproductive biology and genecology of our species, including adaptive traits of families as well as the effect of environment on reproductive success and progeny performance. This is the challenge for future physiologists.

Reproductive Biology

The reproductive biology of forest trees forms the basis of our current and future studies. The reproductive biology of species includes the cycle of events starting from initiation of reproductive structures through to seed dispersal. For most conifers and temperate hardwoods these cycles have been at least partially, if not fully, described. In general, this information is lacking for tropical hardwoods but we expect to see this knowledge base expand rapidly over the next few years. Before a tree begins its reproductive cycle, it must first become sexually mature.

Sexual Maturation

All trees go through a phase of juvenility before flowering occurs and this period can be short (1–2 years) or long (greater than 30 years). There are specific phase changes associated with maturation in woody plants. These include morphological changes (decrease in growth rates, an increase in plagiotropism, a change in foliar morphology, and the onset of reproductive competence) as well as physiological and biochemical changes. While maturation is likely under genetic control, the effect of environment on gene expression is also significant. For example, many species of the family Pinaceae and Cupressaceae can become sexually competent in just a few years from seed. Using a combination of early growth acceleration (extended photoperiod and optimal growing regimes), applied stress (drought and heat during reproductive differentiation), crown-forming and growth hormones (gibberellins), flowering can be induced in just a few years and as low as 1 year. Sexual expression is a result of not only the attainment of ripeness to flower (maturation) but also the exposure to environmental/cultural conditions that stimulate flowering.

Physiology of Flowering

The anatomical and morphological description of flowering in conifers and temperate hardwoods has been thoroughly detailed. There are several critical stages in the reproductive cycle to know and they are most often referenced to calendar date. However, phenological development is mediated by environmental cues (photoperiod, temperature, soil moisture), making calendar dates too variable. Where possible, reproductive stages should be referenced to a readily observable phenological stage of development (i.e., bud burst and bud set) of the shoot or plant.

The reproductive stages of most interest are floral initiation and differentiation, meiosis, anthesis, fertilization, embryo development, and cone maturation. All reproductive structures of conifers and hardwoods differentiate from undetermined terminal or axillary apices. For all species of Pinaceae and Cupressaceae, initiation and differentiation are completed before winter dormancy, with the possible exception of soft (Haploxylon) pines where anatomical identification of seed cone structures does not appear until the spring following dormancy. However, in these species, the biochemical/physiological events leading up to differentiation and anatomical identification may occur prior to winter dormancy.

Conifer apices can abort, remain latent, or be determined as seed cones, vegetative buds, or pollen cones. The development sequence apices undergo is largely determined by their position on the stem and in the crown as well as the physiological state of the tree. Temperature and soil moisture conditions that put the trees into stress during periods of initiation and differentiation are the principal environmental factors determining the fate of apices. Light has also been implicated as a contributing factor but, aside from regulating shoot growth, light does not appear to play a direct role in the flowering of conifers. For tropical species, light (photoperiod) and temperature are important factors affecting flowering. Soil nutrient status (fertilizer) also affects flowering but the results are often conflicting and seldom predictable.

Mechanism of Flowering

We do not know the specific mechanism of flowering in trees nor why trees respond to specific inductive treatments. We do know, however, many of the environmental triggers that induce flowering in most Pinaceae and Cupressaceae species and some tropical hardwoods but we have yet to explain the mode of action of specific induction treatments acting either alone or in combination. Much of what we know today about flower induction in temperate conifers came from observations made in natural stands. Trees growing in open, more exposed sites on drought-prone soils are more conducive to flowering than those growing on sites that are shaded, cool, and moist. While some stress is essential for flowering to occur, it is stress applied at specific stages of phenological development that is important. Both low annual rainfall and above normal temperatures in the preceding year are associated with good flowering. However, we do not know how much (or little) drought and heat is required, although experience suggests that warm springs followed by warm, dry summers in temperate climates are best. We also know that growth in the years preceding flowering is important. Even if optimal meteorological conditions leading to stress differentiation occurs, flowering may not necessarily occur. Flowering the year following a particularly heavy crop year (mast) rarely occurs. For species that form their seed cones in the terminal position (i.e., spruce), then new growth must occur before another flowering event can occur.

Several hypotheses have been proposed to explain flowering in conifers. All implicate flowering in relation to shoot growth and plant hormone metabolism. A nutrient-diversion hypothesis contends that a higher concentration of nutrients is required for buds to differentiate reproductively and treatments which retard shoot growth will favor flowering. A second hypothesis relates bud (meristematic) vigor to flowering. Very-high- or very-low-vigor buds remain vegetative. Buds of moderate activity would preferentially promote female flowering in the upper crown (higher-vigor shoots) and male flowering in the lower crown (lower-vigor shoots). The effect of cultural stress treatments (root-pruning, root restriction, drought, and girdling) would be to slow the growth of vegetative buds and favor (enhance) the development of reproductive buds.

However, these hypotheses do not explain the results of gibberellin $A_{4/7}$ ($GA_{4/7}$) applications which not only promote flowering but can also enhance shoot growth (with no effect on apical bud activity). This suggests that the hormonal promotion of flowering and shoot growth are independent processes. Cultural treatments, such as root-pruning (in Douglas-fir), which also enhance flowering, did so by delaying development and not by increasing nutrient concentrations (total insoluble carbohydrate) in axillary apices. Root-pruning also reduces cell elongation and slows apical bud (mitotic) activity in both lateral and terminal buds.

A plausible hypothesis exists for the enhancement of flowering in conifers based on gibberellin biosynthesis and metabolism, although it remains largely untested. The effect of cultural treatment with and without $GA_{4/7}$ treatments suggests that flowering is under numerous biochemical/physiological controls, all of which must be 'permissive' if reproductive structures are to be differentiated and developed. Furthermore, cultural treatments (root pruning, drought, girdling, fertilizer, high temperature, root flooding) may all act through effects on GA metabolism. The effect of these six cultural treatments seems to increase the less polar endogenous GA-like substances ($GA_{4/7}$, GA_9) while at the same time decreasing the levels of more polar-like GA substances (GA_3). Results from labeled (tritiated and deuterated) GA_4 studies support this hypothesis and further suggest that GA activity is regulated in the shoot cell and their metabolites may be influenced by factors affecting root activity.

Roots may have a direct role in regulating flowering and it may involve cytokinins. The promotion of flowering by $GA_{4/7}$ alone and in combination with root flooding resulted in a marked decrease in cytokinin levels in Douglas-fir shoots harvested during the period of cone-bud differentiation. This led to the suggestion that actively growing roots export substances inhibitory to flowering. Since cytokinins are known to inhibit GA biosynthesis, the decreased levels of cytokinins found during flower promotion treatments may actually raise the levels of less polar GAs and, conversely, the higher levels of root-exported cytokinins during nonstress periods would result in lower GA levels and no flowering response.

While this hypothesis is intriguing, it must still be confirmed for the many species in which flowering has been promoted through application of stress treatments. While we do not have hard evidence that less polar GAs have a direct morphogenic role in the promotion of flowering in conifers, it is currently the best one we have. With the increasing knowledge of physiological processes under genetic control and the rapid expansion of molecular technique, new and innovative techniques can now be applied to test this hypothesis rigorously.

It is also interesting to note that flowering in the Pinaceae species only responds to the less polar gibberellins, $GA_{4/7}$, and species of the Cupressaceae families only respond to a more polar gibberellin, GA_3. For Pinaceae species, the effect is enhanced if treatments are combined with stress-inducing cultural techniques such as drought, root-pruning, and heat. Adjunct stress treatments for Cupressaceae species are less effective. Gibberellins do not seem to affect a flowering response in hardwoods but they do respond to photoperiod and shoot-growth retardation which may result in a reduction of GA concentrations. Applications of the growth retardant paclobutrazol have successfully induced flowering in *Eucalyptus* and in a dipterocarp (*Shorea stenoptera*).

Sex Expression

Because most conifer species produce large quantities of pollen that can be handled relatively easily *ex situ*, developing techniques to increase the ratio of seed cones to pollen cones would facilitate not only improved seed production but also the delivery of genetic gain through seed orchard management.

The management of seed production has long sought after sex-specific flower induction treatments. Most conifer species are monoecious and pollen cones are normally differentiated before seed cones. This has led to the possibility that both specific induction treatments and their timing may favor the response of one sex over the other. Cultural treatments are less specific but GA application may provide our best opportunity to control sex expression. However, the levels of endogenous GA normally applied are so large relative to exogenous levels (estimated to be about 5000 greater), it is difficult to expect such subtle responses at the cellular level. Furthermore, we know very little about other plant hormones and their role in sex expression. Certainly, the balance of gibberellins, auxins, cytokinins, and possibly growth inhibitors (i.e., abscisic acid) has been implicated in other plants (angiosperms) and to a certain extent in conifers but their mode of action in conifers is far from clear. Further, the interaction of known growth regulator response with cultural treatments and photoperiod must be very complex.

Regardless of these uncertainties, the value of sex-specific treatments remains. Current management practices that show promise are crown-pruning techniques that favor shoots with a high potential of pollen or seed cone response and treatment timing (specifically gibberellins) in relationship to shoot phenology. We also have the possibility of sex-specific gametocides, including chemical agents that inhibit pollen development.

Pollination Biology

Our knowledge of pollen biology and handling pollen *ex situ* has made pollen management of conifers an essential activity for breeding programs. Pollen management (supplemental pollination) can also be cost-effective in seed orchards where external pollen supply (contamination) can reduce the genetic worth of seed lots or in young orchards where pollen supply and distribution limit seed production. It can also be an effective tool for producing seed with specific traits (i.e., insect-resistant progeny).

Further restraints to seed production and optimal genetic gain include differential parental contribution and nonrandom mating. Some parents are more fecund than others and nonsynchronous flowering (seed cone receptivity and pollen shed) produce distinct breeding populations within orchard seed lots. Orchard activities to balance parental contribution and random mating among all parents include flower enhancement of selective clones, orchard cooling to reduce synchrony between external orchard pollen flight and within orchard pollen flight, and pollen management.

Pollen management involves the collection, extraction, storage, testing, and reapplication of pollen. To handle pollen successfully, we must be able to maintain and measure pollen viability *ex situ*. Pollen of all Pinaceae species is relatively easy to collect, extract, and store. Optimal storage conditions vary slightly among species. In general, pollen must be harvested as near to natural shedding as possible, dried at low humidity (30–40%) and warm temperatures (25–30°C) to a moisture content between 5 and 10%, and then stored in airtight containers at freezer temperatures (− 30°C or lower). For the few Cupressaceae species tested (i.e., *Thuja plicata*, *Chamaecyparis nootkatensis*), pollen must be handled differently. First, pollen must be extracted under high humidity (70–80% relative humidity) and cool temperatures (15–18°C). Under these conditions, pollen moisture content ranges from about 15% to 20% and pollen viability can be maintained at freezer temperatures.

However, conifer pollen quality can deteriorate quickly, especially under high temperatures and humidity. If pollen is exposed to a wide range of conditions, then it is important to test its *in vitro* viability before using. For conifers, three assays that provide consistently good estimators of field performance are respiration (a measure of oxygen uptake), electrical conductivity (a measure of membrane stability), and germination (pollen tube growth in a nutrient medium). Respiration and conductivity are straightforward assay procedures and yield the most consistent response for a wide number of species tested (Pinaceae and Cupressaceae). Germination can also yield good results but the procedure is very sensitive to assay conditions, in particular cultural technique, media components, and pollen prehydration.

Estimates of a pollen lot's fertility potential (ability to set seed) can be determined from assay response. Seed set rises rapidly with increasing pollen viability but quickly reaches an asymptote determined by the number of viable ovules per cone. Since most studies relating assay response to seed set are done using controlled crossing (isolation bags) procedures, the interpretation of these results is limited to this particular pollination technique. When using viability assay response for pollen lots to be used in pollen mixes (i.e., supplemental pollination), then competition between pollen lots becomes important. Since we expect equal contribution from each pollen lot within a supplemental pollination mix, variation in viability may lead to disproportionate contribution. Now that molecular fingerprinting techniques are routinely available, it is possible to measure paternal contributions and use this information to formulate mixes (equal volumes or adjusted to viability response) and to relate *in vitro* viability response to competition both within supplemental pollination mixes and between endogenous orchard pollen clouds.

Pollination Mechanism

Conifers and most temperate hardwoods are wind-pollinated (anemophilous) whereas most angiosperms are insect-pollinated. Most conifer pollen is shed by a wind shock and then air flow patterns around the receptive seed-cone bud not only aid the probability of pollen entrapment but may also favor pollination from its own species. While pollen capture is not specific (it requires over 1 million per ovule), the mechanism of pollen capture can be very efficient.

Once captured, the mechanism of moving the pollen grain into micropyle is quite different among conifer species. A pollination drop is actively involved in some species but not in others. There is considerable interest and, to a large extent, uncertainty about the actual role of the pollination drop. It has not been detected in species such as *Pseudotsuga*, *Larix*, *Tsuga*, and *Abies*. Where the drop does exist (i.e., *Pinus*, *Picea*, Podocarpaceae) and the micropylar arms of the ovule are inverted, the pollination drop can actively draw the pollen grain into the micropyle as it recedes. In some species, such as *Thuja* and *Chamaecyparis*, the pollination drop simply acts as a medium for the pollen landing on its surface to sink towards the nucellus. The various types of pollination mechanism are based on the presence or absence of a pollination drop and may have evolutionary significance.

The pollination drop may be a more recent occurrence but others argue that ovule secretions must have been part of the primitive pollination mechanism as well. Regardless of its evolutionary significance, conifer pollinations drops play an important role in not only directing the pollen towards the nucellus but also in preparing the grain for germination and, perhaps, even actively selecting the species' own pollen from foreign pollen and other microbes. The constituents of the drop include many simple sugars, amino acids, and proteins. With improving analytical technique, the complexities of ovule secretions and the role they may play in pollen germination, selfing and male selection will become clearer.

Cone Development

The description of conifer cone development from preanthesis to seed formation has been extensively reviewed. However, the effect of cultural and environmental conditions on these processes has been less studied, in particular seed cone development. Most temperate Pinaceae species develop their reproductive structures early in the season when temperatures are cool and soil moisture is adequate. However, development of ovules, pollen uptake, and fertilization may be affected by seed orchard environments prone to drought and high temperatures. Most often, the principal cause of poor seed set in conifers is unpollinated ovules. Even when artificial pollen is applied, on average seed yields do not normally exceed 50–60% potential yields. There are also a considerable number of immature or poorly developed ovules in each cone, typically at the base and tips of the cone. Certainly, cone development and early ovule development are under a certain degree of genetic control but the potential to increase the number of mature ovules through cultural techniques warrants a closer look. This is especially true in seed orchard environments where culture techniques can be easily applied.

Another factor affecting low seed set is cone and embryo abortion. *Pinus* species are most sensitive to pollen supply where a substantial percentage of first-year conelets can abort due to inadequate pollen. However, in mature seed orchards, pollen supply is seldom limiting and cone retention is high. However, under field conditions where drought, high temperatures, and low humidity occur, poor uptake of pollen in *Pinus* species may result in increased cone abortion. It is also possible that drought, high temperatures, and low humidity could restrict fertilization and early embryo development in all species.

Environmental Effects on Reproduction

Orchard environment can affect progeny performance. Progeny from parent trees growing in warmer southern seed orchard environments can display delayed flushing in the spring and extended growing periods and delayed growth cessation in the summer. They also developed frost-hardiness later compared to like genotypes derived from northern sources. This phenomenon has been termed seed orchard aftereffects and the effects can endure for several years, if not the lifetime of the tree. Similar effects have been demonstrated with progeny derived from like parents growing under greenhouse conditions compared to open orchard conditions. Further, progeny derived from seed reared under the warmer environment of greenhouses can also show lower spring and fall frost resistance.

We do not know the mechanism of this phenomenon, nor do we know at which stage of reproductive development the effect occurs. However, several hypotheses have been postulated. Since many of the genes expressed in the sporophyte are also expressed in the gametes, it is possible that gametophytic selection occurs. It is argued that pollination selection does not occur in conifers because the pollination mechanism allows too few pollen grains to enter the micropyle to provide sufficient selection pressure. However, three or four pollen grains in each of 100 ovules per cone and hundreds of cones per tree may provide a population sufficiently large to consider a directional selection of pollen under different temperature regimes. Furthermore, conifers have multiple archegonia (many egg cells) per ovule, which permits the possibility of temperature affecting the selection of many fertilized egg cells. Finally, the effect could also be non-Mendelian and represent a maternal effect that remains to be described.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems; Reproductive Ecology of Forest Trees. **Tree Physiology**: Physiology of Vegetative Reproduction; Shoot Growth and Canopy Development; Tropical Tree Seed Physiology.

Further Reading

Bonnet-Masimbert M and Webber JE (1995) From flower induction to seed production in forest tree orchards. *Tree Physiology* 15: 419–426.

Chalupka W (ed.) (1985) Flowering and seed-bearing in forest seed orchards. *Proceedings of the Symposium of Working Parties S2.01.00 and S2.0501*. Kornik, Poland.

Day ME, Greenwood MS, and Diaz-Sala C (2002) Age- and size-related trends in woody plant shoot development: regulatory pathways and evidence for genetic control. *Tree Physiology* 22: 507–513.

FAO (2001). *Global Forest Resources Assessment 2000. Part 1 Global issues*, pp. 23–38. FAO forestry paper 140 (FRA 2000 main report). Rome: FAO.

Gelbart G and von Aderkas P (2002) Ovular secretions as part of pollination mechanisms in conifers. *Annuals of Forestry Science* 59: 345–357.

Henrik S, Cannell MGR, Johnsen Ø, Ryan MG, and Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytology* 149: 369–400.

Krugman SL and Katsuta M (eds) (1981) *Proceedings of the Symposium on Flowering Physiology.* 17th IUFRO World Congress Meeting, Kyoto, Japan.

Pharis RP, Webber JE, and Ross SD (1987) The promotion of flowering in forest trees by gibberellin $A_{4/7}$ and cultural treatments: a review of the possible mechanisms. *Forestry Ecology Management* 19: 65–84.

Sedgley M and Griffin AR (1989) *Sexual Reproduction of Crop Trees*. London: Academic Press.

Webber JE, Owens JN, and Stoehr MU (eds) (1995) Biology and control of reproductive processes in forest trees. *Selected papers from Symposium Working Party S2.01.05*, Victoria, BC, Canada.

Forests, Tree Physiology and Climate

M Rebetez and Michael Reinhard, WSL Swiss Federal Institute for Forest Snow and Landscape Research, Lausanne, Switzerland
Alexander Buttler, University of Franche-Comté, Besançon, France

Introduction

Climate can be defined as the long-term integration of atmospheric parameters such as temperature, precipitation, wind, insulation, air humidity, or snow cover. It is one of the key factors conditioning the growth of vegetation and it is impossible to dissociate the history of forests, and all flora and fauna, from the history of the earth's climate. Climate controls vegetation patterns and dynamics and, conversely, vegetation also influences the climate. These relationships occur over different spatial and temporal scales.

This article reviews the main aspects of the relationship between climate parameters and forests while the impacts of climate change and environment on forests as well as tree physiology and stress are covered in other articles within this publication.

The Energy Cycle and Vegetation Growth

The sun is the basic source of energy for the earth and the maintenance of its biological systems. This energy reaches the planet by means of electromagnetic radiation. The solar constant represents 2 cal (8.3 J) $cm^{-2} min^{-1}$, but the solar irradiance at the earth's surface, which is the driving force for the functioning of ecosystems, represents less than half of the solar constant (**Figure 1**).

The earth re-emits part of this radiation towards space (mainly in the infrared spectrum). Another part of it is trapped by the greenhouse gases in the atmosphere. The balance between the incoming, outgoing, and absorbed energy keeps the earth's climate virtually constant, at a mean temperature of about 15–16°C (warmer now, due to global warming, than it was a few decades ago). Without any greenhouse effect, which is brought about by the humidity and greenhouse gases such as CO_2 in the earth's atmosphere, the mean temperature on the planet would be −18°C. Thus, the total energy absorbed by the earth depends on the amount of greenhouse gases and of aerosols in the atmosphere. These depend in turn on different factors, including volcanic emissions, human sources linked to the burning of fossil fuels, and methane emissions from warming permafrost and agriculture. Only a small part of the sun's energy is used for vegetation growth, the photosynthetic yield, representing the transformation of radiation into chemical energy, being estimated at 1–1.5% for forest ecosystems. Primary

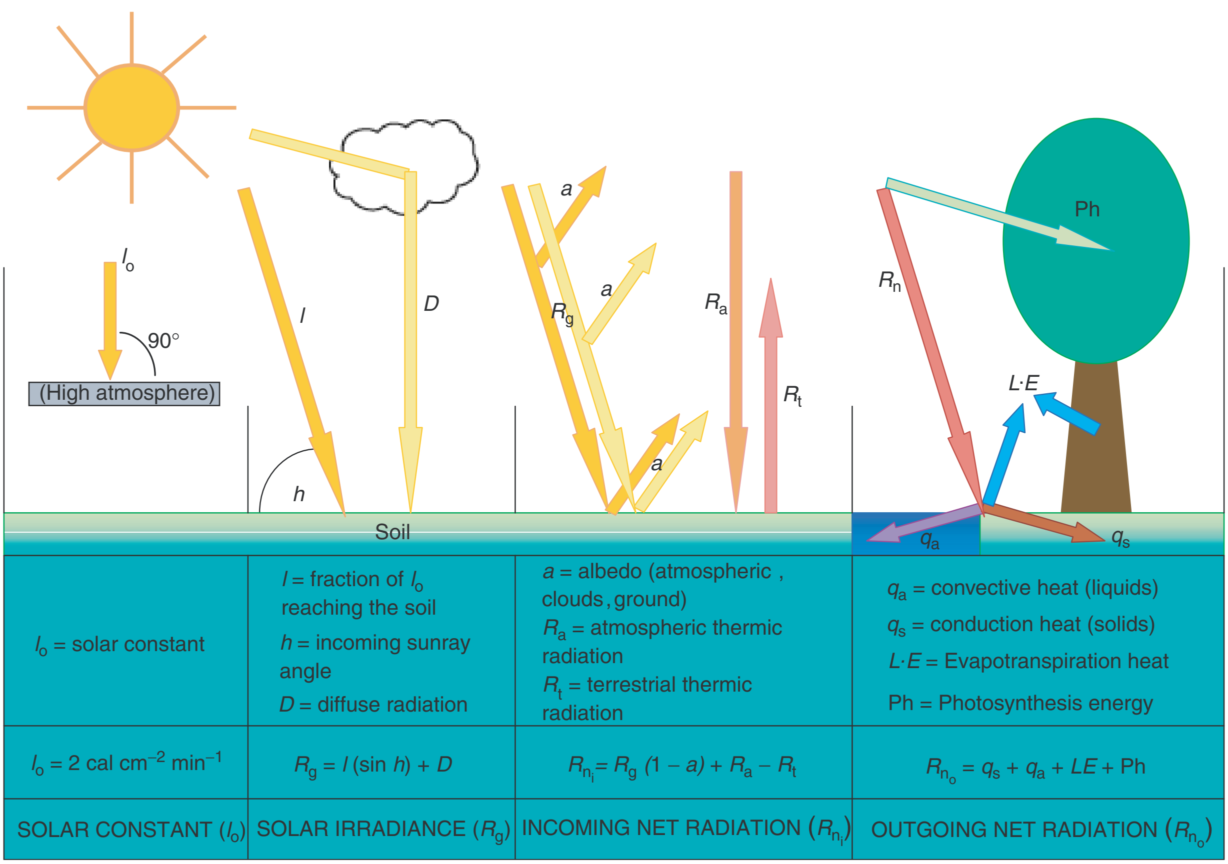


Figure 1 Incoming and outgoing net radiation at the earth's surface. The incoming and outgoing radiation depend on the thickness of the cloud cover, which can act as a shield for the sunrays. The total amount of intercepted radiation at the ground level depends also on the density and thickness of the vegetation canopy. About 98% of the intercepted radiation is reflected or used to heat the tissues and only about 2% is used for photosynthesis. Reproduced with permission from Ozenda P (1982) *Les Végétaux dans la Biosphère*. Paris: Doin.

production contributes to the carbon cycle, and sometimes this organic matter becomes trapped underground as peat, oil, or coal. Through its albedo, the vegetation cover also influences the amount of energy absorbed at the earth's surface.

The energy emitted by the sun is not equally distributed over the earth's surface and this leads to compensating ocean currents and atmospheric circulation. The earth's spherical shape implies a spatially uneven incidence of the incoming solar irradiance, and its intensity changes with latitude. Throughout the year, the intertropical zone receives more energy than polar regions. As the tilt of the earth's axis is not perpendicular to the planet's orbit, the amount of energy received also changes throughout the year, thus determining the seasons. The total amount of energy received by the earth yearly also varies with the amount of energy released by the sun and also with the elliptical shape of the earth's orbit and its eccentricity. These orbital parameters determine climatic cycles on the order of 20 000 to 100 000 years. These differences are relatively small, but important enough to explain major changes in the earth's ice, ocean, and vegetation cover in the past.

The Impact of Climate on Vegetation

Climate and the resulting distribution of vegetation over the earth's surface is primarily determined by the available energy. At a large geographical scale, climatic zones follow one another in parallel from the equator to the poles and determine zonal macroecosystem belts called biomes (**Figure 2**).

The strong warming of the earth's surface in equatorial regions causes air to rise. As the warm, moist air rises, it cools, resulting in frequent precipitation and allowing the development of rainforests. This air circulation pattern is linked to a belt of low atmospheric pressure upon which winds converge (**Figure 3**). The warm air masses circulate back the earth's surface north and south of the equatorial region, in a subsidence movement that is linked to high air pressures. During this process, the air temperature remains relatively high but the

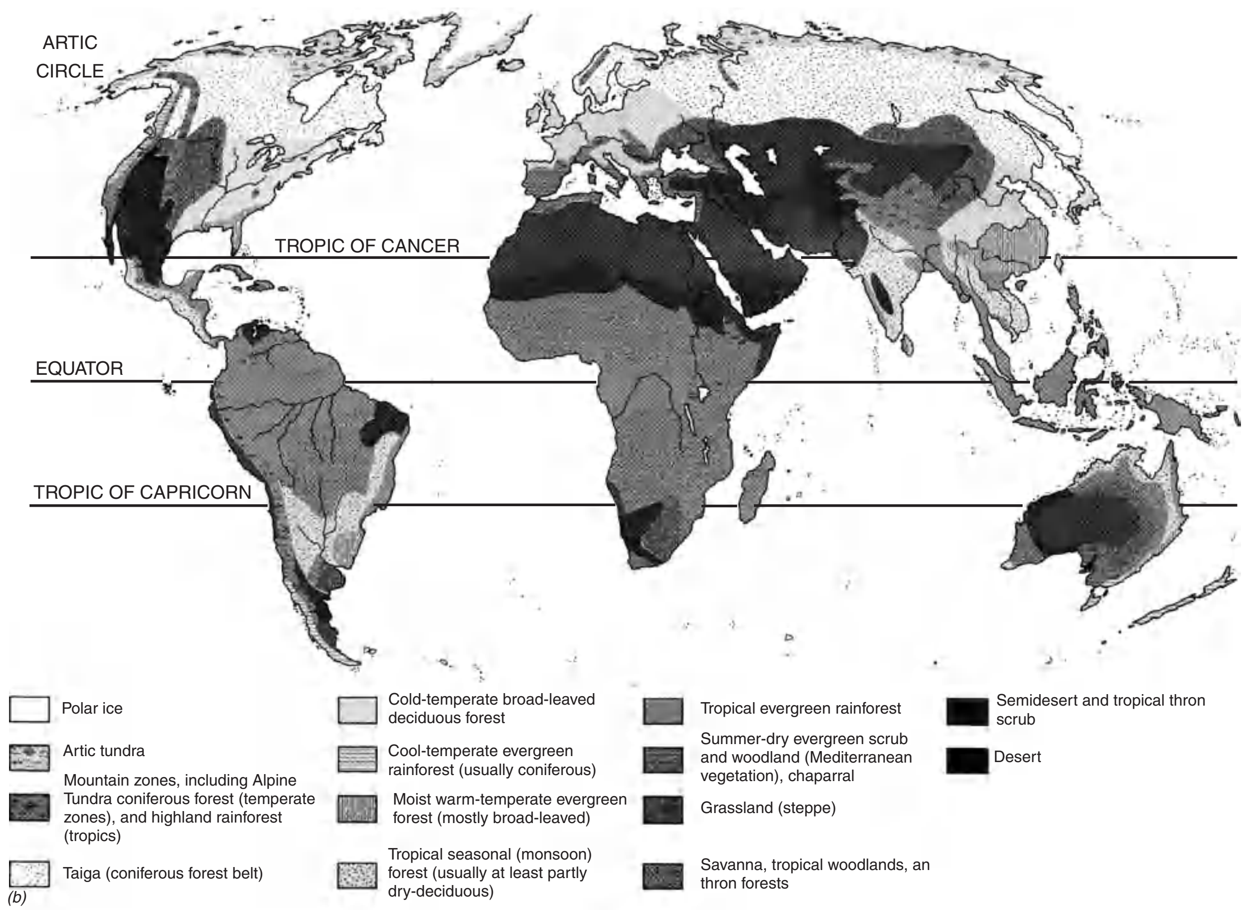


Figure 2 Distribution of the major vegetation types across the globe. Reproduced with permission from Aber JD and Melillo JM (2001) *Terrestrial Ecosystems*, 2nd edn. London, UK: Academic Press.

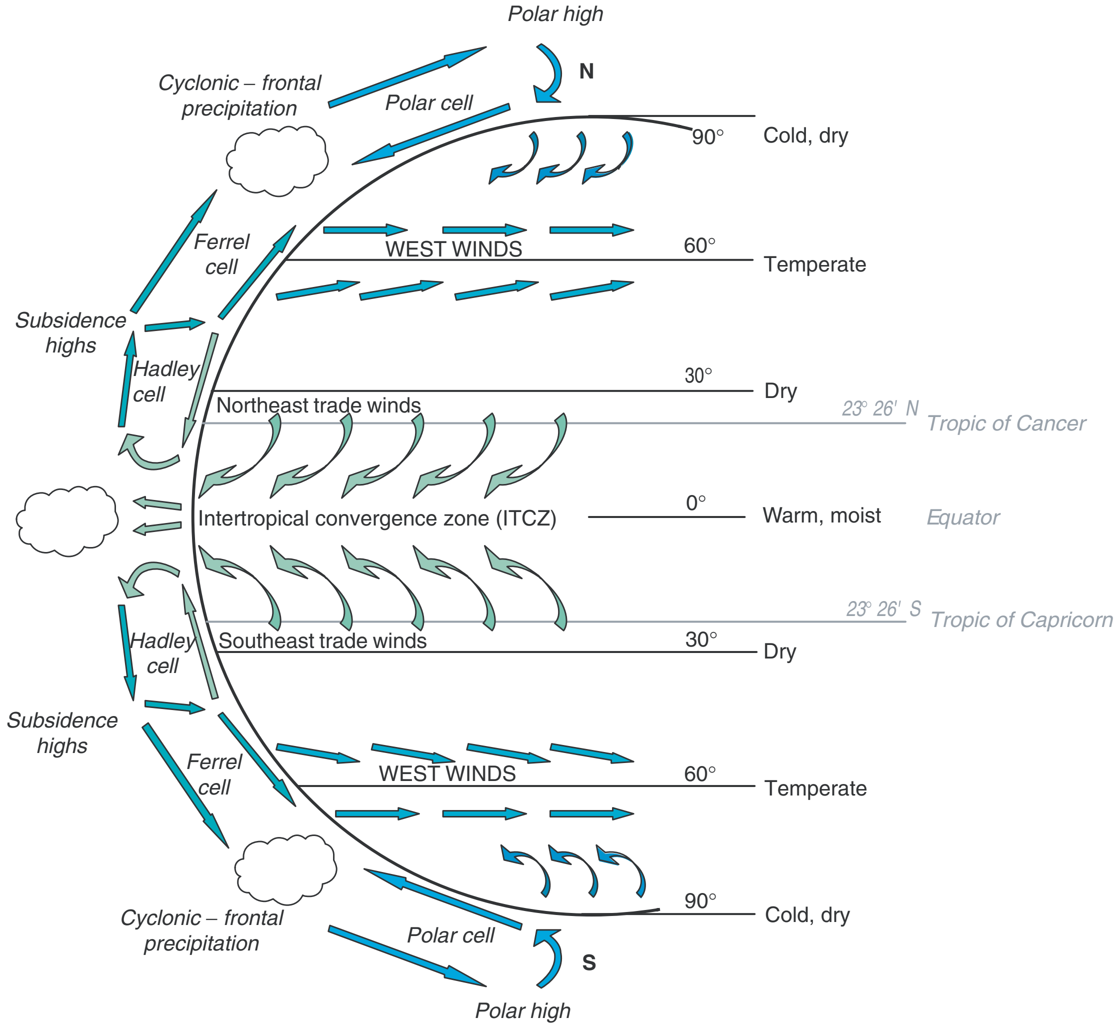


Figure 3 Global earth atmospheric circulation and main winds. The planet's surface receives decreasing solar radiation from the equator to the poles because of the spherical shape of the earth and its tilt. Heated air expands and loses density. There is thus a relation between the temperature gradient of the earth and the atmospheric pressure system. Hence, we would expect the air masses to move from the cold poles (dense air, high pressure) to the warm equators (dilute air, low pressure) to cancel out the pressure gradient. In reality, we observe various cyclonic (lows) and anticyclonic (highs) pressure systems leading to three main components (Hadley, Ferrel, and polar cells) in both hemispheres. Adapted from Whittaker RH (1975) *Communities and Ecosystems*. London: Collier Macmillan and Dincauze DF (2001) *Environmental Archaeology*. Cambridge, UK: Cambridge University Press.

moisture and precipitation decrease progressively, leading to drier climatic zones with more pronounced seasonality. A precipitation gradient of approximately 1 mm year^{-1} km^{-1} occurs from approximately 10° N to 18° N. Below a threshold of approximately 400 mm year^{-1}, the lack of precipitation shapes the steppe and desert vegetation. The Sahara Desert, the Sahel zone, and their transition zone have been defined as having the following rainfall values: Sahara Desert, 0–100 mm year^{-1}; Saharan–Sahelian transition zone, 100–200 mm year^{-1}; and the Sahel proper, 200–400 mm year^{-1}.

At higher latitudes, beyond these anticyclonic zones, the climate is dominated by westerly winds. The Mediterranean climate is characterized by dry and hot summers with wet and mild to cold winters. The temperate climate experiences air masses from the north or south at all seasons: warm air masses from the tropics alternate with cold air from the polar regions. Temperatures can consequently vary from one day to the next and vegetation must be adapted not only to cold winters and hot summers but also to rapid changes, including for instance a return to below-freezing temperatures during a mild spring. At the highest latitudes, temperature and light remain very low throughout the year. The vegetation is limited by the cold and partly by snow or ice cover, resulting in cold deserts. The broad pattern of world biome types can be represented in relation to humidity and temperature (**Figure 4**). The concept

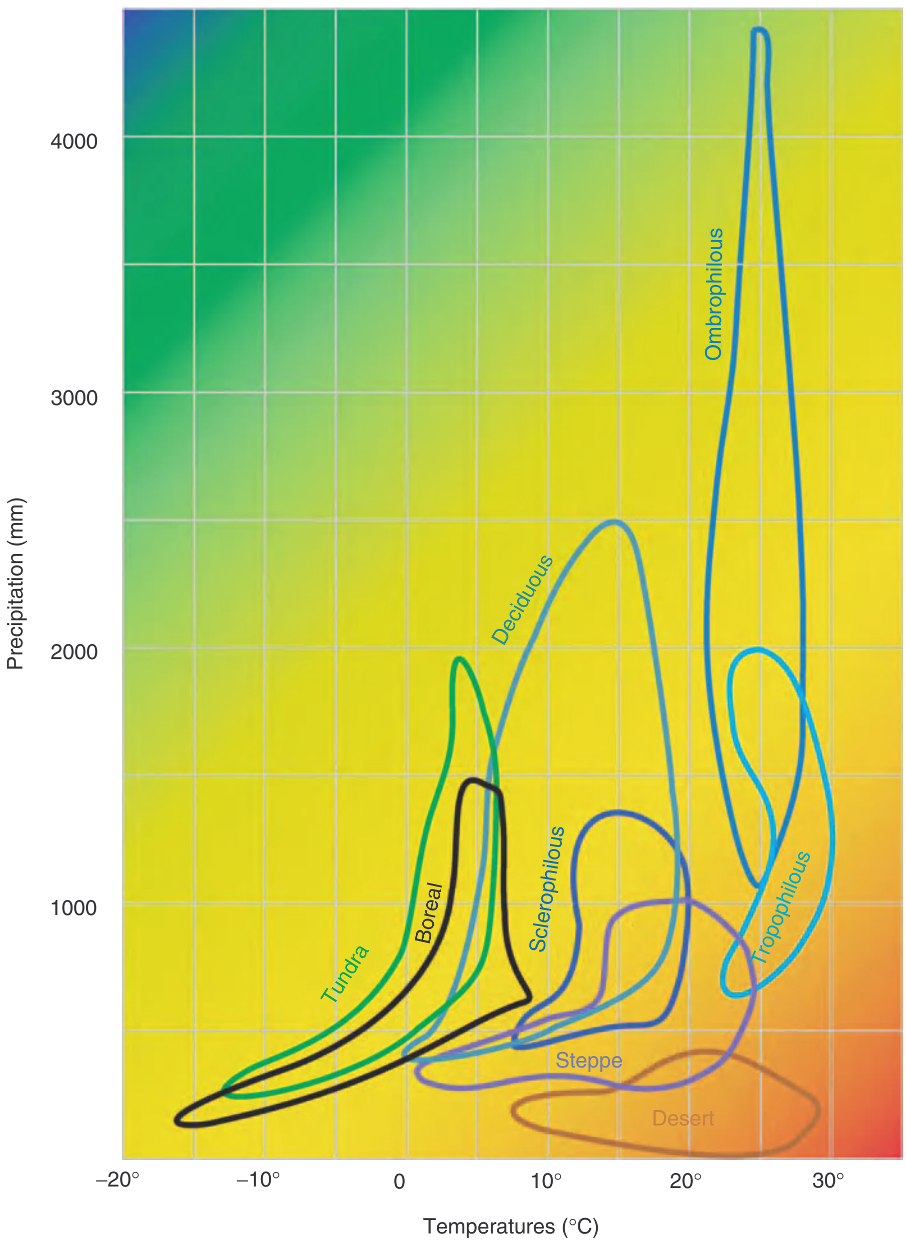


Figure 4 Distribution of vegetation types according to mean annual temperature and precipitation. The planet's vegetation cover is largely linked to temperature and precipitation gradients. This figure gives an insight into the coarse ombrothermic distribution of the major biomes. At finer scale, the species composition determines many other plant communities. Furthermore, the natural distribution and extension of the biomes is altered by human activities. Adapted from Whittaker RH (1975) *Communities and Ecosystems*. London: Collier Macmillan.

of the ecocline can be used to relate communities to climate on a worldwide scale.

The distribution of vegetation on the earth's surface is also influenced by other factors. Because of the uneven distribution of land and water over the globe, the biomes are distributed unequally between the northern and southern hemispheres (**Figure 2**). Regionally, they also depend on proximity to oceans, on the degree of continentality, or on topography. Temperate areas located near oceans are often referred to as 'oceanic,' as the oceans bring moisture and reduce the variation in temperature between summer and winter as well as between day and night. As air masses from the west move over the continent, losing moisture, the 'continentality' increases, which means longer drought periods and greater temperature fluctuations, and consequently the development of dry vegetation types such as steppes and deserts.

At intermediate scales, the regional climate setting can modify the general pattern of vegetation. Greater elevations can be considered as equivalent to higher latitudes. On Mount Kilimanjaro, Mount Everest, and Mont Blanc, the climate is comparable to that of the poles (cold deserts) although these mountains are in tropical and temperate regions. On the sides of these mountains, the climate follows a gradient determined by altitude. The temperature, in particular, decreases with altitude at a mean rate of approximately 0.7°C per 100 meters (depending mainly on the air humidity and pressure), and the vegetation communities reflect these changes (**Figure 5**). The vegetation changes that occur with altitude are similar to those occurring with latitude. For example, 100 meters change in elevation is equivalent to an increase of 1° of latitude. The degree of sun exposure and more generally the topography of the landscape can change the altitudinal distribution of vegetation communities (**Figure 6**). Features such as valleys where temperature inversions occur can host specialized communities and even reverse the altitudinal distribution of vegetation (**Figure 7**).

Light

Light is a fundamental climatic parameter providing the energy for photosynthesis and controlling the availability and production of vegetation. The amount of light and energy that penetrates the forest or is reflected depends on the species composition, which determines the canopy structure, and on other properties such as the color of leaves, their position and density, the age of the stand, and the season (**Figure 8**). The loss of light with increasing distance from the top of the canopy is termed light attenuation, and can be expressed by:

$$\mathrm{IL}/\mathrm{IO} = \mathrm{e}^{-k\mathrm{LAI}(L)}$$

where IL/IO is the percentage of light at the top of the canopy (IO) reaching depth L in the canopy, LAI(L) is the cumulative leaf area (in m^2 of leaf area per m^2 of ground area, called leaf area index) from the top of the canopy to depth L, k is a stand- or species-specific constant, and e is the base of natural logarithms (2.718).

The ground surface in a forest receives progressively less light as the forest grows; at the time of canopy closure, the ground in a pine stand will only be receiving approximately 7–8% of the ambient light. However, as a stand ages beyond this stage, the light penetration gradually increases, reaching approximately 30% of ambient by maturity. In the deciduous forests of temperate zones, the amount of light reaching the ground is highest in spring, being 5–10 times higher than that experienced in summer, when only 1–5% of the ambient light reaches the soil. Combined with the increase of temperature over the growing season, this change in light condition allows phenological shifts of the vegetation that are particularly obvious in the herbaceous strata.

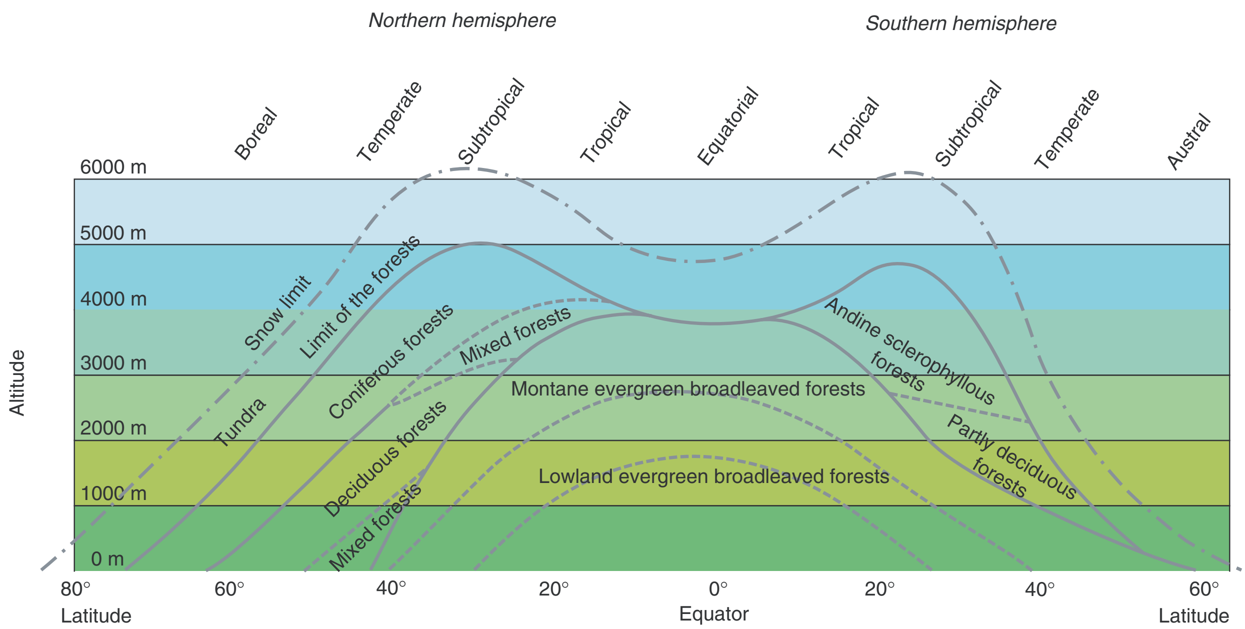


Figure 5 The relationship between altitude, latitude, and main forest types. The snow limit is lower at the equator because of the high precipitation and the related snow amount in comparison to the tropics. In general, coniferous forests mark the limit of the forests in the northern hemisphere, whereas deciduous forests do so in the southern. Adapted from Otto HJ (1998) *Ecologie Forestière*. Paris: Institut pour le Développement Forestier.

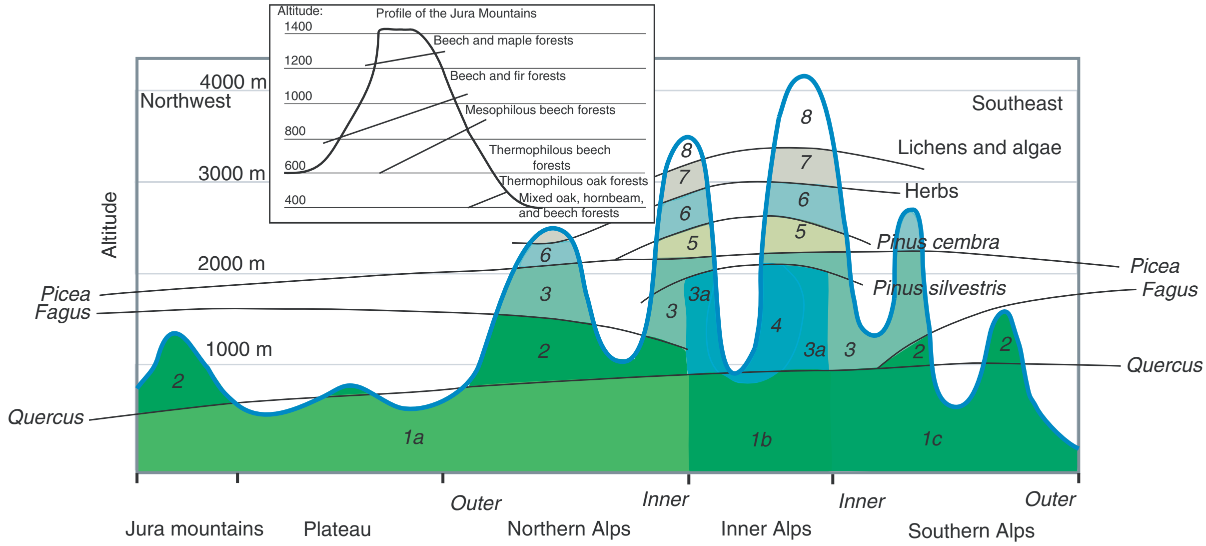


Figure 6 Influence of geomorphology and sun exposure on the altitudinal distribution of trees and vegetation strata and communities: an example from Switzerland with a transect from the Jura Mountains to the Alps. 1, Hilly strata (*Quercus*); 1a, Northern variation, mostly *Quercus robur*, *Q. petraea*, *Carpinus betulus*, and *Fagus sylvatica*; 1b, Inner alpine variation, mostly *Q. pubescens*; 1c, Southern variation, mostly *Q. pubescens*, other *Quercus* spp., and *Castanea sativa*; 2, Montane strata (*Fagus sylvatica–Abies alba*, together with *Picea abies*); 3, Subalpine strata (mostly *Picea abies*); 3a, Continental variation, *Pinus sylvestris* mixed with *Picea abies*; 4, Continental montane strata (*Pinus sylvestris*); 5, Suprasubalpine strata (*Pinus cembra* and *Larix decidua*); 6, Alpine strata, mostly alpine lawns; 7, Sub snow strata, mostly low-statured plants in patchy communities; 8, Snow strata, isolated plants, mostly lichens and algae. Modified from Gallandat JM and Landolt E (1994) Compte Rendu de la 2ème Excursion Internationale de Phytosociologie en Suisse (14–21 Juillet 1991). Veröffentlichung de Geobotanischen Institutes der Eidg. Tech. Hochschule, 119. Heft. Zurich: Stiftung Rübel.

Within the vertical strata of a forest stand, both the quantity and quality of light follow a gradient, which determines the ecological niches for species and contributes to the biodiversity of the stand. Hence, only a small amount of the direct light reaches the lowest forest strata and a distinction must be made between direct and diffuse radiation (**Figure 1**). Radiation within the forest canopy is characterized by the high transmission and reflection of green and infrared light, whereas blue and red–orange light, which are the most useful for assimilation, are depleted towards the lower strata. Photosynthetic assimilation in response to solar radiation has a hyperbolic shape. At the top of the curve is the saturation point (SP), or the light saturated rate of photosynthesis, beyond which plants cannot further increase light absorption. Some authors consider that if solar radiation increases beyond this point, photosynthesis diminishes in a process termed photoinhibition, and at very high levels of radiation photodamage occurs in the form of destruction of photosynthetic pigments and thylakoid structures. However, generally, leaves are well adapted to the local light conditions and their pigmentation allows for the dissipation of excess energy or the capture of energy when it is limited. This means that species growing under full-sun conditions generally show higher rates of photosynthesis and have higher saturation points than those normally growing under partial shade.

These processes play a determinant role in the plant composition of forests as different species have different light requirements. There are heliophyte plants, requiring high quantities of sunlight, and sciophytes, which prefer shade and sometimes still have a positive carbon balance, and finally species that have a rather large ecological amplitude. For instance, mosses and herbs on the forest ground have very low SPs. The amount of global radiation is the most important parameter for the definition of heliophyte and sciophyte types and hence for the vegetation composition in forests. Light conditions are also very heterogeneous horizontally. Light can directly penetrate into forest stands, creating light patches at the soil surface that are of particular importance for the regeneration of vegetation. Such light flecks can cover 20–25% of the ground surface at noon in a tropical forest, contributing 70–80% of the energy reaching the soil.

Plants do not only physiologically adapt to the light, they also do so morphologically. For example, the shape of leaves is smaller and thicker where insulation is important, whereas the opposite occurs in less exposed locations. The same tree species may show very different stature depending on whether it is growing in a dense or open stand. For example,

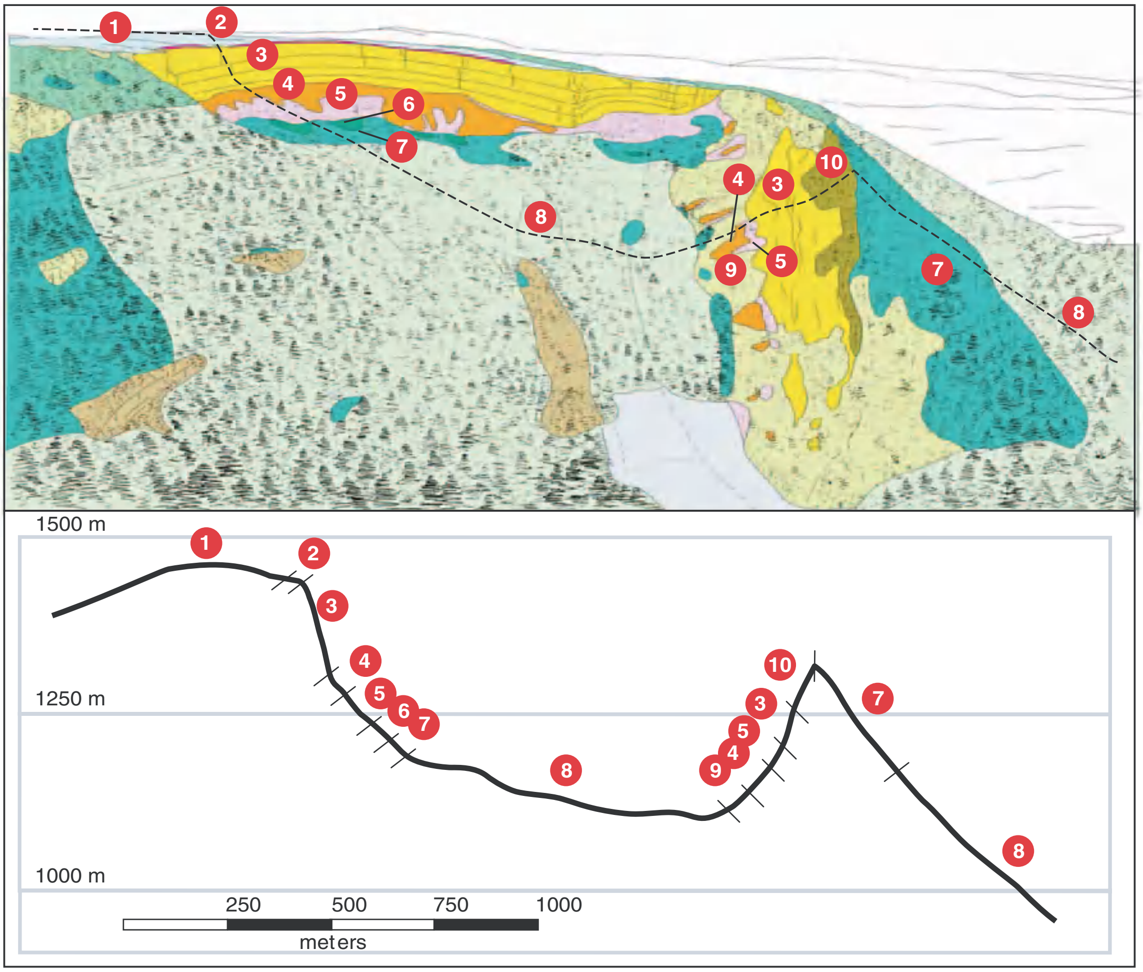


Figure 7 Distribution of the main vegetation types in the Creux-du-Van in the Swiss Jura Mountains. The site is shaped by a 200-m high cliff which encircles a semiclosed depression with a cold local climate. In the scree at the foot of the cliff, a permafrost has built up as a remnant of a local glacier. The figure shows that a spruce subalpine forest is developing in the cold depression and on north-facing slopes, whereas, on the contrary to normal vegetation distribution (see **Figure 6**) beech forests can be found at higher altitudes than the spruce forest. 1, Beech and maple forests, pastures; 2, Rock pioneer vegetation on the cliff; 3, Maple forests and pioneer vegetation on the scree; 4, Subalpine spruce forest on the scree, together with subalpine herbaceous species; 5, Beech and fir forests; 6, Thermophilous beech forest and pine forest. Modified with permission from Büttler A, Gallet F, and Gobat JM (2001) Vegétation et flore. In: *Le Jura*, pp. 77–151. Paris: Collection Bibliothèque du naturaliste, Editions Delachaux et Niestlé.

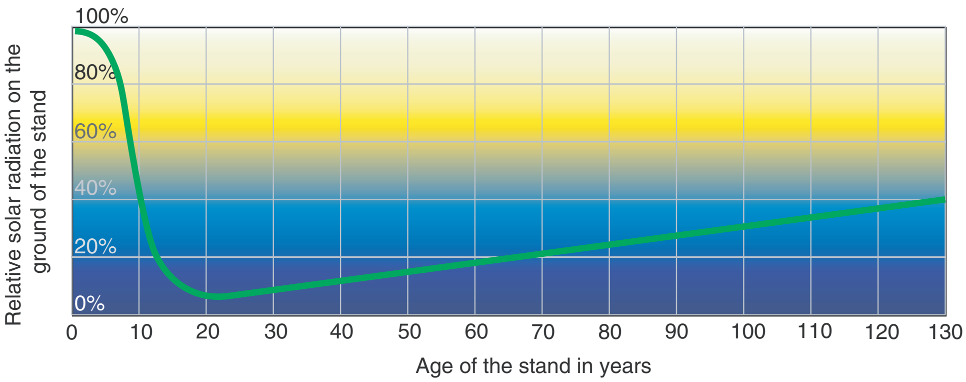


Figure 8 Relationship between the age of the stand and the relative amount of light received on the ground of the forest. On average, forests are thickest at about 20 years of age, which corresponds to the period when the smallest amount of light reaches the forest ground. Later, as the stand grows older, it loosens allowing for more light on the ground. Adapted from Flemming G (1995) *Wald, Wetter, Klima: Einführung in die Forstmeteorologie*. Berlin: Deutscher Landwirtschaftsverlag Berlin.

shaded leaves may have less chlorophyll per unit leaf surface area than sun-exposed leaves.

Temperature

Temperature is very important to poikilotherm organisms such as trees. Poikilotherm organisms assume the temperature of their environment. The lower the temperature, the lower the metabolic activity of the plant and the less the photosynthetic activity. Tree species all have different temperature optima for photosynthesis: a boreal forest tree conducts photosynthesis at far lower temperatures than tropical trees. On average, temperatures are harmful to vegetation when they rise above 50–60°C, which is the protein alteration threshold, and when they drop below 0°C, at the threshold for cellular structural deterioration. At both thresholds, the cell wall stability is critical. However, trees may adapt physiologically where temperatures frequently pass beyond these values. For example, in Siberia, trees have to cope with temperatures as low as −68°C.

Cold is a limiting factor that can cause freeze stress to trees unless they are acclimated. If the temperatures are too low and the growing season too short, trees cannot grow. Freezing damage is more important during daytime, when photoinhibition is also induced, and when vegetation is active, for example at the beginning of the growing season. Ice crystals form inside the plant cell and break the cell walls, which kills the cells. Extracellular freezing may also induce cell dehydration. Freezing within the xylem vessels can be followed, during melting, by the development of occlusions that hamper hydraulic conductivity. Trees therefore need to adapt to temperature, and they do this using particular strategies. In temperate climates, deciduous forests are dormant during wintertime. Trees lose their leaves, which cannot withstand frost, leaving only the relatively resistant dormant buds. Coniferous trees do not lose their needles during the winter season and overcome freezing stress through physiological adaptations. Intracellular freezing is avoided by chemical alteration of the liquids inside the cell, a phenomenon called supercooling. Supercooling is enhanced by partial rejection of water outside the cells, dropping the freezing point of the solute content of the cell. Water can freeze outside the cell, whose walls are able to deform. However, despite the use of both supercooling and extracellular freezing, most coniferous trees need a time to adapt and become frost resistant for the winter, a process called frost hardening. If the temperature drops too quickly, then even coniferous trees suffer from freezing stress, resulting in the development of injury to the foliage. Hence, winter temperatures set the broad geographic distribution of many tree species in both the northern and southern hemispheres. Under natural conditions, this ecological limitation can be recognized on mountains by the upper growing limit of the trees – the treeline.

High temperatures can also disturb or disrupt photosynthetic activity and harm the plant. The rate of photosynthetic activity depends on the species. Observations suggest that there is a relationship between latitude and the sensitivity of photosynthesis in a species to temperature. However, there is also evidence of considerable plasticity in this relationship. Several factors can lead to the decline of photosynthetic activity at high temperature, including the more rapid increase in respiration rate than photosynthesis that accompanies increasing temperature; the breakdown of temperature-intolerant enzymes thought to be critical for photosynthesis; the alteration of the cell structure, cell membrane thinning, and cell leakage; and stomatal closure and the inhibition of the carbon dioxide, water, and oxygen exchange essential for photosynthesis. Plants can adapt physiologically to high temperatures. For example, some leaves have a reflective coating. Other forms of adaptation concern the form or the orientation of the leaves, which may be vertical in order to reduce the exposure to the sun. For example, if a leaf orientated perpendicular to the sun absorbs 1.0 cal (4.19 J) of energy $cm^{-2} s^{-1}$, then one orientated at 60° to the sun will only absorb 0.5 cal (2.09 J) $cm^{-2} s^{-1}$. In cases when there is sufficient water available, another adaptive mechanism is to increase the transpiration rate, which then cools the leaves.

At a local scale, temperatures are controlled within forest ecosystems by the strong moderating effect of the stand on radiation. In deciduous forests, daytime temperatures are highest within the crown during the growing season, and highest at the soil surface once the leaves have been shed. Temperatures inside forests, and particularly at the ground surface, are of major significance as they have such a bearing on physiological processes. The temperatures inside forest stands are regulated, whereas the temperatures outside wooded areas can vary greatly between day and night, and over the seasons. Forests reduce the diurnal temperature range: days are cooler and nights are warmer than they are outside the forest. However, on average, temperatures are cooler in forests than in nearby open areas. The differences are greatest at the ground level. For instance, the average difference between field and forests is about 1 K at ground level, 0.7 K at about 2 m above the ground, and 0.3 K at the crown level. This is the result of the poor distribution of light and of the high rate of evaporation within the forests. Tree crowns retain cool air during the day, and at night, they capture the thermal radiation near the ground. In winter, snowless crowns have a lower albedo than the surrounding fields and, hence, temperatures are higher in the forests when there is snow on the ground. The spatial heterogeneity of the forest, and in particular the presence and distribution of larger gaps in the stands, can alter the thermal exchanges within the forest and its temperature gradients. This can be critical for the regeneration of trees.

Precipitation and Water Availability

Water availability at a particular location and the hygrometric condition of the atmosphere are of the utmost importance for terrestrial organisms, as their survival depends on the desiccation rate in conjunction with temperature. For many species, precipitation is a more important determinant of survival than temperature per se. Precipitation is a primary determinant of vegetation structure, with trees occurring only where annual precipitation is in excess of 300 mm. Vegetation needs water to achieve photosynthesis as much as it needs optimal temperatures and light. Moreover, plants need water for physiological activities such as protein synthesis or cell growth, and to maintain the rigidity (turgor) of the cells. Eventually, water is necessary for nutrient transportation in plants. Water is transported in vascular plants by physical processes: water moves from the high vapor pressure at the roots to the low pressure at the stomata. Water leaves trees through the stomata, which are usually located under the leaves, and this loss creates an upward water flux from the soil to the plant. The loss of water is termed transpiration, and the rate at which it occurs depends on the air temperature, humidity, and wind conditions, and on the particular stomata shape and behavior. Evapotranspiration is the total amount of water transmitted into the atmosphere by vegetation transpiration added to the total amount of evaporation from the plant and ground surfaces at the same location. The total yearly transpiration of a temperate forest stand ranges from 200 to 600 $l\,m^{-2}$. Thus, vegetation cover largely influences air humidity.

Observations indicate that there is a relationship between annual precipitation and the main vegetation types. This is particularly true for regions with extreme precipitation. However, this relation is blurred at regional and local scales. This is because of annual precipitation patterns, which regulate the available and usable water quantity for vegetation. Other parameters such as topography, soil, and the vegetation itself can influence the hydrological budget at a site. The fate of the rainwater depends partly on the forest stand. In temperate deciduous forests, the canopy can intercept between 10% and 40% of the annual precipitation, which is subsequently lost from the stand through evaporation. Higher interception rates have been reported for coniferous forests.

Trees need to adapt to hydrological conditions as well as to light and to temperature. Hygrophyte plants grow in environments close to the water saturation point while xerophyte plants live in dry environments. In water-saturated environments, trees are adapted to the poor oxygen availability in the soils; these include poplar (*Populus* spp.), willow (*Salix* spp.), alder (*Alnus* spp.), *Taxodium distichum*, *Nyssa* spp., mangroves, and a few palms, such as *Nypa fruticans*. The diffusion of oxygen in water-saturated soils is about 10 000 times slower than in dry soils. Consequently, plants need to adjust their roots to the conditions that they are growing in: aerial roots from stems, ventilating tissue (aerenchyma) along the stems, and longitudinal air spaces along roots are examples of observed adaptations.

Drought is also an important factor limiting vegetation. It influences the distribution of plants and occurs when a deficit develops between precipitation and evapotranspiration, leading to a reduction in the soil water content. Water stress occurs when, as a result of water deficit, the relative water content of the plant tissue decreases. Many plants cannot extract water from soils when the matric potential (a measure of the attraction between soil particles and water in the soil) falls below −1.5 Mega Pascals (MPa) – termed the permanent wilting point. Plants adapted to very dry conditions have permanent wilting points well below −1.5 MPa, such as the dryland vegetation described below. A lack of water will drastically disturb photosynthetic activity: the plant closes its stomata to avoid desiccation and to maintain the cell's rigidity and, hence, uptake of carbon dioxide for photosynthesis is halted. Trees that adjust to dry conditions are called water-stress avoiders because they develop particular resistance strategies. A general, long-term response to water stress is for the osmotic potential of leaf cells to be altered through an increase in the concentration of cations, sugars, and low-molecular-weight solutes in cells. This increases the differences in water potentials between leaf and soil and decreases the gradient between leaf and atmosphere, facilitating the movement of water from the soil to the leaf and reducing the rate of water movement from the leaf to the atmosphere. Other mechanisms also occur. For instance, the baobabs (*Adansonia* *digitata*) use their thick trunks to store water, which is then used during dry periods. They can store up to 120 000 l of water and at maturity have a circumference of about 20 m. Some shrubs develop a particularly deep root system that can reach groundwater located at considerable depths. For example, mesquite shrubs (*Prosopis* spp.) develop roots penetrating as deep as 53 m. Families such as *Olea*, *Myrtus*, and *Phillyrea*, which are fairly tolerant of fluctuations in water content, are termed hydrolabile. Families such as *Laurus*, *Arbutus*, and the evergreen *Quercus* species cope with water stress by adjusting transpiration rates; this behavior is termed hydrostable. Dormancy is another adaptation. Some trees adapt by shedding leaves during the dry season. However, plants retaining their leaves during the dry season are often adapted to water stress by having hard and waxy leaves, termed sclerophyllous leaves.

Precipitation and moisture in their solid form, snow and ice, are also important ecological factors in the mountains and in cold climates. They act as water reservoirs during the summer. Snow can protect against desiccation and against cold temperatures. However, snow can also harm trees because of its weight. The length of the snow cover season influences the spatial distribution of plant communities, and topography has an influence on the length of snow cover. A snow depth of 20 cm will prevent between 85% and 99% of the ambient light reaching the ground, depriving plants of the light necessary for photosynthesis. Fog and dew are other factors that can play an important role in some circumstances, for example in providing a significant source of water in what would otherwise be relatively dry ecosystems (*see* **Hydrology**: Hydrological Cycle).

Wind

Winds emerge from the atmospheric pressure system. Their strength depends on the difference between high- and low-pressure areas, modulated by topographical features of the earth's surface such as mountains and valleys. At ground level, air masses always move from high to low pressure at all the global, regional, and local scales, contributing to the precipitation distribution. As a result of the earth's rotation, winds in circular air movement patterns move to the left in the northern hemisphere and to the right in the southern hemisphere.

Within forest stands, wind influences temperature and moisture gradients. Where winds blow strongly and constantly, trees develop specific features reflecting the dominant wind direction. This phenomenon is called anemomorphism and is particularly frequent in coastal zones and some mountain regions. Where winds are too strong, arborescent species cannot grow and give way to shrubs and grass fields. Trees often grow up to a limit of 2300 m above sea level in the European Alps, for example, whereas because of wind they barely reach 1450 m in the French Auvergne, located only a few hundreds of kilometers away.

Locally, forests can act as windbreaks. Next to the forest boundary, turbulence is produced, altering the effect of the wind. For deciduous forests, this effect is most effective during the growing season. In many regions of the world, trees are used to shelter crops, buildings, and other features from wind.

See also: **Environment**: Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. **Hydrology**: Hydrological Cycle. **Tree Physiology**: Canopy Processes; Stress.

Further Reading

Aber JD and Melillo JM (2001) *Terrestrial Ecosystems*, 2nd edn. London, UK: Academic Press.
Barry RG and Chorley RJ (1995) *Atmosphere, Weather and Climate*, 6th edn. London: Routledge.
Berger A (1992) *Le Climat de la Terre: Un Passé pour Quel Avenir?*. Brussels: De Boek Université.
Büttler A, Gallet F, and Gobat JM (2001) Vegétation et flore. In: *Le Jura*, pp. 77–151. Paris: Collection Bibliothèque du naturaliste, Editions Delachaux et Niestlé.
Dincauze DF (2001) *Environmental Archaeology*. Cambridge, UK: Cambridge University Press.
Flemming G (1995) *Wald, Wetter, Klima: Einführung in die Forstmeteorologie*. Berlin: Deutscher Landwirtschaftsverlag Berlin.
Gobat JM, Avagno M and Matthay W (1998) *Le sol vivant. Bases de Pédologie et biologie des sols*. Collection géver l'environnement. Lausanne, Switzerland: Presses Polytechniques et Universitaires Romandes.
Gordon M (1984) *Ecologie de la Végétation Terrestre*. Paris: Masson.
Kimmins JP (1987) *Forest Ecology*. New York: Macmillan.
Lacoste A and Salanon R (1999) *Eléments de Biogéographie et d'Ecologie Végétale*, 2nd edn. Paris: Nathan.
Larcher W (2003) *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups*, 4th edn. Berlin: Springer-Verlag.
Lawford RG, Alaback PB, and Fuentes E (1996) *High-Latitude Rainforests and Ecosystems of the West Coast of the Americas*. New York: Springer-Verlag.
Lüttge U (1997) *Physiological Ecology of Tropical Plants*. Berlin: Springer-Verlag.
MacDonald GM (2003) *Biogeography: Introduction to Space, Time and Life*. New York: John Wiley.
Mitscherlich G (1982) *Wald, Wachstum und Umwelt: Eine Einführung in die Ökologischen Grundlagen des Waldwachstums*, 2nd edn. Frankfurt am Main, Germany: D. Sauerländer's Verlag.
Otto HJ (1998) *Ecologie Forestière*. Paris: Institut pour le Développement Forestier.

Ozenda P (1982) *Les Végétaux dans la Biosphère*. Paris: Doin.

Tucker CJ, Dregne HE, and Newcomb WW (1991) Expansion and contraction of the Sahara Desert between 1980 and 1990. *Science* 253: 299–301.

Tyree MT and Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Biology* 40: 19–38.

Walter H (1977) *Vegetationszonen und Klima*. Stuttgart, Germany: Ulmer.

Whittaker RH (1975) *Communities and Ecosystems*. London: Collier Macmillan.

Physiology of Vegetative Reproduction

R R B Leakey, James Cook University, Cairns, Queensland, Australia

Introduction

Vegetative regeneration is both a natural process and an artificial process. The artificial process is used by agriculturalists, horticulturalists, and foresters to capture and multiply individual genotypes, and so to produce cultivars and clones. Clonal approaches to forestry and horticulture have a history going back more than 800 and 3000 years respectively, originating in China. Typically the process is used to develop superior planting stock, although there are also many applications in research where clonal uniformity is a powerful tool in the separation of genetic effects from physiological and environmental impacts on growth processes in plants.

The level of understanding about vegetative regeneration using stem cuttings has progressed enormously since the 1970s, the period when clonal forestry was becoming a reality in Europe, USA, tropical Africa, and Latin America. Although the focus of this review is primarily on the physiology of rooting cuttings, some mention is also made of related issues in air-layering/marcotting, grafting/budding, and different *in vitro* propagation methods.

This contribution draws heavily on studies done with *Triplochiton scleroxylon*, a tropical hardwood of West Africa, because of the large number of relatively comparable experiments done using a similar type of material (single-node leafy cuttings) under similar environmental conditions, to seek some physiological principles of wider relevance. In addition, the review offers some suggestions on how future research should be implemented to enhance the identification of underlying physiological principles determining successful rooting of stem cuttings. The problem that needs to be overcome is the high level of interaction between the large number of factors preseverance, postseverance, and in the propagation environment.

Rooting Stem Cuttings

Stem cuttings can come in many forms but the two major groups are leafy softwood cuttings from relatively unlignified, young shoots (**Figure 1**), and leafless hardwood cuttings from older and more lignified shoots which typically have already shed their leaves due to the onset of winter or a dry season. It is important to understand that the factors determining the rooting of these two types of cuttings are very different: leafy cuttings depend on current photosynthates produced in the propagation bed, while hardwood cuttings depend on the hydrolysis and availability of carbohydrates stored within the stem tissues.

When trying to root leafy stem cuttings, there are four stages when a good physiological understanding of the factors influencing rooting ability is necessary: (1) in the propagation environment; (2) postseverance; (3) in cutting origin and environment; and (4) in the preseverance stockplant environment.

The Propagation Environment

The most important aspect of the propagation environment is that it encourages physiological activity (photosynthesis and transpiration) in the leaf to minimize the physiological stresses experienced by the tissues, from transpiration and respiration, and encourages meristematic activity (mitosis and cell differentiation) in the stem. The transport of assimilates and nutrients from the leaf to the base of the stem, and of water from the base of the stem to the leaf, are also important. Recent physiological measurements confirm general experience that the duration of physiological shock arising from severing a cutting from its stockplant and inserting it in a propagator can be minimized by controlling the propagation environment. Minimizing this shock enhances rooting.

There are many different types of propagation systems for stem cuttings, but the most common are: (1) fogging systems; (2) intermittent mist (**Figure 2**), controlled by a range of different sensors; and (3) airtight, watertight, high-humidity, nonmist propagators (**Figure 3**). These are all very effective, but vary in their cost and sophistication. The nonmist

Figure 1 A rooted cutting of *Milicia excelsa*.

Figure 2 A typical mist propagator.

propagators have the advantage of being very low cost and simple and so are highly suitable for use in developing country or rural situations where electricity and piped water are not available. The basic principles behind all these systems are that the cuttings are well supplied with water at the cutting base while the leaves are in a cool, shady environment with low vapor pressure deficit (VPD) to

Figure 3 A nonmist propagator – a watertight, airtight box when the lid is closed. Inset: cross-section of the propagation medium showing layers of saturated gravel and unsaturated but moist rooting medium.

minimize water stress. Moist leaves also keep the cuttings cool due to the evaporation of water from the leaf surfaces. While shading is beneficial, leafy cuttings need enough light to photosynthesize. Interestingly, the highest values of photosynthesis in severed cuttings have been found at relatively low levels of irradiance.

Comparative studies between different propagation systems for cuttings (e.g., mist and nonmist) found that nonmist propagators provided as good an environment for rooting as mist, if not better. Under mist, air and leaf temperatures and VPD were consistently higher than under nonmist systems. There were also differences in the frequency of peaks in VPD associated with peaks in irradiance. Peaks of VPD can also occur as a result of misting frequency, and its spatial distribution on the propagation bed. In a second study, using cuttings of four tropical trees (two from the moist tropics and two from the dry tropics), significant water deficits did sometimes develop in the leaves of the cuttings under both systems. The patterns of variation in relative water content (RWC) were similar to those of water potential and stomatal conductance. Interestingly, the species differences in RWC and stomatal conductance seemed to be more closely related to leaf morphology than to their environment of origin. Leaf morphology may also account for differences between the four species in optimum leaf areas, indicating the need to report full details of as many of the long list of morphological and physiological pre- and postseverance factors affecting rooting as possible if a good understanding of the vegetative propagation process is to be achieved.

Few studies have been done on the effects of the light environment on photosynthesis during propagation because of the difficulty of measuring gas exchange in cuttings with wet leaves; however, the use of a nonmist propagator has allowed measurements on the rates of photosynthesis, stomatal conductance, and chlorophyll fluorescence ratio to be made on cuttings with and without shade. A study on *Cordia alliodora* confirmed that photosynthesis does occur in severed cuttings in the propagation bed. Photosynthetic efficiency under two levels of irradiance (24–53 and 106–159 μmol m^{-2} s^{-1}) was found to be more closely related to rooting ability than photosynthetic rate, the latter being greatest at the higher irradiance, while rooting ability was either unaffected or reduced by irradiance, depending on the cutting's leaf area and presumably the balance between photosynthesis and transpiration. The number of roots produced was, however, closely related to photosynthetic rate. Further work is required to look at the interactions between propagation light environments and pre- and postseverance factors. The composition of the rooting medium, usually open compost or fine gravel, is often critical for rooting and can vary between species, and cultivars/clones. In addition to holding the cutting firm, it has to provide moisture and allow respiration from the tissues. Anoxia at the cutting base usually encourages rotting, so the gas-filled pore space (air-to-water ratio) of the medium needs to be optimized by the use of various-sized particles (sand and gravel) and a water-holding medium (perlite, peat, or other organic products). The oxygen diffusion rate also needs to be adequate for respiration. In *Milicia excelsa* the moisture content of the medium was positively related to the numbers of roots formed and negatively related to mortality and leaf abscission.

In temperate environments propagation beds, especially those for leafless hardwood cuttings, typically have some bottom-heat provided by heating pipes or cables to promote meristematic activity at the cutting base, while the leaves remain cool. Sprouting by cuttings in the propagation bed often has negative impacts on rooting, presumably by creating a competing sink for assimilates. Consequently a lower air temperature than bed temperature can be advantageous. This differential, although more difficult to achieve, can also be important in the tropics.

For successful rooting, cuttings have to have a positive carbon balance (i.e., producing assimilates faster than they are losing them through respiration). However, very little is known about the overall respiration rates of cuttings under different environmental conditions, or about the ways in which cutting origin, leaf area, and stem length/diameter affect respiration losses. This has, however, been investigated using an oxygen electrode to measure respiration in leafy, single-node cuttings of *Prosopis juliflora*. It was found that respiration rate per gram of dry matter decreased linearly down a shoot, as stem diameter increased. This can be attributed to an increase in nonrespiring lignified tissues, although the greater mass of cuttings with larger diameters more than compensated for these losses and the larger cuttings had a greater overall rate of respiration. Perhaps more importantly, however, the respiration rate of the cutting base (1-cm-long section) was greater than that of the stem above it. This, it has been suggested, provides a concentration gradient which drives assimilate transport basipetally to the cutting base and is a key factor in the rooting process.

Postseverance Treatments

There is probably a larger body of literature on the effects of postseverance treatments than on any other aspect of rooting cuttings. One characteristic of this literature is the apparent lack of consistent results between, and even within, species. This lack of any clear principles defining the rooting process has led to a plethora of papers reporting apparently situation-specific results, rather than to enhanced understanding. To reverse this process it is important to seek the factors that create the variability in responses to different treatments and factors affecting rooting ability.

Probably the most important of the postseverance factors are the application of auxins, leaf area, and cutting length/diameter. Consequently, to develop a practical rooting protocol for leafy stem cuttings of a previously unstudied species, it is first desirable to determine experimentally the optimal auxin application, optimal leaf area, and optimal cutting length and, if possible, to investigate experimentally their interactions within each propagation environment.

Auxin applications The application of root-promoting growth-regulatory substances (auxins) is the most common treatment to enhance rooting in stem cuttings. It is also probably the single most effective treatment to achieve successful propagation. In addition to effects on cell differentiation, auxins promote starch hydrolysis and the mobilization of sugars and nutrients to the cutting base, although increasing auxin concentrations does not result in respective increases in cutting dry mass. However, behind this apparently ‘cure-all’ treatment there lies a considerable body of evidence showing that auxin applications are interactive with other treatments, types of material, and the environmental variables affecting the rooting capacity of cuttings. This high degree of interaction is probably the reason why the literature is full of apparently contradictory statements about the precise physiological role of auxins in the rooting process, a situation that cannot be resolved when authors do not present definitive information about either the physiological condition of their material or the propagation environment used.

Typically cuttings treated with auxins root more rapidly and produce more roots, usually with a higher percentage of cuttings rooted. Usually, indole-3-butyric acid (IBA) is found to be the most effective root-promoting auxin, but occasionally α-naphthalene acetic acid (NAA) can be as effective, as in *Parkia biglobosa*. However, tree species and even clones can appear to respond differently to individual and mixed applications of auxin at differing concentrations, even when many other factors are constant. Interestingly, however, clones of *T. scleroxylon*, which appeared to have different dose–response curves, all rooted equally well at 40 μg auxin per cutting.

Leaf area Usually the rooting of softwood cuttings is dependent on the presence of a leaf, and indeed in the physiological processes of this leaf. Cuttings without a leaf very quickly become moribund, while the most common reason for these cuttings failing to root is the death of the leaf due to rotting, necrosis, bleaching, or leaf abscission. All these causes of failure are due to either the use of inappropriate tissues (too old (senescent), photosynthetically inactive (below compensation point; water-stressed; starch-filled), diseased, pest-infected), or to an undesirable rooting environment (too hot, too wet, too dry). The most common symptoms are leaf shedding, leaf rot, and stem rot.

Studies of the role of the leaf have indicated that rooting ability is maximized when the severed cutting is photosynthetically active and producing assimilates for the development and elongation of the root primordia, and when the leaf is not suffering water stress (**Figure 4**). Consequently, there often seems to be an optimum leaf area at which the balance between photosynthesis and transpiration is optimal. This varies between species and clones, depending on specific leaf area (leaf thickness), stomatal density, leaf morphology (waxiness, etc.) and the age of the leaf (node position). Optimizing the balance between photosynthesis and transpiration seems to be particularly important in difficult-to-root material, with easy-to-root species not being very sensitive to leaf area. Cuttings with a leaf that is too small rapidly decline in their carbohydrate (sugars and starch) contents, while those with an appropriate area increase in carbohydrate content (and hence dry matter), at least until the roots start to develop, creating a sink for assimilates. One study has found that there is a relationship, which develops after severance, in cuttings with differing leaf areas, between rooting ability and the content of reflux-extracted soluble carbohydrates, which suggests that rooting is promoted by the production of specific sugars during the period that the cuttings are in the propagator. Cuttings with an overly large leaf suffer from transpiratory water loss and stress, and close their stomata, thereby limiting their capacity to photosynthesize, and often triggering leaf abscission. As mentioned earlier, leaf area is an important variable interacting with the level of irradiance in the propagation environment. Consequently, statements about the optimal leaf area for rooting have to be linked to statements about the specific propagation environment.

Despite the importance of current assimilates for rooting in leafy softwood cuttings, there is evidence that the level of dependency does vary between species, with some species also being able to utilize stored reserves in the same way as hardwood cuttings, perhaps reflecting differences in stem anatomy. In *Larix* × *eurolepis* cuttings, for example, a dual ^{13}C and ^{15}N labeling approach indicated that more than 80% of total carbon in the roots was newly assimilated carbon, while 20% was from stored reserves.

Cutting length Cuttings can either be cut to a constant length (in which case they will usually vary in the number of nodes present) or can be cut to the available internode length of a predetermined number of nodes (**Figure 5**). The decision about which

Figure 4 Using a 'pressure bomb' to assess the leaf water potential of *Triplochiton scleroxylon* cuttings.

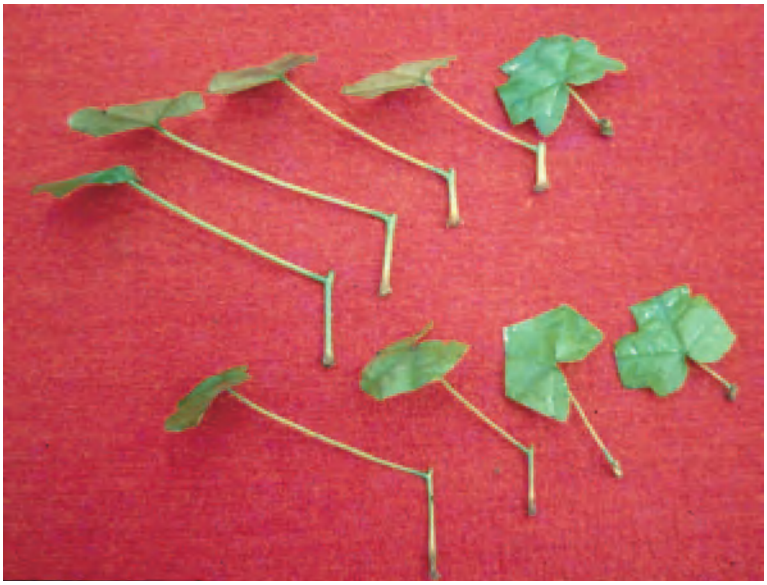


Figure 5 Variation in length and diameter in single-node cuttings from a two-shoot stockplant of *Triplochiton scleroxylon*, arranged in node order from the shoot apex. Top shoot: nodes: 1–5; second shoot: nodes 1–4.

option to take will have big impacts on the rooting ability, as long cuttings usually root best. From the practical point of view, the number of cuttings rooted is maximized by using a constant length, close to the optimum. This has the additional advantage that all the cuttings will penetrate the rooting medium to the same depth and that the leaf will be held the same height above the medium. From the research point of view, however, much can be learnt about the sources of variation by using a fixed number of nodes and utilizing the pattern of variation in internode length found within a stem (**Figure 5**). In the latter case, it is important to remember that internode length varies sequentially down a stem and thus is not an independent variable.

Stockplant Factors: Cutting Origin and Environment

There are two major sources of variation in stockplants. These are attributable to: (1) within-shoot factors and (2) between-shoot factors, both of which are strongly influenced by the stockplant environment. Additionally, there are other endogenously controlled growth changes, such as recurrent flushing, which can affect rooting ability.

Within-shoot factors Within any shoot there are numerous gradients of variation associated with the chronological aging of shoots as they grow longer. For example, from the top to the bottom, there is a gradient in age that affects the leaf size, leaf water potential, leaf carbon balance, leaf senescence, internode length, internode diameter, stem lignification, nutrient and stem carbohydrate content, and respiration. These gradients mean that no two cuttings are physiologically identical and, hence, no two cuttings have the same rooting capacity. Consequently, it is possible to use these gradients node by node as a diagnostic tool for how physiological factors affect rooting. For example, one of the unresolved issues that could be addressed is the importance of the relative concentrations of carbohydrates and nutrients in cutting tissues, which vary between node positions and over time. There is evidence of stored reserves being depleted early in the rooting process in *Larix* hybrid, and in *Khaya ivorensis*.

Comparing the typical with inverse relationships between cutting length and node position allows the study of within-shoot variation and has found that cutting length (in reality probably cutting volume) has a major influence on rooting ability. It seems that this may be due to the need for storage capacity for current assimilates until the new roots form a sink for these carbohydrates. The importance of this is supported by a negative relationship between leaf area and cutting length, suggesting that short cuttings cannot provide the storage capacity for assimilates coming from a large leaf.

Between-shoot factors Even in the simplest type of stockplant, a seedling that has been cut back once previously (**Figure 6**), there are considerable differences in rooting ability between the lateral shoots, with those from upper shoots being best. In *T. scleroxylon*, the percentage of cuttings rooted declines as

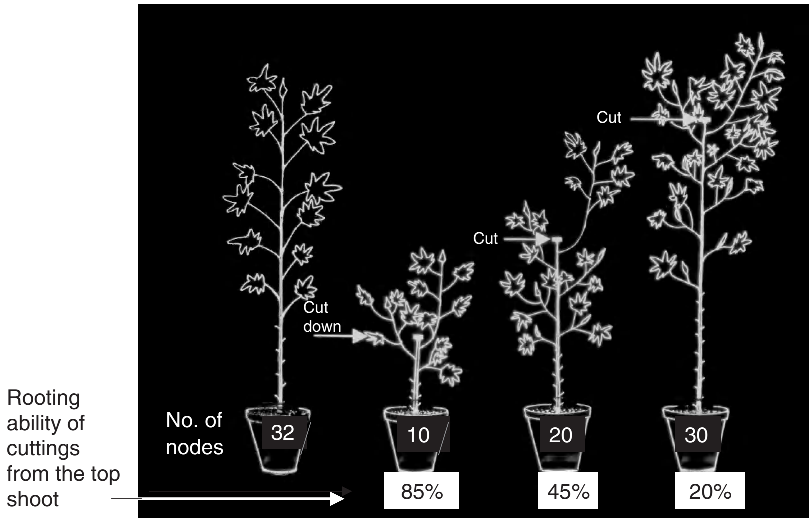


Figure 6 Effects of the number of shoots and stockplant height on rooting ability of *Triplochiton scleroxylon* cuttings from the top shoot. After Leakey RRB (1983) Stockplant factors affecting root initiation in cuttings of *Triplochiton scleroxylon* K. Schum., an indigenous hardwood of West Africa. *Journal of Horticultural Science* 58: 277–290.

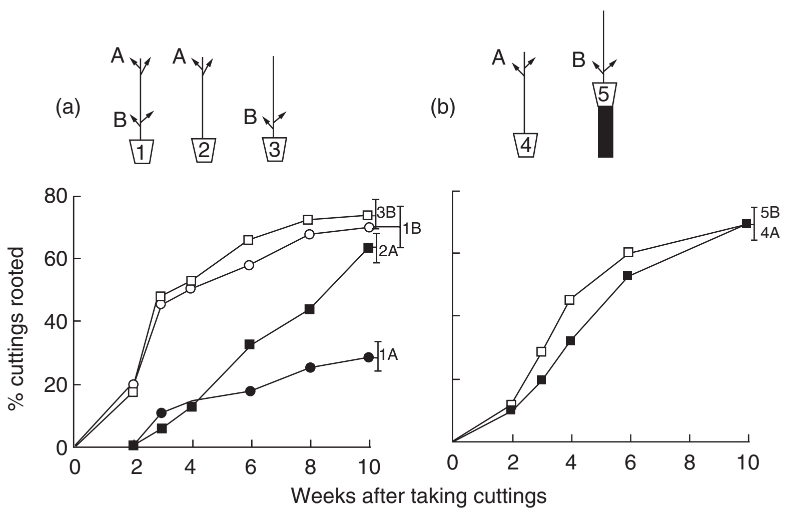


Figure 7 Effects of the number and position of shoots in stockplants of *Triplochiton scleroxylon*, relative to a light source. After Leakey RRB (1990) The domestication of tropical forest trees: a strategy for increased production and for conservation. In: Werner D and Müller P (eds) *Fast Growing Trees and Nitrogen Fixing Trees*, 1990 © Elsevier GMbH. Stuttgart, Germany: Gustav Fischer Verlag.

the height of the stockplant increases, there being a relationship between percentage rooting and the number of shoots per plant. The rooting ability of cuttings from lower shaded shoots can, however, be enhanced by the use of fertilizers, or by reorienting the stockplant (angled or horizontal) to alter the patterns of correlative inhibition. The rooting ability of cuttings from the upper shoots can be enhanced by removal of the lower shoots, implying that intershoot competition is a factor in determining rooting ability. Under situations of low but equal competition, basal shoots have a higher rooting ability than upper shoots. However, if basal and upper shoots are under similar light environments, their rooting ability becomes very similar (**Figure 7**).

In more complex stockplants, cuttings from first-order lateral shoots of *Cryptomeria japonica* rooted better than those from second-order laterals, indicating the need for better physiological and morphological understanding of such structural variation.

Preseverance Stockplant Environment

As seen above, both nutrients and light have been confirmed to have major effects as preconditioning agents on rooting ability, a finding confirmed in

Albizia guachapele. When this was tested experimentally in *T. scleroxylon*, it was found that there are complex interactions between nutrients and the quantity and quality of light, which affected photosynthesis and the carbohydrate status of cuttings. Photoinhibition and high starch concentrations in cuttings appeared to inhibit rooting, while active photosynthesis was associated with good rooting. Both low irradiance and low red-to-far-red ratios independently enhanced rooting ability, but in many natural systems these characteristics of shade occur together and probably have additive benefits. The mechanisms for this enhancement seem to be both morphological and physiological; cuttings from shaded stockplants of *Eucalyptus grandis* have longer internodes, greater specific leaf area, greater codominance between shoots, lower rates of preseverance net photosynthesis, lower chlorophyll concentration, but higher rates of net photosynthesis per unit of chlorophyll, and many other differences in gas exchange characters (**Figure 8**). These characteristics of preseverance physiology and morphology subsequently enhanced the cuttings' postseverance physiological status and promoted high rooting ability.

Figure 8 Using a portable gas analyzer to assess rates of preseverance net photosynthesis and transpiration in stockplants of *Zizyphus mauritiana*.

In *T. scleroxylon*, analysis of deviance indicated that the effects of light quality on rooting were entirely attributable to increased internode length. The changes in these stockplant factors are largely attributable to changes in the physiological condition of the shoots and are often related to vigor; thus they can be seen as a component of physiological aging.

The effects of preseverance light quality on rooting ability have now been demonstrated in a number of different taxa but, as expected, there are differences in stem and leaf morphology. Shoot etiolation under low irradiance and the preseverance elimination of light from the area of the cutting base independently and additively enhance subsequent rooting ability, having histological effects on stem development and retarded sclereid development. There is also some evidence of etiolation on levels of rooting cofactors and sugar concentrations. This newer understanding of preseverance factors is important as it involves easily overlooked differences in the ambient environment. This contrasts with the manipulative treatments like bark girdling, which have also been used to enhance rooting.

Stockplant Management

The importance of all of the above stockplant factors clearly indicates the opportunity to enhance the rooting ability of cuttings through stockplant management (especially a combination of pruning, fertilizer use, and light management) to promote the appropriate morphological and physiological conditions of the shoots. Field trials in the tropics have indicated that using nitrogen-fixing species like *Leucaena leucocephala* to provide a shading canopy above a stockplant hedge can be very beneficial. Hedging approaches have been tested over long periods, and found to be robust with no loss of rooting ability with time, although rooting success is affected by the height of hedges and the types of shoots used.

Efforts to improve stockplant management in *Larix* have included the extension of the photoperiod with artificial illumination in the fall, but without success, and the use of cytokinins to promote the outgrowth of short shoots. In *T. scleroxylon*, however, the injection of auxins preseverance was found to enhance rooting ability, with earlier injection dates enhancing the rooting ability of short cuttings.

Phase Change

The relative importance of ontogenetic and physiological aging is one aspect of the impact of stockplant physiology relating to rooting ability that is unresolved. As trees grow they develop a gradient towards reproductive maturity (ontogenetic aging) and after a time reach a threshold above which the newly developing shoots have the capacity to fruit and flower, while those below the threshold are still juvenile (**Figure 9**). The transition from juvenility to the state of maturity is called phase change. There are large numbers of reports in the literature that cuttings from mature shoots are very much more difficult to root than those from juvenile (seedling or coppice) shoots and attributed this to phase change. Increasingly, however, there are reports of old mature trees being propagated by cuttings, with reasonable success, especially in the early spring. However, a good understanding of the reasons why mature trees are difficult has never been achieved.

The importance of physiological aging in the rooting of cuttings from mature trees is illustrated by recent unpublished data in *Prunus avium* (**Figure 10**), which indicate that by comparison with leafy juvenile shoot cuttings, the rooting capacity of mature softwood cuttings was limited by the availability of stored reserves, while mature hardwood cuttings were constrained by leaf abscission. Other evidence that the poor rooting ability of mature shoots can be attributed to physiological aging rather than to ontogenetic aging is seen in the high rooting ability of ontogenetically mature and flowering plants formed when cuttings from mature tree crowns are successfully propagated and then used as stockplants (**Figure 9**). Although often plagiotropic, such plants have the vigor of juvenile seedlings and coppice shoots. To examine this experimentally within the crown of mature trees is difficult as it requires the formation of physiologically young shoots within an ontogenetically mature crown. This is not achieved by pollarding, but further research is needed to elucidate the relevance of phase change to rooting.

Observations of leaf shape and other morphological characters indicate gradients as trees grow older and these changes have been examined in detail, often using ivy (*Hedera helix*) as a model plant. This raises two questions: (1) are the changes in leaf shape relevant? (2) do we need to have a maturity factor, or are the conditions in mature cuttings just a severe case of the complex interactions arising from the sorts of stockplant variables examined above? Regarding leaf shape in ivy, there may be an error in the belief that the juvenile leaf form converts to the mature form as a result of ontogenetic aging, as the juvenile form is associated with the vine stems

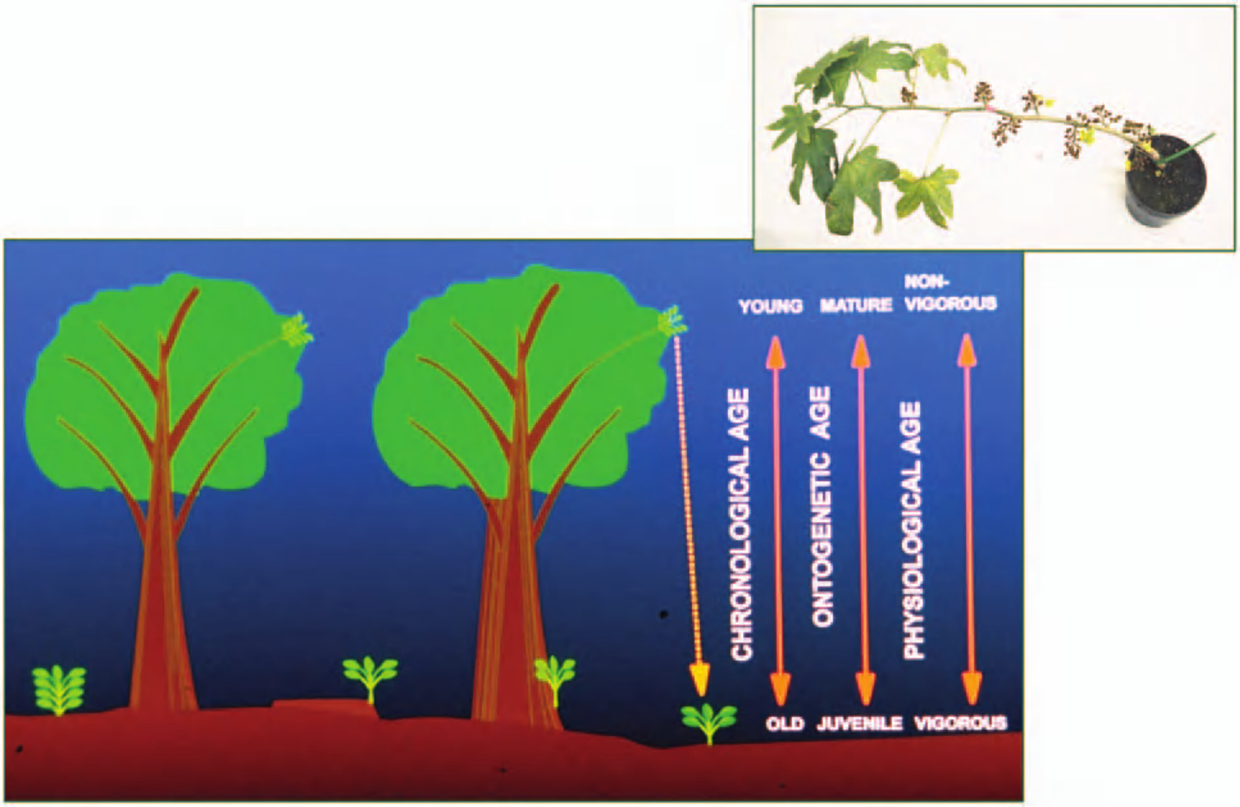


Figure 9 Gradients of aging and maturity in trees. Inset: an easily rooted mature cutting of *Triplochiton scleroxylon*, illustrating its plagiotropic habit and ability to flower.

Figure 10 Cherry (*Prunus avium*) cuttings from juvenile root suckers (1- and 2-year-old wood), young lateral softwood in a mature crown and terminal woody shortshoots in a mature crown.

(the mainstem) and the mature form is associated with free-standing branches, which happen to be where ivy, like many other woody plants, flowers. Different leaf arrangements and shapes in mainstems and branches are very common in woody plants. It is not clear therefore whether the reported differences in genetic material between these two tissue types is a result of ontogenetic phase change or to epigenetic differences between different tissues. In other species, there are changes in leaf morphology up the mainstem, as in *Acacia mangium*, in which the pinnate true leaf on seedlings changes to a mature phyllode. The unreliability of the phyllode as a marker of phase change was shown in a rooting trial from coppice stumps in which the rooting ability of cuttings with phyllodes was greater than that of cuttings with true leaves.

The felling and subsequent coppicing of mature trees are generally regarded as the best way to return to the juvenile state. However, while this was successful in *Milicia excelsa*, the rooting ability of cuttings from coppice shoots was still negatively correlated with the age of the stump. Similarly, in *Vochysia guatemalensis*, increasing stump diameter also had a negative effect on rooting, with larger stumps producing more shoots, and intershoot competition perhaps reducing rooting success.

There are some anomalies in the phase change literature. For example, in *Picea mariana*, cuttings from flowering crowns of 9-year-old trees rooted better than those from nonflowering trees of the same age and origin, while in *Cunninghamia lanceolata*, burying mature shoots horizontally in the soil apparently results in new juvenile shoots.

This topic of how to propagate mature tissues is the major constraint to many tree improvement programs focusing on cultivar development through vegetative regeneration.

Genetic Variation in Rooting Ability

Experience has suggested that there are genetic differences between species, and even between provenances and clones within species, which result in differences in rooting ability, although more and more formerly unrootable species and clones are now being rooted relatively easily as understanding improves. This suggests that, as the within-clone factors affecting rooting ability are optimized, the apparently innate genetic differences in rooting ability are actually attributable to genetic differences in the morphological and physiological factors that govern rooting ability. This view is supported by the use of stepwise regression to analyze data from rooting experiments, which commonly finds that the factors explaining much of the variance are cutting length, leaf abscission, and leaf area, and that the genetic differences between clones explain relatively little of the variance. This conclusion is in contrast to some recent studies, which have sought to detect quantitative trait loci affecting vegetative propagation. No very clear evidence has been found to indicate that there is genetic control of rooting ability *per se*. Some trees, like many herbaceous weeds, do regenerate vegetatively naturally (e.g., from root suckers), but it is difficult to see in evolutionary terms why there would be a genetic trait for rooting ability in detached shoots of trees.

Failure to Root

To learn more about the processes affecting rooting, there is also a need to pay much more attention to the causes of rooting failure. Some cuttings, as stated earlier, display different symptoms of death from leaf abscission to different patterns of rooting, which can be attributed to water stress, photoinhibition, anoxia, and negative carbon balance. Other cuttings neither die nor root. More information needs to be collected on all these responses to attempted propagation.

Integration by Modeling

The complexity of the rooting process in leafy stem cuttings alone makes it a very appropriate subject for modeling. Based on the *T. scleroxylon* data set, a mechanistic model of carbohydrate dynamics during the rooting process provides a framework for many of the other factors discussed above to be examined and compared with research results. Hopefully in future it will be possible to use this and other models to test differences in experimental methods and materials and so interpret the often contradictory experimental results.

Apparent Absence of Principles Determining Rooting Success

Recording Materials and Methods

On top of the highly interactive nature of the multitude of factors influencing the physiological condition of cuttings, there is an overarching methodological issue that needs to be resolved. Typically, people taking cuttings do not collect their cuttings in the same way, and more importantly, do not report what they have done precisely. Because of the impacts of all the interactive processes discussed above, two people propagating the same species under relatively similar conditions can obtain results that appear to be contradictory, while in fact their results are expressions of the different physiological and morphological condition of the tissues being propagated. Researchers need to address these deficiencies in their techniques and to address the impacts of all the variables experimentally before we can expect to understand fully the fundamental physiological principles determining the success of vegetative propagation.

Percentage Rooting – A Poor Measure of Success

To make matters worse, almost all research papers use the percentage of cuttings rooted as the prime measure of rooting success. Taking a simple example, even if auxin application, leaf area, and rooting environment are all optimized, when all the available cuttings are collected from a managed juvenile stockplant (**Figure 11a**), they are likely to have a fairly low rooting percentage and hence create a relatively low number of new plants. This is because of the inclusion of all of the inherent variations in cutting size and shoot position. If, on the other hand, the same people go to an identical plant and, because they know more about the species they are propagating and are aware that cuttings from the top two shoots are likely to have the greatest capacity to root (**Figure 11b**), restrict their collection to these shoots (so maximizing the use of their time and resources), they will root the same number of cuttings, but can claim an improved rooting percentage. In a third situation, where they have more understanding of stockplant management, and grow their stockplants under the shade of other plants and provide nutrients, the stockplant has greater codominance between shoots and produces more material to harvest. In this case, the shoots are morphologically and physiologically in a better condition to root well (**Figure 11c**). Consequently, more cuttings can be

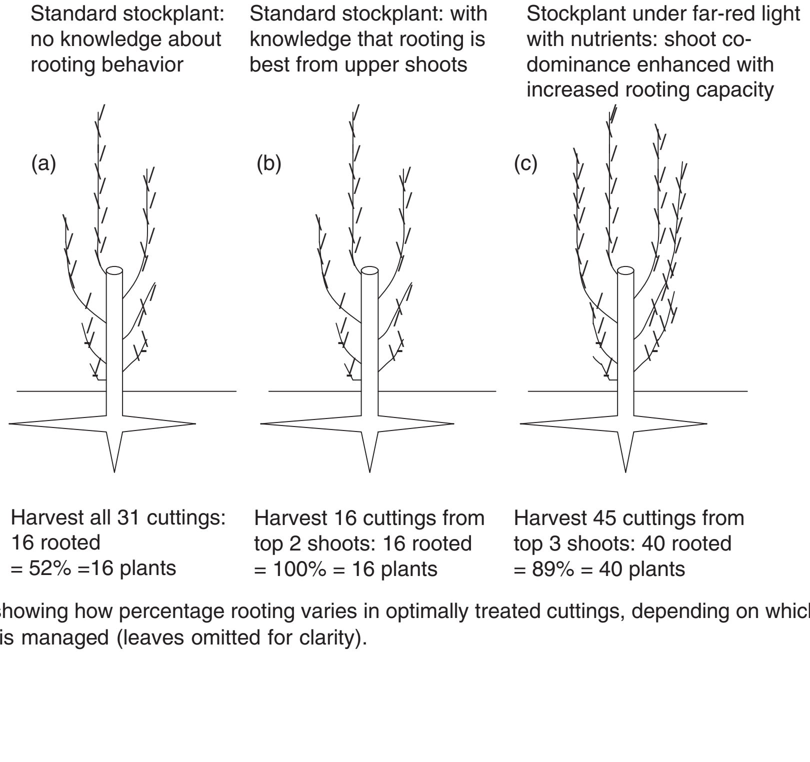


Figure 11 Diagram showing how percentage rooting varies in optimally treated cuttings, depending on which cuttings are used and on how the stockplant is managed (leaves omitted for clarity).

collected, and a third shoot can be included, resulting in a much larger number of cuttings rooted, but the percentage rooting may be lower than that in **Figure 11b**. Which of these results is of greatest practical value, and how well does the measure of percentage cuttings rooted represent the overall rooting capacity of the cuttings collected? Clearly, if the understanding of vegetative propagation is to advance, we have to be more rigorous in describing the source of our cuttings, and we have to improve the way we quantify rooting capacity.

Many authors do use additional measures of rooting success; for example, the number of roots per cutting, the mean or total length of roots produced, the mass of roots produced, and graphs often show differences in the rate of rooting. Interestingly, these measures of success are often unrelated to rooting percentage, and it is probably only when these different measures are well correlated that there is a good measure of rooting ability. These methods of quantifying rooting ability and their relationships require further research.

Other Propagation Systems

Grafting/budding, marcotting (**Figure 12**), root cuttings, and *in vitro* culture (**Figure 13**) are all systems that are used to multiply ontogenetically mature shoots that are very difficult to propagate by cuttings. This is especially important for the propagation of fruit trees or selected phenotypes in a forest tree seed orchard where ontogenetic maturity has to be retained.

In contrast with *in vitro* systems there have been relatively few major advances in grafting and marcotting in recent years, although they are still widely applied. Nevertheless, there is a need for improvements to make them more robust and reliable as low-technology options for mature tree propagation. Probably the most important area for future research is an investigation of how to use preseverance treatments and environment to enhance the rate and success of both the propagation and the subsequent establishment and growth of the young propagule.

Constraints on space here make it impossible to review fully the progress in other propagation systems. *In vitro* systems, which potentially have much greater multiplication rates and allow for biotechnological developments through genetic manipulation, continue to be an area of rapid development, meriting an independent literature review. Some easy rooting of shoots from mature *in vitro* cultures has been reported but the mechanism remains unclear. *In vitro* micrografting has also been used to improve the rooting ability of mature shoots. There is a need for better understanding of the use of these systems to promote easy propagation from a range of mature tissues. Evidence suggests that some physiological rejuvenation occurs after serial subculturing *in vitro* (with and without an assortment of culture medium supplements) but the physiological processes

Figure 12 Marcotting or air-layering on a tree of *Dacryodes edulis*.

Figure 13 *In vitro* micropropagation of (a) *Khaya ivorensis* and (b) *Nauclea diderrichii* showing the proliferation and rooting phases respectively.

involved are still unknown. Additionally, there is a need for more research on the role of preseverance factors on the opportunities for more robust *in vitro* propagation. For example, light quality has been found to be important for root formation in *Betula* shoot cultures *in vitro*, while darkness was important for micrografting *Picea* shoots *in vitro*.

Against the advantages of *in vitro* systems are the facts that they are costly and require specialist facilities and staff, making them inappropriate for some developing-country applications.

Conclusions

Within any of the numerous different types or systems of propagating trees, there are large numbers of factors that determine whether or not the propagule is in a good physiological condition, to form a functional plant and grow. For example, when propagating from single-node, leafy cuttings from juvenile shoots, the factors that will determine the level of success are:

stockplant environment × stockplant management
× topophytic variables × node position
× nursery management × postseverance treatments
× propagation environment

Each of these factors are themselves multifaceted and influenced by the ambient environment (light quality and quantity, water, temperature, nutrients) of the stockplant garden, the nursery, or the propagation bench. For example, in the stockplant garden the environment (light, water, and nutrients) and the management of stockplants can have both short-term impacts on rooting ability by determining the levels of water or heat stress experienced by the tissues being propagated before severance from the stockplant, or long-term impacts on rooting ability through their effects on the morphology or physiological condition of the shoots. Similarly, once the cuttings have been severed from the stockplant the environment of the nursery and the handling of the severed cuttings before and after insertion in the propagation bed will also determine the levels of stress that the cuttings experience. In addition, the cuttings are also affected by the activities of the person doing the propagation and particularly the care taken by this person to minimize the levels of stress experienced by the cuttings (e.g., maintenance in a cool, shady, moist environment; reduction of transpiration by leaf trimming). The human element in this is what is commonly called having 'green fingers' and reflects the person's sensitivity to the needs of the plant material.

See also: **Genetics and Genetic Resources**: Propagation Technology for Forest Trees. **Silviculture**: Natural Regeneration of Tropical Rain Forests. **Soil Biology and Tree Growth**: Tree Roots and their Interaction with Soil. **Tree Physiology**: Root System Physiology.

Further Reading

Davis TD, Haissig BE, and Sankhla N (1988) *Adventitious Root Formation in Cuttings*. Portland, OR: Dioscorides Press.

Dick JMcP and Dewar RC (1992) A mechanistic model of carbohydrate dynamics during the adventitious root development in leafy cuttings. *Annals of Botany (London)* 70: 371–377.

Hartmann HT, Kester DE, Davis FT, and Geneve RL (1997) *Plant Propagation: Principles and Practices*, 6th edn. Upper Saddle River, NJ: Prentice-Hall.

Jain SM and Ishü K (2003) *Micropropagation of Woody Trees and Fruits*. Dordrecht, The Netherlands: Kluwer Academic.

Leakey RRB (1981) Adaptive biology of vegetatively regenerating weeds. *Advances in Applied Biology* 6: 57–90.

Leakey RRB (1983) Stockplant factors affecting root initiation in cuttings of *Triplochiton scleroxylon* K. Schum., an indigenous hardwood of West Africa. *Journal of Horticultural Science* 58: 277–290.

Leakey RRB (1985) The capacity for vegetative propagation in trees. In: Cannell MGR and Jackson JE (eds) *Attributes of Trees as Crop Plants*, pp. 110–133. Monks Wood, UK: Institute of Terrestrial Ecology.

Leakey RRB (1990) The domestication of tropical forest trees: a strategy for increased production and for conservation. In: Werner D and Müller P (eds) *Fast Growing Trees and Nitrogen Fixing Trees*, pp. 22–31. Stuttgart, Germany: Gustav Fischer Verlag.

Leakey RRB, Newton AC, and Dick JMcP (1994) Capture of genetic variation by vegetative propagation: processes determining success. In: Leakey RRB and Newton AC (eds) *Tropical Trees: The Potential for Domestication and the Rebuilding of Forest Resources*, pp. 72–83. London, UK: HMSO.

Longman KA (1993) *Rooting Cuttings of Tropical Trees. Tropical Trees: Propagation and Planting Manuals*, vol. 1. London, UK: Commonwealth Science Council.

Mudge KW and Brennan EB (1999) Clonal propagation of multipurpose and fruit trees used in agroforestry. In: Buck LE, Lassoie JP, and Fernandes ECM (eds) *Agroforestry in Sustainable Agricultural Systems*, pp. 157–190. New York: CRC Lewis.

TROPICAL ECOSYSTEMS

Contents

Acacias

S Harris, University of Oxford, Oxford, UK

Introduction

Acacias are emblematic landscape trees, whether they are the flat-topped trees that pepper the African savanna, the swollen thorn ant acacias of Central America or the wattles of the Australian outback. Many acacias are adapted to poor soils and disturbed conditions, often in hostile environments, where they are colonizers. It is these conditions that are often faced by tropical foresters, especially where human activities have modified the environment. Thus, acacias, particularly the Australian species, are important forestry trees and multipurpose tree species in the tropics. Acacias belong to the speciose genus *Acacia* and the monotypic genus *Faidherbia*. It is the purpose of the present article to introduce the basic systematics and distribution of the acacias, together with data on genetic variation and hybridization. The ecological and reproductive diversity of the acacias is presented, together with an overview of their utility.

Systematics

Acacia is a widespread genus of tropical–subtropical tree and shrub legumes distributed from Central/South America through Africa to Southeast Asia and Australia. Macrofossils (wood, leaves, phyllodes, flowers) attributed to *Acacia* have been reported from the Dominican Republic (Early Miocene/Late Eocene) and Australia (Early Pleistocene/Lower Pliocene). In contrast, microfossils (pollen) have been reported from Cameroon (Late Eocene), Puerto Rico (Oligocene), New Zealand, Patagonia, and Sudan (Miocene), and Australia (Late Middle Eocene to Quaternary).

Table 1 Characters that separate subgenus *Acacia* and the monotypic genus *Faidherbia* (*F. albida*, synonym *A. albida*)

Character	*Subgenus* Acacia	Faidherbia
Leaf phenology	Lost in dry season	Present in dry season
Seedling morphology	Pinnate eophyll	Bipinnate eophyll
Petiolar gland	Present	Absent
Stamen fusion	Free	Shortly fused
Polyad structure	Commonly 16	26–32 (rarely 16)
Pollen pores	Three	Four
Pollen exine	Smooth/reticulate	Areolate
Pollen size	23–64 μm	90–124 μm
Wood rays	Multiseriate	Uniseriate
Involucel	Present	Absent
Pod fibers	One layer	Two layers
Cotyledons	Petiolulate	Sessile

More than 5000 *Acacia* names have been described, comprising some 1300 species; more than 950 species occur in Australia, with approximately 230 species in the New World, 135 species in Africa, 18 species in India, and a few others in Asia and as island endemics. The genus *Acacia* is one of two members (the other is the African monotypic genus *Faidherbia*) (**Table 1**) of the mimosoid legume tribe, Acacieae. The Acacieae is closely related to the tribe Ingeae, although there appear to be no consistent characters that distinguish them.

Acacia species are woody trees, shrubs, or lianas which may have prickles. The leaves are bipinnate or modified as phyllodes (rarely reduced or absent). Petiolar glands are usually present, as are stipules that may be spinescent. Flowers are tetramerous or pentamerous, with white or yellow (rarely pink) petals and are either all hermaphrodite or a hermaphrodite–male mixture on a single tree. Flowers are organized into heads, and flower heads organized into axillary, racemose or rarely paniculate inflorescences (**Figure 1**). Flowers have free to united sepals, with numerous stamens that are usually free (rarely united at the base into a very short tube) and a single (usually), sessile or stalked ovary. Pods are dehiscent or indehiscent, usually flattened, and very variable in shape, ranging from straight to highly contorted. Seeds are unwinged and nonendospermous, usually with a hard seed coat and with or without an aril.

Acacia taxonomy has been in a state of flux since the genus was first described by Miller in 1754, although it was not until Bentham's work in the mid-1800s that the present generic limits were

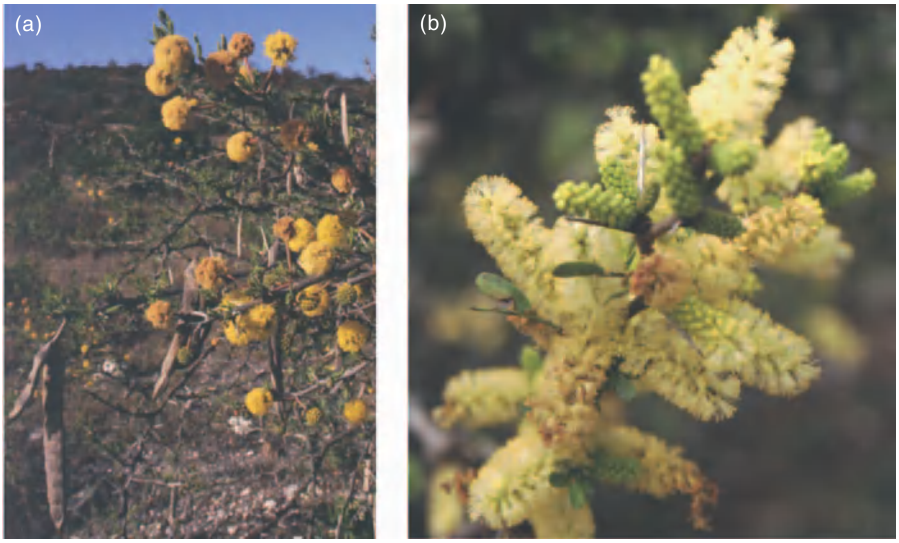


Figure 1 Globose and spicate inflorescences in the genus *Acacia*. (a) Globose inflorescence of *A. schaffneri* (Mexico); (b) spicate inflorescence of *A. amentacea* (Mexico).

established. Bentham divided *Acacia* into six series (**Table 2**), based primarily on vegetative characters (foliage and spinescence) and secondarily on inflorescence characters; fruit was largely ignored. In the 1970s, Vassal recognized three subgenera (*Acacia*, *Aculeiferum*, and *Phyllodineae*) (**Table 2**), and moved the African species *Acacia albida* to the monotypic genus *Faidherbia*. In the mid-1980s, Pedley concluded that the genus *Acacia* was too broadly conceived and three genera should be recognized (although most botanists have not accepted these changes): *Acacia* (=*Acacia* subgenus *Acacia*), *Senegalia* (=*Acacia* subgenus *Aculeiferum*), and *Racosperma* (=*Acacia* subgenus *Phyllodineae*) (**Tables 2** and **3**).

Most recent evolutionary studies, whether based on DNA or morphological data, concur with Pedley that the genus *Acacia* is not monophyletic. However, the appropriate division of the genus is unclear. Some workers suggest that subgenera *Aculeiferum* and *Phyllodineae* group together and are distinct from subgenus *Acacia*, others have suggested that subgenera *Aculeiferum* and *Acacia* group together and are distinct from subgenus *Phyllodineae*, whilst more radical still is the suggestion that the currently circumscribed *Acacia* should be split into five different genera. The formal splitting of the genus *Acacia* is likely to result in a large number of changes of scientific names.

Complex patterns of morphological variation, the paucity of material, poor understanding of distribution in some species and the recognition of numerous infraspecific taxa (e.g., *A. tortilis* and *A. nilotica*) can confound species delimitation. For example, *A. farnesiana* is prostrate in Mexican sand dunes, whilst *A. longifolia* subsp. *sophorae* shows a similar habit in the sand dunes of southwestern Australia. Some species have very wide distributions (*A. tortilis*, throughout tropical Africa and into the Middle East and India), whilst other species have very restricted distributions (e.g., *A. dorsenna*, known only from one area in Western Australia).

Table 2 Major classifications of the genus *Acacia*

Bentham	*Vassal*	*Pedley*
Acacia	*Acacia*	
series *Gummiferae*	subgenus *Acacia*	*Acacia*
	Section *Acacia*	
series *Vulgares*	subgenus *Aculeiferum*	*Senegalia*
	Section *Monacanthea*	Section *Senegalia*
	Section *Aculeiferum*	
series *Filicinae*	Section Filicinae	Section *Filicinae*
	subgenus *Phyllodineae*	*Racosperma*
series *Botrycephalae*		
series *Phyllodineae*	Section *Uninervea*	Section *Racosperma*
	Section *Heterophyllum*	Section *Plurinervia*
		Section *Lycopodiifolia*
series *Puchellae*	Section *Pulchelloidea*	Section *Pulchella*
	Faidherbia	*Faidherbia*

Table 3 Major subgeneric characteristics of the genus *Acacia*

Characteristic[a]	*Subgenus* Acacia	*Subgenus* Aculeiferum	*Subgenus* Phyllodineae
Distribution	New World, Africa, Asia [Australia]	New World, Africa, Asia [Australia]	Australasia [Hawaii, Mascarene Islands]
Phyllodes	Absent	Absent	Present, rarely absent
Stipular spines	Present	Absent	Absent, rarely present
Prickles	Absent	Present, rarely absent	Absent
Anther gland	Present or absent	Present or absent	Absent
Pod fibers	Single layer	Two layers	Two layers
Pollen	Colporate	Porate [extraporate]	Extraporate [porate]
Ploidy	$2x$, $4x$, $8x+$	$2x$, rarely $4x$, $8x$	$2x$, rarely $4x$, $6x$
Mean 1C DNA content (standard error)	1.130 (0.032)	0.997 (0.074)	1.435 (0.011)

[a]Square brackets indicate that characteristic is rarely found.

Genetics

Chromosome number and structure varies across the genus from $2n=2x=26$ to $2n=16x=208$, with homogeneous to heterogeneous karyotypes, and nuclear DNA contents (1C, i.e., the amount of DNA in the haploid set of chromosomes) from 0.53 pg to 2.1 pg. Chromosome number in subgenus *Acacia* ($2x$, $4x$, $8x+$) is more variable than the other two subgenera, whilst 1C DNA content is greater in subgenus *Phyllodineae* than either of the other two subgenera (**Table 2**). However, variation in chromosome numbers can be found within species; for example, tetraploid individuals occur in populations of the normally diploid *A. dealbata*.

Differences in chromosome numbers would imply that polyploidy has been important in the evolution of the genus *Acacia*. The origin of the Australian allohexaploid *A. colei* is thought to have been through allopolyploidy, involving the diploid *A. neurocarpa* and the tetraploid *A. elachantha*, through a triploid, presumably sterile, intermediate. In the case of the African triploid *A. laeta*, this is thought to have arisen through hybridization between the two diploid species, *A. mellifera* and *A. senegal*. In general, natural hybridization between *Acacia* species appears to be relatively rare, although putative hybrids have been recorded from all the major areas of the genus's distribution. Furthermore, hybrids may have considerable potential in forestry; for example, the hybrid between the economically important species *A. auriculiformis* and *A. mangium*, has desirable commercial characteristics.

Few investigations of the distribution of genetic variation within and among natural populations of acacias have been conducted; those that have been undertaken have mainly used allozyme markers (**Table 4**). The occurrence of ploidy differences, particularly in subgenera *Aculeiferum* and *Acacia*, means that genetic diversity investigations are complicated by the possibility of more than two alleles at a locus within an individual and hence in the calculation of allele frequencies (e.g., high genetic diversity and low population differentiation in *A. karroo* may be a reflection of this problem). This may be one of the reasons that the majority of investigations of neutral marker diversity have focused on diploid Australian *Acacia* species. Furthermore, estimates of genetic diversity may be affected by population sampling and choice of loci (e.g., *Faidherbia albida*, *A. mangium*). Acacias tend to show high levels of genetic diversity and differentiation compared to other long-lived, woody perennials (**Table 4**). High genetic differentiation appears to be associated with disjunctions in genetic diversity, for example, the genetic differentiation of *A. melanoxylon* populations in eastern Australia into northern and southern types or the disjunction of genetic diversity between East and West African populations of *Faidherbia albida*. Such disjunctions have been interpreted as the result of changes in population size following major environmental perturbation. In the diploid *Acacia* species, low differentiation appears to be associated with restricted distributions (e.g., *A. anomala*).

Acacia mangium is one of the most widely planted and economically important *Acacia* species, yet very low levels of neutral genetic diversity and population differentiation have been reported. This illustrates the importance of having knowledge of both neutral

Table 4 Examples of the patterns of genetic diversity and population differentiation in natural populations of *Acacia* species sampled from across their native ranges and based on allozyme data

Taxon	*Number of populations*	*Number of loci*	*Mean population diversity*	*Total genetic diversity*	*Population differentiation*
Faidherbia albida	22–30	6–10	0.128–0.454	0.286–0.516	0.123–0.422
Acacia acuminata subsp. *acuminata*	6	16	0.237	0.266	0.108
A. acuminata subsp. *burkittii*	5	16	0.287	0.318	0.098
A. anomala	6	15	0.336	0.356	0.056
A. aulacocarpa	22	30	0.111	0.298	0.626
A. auriculiformis	13–18	18–22	0.098–0.122	0.134–0.149	0.181–0.270
A. mangium	11–13	18–30	0.017–0.064	0.025–0.070	0.086–0.311
A. mearnsii	19	22	0.179	0.201	0.108
A. karroo	12	10	0.84	0.88	0.050
A. melanoxylon	27	30	0.215	0.345	0.377
A. oldfieldii	2	16	0.166	0.178	0.069
Long-lived, woody perennials	Mean = 9.2	Mean = 18.1	0.148	0.177	0.084

and adaptive variation before conservation and utilization decisions are made. Furthermore, *A. mangium* is the *Acacia* species for which the most comprehensive genetic map is available.

Ecology

The ecological diversity of the genus *Acacia* is reflected in its morphological diversity, where species occupy habitats as diverse as the arid centre of Australia and wet neotropical forests. *Acacia* species are important ecosystem components, especially in Australian and African savannas where they may be important colonizing species (e.g., *A. melanoxylon*). However, *Acacia* species tend to be more abundant in arid and semi-arid areas than in wet ecosystems. The majority of *Acacia* species show adaptations to water stress, for example, reduced photosynthetic surface areas (e.g., the Australian *Acacia* species *A. willardiana* of the Sonoran Desert), although some are adapted to periodic flooding (e.g., *A. xanthophloea*). Some species (e.g., *A. erioloba*), survive the extremes of the desert environment, including freezing, and may have very long (6–12 m) tap roots. The ant acacias show a mutualistic arrangement, where ant colonies protect the plant from herbivory and the leaves may produce Beltian bodies (protein-rich structures) as an ant food source. The association between ants and *Acacia* species appears to have arisen on more than one occasion, on at least two continents; the Central American swollen thorn ant acacias (e.g., *A. melanoceros*) support *Pseudomyrmex* colonies, whilst the African whistle-thorn acacias (e.g., *A. seyal*) support *Crematogaster* colonies. African and Australian *Acacia* species are also important hosts for members of the parasitic angiosperm families Loranthaceae and Santalaceae.

Dominant acacias (e.g., *A. aneura*) may have important roles in the landscape, although changes in human activities (e.g., pasture management) may cause considerable changes in an *Acacia*-dominated landscape; for example, the Central American ant acacia *A. melanoceros* is sensitive to forest fragmentation. In contrast, some species are very tolerant of human-mediated disturbance; for example, *A. dealbata* regenerates freely following windthrow. Such differences appear to be at least partially related to life-history traits. For example, *A. melanoceros* matures in 8–14 years compared to the 4–5 years of *A. dealbata*, whilst the resprouting ability of *A. melanoceros* is poor compared to the vegetative regeneration of *A. dealbata*. Furthermore, *A. melanoceros* seeds germinate quickly compared to those of *A. dealbata* that form a long-lived seed bank. Another major effect of humans on the distribution of acacias has been the intercontinental movements of species, for example, Australian species being moved to Africa and the New World and African species being moved to Australia. The consequences of such movements have been unpredictable; some species are highly productive (e.g., *A. mangium* in India), whilst others are very destructive (e.g., *A. nilotica* in Australia).

Distributions of *Acacia* species and range limitations may depend on soil and climatic factors; for example, *A. erioloba* is confined to soils of the Kalahari sand sheet in southern Africa, whilst the northern limit of *A. farnesiana* in the USA may be due to low temperatures. However, more complex interactions may occur; for example, phyllode size in the coastal species *A. melanoxylon* appears to be related to both distance from the coast (aridity) and seasonal rainfall patterns. Seasonality reveals additional patterns of ecological variation in acacias. Some species lose their leaves all at once, e.g., Sudanese *A. nubica* (at the end of the long dry season), whilst *A. tortilis* sheds its leaves progressively as the dry season advances. Most Australian acacias are adapted to fire; thus germination may be facilitated by fire or vegetative regeneration may be stimulated, as with some African acacias, where coppice growth is facilitated (e.g., *A. stolonifera*).

Acacias, as legumes, are generally capable of forming symbiotic relationships with the bacterial genus *Rhizobium*, producing root nodules and fixing atmospheric nitrogen. However, both nodulating and nonnodulating species are found in the genus *Acacia*. Nonnodulation is restricted to the southern USA, Central and South American, African and Asian members of subgenus *Aculeiferum* section *Monoacanthea* (e.g., *A. brevispica*); nonnodulation is unknown in Australian *Acacia* species. In addition to root nodules, acacias also have mycorrhizae.

Thirty-five *Acacia* taxa are listed as under threat by the IUCN, although this is likely to be an underestimate given that no Australian *Acacia* species are represented. Of those species under threat, the majority are threatened due to either agriculture or habitat degradation. Secondary effects of large mammal conservation may also have effects on *Acacia* conservation; as an example, the introduction of giraffes into South African savannas has driven accessible *A. davyi* populations to extinction.

Reproductive Biology

In *Acacia* species, the pollination unit is the flower head and pollen is released as polyads. Three mechanisms to promote outcrossing predominate in *Acacia* species:

1. Protogyny, where the stigma is receptive to pollen before pollen in the same flower is released.
2. Andromonoecy, where male and hermaphrodite flowers occur on the same plant, e.g., 17–50% male flowers are found per head in *A. suaveolens*.
3. Gametophytic self-incompatibility, where successful fertilization is determined by the genotype of the pollen, e.g., *A. retinoides*.

The structure of the *Acacia* inflorescence suggests that the majority of species are pollinated by insects, including Coleoptera, Diptera, Hymenoptera, and Lepidoptera, although others are pollinated by small mammals and nectarivorous birds; there is evidence that *A. nigrescens* is giraffe-pollinated. Genetic investigations of *Acacia* mating systems have shown that the species are highly outcrossed. However, reports of isolated individuals (e.g., *A. karroo*, *Faidherbia albida*) setting seeds imply that selfing may occur, whilst reports of polyembryony (e.g., *A. karroo*, *A. farnesiana*, *A. nilotica*) suggest that apomixis may also be important in some species.

In addition to sexual reproduction, some *Acacia* species also reproduce asexually by root suckering. For example, allozyme analysis of two disjunct regions of the rare Australian species *A. anomala* supports the view that one region is primarily outcrossing and the other is clonal, where each population in the latter region contains individuals with identical, multilocus genotypes.

Seed dispersal in acacias is usually by gravity or mechanical means. However, both insects and vertebrates may play important roles in seed dispersal and the facilitation of germination. In a few species, bird dispersal seems to be a common strategy. For example, the Central American ant acacias often have brightly colored fleshy arils that may attract birds, whilst the attractiveness of some species (e.g., *A. cyclops*) may be enhanced by seeds being suspended from the pod. In addition, it has been suggested that the aril of acacia seeds may be attractive to ants. For example, in the mechanically dispersed Australian species *A. linifolia*, secondary ant-dispersal may occur. Browsing vertebrates, particularly in Africa, play an important, if less selective role in seed dispersal; elephants and antelopes ingest large numbers of seeds which are then deposited in their faeces (e.g., *A. erioloba*). Such treatment scarifies the seed and provides a fertile germination medium. Other species, e.g., *Faidherbia albida*, appear to be dispersed by water, the fruits being buoyant, and deposit their seed when rotted, although the relative importance of water versus mammal dispersal in this case is unclear. Humans are an important means of long-distance dispersal of acacia seed, whether it is seed for establishing plantations, movement of multipurpose species with human migration, or transport by their livestock.

Many *Acacia* seeds have hard seed coats and need to be scarified before they will germinate; there are reports of acacia seed remaining viable in the soil for up to 60 years. The seeds of other species (e.g., *A. harpophylla*) lack impervious seed coats, lose viability rapidly, and have short lifespans. Despite their hard seed coats, many acacia seeds may be lost through infection of developing ovules by beetle larvae (Bruchidae) at the early stages of fruit development. Such losses are more significant in the New World and African acacias than in the Australian acacias, where the diversity of Bruchidae is relatively low.

Silviculture

Acacia diversity is reflected in the range of silvicultural practices applied to species management. The most widely planted *Acacia* species (*A. auriculiformis*, *A. mangium*, and *A. melanoxylon*) are generally light-demanding and adapted to a range of soil types. For example, *A. mangium* grows on acidic soils, whilst *A. auriculiformis* is particularly adaptable and grows well on sandy to heavy clay, often shallow soils. Furthermore, *A. auriculiformis* will tolerate flooding and very acidic soils, e.g., acid mine spoil in northern Australia.

Acacia saplings may be raised by vegetative propagation, although grafting may not be suitable for large-scale sapling production and stem cutting may only be possible from seedlings. Therefore, acacia plants are usually raised from seed. Acacia seeds can be stored for long periods, although they usually need scarification before they will germinate. Scarification may occur naturally by passage through animal guts, which has been promoted as a means of obtaining seed for plantation establishment. However, for most purposes other scarification treatments are necessary (e.g., mechanical or chemical damage to the seed testa or treatment with boiling water). Burning may also promote the germination of acacia seeds and is a common silvicultural practice, since accumulated litter is removed, even-aged stands are produced, and pests are destroyed. However, the practice may also increase the likelihood that some species become problem invaders, due to loss of seed dormancy (e.g., *A. brevispica*, *A. catechu*).

Acacia plantations are usually established from container-grown plants inoculated with rhizobia;

saplings are usually transplanted at about 6 months old. However, direct sowing of seed has been recommended in some cases, for example, *A. decurrens* in South Africa, where a well-developed taproot may be damaged during transplantation. Acacia seedlings are usually frost-sensitive, although once established species may be frost-hardy; for example, *A. melanoxylon* plantations will withstand frosts to $-7°C$.

Optimal spacing depends on the species and the products of interest. In order to produce high-quality *A. mangium* logs it is necessary to plant at densities that range from 900 to 1680 stems ha^{-1} which, combined with regular pruning and extensive thinning, will yield suitable timber after 15–20 years. In contrast, plantations for chipping, pulpwood, and firewood are not generally pruned or thinned and are harvested at 6–7 years.

Plantation management will depend on the species. *Acacia auriculiformis* responds well to pollarding and can be coppiced, whilst *A. mangium* is generally unsuitable for multiple rounds of coppicing. *Acacia melanoxylon* is susceptible to windthrow and must be sheltered if high-quality timber is to be produced; for example, in Tasmania it is grown with either *Pinus radiata* or *Eucalyptus* species. Rotation times will depend on the species; for example, *A. auriculiformis* produces stems of 15–20 cm diameter after 10–12 years, whilst *A. melanoxylon* will produce stems of more than 50 cm diameter after 70 years.

Utilization

Wood Products

In general, *Acacia* species have good biomass potential and, because of their high calorific value, are good fuelwoods. Large plantations of *A. mangium*, for paper pulp production, occur in Indonesia and Malaysia, where it is also an important building and furniture timber. *Acacia auriculiformis* is used for fuelwood, whilst the *A. mangium* × *A. auriculiformis* hybrid also has very good wood properties. *Acacia melanoxylon* is the best-known and highly valued temperate *Acacia* timber species, with harvesting from natural Tasmanian forests and plantations in New Zealand, South Africa, and Chile. *Acacia* species are important timber species in their native countries, e.g., *A. galpinii* and *A. nilotica* in Africa. In Western Australia, *A. acuminata* and *A. trachycarpa* are important *Santalum* hosts in commercial sandalwood production.

Tannin

Acacia mangium bark is a major source of vegetable tannin (used in leather and adhesive manufacture), the main producers of which are Brazil, China, Kenya, India, South Africa, Tanzania, and Zimbabwe. *Acacia decurrens* is also used, whilst historically *A. mearnsii* was planted for its tannin-rich bark.

Human Food

Acacia seeds typically have high nutritional values and few toxic or antifeedant compounds. Seeds of Australian tropical arid zone species, e.g., *Acacia colei* and *A. tumida*, are showing promise as a human food sources in semi-arid regions of the Sahel, where they were originally introduced for fuelwood and amenity planting. In Australia, *Acacia* (e.g., *A. murrayana*, *A. victoriae*) seeds are used as flavourings in the developing bushfood industry. African *Acacia* species (e.g., *A. senegal* and *A. seyal*) are important sources of edible gums.

Fodder

Acacia species are an important food component for African savanna mammals, whilst there are significant economic uses of *Acacia* foliage and green pods as livestock fodder, especially in times of drought (e.g., *A. tortilis*). In Australia, the *A. aneura* group is a particularly important fodder for sheep in the arid-zone rangelands, whilst *A. saligna* has been used outside Australia as fodder for sheep and goats in North Africa and South America. However, the foliage for some species is very toxic to livestock (e.g., *A. georgiana*). *Acacia* species may also be important fodder for wild species (e.g., *A. erioloba* in South Africa).

Ornamentals, Oils, and Medicines

In southern Europe, Australian *Acacia* species (e.g., *A. dealbata*, *A. retinodes*) have extensive ornamental value. In southern France, oil from *A. dealbata* and *A. farnesiana* flowers is used as a fixative and blending agent in perfume manufacture. Traditional medicines are extracted from some *Acacia* species, particularly *A. nilotica* and *A. catechu* in India.

Land Amelioration

Acacia species have been used for sand stabilization, *Imperata cylindrica* control, mine spoil rehabilitation, and improvement of soil quality. For example, *A. saligna* has potential for the mitigation of salinity, whilst *A. ampliceps*, *A. maconochieana*, and *A. stenophylla* have been very successful in highly alkaline, saline soils in Pakistan. *Acacia karroo* is an important species for land reclamation in southern Africa, and *A. dealbata* and *A. melanoxylon* are important species for sand dune stabilization in Chile.

Weediness

Some *Acacia* species have become serious weeds. Exotic Australian *Acacia* species (e.g., *A. saligna*, *A. cyclops*, *A. melanoxylon*, and *A. dealbata*) have caused serious weediness problems in South Africa, Portugal, and Chile, whilst New World and African *Acacia* species (e.g., *A. farnesiana*, *A. nilotica*) have caused problems in Australia. The weediness of *Acacia* species means that their use in agroforestry and amenity situations must be considered very carefully.

See also: **Biodiversity**: Biodiversity in Forests. **Ecology**: Reproductive Ecology of Forest Trees; Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics. **Landscape and Planning**: Landscape Ecology, Use and Application in Forestry. **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest; Forest Biodiversity Prospecting; Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Tree Breeding, Practices**: Tropical Hardwoods Breeding and Genetic Resources. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Dry Forests; Tropical Moist Forests; Woody Legumes (excluding Acacias).

Further Reading

Barnes RD, Fagg CW, and Milton SJ (1997) Acacia erioloba: *Monograph and Annotated Bibliography.* Tropical Forestry Papers no. 35. Oxford, UK: Oxford Forestry Institute.

Doran JC and Turnbull JW (1997) *Australian Trees and Shrubs: Species for Land Rehabilitation and Farm Planting in the Tropics*. ACIAR Monograph no. 24. Canberra: Australian Centre for International Agricultural Research.

Guinet P and Vassal J (1978) Hypotheses on the differentiation of the major groups of the genus *Acacia* (Leguminosae). *Kew Bulletin* 32: 509–527.

Janzen DH (1974) Swollen-thorn Acacias of Central America. *Smithsonian Contributions to Botany* 13: 1–131.

Maslin BR (2001) *Flora of Australia*, vol. 11A/B, Mimosaceae, *Acacia*, Part 1–2. Canberra: Commonwealth Scientific and Industrial Research Organization Publishing.

Maslin BR, Miller JT, and Seigler DS (2003) Overview of the generic status of *Acacia* (Leguminosae: Mimosoideae). *Australian Systematic Botany* 16: 1–18.

New TR (1984) *A Biology of Acacias: A New Source Book and Bibliography for Biologists and Naturalists*. Melbourne, Australia: Oxford University Press.

Pedley L (1986) Derivation and dispersal of *Acacia* (Leguminosae), with particular reference to Australia, and the recognition of *Senegalia* and *Racosperma*. *Botanical Journal of the Linnean Society* 92: 219–254.

Ross JH (1979) A conspectus of the African *Acacia* species. *Memoirs of the Botanical Survey of South Africa* 44: 1–155.

Turnbull JW (1986) *Multipurpose Australian Trees and Shrubs*. Canberra: Australian Centre for International Agricultural Research.

Bamboos, Palms and Rattans

I R Hunter and N Bystriakova, International Network for Bamboo and Rattan, Beijing, China

Taxonomy/Genetics

Bamboos: Poaceae (Gramineae)

The family Poaceae comprises about 12 000 species in about 700 genera. Twelve subfamilies are recognized, of which the Bambusoidea is one. This subfamily includes approximately 1200 species within the tribes Bambuseae (woody bamboos) and Olyreae (olyroid or herbaceous bamboos).

Bamboos are forest grasses. The most ancient grasses were tropical forest dwellers but, as the higher grasses diversified into open areas, the true bamboos were the only major lineage of the family to adapt to the forest habitat. Bamboos are set off from other grasses by the predominance of certain 'bambusoid' structural characters, many of which are considered to be 'primitive'. The most easily recognizable vegetative features that distinguish the bamboos are the prominent development of a rhizome system, the woodiness and strong branching of the culms, the presence of petioles on the leaf blades, and the difference in form between the sheaths clothing young culm shoots and those borne on the leafy twigs. To these may be added floral characters such as well-developed lodicules, in most species three in number, and a style consisting typically of a single column, bearing one, two, or three (rarely more) stigmas.

The bambusoid grasses are naturally distributed in all continents except Europe and Antarctica. Bamboos appear more or less prominently in the natural vegetation of many parts of the tropical, subtropical, and mild temperate regions. The approximately 1100 species of woody bamboos are distributed from 46° N to 47° S latitude and from sea level to 4300 m in equatorial highlands, whereas the approximately 110 species of herbaceous bamboos occur overwhelmingly in the New World, with only two Old World representatives. The herbaceous bamboos occur principally in moist forests between 29° N and 34° S latitude and are only occasionally found above elevations of 1000 m, rarely to 2700 m. The natural distribution of bamboo in the world has been greatly modified by human intervention.

Of the 60–70 genera of woody bamboos, only *Arundinaria* occurs in both the Old World and New World. Currently, 20 genera of solely New World woody bamboos are recognized, so there are 21 New World woody genera. Although nearly twice as many Old World genera are recognized, there are approximately 430 species of New World woody bamboos, compared with 500–600 Old World species.

In the Old World, the monsoon-belt of Southeast Asia with southern China is the main center of diversity of the bambusoid grasses. In the New World, Brazil (including the Amazon basin and the Atlantic forests) has the greatest diversity of genera and species, followed by the Andes (Venezuela to Bolivia) and Mexico and Central America.

Bamboos have a great industrial and cultural significance, particularly in East Asia, although fewer than 100 species are generally used.

Palms: Arecaceae (Palmae)

The family Arecaceae is a large group comprising approximately 2500 arboreal species to be found throughout equatorial, tropical, and subtropical areas of the world where they feature as a very peculiar element of the landscape. The main geographical areas having played the role of differentiation centers are Africa's equatorial coasts, the Indonesian region, the Sunda Isles, Oceania, Brazil's coasts, Amazonia, and the Antilles. It was during the Cretaceous period that this group had its largest diffusion and differentiation, leaving behind several fossil remains of trunks and leaves.

The family is traditionally divided into a number of subfamilies: (1) Phytelephasieae, characterized by flowers without a perianth, a large number of stamens in male flowers and female flowers bearing a multilocular ovary (4–9 locules), and infructescences (*Phytelephas*); (2) Coryphoideae, exhibiting floral characters typical of the family: free carpels, berry-like fruits, pinnate or fan-shaped leaves (*Phoenix*, *Chamaerops*, *Trachycarpus*, *Livistona*, *Sabal*, *Washingtonia*); (3) Borassoideae, characterized by fan-shaped leaves, perianth typical of the family, syncarpous ovary (*Hyphaene*, *Borassus*, *Lodoicea*); (4) Lepidocaryoideae, characterized by syncarpous ovary and fruits covered with imbricate scales (*Raphia*, *Metroxylon*, *Calamus*); (5) Ceroxyloideae, characterized by syncarpous ovary and pinnate leaves (*Arenga*, *Ceroxylon*, *Areca*, *Cocos*); (6) Nipoideae, characterized by male flowers bearing three connate stamens, and unilocular ovary (*Nipa*).

Habits of palms are quite typical, in that they are characterized by a tall, unbranched stem (up to 80 m tall in the genus *Cocos*) or, rarely, by a dichotomous branching stem (*Hyphaene*), and of the same diameter all along from base to top; at the apex they bear a rosette consisting of coriaceous, either palmate or pinnate, leaves, up to some meters long. The stem may remain quite slender, in which case it turns to a creeping habit (rattan/*Calamus*), or otherwise it may be very short in acaulescent species (*Phoenix acaulis*). Another feature peculiar to this family is that the stem reaches its ultimate growth in diameter before it starts its growth in height. Indeed, palms lack any secondary growth. Inflorescences are spadix-like, at first enveloped by a spathe or by leaf sheaths opening up at anthesis.

The fruit may be either a berry (e.g., *Phoenix*) or a drupe (e.g., *Cocos*). Only one fertilized locule carries on developing, whilst all others wither, so that the fruit contains one seed only. Pollination is mostly anemophilous; accordingly, the plant produces a large amount of pollen for this purpose.

The Arecaceae include plants of enormous economic importance for human beings, amongst them the coconut palm (*Cocos nucifera*) and the date palm (*Phoenix dactylifera*). Several species are employed in the production of vegetable fibers (*Sabal*, *Chamaerops*, *Trachycarpus*, *Borassus*). African oil palm (*Elaeis guineensis*) supports a huge industrial oil industry. Rattans are the basis of a large furniture and matting industry. Other palms with high potential as food sources include *Bactris gasipaes*, *Euterpe oleracea*, *E. precatoria*, *Jessenia bataua*, *Mauritia flexuosa*, and *Orbignya phalerata*.

Palms are also used in milder temperate-climate regions to provide trees for parks, gardens, squares, and avenues. Among the most widely used to this end are *Phoenix canariensis*, *P. dactylifera*, *Washingtonia filifera*, *W. robusta*, *Syagrus romanzoffiana*, and *Trachycarpus fortunei*.

Rattan: Calamoideae

Rattans belong to the Calamoideae, a large subfamily of palms. There are around 600 different species of rattan belonging to 13 genera and these are concentrated solely in the Old World tropics; there are no true rattans in the New World. All of the species within the Calamoideae are characterized by overlapping reflexed scales on the fruit and all of these climbing palms are spiny, a necessary preadaptation to the climbing habit. Of the 13 genera of rattan, three are endemic to Africa: *Laccosperma* (syn. *Ancistrophyllum*), *Eremospatha*, and *Oncocalamus*. Although some species within these genera are utilized locally and form the base of a thriving cottage industry, they have not, until recently, attracted much attention from commercial concerns.

The largest rattan genus is *Calamus*, with *c.* 370 species; it is represented in Africa by one very variable species, *C. deerratus*. *Calamus* is predominantly an Asian genus and ranges from the Indian subcontinent and south China southwards and east through the Malaysian region to Fiji, Vanuatu, and tropical and subtropical parts of eastern Australia. Most of the best commercial species of rattan are members of this genus. The remaining rattan genera, *Calospatha, Ceratolobus, Daemonorops, Korthalsia, Myrialepis, Plectocomia, Plectocomiopsis, Pogonotium,* and *Retispatha*, are centered in Southeast Asia and have outliers further eastwards and northwards.

Rattans can be clustering (clump-forming) or solitary; some species, such as *Calamus subinermis*, can be both. Other species are acaulescent, having no discernible stem at all. Clustering species sometimes possess up to 50 stems of varying ages in each clump and produce suckers that continually replace those stems lost through natural senescence or through harvesting. Some clumps can be harvested many times on a defined cycle if the light conditions are conducive to the remaining suckers being able to develop and elongate.

Rattans display two main modes of flowering. In one, a period of vegetative growth is followed by the simultaneous production of flowers. Flowering and fruiting are followed by the death of the stem itself. In single-stemmed palm species, the whole organism dies after fruiting. However, in clustering species of rattan the plant coppices from the base and it is only the individual stem that dies. In the other form of flowering, flowers are produced continually and flowering and fruiting do not result in the death of the stem. All the species of *Korthalsia, Laccosperma*, *Myrialepis*, *Plectocomia*, *Plectocomiopsis*, and a few species of *Daemonorops* flower and die. Furthermore, in many of these species, stems tend to be of low quality due to the presence of a soft pith which results in poor bending properties. Such stems are also more prone to subsequent insect attack due to increased starch deposition.

Rattan fruits are often brightly colored (white, yellow, orange, or red) and attractive to birds and mammals. Birds (e.g., hornbills) and primates are the main dispersers of rattan seeds. In the Asian taxa, the seed is often covered with a fleshy seed coat. Incomplete removal of this coat often results in delayed germination, suggesting that it contains some chemical germination inhibitors. However, once this outer layer is fully removed, the germination of commercial species such as *Calamus manan* and *C. caesius* is both rapid and uniform. In contrast, in African rattan species it can be rather prolonged and it may take between 9 and 12 months before germination commences.

Ecology

Bamboo

Bamboos range in height from a few centimeters to 20 meters or more. The shorter species exist either as understory to forest stands or as edaphic or climatic climaxes (particularly in altitudinal belts on mountains). They are associates of most temperate and tropical moist or dry forest types. Bamboos are generally very tolerant of poor soils. The minimum rainfall to form closed stands seems to be around 600 mm year^{-1}. Bamboo species vary greatly in cold tolerance; some will not tolerate any frost but others tolerate temperatures down to $-30°C$.

Bamboo understory species prefer light overhead shade. Bamboos may interact with fire in that they and grasses are reduced with fire exclusion. Soil impoverishment, through frequent burning, may promote development of a bamboo-dominated forest understory. Bamboo may aggressively colonize forest gaps and exclude light-demanding pioneer tree species. Under these circumstances forest composition can gradually change to be bamboo-dominant.

Pure bamboo stands occur naturally in several parts of the world. Altitudinal belts occur on East African mountains at 2400–3000 m. Bamboo forest, a type of open rain forest characterized by the dominance of arborescent bamboos of the *Guadua* genus, covers over 50% of Acre state in the southwestern Brazilian Amazon.

There is a close ecological link between bamboo forest and certain rare species – Amazonian bird species and, notably, the panda. However some bamboo stands may have a lower wildlife biodiversity than other natural forests.

Many bamboos are semelparous – they flower once after a long interval and then die. There are other plant genera with similar habits – *Agave, Ensete, Kalanchoe, Lobelia*, *Orchis*, and *Yucca*. It is not known what triggers such flowering or what benefit it is to the plant to behave in this way, although there are three main theories: bet-hedging, reproductive effort, and demographic models. Flowering seems to occur in waves, starting in one place and then migrating through nearly the entire species. The time taken to go through the wave may range from a few years to many decades. Contemporaneous flowering may occur even in ornamental bamboo plants continents away from their native range. For example, in the 1990s millions of plants of *Fargesia murieliae*, an ornamental bamboo, flowered in western Europe. As all plants were ramets of a single ortet introduced into Europe about 80 years ago, the simultaneous flowering of all these ramets constituted a single giant compound inflorescence. Species moved within their range retain the flowering pattern of their home range. One major cohort of *Bambusa arundinacea*, widely distributed in India, has been recorded as seeding in 1868–1872, 1912–1916 and 1958–1962. On the other hand, in *Melocanna baccifera* some populations have a flowering cycle of 30–35 years, and others may have a longer (45, 60, 65 years) or shorter (7–10, 19–21, 25, 26, 27 years) cycle.

Mass flowering and dying of bamboo are important events in the ecology of their associations leading variably to such consequences as enhanced tree seeding in gaps or to explosions of rodent populations. Flowering remains largely unpredictable, unless written or oral history has accumulated, and the subsequent dying is a major although infrequent problem in the management of bamboo as a crop.

Intensification of bamboo management leads to more diseases – particularly blights and rots. Some bamboos may form a nitrogen-fixing association with azotobacteria.

Palms

Palms exist as canopy constituents of forest associations; as understory species in forests and as edaphic or climatic climax, or more properly, survivor species. Many palm species are more tolerant of harsh conditions (salt, alkali soils, harsh temperatures, drought, permanent water-logging) and are hence sometimes, along an environmental gradient, amongst the last plants to be found on such highly degraded sites. In forest associations it has been noted that palms are often found on the poorer soils.

Rattan

With habitats ranging from sea level to over 3000 m elevation, from equatorial rainforests to monsoon savannas and the foothills of the Himalayas, there is a huge range of ecological adaptation among rattans. However, rattans are predominantly plants of primary rain and monsoon forest. Rattans are distributed in tropical and subtropical areas in the Asia-Pacific region and Africa. No rattans are found growing naturally in other tropical and subtropical areas, or in the temperate regions.

Throughout their natural range, rattan species are found in a wide range of forest and soil types. Some species are common components of the forest understory, whilst some rely on good light penetration for their development; hence several species are found in gap vegetation and respond very well to canopy manipulation, particularly that caused by selective logging. Other species grow in swamps and seasonally inundated forest whilst others are more common on dry ridge tops.

Despite this wide range of ecological conditions, the majority of rattans need adequate light for their full growth and development. Although the seeds will germinate under a wide range of light conditions, the resultant seedlings will remain for long periods on the forest floor awaiting sufficient light for them to develop, such as may occur after a tree fall.

Date Palm

The date palm is a native of North Africa but has been so extensively cultivated there for thousands of years that no natural stands are thought to remain and no information on its native ecology is available.

It is cultivated and naturalized throughout the desert regions between 15° and 35° N, from the Canary Islands and Morocco in the west to India in the east. It has been recorded from all the inland and littoral parts of North Africa, from the southern parts of the Balkan peninsula and Asia minor, from Syria, Palestine, Jordan, Iraq, Arabian peninsula, Iran, and Pakistan. It is cultivated as an ornamental in southern Europe, but seldom matures fruit except in extreme southern parts of Italy and Spain. The date palm is cultivated in Arizona and California, USA, and Queensland, Australia. There is evidence of date usage 8000 years ago in India as well as its cultivation in Sumeria and ancient Egypt.

Date palm is reported to tolerate annual precipitation of 30–400 mm – a full-bearing orchard requires only 250 mm of rainfall (by rainfall or irrigation). It is grown ideally where the permanent water table is within root-reach of the soil surface. Annual temperature should be warm temperate to tropical and soil pH slightly acid to strongly alkaline. Any good soil that is not too heavy will do. Dates do well even where there is a crust of salt on the surface. Daytime temperatures of 50°C are tolerated. For proper ripening of fruit, the mean temperature between the period of flowering and ripening should be above 21°C, rising to 27°C, for at least a month. There must be no rain during flowering time. Winter temperatures below −8°C are harmful.

Oil Palm

The oil palm (*Elaeis guineensis*) is originally a native of Africa but is now widely distributed as an exotic plantation species. It is widespread in the moist tropical forests of Africa. However, even in its native range its ecology has been greatly modified by domestication. Considerable attention is now directed to its genetic range. The Palm Oil Research Institute of Malaysia has the largest collection of *Elaeis guineensis* and *E. oleifera* germplasm in the world. Palms in over 1000 ha of germplasm gardens are being evaluated for oil yield, kernel content, height, harvest index, fatty acid composition, carotene, and vitamin E contents.

Raffia Palm

The raffia palm often occurs pure or in mixtures with mangroves and palms in wetlands and freshwater swamps in Africa. Although *Raffia regalis* is found on dry soils, and *R. farinifera* in lower mountain regions in Cameroon, the raffia palms in southern Benin are confined to freshwater swamps where the natural vegetation is forest. However, human activity has transformed this forest into a 'raphiale' where *R. hookeri* has become the main arborescent species. One sole species, *R. taedigera*, occurs in Latin America in a particular kind of swamp forest which is composed of a nearly pure stand of *R. taedigera*, growing in clumps. The leaves of *R. taedigera* grow to nearly 15 m in length and upon falling seem to eliminate the few other species of trees that might grow in water. There is conflicting evidence as to whether *R. taedigera* is actually native or introduced long ago from Africa.

Silviculture

Bamboo

Bamboos can be classified into two main types – sympodial (clumping and largely tropical) bamboos and monopodial (running and largely warm temperate bamboos). Monopodial bamboos spread by creeping rhizomes. They will naturally invade and thicken up. They can be very easily propagated by simple cuttings from the rhizomes. It is more difficult to make such cuttings from sympodial bamboo. However, techniques such as soil-layering, air-layering, and branch or culm cuttings are usually successful.

Bamboos do not suffer from a quality-degrading 'edge effect' like trees and so can be grown successfully in single clumps or in dense plantations. Bamboo shoots emerge and grow rapidly, reaching full height (which can be up to 20 m) in 40 days. In China a combination of edible shoot harvesting and respacing is used to keep a density of approximately 2500–3000 stems per hectare. Bamboo culms become mature at 4 or 5 years of age. Bamboo clumps therefore are best managed by selectively cutting the mature culms. Managed in this way, the evergreen canopy is never broken, thus maximizing soil and water conservation values. However, periodic clear-cutting has also been used successfully. Fertilizer and insecticide have been used to increase productivity. Managed conservatively, plants should last until the next flowering cycle, 50–100 years depending on species.

Bamboos have been planted in large-scale plantations; however, much of the 'bamboo seas' prevalent in China have resulted from an intensification of management in east coast monsoon forest scrub, by which farmers have gradually replaced all other species with bamboo.

Palms

In natural forests palms often occupy the poorest sites. Coconut palm lives on the edge of salty, wind-blown oceans. Date palms live in furnace-like deserts. Many palm species are extraordinarily tolerant of tough sites. Silviculture is not therefore usually problematical.

Oil palm From 1967 through to 1997, oil palm was one of the fastest-growing subsectors of the Indonesian economy, increasing 20-fold in planted area and showing a 12% average annual increases in crude palm oil production. The Malaysian oil palm industry has seen unprecedented growth in the last four decades to emerge as the leading agricultural industry in the country. From a mere 55 000 ha in 1960, the area under the crop grew more than 50-fold to 2.82 million ha in 1997. There are now, globally, 5.5 million ha of plantations. Oil palm grows well on desaturated ferrallitic soils of low fertility. Normally, however, the site is substantially, modified by cultivating, weed control, and fertilizing to achieve maximum growth. Oil palm silviculture is the subject of a highly focused and site-specific research effort. In that respect it has more in common with the major forest plantation genera such as *Acacia*, *Eucalyptus*, and *Pinus* than other palm species. Research reports indicate major efforts to control site-specific pests and diseases in monocultural plantations. Considerable effort is being applied to integrated pest management to reduce the use of pesticides. Oil palm cultivation is clearly associated with the destruction of primary or secondary rainforest and raises significant environmental issues.

Rattan Most of the rattan currently harvested comes from naturally occurring plants in tropical rainforests and is not managed silviculturally in any way. Some village communities have evolved indigenous management techniques. Generally, however, even known good practice techniques in cutting, such that the whole plant does not die, are not applied. Rattan can be grown in plantations. As a scrambling climber it does need overhead support. As a plant it also seems to need part shade in order to develop into a vine. There are many reports of it being grown in conjunction with and over other crops, such as old rubber trees. However, the cost of plantation-grown rattan is much higher than naturally grown rattan and the quality is sometimes poorer. Consequently, there is as yet little active silvicultural management. The global management of rattan could be described as in transition from weakly regulated exploitation of a natural resource towards some kind of resource management in the future as natural resources become depleted.

Rattan is usually grown from seeds collected from wild stands. The seeds of some species are slow to germinate, needing many months in specially prepared sandy seedbeds. Nursery technique therefore needs local experimentation and adaptation to be successful.

Coconut The coconut palm grows readily from the nut. It thrives on sandy, saline soils; it requires abundant sunlight and regular rainfall over the year. Coconut can be and is grown in plantations on a range of soils well away from the sea. It is often interplanted with other crops and sometimes with N-fixing crops to reduce fertilizer need.

Date palm The date palm is propagated by seed or offshoots. Seedlings are first planted in nursery rows and later transplanted to their permanent location. Normal healthy trees may produce 10–30 or more offshoots. These will root if their bases are encased in soil. Date palms are planted between 6 and 9 m apart, with one male per 50 or more females. Date palms are sensitive to cold. In early stages, manuring is productive and palms may be intercropped with low crops like barley, pulses, and wheat. When the palms are taller, fruit trees can be intercropped. Pruning of the leaves, artificial pollination, and thinning of the fruits are also recommended. Pollination is helped by placing cut portions of the male flower spikes in the receptive female inflorescence. In Egypt, dates usually flower in February and March, ripening in August and September. Precocious trees may start fruiting at 3 years, but full crops are not usual until 5–8 years old. Old or damaged trees can be rejuvenated by air-layering the top and retransplanting it. Trees may bear for a century or more.

Utilization

Bamboo

Bamboos are used for the widest range of products imaginable. As bamboo tubes they are used as structural members for housing, for water pipes, and for musical instruments. In the split form bamboo is used to make baskets and household containers. Split and made into mats it is further fabricated into plywood. Split and carefully squared, it is made into panels and parquet flooring. As a fiber it is made into fiberboard, paper, and (experimentally) textiles. The shoots are harvested in the spring, cooked and eaten.

There is a very large internal consumption of products in each producing country. There is a substantial trade in bamboo products between countries. World trade is known to be at least US $2 billion per year. Since many products are not identified as being of bamboo in the trade statistics, total trade can only be estimated, but is conservatively thought to be over three times greater. China is the world's largest producer and accounts for approximately half of the world exports. Indonesia, the Philippines, and Vietnam are significant exporters. The EC and USA receive nearly 80% of world imports.

Palms

Palm wine, an important indigenous product, is the fermented sap from numerous species of palm trees. In Ivory Coast, it is extracted from oil palm (*Elaeis guineensis*), borassus palm (*Borassus aethiopum*), and raffia palm (*Raphia hookeri*).

Rattan

The most important product of rattan palms is cane; this is the rattan stem stripped of its leaf sheaths. This stem is solid, strong, and uniform, yet highly flexible. The canes are used either in whole or round form, especially for furniture frames, or split, peeled, or cored for matting and basketry. Other plant parts of some species of rattan – fruits, leaves, roots, and palm heart – are also utilized and contribute to the indigenous survival strategies of many forest-based communities.

However, it is for their cane that rattans are most utilized. Rattan canes are used extensively across their range by local communities and play an important role in subsistence strategies for many rural populations. The range of indigenous uses of rattan canes is vast: from bridges to baskets; from fish traps to furniture; from crossbow strings to yam ties. It is estimated that 80% of the known rattan species is of limited commercial value due to inflexibility and being prone to breakage or possessing other poor mechanical properties, or due to biological rarity.

Coconut Palm

Coconuts are the main product of the coconut palm, and are used as whole fruits or for their parts: fibers, milk, kernel (or flesh), and husk. Coir mats are made out of coconut fiber. World production of coconuts exceeds 50 million tonnes. Indonesia, Philippines, and India between them account for over 70%.

Other parts of this plant are used too, notably its leaves to make baskets and roofing thatch. Apical buds of adult plants are an excellent palm-cabbage and an alcoholic drink known as toddy or palm wine is extracted from its sugar sap, tapped from the flowers.

Raffia

The leaves are the main products. Raffia fiber is used in floriculture and horticulture to make very tough ties, as well as a number of woven articles (mats, baskets, and hats). Raffia is tough yet very flexible and resilient leaf petioles are employed, instead of bamboo, to build houses and make various kinds of furniture. Sago, a kind of flour, is extracted from the stem pith which, before blooming, is extremely rich in starch.

Date

The fruit is the main product. Dates, due to their high sugar content, are the basic food for the people of North Africa, Arabia, and Iran. Hundreds of varieties are grown for commercial purposes. The individual varieties are recognized and prized much in the same manner as wines. Total world production exceeds 6 million tonnes. Egypt, Iran, United Arab Emirates, Saudi Arabia, Iraq, Pakistan, and Algeria (in that order) account for over 85% of world production. A considerable export trade exists to many other countries.

Palm Oil

The seeds are the main product. Prime oil, commercially known as palm kernel oil, is extracted from the seeds, which are first shelled and ground, then hot-squeezed. It is seldom extracted by means of chemical solvents. Oil content per seed ranges between 43% and 51%. This oil is very similar to coconut oil, from which it differs in its higher content of oleic acid; it is solid and buttery below 20°C, yellowish-white in color, pleasantly flavored, and it smells somewhat like coconut.

Palm kernel oil possesses a variable acidity degree, usually not exceeding 15%. It is employed for nutritious purposes as a kind of margarine or vegetable butter, or again as a partially hydrogenated oil; to this end, it is suitably refined and decolorized.

A kind of high-acidity oil, therefore of a purer quality, is extracted from the fibrous flesh of fruits after they have been hot-squeezed. This oil, whose content per fruit ranges between 40% and 70%, is mostly employed in making soaps and cosmetics or as a machinery lubricant.

During the last three decades world production of palm oil has increased from 0.9 million tonnes in 1967 to 17.4 million tonnes in 1997 from 5.5 million ha of plantations. Malaysia produces 50% of world production of oil palm fruit and Indonesia 29%.

See also: **Landscape and Planning**: Landscape Ecology, the Concepts. **Silviculture**: Managing for Tropical Non-timber Forest Products; Natural Stand Regeneration; Treatments in Tropical Silviculture.

Further Reading

Abd-Razak O, Abd-Latif M, Liese W, and Norini H (1995) *Planting and Utilization of Bamboo in Peninsular Malaysia*. Research Pamphlet Forest Research Institute Malaysia. 1995, no. 118. Kuala Lumpur: Forest Research Institute of Malaysia.

Dransfield J and Manokaran N (eds) (1993) *Plant Resources of South-East Asia*, no. 6 *Rattans*. Wageningen, the Netherlands: Centre for Agricultural Publishing and Documentation (PUDOC).

Dransfield S and Widjaja EA (eds) (1995) *Plant Resources of South-East Asia*, no. 7, *bamboos*. Leiden, the Netherlands: Backhuys.

Farrelly D (1996) *The Book of Bamboo: A Comprehensive Guide to this Remarkable Plant, its Uses, and its History.* London: Thames & Hudson.

Hartley CWS (1988) *The Oil Palm*. Harlow, UK: Longman.

Jacquemard JC (1995) *Le Palmier à Huile*. Le Technicien d'Agriculture Tropicale, no. 33. Paris: Editions G-P Maisonneuve et Larose.

Ohrnberger D (1999) *The Bamboos of the World. Annotated Nomenclature and Literature of the Species and the Higher and Lower Taxa*. Amsterdam, The Netherlands: Elsevier Science.

Piggott CJ (1990) *Growing Oil Palms: An Illustrated Guide*. Kuala Lumpur: Incorporated Society of Planters.

Tomlinson PB (1990) *The Structural Biology of Palms*. Oxford, UK: Oxford University Press.

Uhl NW and Dransfield J (1987) *Genera* Palmarum. *A Classification of Palms Based on the Work of H.E. Moore Jr.* 610pp. Lawrence, KS: L.H. Bailey Hortorum and the International Palm Society.

Dipterocarps

B Krishnapillay, Forest Research Institute Malaysia, Kepong, Malaysia

Introduction

The dipterocarp forests of Southeast Asia constitute a dominant and particularly valuable component of the world's tropical rainforest. As a family of plants, Dipterocarpaceae may perhaps hold the distinction of being the best-known trees in the tropics. Their ecosystems are extremely diverse. They are uneven in their age and multilayered. They grow all the year round under warm temperatures and on sites where there is a large amount of rainfall. However, those growing in the seasonal forest are generally medium sized with the tallest trees being around 20 m with a maximum diameter of about 50 cm. Generally dipterocarps have been observed to occur on soils with very low fertility. Currently the dipterocarps dominate the international tropical timber market, and therefore play an important role in the economy of many Southeast Asian countries. In addition to timber, this family of trees also produces other non-timber products like resins and oleoresins.

Distribution

The present distribution patterns of dipterocarps are thought to reflect routes of colonization and past climatic conditions. They are distributed over the tropical belts of three continents of Asia, Africa, and South America (**Figure 1**). They occupy several phytogeographical zones that mainly conform to climatic and ecological factors. However, in Southeast Asia the Wallace line, which runs east of Philippines and between Borneo and Celebes, is a major phytogeographic boundary for dipterocarps. This phenomenon cannot be explained in terms of climatic differences but requires the intervention of continental drift.

Worldwide there are about 16 genera and about 580 species in the family. Seven main phytogeographical regions are classically recognized within this distribution area

1. Malesia, which constitutes Peninsular Malaysia, Sumatra, Java, lesser Sunda Islands, Borneo, Philippines, Celebes, the Moluccas, New Guinea and the Bismarks. The northern frontier of Peninsular Malaysia delimits this part.
2. Mainland Southeast Asia, which includes Burma, Thailand, Cambodia, Laos, Vietnam, and South China.

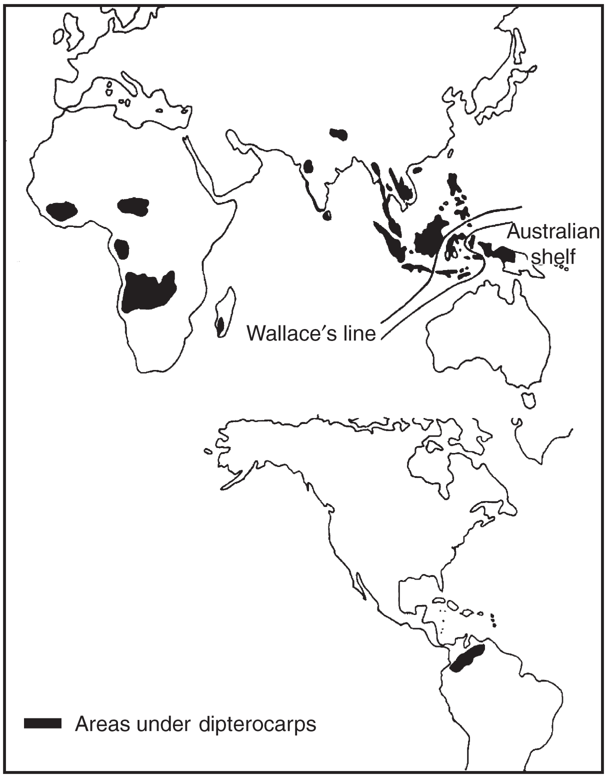


Figure 1 Phytogeographical distribution of the family Dipterocarpaceae worldwide.

3. South Asia, which constitutes India, the Andaman Islands, Bangladesh, and Nepal.
4. Sri Lanka.
5. The Seychelles.
6. Africa, which constitutes Madagascar, a narrow strip from Mali to Sudan in the northern hemisphere, and Congo.
7. South America, which constitutes Araracuara (Colombia), Venezuela, and Guyana.

The South American region corresponds to Guyana, Venezuela and part of the Colombian Amazon, which overlies the Guyana shield. The African region includes a continental area and an insular part in Madagascar. The Asian region corresponds to the Indo-Malesian area, which concentrates a high number of genera and species in the equatorial forest. This area is limited northward by the Himalayan foothills, then approximately by the borders of Assam, Arunachal Pradesh, Burma, Laos, and Vietnam and penetrating into South China including Hainan Island. On the extreme southwest the large belt of Asian dipterocarps reaches the Seychelles and covers India and Sri Lanka. Its eastern border corresponds to New Guinea. The Sundalands delimit the most southern part. No dipterocarp species are found in Australia.

In Asia, dipterocarps occupy a large variety of habitats. They are found from the coast to the inland, from riverine to swampy conditions. They occur on dry land on undulating to level terrain, on ridges, on slopes, in valley bottoms, on soils that are deeply weathered and shallow, from well drained to poorly drained conditions, and both on soils rich or poor in nutrients. This to a great extent shows the wide versatility of the species in terms of its ecology. In Peninsular Malaysia the altitudinal zonation of their main habitats types ranges from 0–300 m (known as lowland dipterocarp), 300–750 m (called hill dipterocarp forest), and 750–1200 m (known as upper dipterocarp forests).

The freshwater swamps, especially in drier parts, are rich in the species while in the true peat swamps occurrence is relatively poor. The dipterocarp flora is also poor on limestone and riverine fringes. Asian dipterocarps are limited altitudinally by climatic conditions and the conjunction of altitude and other natural barriers, such as large rivers and watersheds. These have obstructed the distribution of species in Borneo. For example the northwest and northeast of Kalimantan, Sarawak, Brunei, and Sabah are much richer in species than the rest of Kalimantan. The ever-wet areas are also richer in species than the seasonal ones as seen in Sri Lanka by the concentration of species in the southwest quarter, or in the Thai–Malaysian transition belt or from Java to the lesser Sundas.

The genera and species in Asia show much greater diversity compared to Africa and South America. As expected the higher numbers clearly occur in the ever-wet regions. **Table 1** shows the number of genera and species found in the different phytogeographical regions.

Ecological Distribution

For clarity in understanding the ecosystem of dipterocarps, the well-illustrated description from Peninsular Malaysia is referred to in this text. In the other parts of Asia, the ecological conditions are somewhat similar and with very minor variations. The ecosystems in which dipterocarp species are distributed can thus be divided into the following categories based on the altitude and forest type in which they occur.

Table 1 Distribution of genera and species of dipterocarps according to the seven phytogeographical regions

Phytogeographical region	*Number of genera*	*Number of species*
Malesia	14	465
Mainland Southeast Asia	8	79
Sri Lanka	7	45
South Asia	9	58
Seychelles	1	1
Africa and Madagascar	3	49
South America	1	1

The Lowland Dipterocarp Forests

These can also be classified as lowland evergreen rainforest formation. The bulk of the exploitable forests are in this category, which embraces all the well-drained primary forests of the plains, undulating land, and foothills up to about 300 m altitude. In most localities the dipterocarps form a high proportion of the emergent and dominant strata of the forest. Exceptionally, dipterocarps may be almost absent, while occasionally, over small areas, they may be so abundant that large trees of other families are few and scattered. In these lowland dipterocarp forests about 130 species of dipterocarps, representing all the main groups, occur. In any one forest reserve there may, exceptionally, be as many as 40 species, but between 10 and 30 is a more usual number. In most lowland reserves *Shorea* is represented by two or three species, and is the most conspicuous woody component of the forest. Usually one or two species of *Dipterocarpus* are also present.

The Hill Dipterocarp Forests

These too can also be classified as a lowland evergreen rainforest formation. They are the climax vegetation of the altitudinal zone immediately above the lowland dipterocarp forests. On inland ranges the altitudinal limits are approximately 300–750 m, but on isolated mountains, or on coastal ranges, this zone may be depressed to much lower altitudes. The lines delimiting the hill dipterocarp forests cannot be drawn strictly along the topographical contours; they descend the ridge and ascend the valleys, and the lower limit may range between 150 and 450 m on the same hill system.

The main difference between the hill dipterocarp forests and the lowland dipterocarp forests is in specific composition of the dominants of the upper strata of the vegetation. There is usually a slight diminution in size of the larger trees accompanied by a slight increase in number per unit area on ridge tops and towards the upper limits of the hill dipterocarp forests. Many of the lowland dipterocarps are represented in the hill forests, although they become scarce towards the upper limits of these forests, but many species appear in the hill forests that never, or only very exceptionally, occur in the lowland forests. Predominant among these is *Shorea curtisii*, one of the *Shorea* group that tends to be gregarious on ridges; it is readily distinguished in the forest, and is a useful indicator of hill dipterocarp forest. Where this species is abundant the light-colored crowns of the *S. curtisii* trees mark the hill dipterocarp forest zone as a blue–gray band along the mountainsides.

In these forests all the main dipterocarp groups, except perhaps *Dryobalanops* and *Pentacme*, are represented. At the lower levels of the zone, where many of the lowland dipterocarps still persist, the forests are the richest both in species and volume of dipterocarps. Beyond the limits of the lowland species the number of dipterocarp species represented is usually less per unit area than in the lowland forests, although *Vatica* is usually better represented. This reduction in species, however, is often more than offset by the greater number of individuals, thus fully maintaining the predominance of the dipterocarps in these forests.

In the hill dipterocarp forest zone on coastal hills, or on hills that the geologically recent recession of the sea has rendered inland, several dipterocarps are represented, which are absent or rare on ranges remote from the sea, for example, *Shorea glauca*, *S. lumutensis*, *S. gratissima*, *Dipterocarpus rotundifolius*, *D. penangianus*, and *Cotylelobium malayanum*. These hill forests too represent a great potential wealth.

The Upper Dipterocarp Forests

These are also classified as tropical lower-montane evergreen rainforest subformation, which is a transition zone between the tropical lowland evergreen rain forest and the tropical upper montane rainforest of the higher mountains. This is the zone into which the hill dipterocarp forests blend. It is represented only on the higher mountains, the altitudinal limits being approximately from 750 to 1250 m altitude on inland ranges, but on isolated mountains or coastal ranges, where the vegetation zones tend to be depressed and telescoped, it may be represented by a narrow belt lying between 600 and 900 m altitude.

There is a marked difference in floristic composition of the vegetation as one passes from the hill dipterocarp forests into the upper dipterocarp forests. Almost all the lowland forms are absent and the montane forms, which predominate in the next highest zone, become more and more in evidence. The dipterocarps are represented by only a few species, but these are so characteristic, and sometimes so abundant in these forests, that it is desirable to recognize a separate forest zone of which they are the chief indicator species. The predominant, typical species is *Shorea platyclados*. However, *S. ovata*, *S. ciliata*, *S. submontana*, *Hopea montana*, *Dipterocarpus retusus*, *D. costatus*, and *Vatica heteroptera* are also characteristic. These forests are mainly of value for soil protection, but limited areas rendered accessible by the roads to hill stations may produce commercial timber.

The Montane Oak Forests

These forests can also be classified as tropical lower-montane evergreen rainforest subformation. The upper dipterocarp forests form the lower levels of this subformation, and the montane oak forests the upper. The altitudinal range of the montane oak forests is usually between 1050 and 1500 m. These altitudes are above the normal range of dipterocarps.

Peat Swamp Forests

These are classified as tropical woodland formations but they are most closely allied to the tropical freshwater swamp forest. They belong to a vegetative formation that occupies vast alluvial flats along the northwest and southwest coasts of Borneo, around the coasts of the Rio and Lingga archipelagos, on the east coast of Sumatra, and on the west, and to some extent the east coast of Peninsular Malaysia. All the chief timber-producing families of the lowland dipterocarp forests are represented in the peat swamp forests, but the number of species of each is comparatively small. These species are, with very few exceptions, entirely different from any found on dry land, but most of them are widely distributed throughout the peat swamps. Dipterocarps are important components of the peat swamp forests. The number of species is small, but they show a marked gregarious tendency and frequently form a high proportion of dominant and emergent trees of the forest. Species like *Shorea albida*, *S. rugosa*, *S. teysmanniana*, *Anisoptera marginata*, *S. platycarpa*, *S. dealbata*, *Dipterocarpus coraceus*, *D. chartaceus*, *Hopea resinosa*, *H. mengarawan*, and *Vatica wallichii* are commonly found in this habitat.

Riparian Fringes

The narrow strips of vegetation found along, and characteristic of, river courses are regarded here as riparian fringes. These have also been classified as tropical riparian woodland formation, but it is perhaps more appropriate to regard them as a series of edaphic formations zoned from river mouth to source. A constant supply of telluric (rising from the soil) moisture is the predominant edaphic factor, while the zones are determined mainly by the incidence of tidal influence, width of stream, rate of flow, and altitude. At the mouth of a stream, the first zone, which is under saline influence, is inhabited mainly by mangrove swamp species. Further upstream a transition zone occurs, which is still under tidal influence but in which the water is mainly fresh. This riparian zone is not normally inhabited by dipterocarps, but *Vatica wallickii* has been reported to occur towards its upper limits. Beyond tidal influence there is a pronounced change in specific composition of the riverbank flora. Many of the species are particularly adapted to this riparian habitat. Some have narrow leaves to reduce resistance to flood water, the so-called stenophyllous plants, while some have fruits specially adapted for dissemination by water or capable of germinating and establishing themselves under water. Several dipterocarps are characteristic of these communities. The best known and most abundant is *Dipterocarpus oblongifolius*, but in the same category *Shorea sumatrana*, *S. palembanica*, and *Hopea odorata* could also be placed. The gnarled trunks of these trees overhang the streams, forming what have been called gallery forests. The following species also frequently occur in this zone of riparian vegetation, but they are less characteristic of the differentiated riparian fringe than of any damp soil in the vicinity of streams or of land subject to periodic inundation. These would include *Shorea assamica*, *S. macrantha*, *S. hemsleyana*, *Hopea kelantanensis*, *H. mengarawan*, *H. sangal*, *Dryobalanops oblongifolia*, *Vatica bancana*, *V. lobata*, and *V. wallichii*. The upper reaches of the larger rivers are in the montane forest zone and no dipterocarps are represented in the riparian fringes.

Heath Forests

In Borneo there are large areas of lowland primary forest to which the provisional name 'heath forest' has been applied. These forests are an edaphic climax type, developed on pale, light-textured, acid sandy soils that seem to resemble a European podsol. *Shorea glauca* occurs gregariously in this forest type. The only dipterocarps in addition to *S. glauca* found in this zone are *Hopea semicuneata* and *Vatica odorata*.

Limestone Rocks

The limestone rocks, which are such a striking feature of the Asian landscape, bear a very different vegetation from that of the surrounding forest. This vegetation contains a calciphilous, or chalk-loving, element, as well as a cremnophilous, or cliff-dwelling element. The small trees and shrubs that dominate this vegetation can mainly be classed in the latter category. It has been stated that dipterocarps shun chalk, and it is true that they are absent from most of the limestone hills. This is probably because xerophyllous, adaptable dipterocarps have lacked access to them. On the limestone hills of Langkawi, Perlis, and the north of Kedah in Peninsular Malaysia, several dipterocarps, that have adapted and that withstand seasonal desiccation in territories to the north, have established themselves. These are *Hopea ferrea*, *Pentacame siamensis*, *Shorea talura*, and *Vatica cinerea*. All these species are also the inhabitants of the semi-evergreen or moist deciduous forests of Burma and Thailand. All these species occur also on soils other than limestone, but *H. ferrea* seems to show a distinct preference for limestone, or perhaps it would be more correct to say that it is unable to maintain itself in competition with other species except on limestone.

BRIS Formations

This is the name adopted to describe a type of vegetation that is occasionally found on the coasts of Borneo, Sumatra, the Malay Peninsula, and the intervening islands. BRIS is the abbreviation for Beach Ridges Interspersed with Swales. These BRIS formations are stretches of white sand, deposited by a combination of river and tidal action. They are most common immediately behind the beaches, but the older formations may occur inland as islands among more recent and dissimilar alluvial deposits. The vegetation of these areas is typically sparse grassland, interspersed with shrubs, among which *Rhodomyrtus tomentosa* is usually conspicuous, and solitary or grouped, small, frequently gnarled, dwarfed trees. Two species of dipterocarps have been reported to grow in such sandy formation. These include *Shorea talura* and *Cotylelobium* sp.

The Family of Dipterocarps

The family of dipterocarps contains 16 genera and 580 species. The genera have further sections and subsections. Details up to the section level are given in **Table 2**, which shows that there is a largely discrete distribution of this family in the neotropics, Africa, and Asia.

Non-Timber Products

Production of oleoresins is characteristic of most members of the family. The volatile portion consists mainly of sesquiterpenes that are used for caulking and varnish. Also, the fruits of many *Shorea* and sometimes *Dryobalanops* are boiled as vegetables. The fruits of *Shorea* section *Pachycarpae* and some others are rich in fat. The seeds contain up to 70% fat, which is similar to cocoa butter but has a higher melting point and is favored for manufacturing

Table 2 Genera and sections of the family Dipterocarpaceae

Genus	*Section*
Hopea	*Hopea*
	Dryobalanoides
Neobalanocarpus	—
Shorea	*Shorea*
	Richetioides
	Anthoshorea
	Mutica
	Ovalis
	Neohopea
	Rubella
	Brachypterae
	Pachycarpae
	Doona
	Pentacame
Parashorea	
Dryobalanops	
Dipterocarpus	
Anisoptera	*Anisoptera*
	Glabrae
Upuna	
Cotylelobium	
Vatica	*Sunaptea*
	Vatica
Stemonoporus	
Vateria	
Vateriopsis	
Monotes	
Marquesia	
Pakaraimaea	

chocolates and cosmetics. Camphor is another product from dipterocarps especially from *Dryobalanops*, which is used as incense (*see* **Non-wood Products**: Resins, Latex and Palm Oil).

Diversity and Conservation in Dipterocarps

Chromosome number is one of the genetic mechanisms responsible for diversification at intraspecific and specific levels. It has been found that dipterocarp species and genera are remarkably uniform with respect to chromosome number. Polyploid species are known only in two genera, namely *Hopea* and *Shorea*, while aneuploidy has been observed only in the genera *Anisoptera* and *Dipterocarpus*. These two ploidy levels assist in diversification at the species level. Breeding systems is another primary determinant of the pattern of genetic diversity in natural populations of dipterocarps. Studies indicate that in this family self-incompatibility exists in a large number of the species and hence most of these species are outcrossers. This mechanism provides the populations to have a high level of genetic diversity (*see* **Genetics and Genetic Resources**: Genetic Systems of Forest Trees).

Concerning conservation, as exploitation of these species for timber has been going on at a rapid phase in the Asia-Pacific regions, national governments have come to the realization that conservation of samples of relatively intact forest is necessary for balanced land use. National parks and other forms of protected area are some of the most universally adopted mechanisms for conservation of the species in this family (*see* **Ecology**: Biological Impacts of Deforestation and Fragmentation).

Conclusion

As can be seen the dipterocarps form an intricate part of the natural forest system in the tropics. The family exhibits a wide variation of characteristics in its growth and occurrence over a range of habitats.

As a forest ecosystem, the dipterocarp forests are a habitat for hundreds of thousands of animal and plant species that form an intrinsic network of interactions. The question being asked all over the world is whether such a complex ecosystem can tolerate anthropogenic disturbances such as timber extraction. However, to date there is still no clear answer to the long-term effects of logging of such forest on species diversity and continued sustenance of such an ecosystem. There is an urgent need to quickly bridge these gaps in knowledge to ensure that this natural treasure so vital to the well being of our planet is conserved and sustainably used to ensure perpetuity of these valuable resources.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation. **Genetics and Genetic Resources**: Genetic Systems of Forest Trees. **Non-wood Products**: Resins, Latex and Palm Oil. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Dry Forests; Tropical Montane Forests.

Further Reading

Appanah S and Weinland G (1993) *Planting Quality Timber Trees in Peninsular Malaysia*. Malayan Forest Record no. 38. Kepong, Malaysia: Forest Research Institute Malaysia.

Appanah S and Turnbull JM (1998) *A Review of Dipterocarps: Taxonomy, Ecology and Silviculture*. Bogor, Indonesia: Centre for International Forestry Research.

Ashton PS (1964a) *Ecological Studies in Mixed Dipterocarp Forest of Brunei State*. Oxford Forestry Memoirs no. 25. Oxford, UK: Oxford University Press.

Ashton PS (1964b) *A Manual of Trees of Brunei State*. Oxford, UK: Oxford University Press.

Ashton PS (1982) Dipterocarpaceae. *Flora Malesiana*, Series I (9): 237–552.

Ashton PS (1990) Dipterocarpaceae. In: Dassanayake MD and Fosberg FR (eds) *A Revised Handbook to the Flora*

of Ceylon, vol. 1, pp. 364–423. Washington, DC: Smithsonian Institution Press.
FAO (1985) *Dipterocarps of South East Asia*. RAPA Monograph no. 1984/85. Bangkok, Thailand: Food and Agriculture Organization. Regional Office for Asia and the Pacific.
Jordan CF (1985) *Nutrient Cycling in Tropical Forest Ecosystems*. New York: John Wiley.
Jordan CF (1994) Ecology of tropical forest. In: L Pancel (ed.) *Tropical Forestry Handbook*, vol. 1, pp. 165–197. Berlin, Germany: Springer-Verlag.
Kostermans AJGH (1985) Family status for the Monotoideae and the Pakaraimoideae, Dipterocarpaceas. *Taxon* 34: 426–435.
Kostermans AJGH (1992) *A Handbook on the Dipterocarpaceae of Sri Lanka*. Colombo, Sri Lanka: Wildlife Heritage Trust of Sri Lanka.
Krishnapillay B (2002) *A Manual for Forest Plantation Establishment in Malaysia*. Malayan Forest Records no. 45. Kepong, Malaysia: Forest Research Institute Malaysia.
Meijer W and Wood GHS (1964) Dipterocarps of Sabah (North Borneo). In: Sabah Forest Department (ed.) *Sabah Forest Records* no. 5, pp. 1–344. Sandakan, Borneo: Sabah Forest Department.
Schulte A and Schone D (eds) (1996) *Dipterocarp Forest Ecosystem: Towards Sustainable Management*. Singapore, Malaysia: World Scientific Publishing.
Smitinand T, Santisuk T, and Phengklai C (1980) The Manual of Dipterocarpaceae of mainland South-East Asia. *Thani Forestry Bulletin of Botany* 12: 1–137.
Smitinand T, Vidal JE, and Pham HH (1990) Dipterocarpaceae. *Flore du Cambodge du Laos et du Vietnam* 25: 3–112.
Symington CF (1943) *Foresters' Manual of Dipterocarps*. Malayan Forest Record no. 16. Kuala Lumpur, Malaya: Forest Department.
Whitmore TC (1975) *Tropical Rainforest of the Far East*. Oxford, UK: Clarendon Press.
Wyatt-Smith J (1963) *Manual of Malayan Silviculture for Inland Forests*, vol. 1. Malayan Forest Record no. 23. Kuala Lumpur, Malaya: Forest Department.

Eucalypts

R J E Wiltshire, University of Tasmania, Tasmania, Australia

Eucalypts and the Australian Vegetation

Eucalypts are remarkably prevalent in the woody vegetation of Australia, dominating an estimated 127 million ha of forest, comprising nearly all vegetation types in Australia (302 communities) and occurring as codominants in a further 30 communities, with the exceptions of rainforest, the vegetation of the central arid zone, and higher montane regions. This natural distribution includes a wide variety of habitats from sea level to the alpine treeline, from the tropics to below 43° S latitude. Although this natural distribution is almost exclusively confined to Australia (except for a handful of tropical species to the north), eucalypts have been introduced to more than 90 countries where they have a multitude of uses, including industrial plantations conservatively estimated at 9.5 million ha in area (*see* **Tree Breeding, Practices**: Genetic Improvement of Eucalypts).

The genus *Eucalyptus* (family Myrtaceae) was named in 1788 by Charles-Louis L'Heritier de Brutelle, from a specimen of *E. obliqua* collected in 1777. Since then over 700 species have been recognized, derived from 13 main evolutionary lineages. The current taxonomic status of the eucalypts is still debated, especially the inclusion of the bloodwoods (*Corymbia* and *Angophora*) within *Eucalyptus*, or as separate genera (*see* **Tree Breeding, Practices**: Genetic Improvement of Eucalypts).

Eucalypts are highly variable in form, ranging in habit from forest trees, generally of between 30 and 50 m in height, but in some species more than 70 m (*E. deglupta*, *E. diversicolor*, and *E. grandis*, with the tallest flowering plant in the world *E. regnans* approaching 100 m in height), to woodland trees 10–25 m high, largely single-stemmed but spreading, to mallees that are multistemmed from the ground level, usually less than 10 m in height, and to some eucalypts that grow as shrubs less than 1 m in height, such as the subalpine yellow gum *E. vernicosa*.

Classifications of Eucalypt Forests in Australia

Most classifications of Australian vegetation are derived from Specht's structural classification, based on the life form and height of each stratum and the foliage cover of the tallest stratum. Eucalypts are not a major component of the closed forests (tropical and temperate rainforests) that comprise 3% of the Australian forest, but do dominate an estimated 78% of the forested area in Australia (from the most recent estimates of the National Forest Inventory or NFI). The NFI classification includes four broad classes of eucalypt forest: tall, medium, and low eucalypt forest, and mallee (**Figure 1**).

Tall Eucalypt Forests (Tall Open Forests)

Tall eucalypt forests (tall open forests or wet sclerophyll forests in previous classification schemes) are those that exceed 30 m in height with a projected foliage cover of 30–70%. These forests occupy

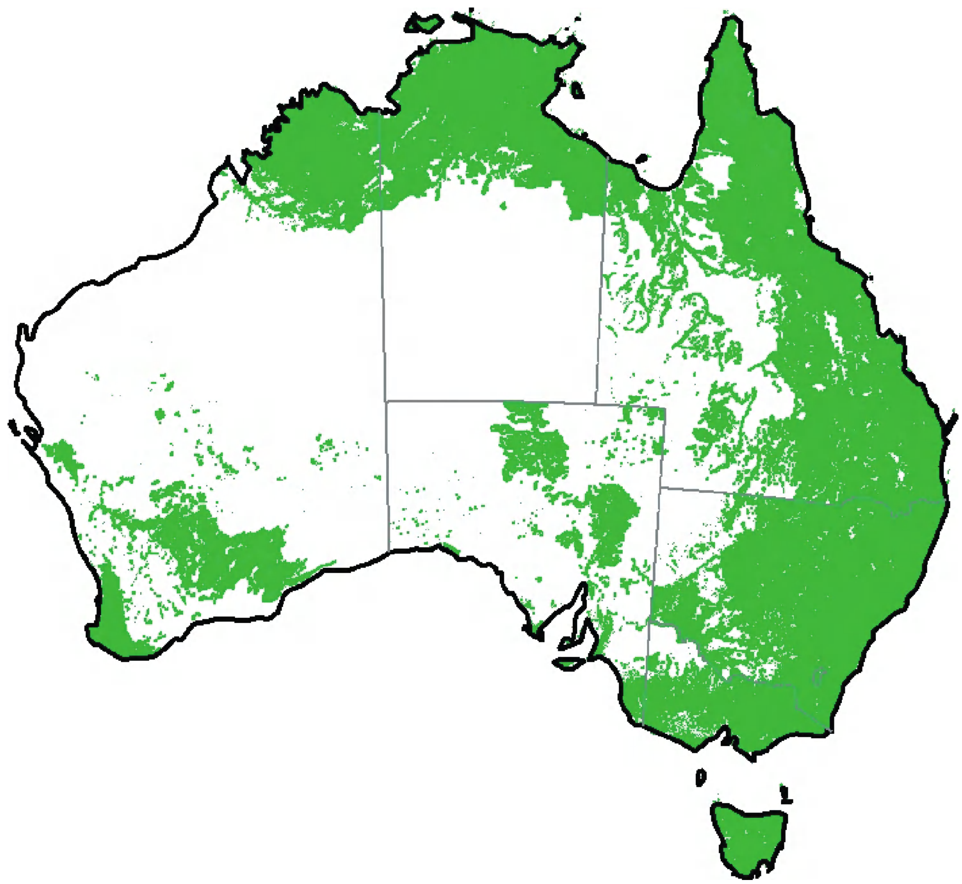


Figure 1 The distribution of eucalypt forest Australia (National Forest Inventory 2003).

8.7 million ha (5% of the total forest area) in Australia and can be extremely productive, with mean aboveground biomass estimates of 492 t ha^{-1} for *E. regnans*. One estimate of standing merchantable volume of 60-year-old unstocked, unthinned stands of *E. regnans* in Victoria was 839 m^3 ha^{-1}. These forests reach their greatest heights (>70 m) in areas of relatively high rainfall (>1000 mm year^{-1}) on soils of reasonable fertility in southeastern Australia (Victoria and Tasmania) and in the karri forests of southwestern Australia.

The understory vegetation in the southeastern tall forests is comprised of mesomorphic shade-tolerant trees such as *Bedfordia salicina* and *Olearia argophylla* (Asteraceae), *Pomaderris apetala* (Rhamnaceae), and some *Acacia* species (e.g., *A. dealbata* and *A. melanoxylon*). Beneath this layer, light is extremely limited and the vascular plants are restricted to tree ferns (*Cyathea* spp. and *Dicksonia antarctica*) and groundcover ferns (such as *Blechnum*, *Histiopteris*, and *Hypolepis*). The understory of the southwestern karri (*E. diversifolia*) forests lacks the tree ferns and the closed forest species, with the dominant understory species often more scleromorphic shrub species of the Rhamnaceae (*Acacia*); Casuarinaceae (*Allocasuarina*); Myrtaceae (*Agonis*); Proteaceae; (*Banksia*, *Persoonia*); Rutaceae; and Fabaceae.

These tall open forests are often comprised of a single cohort of eucalypts (**Figure 2**), recruited after a devastating fire. In an elegant model proposed by Gilbert in 1959, eucalypt tall forest can be viewed as a disclimax vegetation type, dependent on disturbance by fire within the lifespan of the dominant species (350 years). *Eucalyptus regnans* in southeastern Australia, for instance, is killed by wildfire but releases vast numbers of seed (perhaps more than 1 million ha^{-1}) into an ash-enriched seedbed devoid of competitor species, except for soil-stored seeds, such as *Acacia* species, and seed dispersed from adjacent unburnt areas. There is intense competition between individuals as the density decreases from a reported count of 494 000 seedlings ha^{-1} to 400 stems ha^{-1} at 40 years to as few as two trees ha^{-1} 350 years after fire. Seedling establishment is virtually impossible for eucalypts beneath the light-limited conditions of the dense canopy and is restricted to very shade-tolerant rainforest species. Consequently, there is a successional transition from the eucalypt dominants over an understory of short-lived (<100 years) *Acacia* species, to a forest of

Figure 2 Tall open forest (wet sclerophyll) with even-aged *Eucalyptus regnans* over *Acacia* spp. *Bedfordia*, and *Pomaderris*. Sandspit Reserve, Tasmania.

emergent eucalypts (perhaps 70 m in height) over a canopy of shade-tolerant rainforest species (such as *Nothofagus cunninghamii*) if fire is excluded from the community for more than 150 years. If 350 years elapse without fire, the eucalypts senesce and the community becomes a closed forest or cool temperate rainforest. In Tasmania, these transitional forests (**Figure 3**) are termed 'mixed forest' by foresters, to distinguish them from the politically sensitive 'cool temperate rainforest,' although environmental groups have countered with the term 'old-growth forests.' Therefore, it has become a largely political argument whether such forest should be classified as 'eucalypt with rainforest understory' or 'rainforest with eucalypt emergents,' while the reality is a transitional form between the eucalypt forest and rainforest.

Medium-Height Eucalypt Forests

Medium-height eucalypt forests are those ranging between 11 and 30 m in height. The NFI estimates there are 83 million ha of medium eucalypt forest, or 51% of the total forest cover. Most of these forests are woodlands (64%), where the crowns of the trees do not touch, the canopy is very open, and there is often a significant grassy understory, so that in the past they have often been described as 'savanna'. These forest types contain about 80% of all eucalypt species and occur in four main areas: (1) the warm temperate southwest; (2) a broad band across tropical northern Australia; (3) subtropical and warm temperate eastern Australia; and (4) cool temperate southern Australia. The NFI has classified these medium-height woodlands on the basis of the understory: tall, low, or grassy.

Medium-height woodlands with tall understories These communities extend across northern Australia and occur inland in the east and southeast of the continent. Depending on whether the forests are in the northern or temperate regions, the understory includes palms (*Livistona*) and cycads or sclerophyllous shrubs such as acacias, banksias, and casuarinas. In the temperate regions, the natural distribution of these forests has been severely reduced by clearing for agriculture and most only exist as remnant patches in an agricultural landscape. In southern Queensland, central New South Wales, and northern

Figure 3 'Mixed forest' or tall open forest *Eucalyptus regnans* over a rainforest understory. Tahune Forest Reserve, Tasmania.

Victoria, they occur in dry areas (400–600 mm annual rainfall) and are often referred to as box and ironbark woodlands.

Medium-height woodlands with low understories These communities have also been extensively cleared in the Western Australian wheatbelt, where the jarrah (*E. marginata*) forest gives way to *E. wandoo* (wandoo) that may be 12–18 m tall and *E. salmonophloia* (salmon gum) woodlands that may reach 30 m in areas that receive little more than 200–300 mm rainfall annually. In the east, *E. largiflorens* often dominates the areas bordering the floodplains of the Murray Darling basin. In addition to a sclerophyllous shrub understory, these woodlands often have a succulent saltbush (Chenopodiaceae) understory.

Medium-height woodlands with grassy understories The grassy understory woodlands have undergone considerable floristic change in many areas due to the combined effects of grazing by introduced animals, altered fire regimes, nutrient enrichment, and plant species introductions. The understory of some *E. melliodora* (yellow box) woodlands of the southern tablelands of New South Wales, for example, is now composed nearly entirely of species of Mediterranean origin, due to the intense grazing pressure.

About one-quarter of the medium-height forests have a dense canopy. Like their sparse-canopy (woodlands) counterparts, these forests have been classified by the NFI into three types depending on the height and nature of the understory.

Medium-height open forests with a tall sclerophyllous understory These forests occur where annual rainfall is between 600 and 1000 mm. Understory components tend to be similar to those in medium-height woodlands with a tall understory.

Medium-height open forests with a low understory This vegetation type is often called 'dry sclerophyll' to differentiate them from 'wet sclerophyll' or tall eucalypt forests. The 'dry sclerophyll' refers to the often xeromorphic leaf type of the understory species, by comparison with the broader, softer leaves of the taller forests. These forest types are also 'dry' in that they usually occur in areas receiving less than 600 mm of rain a year, and on poorer soils, and are widespread throughout temperate Australia, although small areas also occur in the tropics.

Medium-height open forests with a grassy understory Grassy understory may develop on more fertile soils. These types of forest occur predominantly in north-east New South Wales and eastern Queensland. Smaller areas also occur on soils derived from igneous substrates in Tasmania, on the floodplains of the Murray River (in the form of *E. camaldulensis* forests), and in tropical Australia.

Low Eucalypt Forests

22 million ha of forest, or 14% of total forest cover, is nonmallee eucalypt forest less than 10 m tall. Most of these forests occur in arid regions in association with *Acacia* species. Generally they contain a similar range of eucalypt species to that in adjacent medium-height forests, including *E. baxteri* in South Australia, *E. populnea* and *E. largiflorens* in western New South Wales, *E. populnea* in southern Queensland, and *E. alba*, *E. brevifolia*, *E. miniata*, and *E. tetradonta* in northern Queensland, the Northern Territory, and the Kimberley region of Western Australia. Low eucalypt forests also occur in the subalpine regions of New South Wales, Tasmania, and Victoria. The best known of these are the subalpine snow-gum forests of Tasmania and the Snowy Mountains in southeast Australia *(E. coccifera* and *E. pauciflora,* respectively).

Mallee

Mallee is a unique type of vegetation consisting of low-growing, multistemmed eucalypts generally 2–10 m tall, with a low canopy coverage. These even-sized stems arise from a large lignotuber, or mallee root, after the crown is killed by fire, drought, or herbivore damage. Over 100 species of eucalypt have a mallee form, with the greatest number occurring in Western Australia. Mallee forests have a wide distribution across the south of the continent (about 15 million ha or 9% of Australia's forests), primarily in regions with 250–400 mm of rain a year. South Australia has 40% of Australia's mallee forests. A further 32% are found in Western Australia and the remainder mostly occurs in southwest New South Wales and northwest Victoria. In more arid areas, mallee is usually replaced by acacias and at the upper rainfall limit by single-stemmed forms, sometimes of the same species. Mallee understories may include hummock grasses, sclerophyll shrubs, and semisucculent shrubs.

Ecological Processes Controlling Distribution

Nutrient Availability

The Australian continent is a very old landscape, produced by extensive erosion and weathering, with exposed portions of the Precambrian shield (600–400 million years ago) strongly influencing the western two-thirds of the continent. Due to tectonic stability, there has been little rejuvenating activity since the beginning of the Tertiary, about 60 million years ago, except volcanic activity during the Oligocene along the eastern and southeastern ranges, and glaciations in the southeast and Tasmania during the Pleistocene. Many of the parent materials are sedimentary and so have undergone one or more cycles of weathering and erosion. The smaller-size fractions of the soil, most closely associated with nutrient elements, are lost during these processes. Consequently, the soils in Australia are generally very low in nutrients, particularly phosphorus and nitrogen, but also sulfur and potassium, and the trace elements molybdenum, copper, zinc, boron, and manganese. The average P concentration in Australian soils is 0.03%, but can be as low as 0.003%, compared with a range of 0.04–0.09% for soils in North America (**Table 1**).

Table 1 Nutrient pools in some eucalypt ecosystems in Australia: chemical content in soil 0–100 cm depth

Annual rainfall (mm)	*Parent material*	*Eucalypt community*	*N ($g\,m^{-2}$)*	*P ($g\,m^{-2}$)*	*Ca ($g\,m^{-2}$)*	*Mg ($g\,m^{-2}$)*	*K ($g\,m^{-2}$)*
330	Quaternary alluvium	Tall woodland	1490	740	4530	1140	450
380	Quaternary alluvium	Tall woodland	680	870	3420	1450	840
635	Siltstone	Low woodland	880	170	1380	2020	460
1090	Sandstone	Forest	600	320	300	220	60
1575	Shale	Tall forest	1370	230	40	80	40
1625	Sandstone	Forest	350	110	120	120	70
2135	Basalt, colluvium	Alpine woodland	1620	4920	100	30	60

Reproduced, with permission, from Keith H (1997) Nutrient cycling in eucalypt ecosystems. In: Williams JE and Woinarski JCZ (eds) *Eucalypt Ecology: Individuals to Ecosystems*, pp. 197–226. Cambridge, UK: Cambridge University Press.

Climate

The broad floristic and structural distribution of eucalypt communities is strongly influenced by climate but, within a climatic region, soil nutritional properties (nutrients, soil moisture, aeration, and root penetration) and topography (elevation, aspect, and slope) strongly influence local patterns of distribution of eucalypt species. These factors are interrelated. For example, on a uniform granitic parent material, the vegetation in wetter forests of southeastern Australia may vary from cool-temperate rainforest in gullies, to wet sclerophyll forest on southerly aspects, to dry sclerophyll forest on the warmer, drier northerly aspects. The deeper soils of the rainforest and wet sclerophyll forests may have twice the P content of the dry sclerophyll forest topsoil because of the warmer microclimate and increased weathering of the parent material, and greater erosion associated with more frequent fires.

Eucalypts and Fire

Fire is an integral part of the Australian environment and has played a pivotal role in shaping the forest ecosystems, greatly expanding the range of eucalypts across the continent. Even prior to the arrival of humans in Australia (an estimated 60 000 years ago), eucalypts were an extensive part of the forest vegetation, especially in the arid and semi-arid areas with a high incidence of lightning strikes. With extensive use of fire by the indigenous Australians (for hunting and the creation of specific vegetation types), eucalypt forests have expanded further at the expense of other forest types, such as tropical rainforest, cool temperate rainforest, cypress pine (*Callitris* spp.), *Casuarina* spp., and araucarias.

The arrival of Europeans with their different attitudes to the use of fire have led to further changes to the Australian landscape, as farmers and graziers used fire to clear bush and stimulate grass regrowth; miners used fire to clear vegetation indiscriminately while prospecting; and foresters have used frequent, low-intensity fires for hazard reduction to protect timber resources. The use of fuel reduction burning regimes is currently widespread throughout Australia, not only by forestry agencies, but also by nature conservation bodies, local councils, and private property owners. However, the use of fire as a means of minimizing damage requires further sophistication, or wider application, as attested by recent (January 2003) catastrophic fires in which 500 homes were destroyed in the national capital, Canberra, and surrounding areas.

'Natural' fire regimes (although many are lit by humans) vary in different parts of Australia due to variation in climate, soil, and vegetation. In the seasonally wet northern savannas, less intense fires may occur every 1, 2 or 3 years, whereas in the wet southern forests, severe fires may occur only after one, two, or three centuries. The intensity of the fire is a consequence of the nature and amount of fuel, although this is moderated by the weather, wind direction, and topography. Eucalypts produce large amounts of fuel that accumulates with time since the last fire until it reaches equilibrium. Those litter loads may be relatively low and consist largely of annual grasses in arid and semi-arid northern low eucalypt forests, or may accumulate to $40\,\mathrm{t\,ha^{-1}}$ of eucalypt leaves, bark, and litter in the wetter forests of southern Australia. Thus, the intensities of eucalypt fires can vary from $10\,\mathrm{kW\,m^{-1}}$ of fire edge in light litter fires to $100\,000\,\mathrm{kW\,m^{-1}}$ in firestorms – 25 times higher than the maximum for forest fire control. The temperatures in such extreme fires may reach 1000°C and, if the fuel load beneath them is high, the tree crowns will become involved in the flame front and explode as the essential oils are vaporized. Under the worst combination of dry, hot weather and high winds, such fires are uncontrollable and exacerbated by 'fire-spotting' many kilometers in advance of the fire-front as ribbons of eucalypt bark and glowing embers are caught in the high winds and updrafts caused by the fire.

Unsurprisingly, much of the Australian flora shows adaptive responses to fire. This includes stimulation to flower after fire, as in some orchid species and the grasstree genus *Xanthorrhoea*. A more common response to fire is seen in serotinous species of *Banksia*, *Casuarina/Allocasuarina*, and most species of *Eucalyptus*, to release seed stored in woody, aerial fruits in response to heat and/or desiccation. The postfire environment is optimal for germination, with litter, pathogens, herbivores, and competitors removed, and a readily available source of nutrients from the ash. In other genera, most notably the acacias, fire provides a heat shock that stimulates germination of soil-stored seed, and it has been shown that smoke provides a germination cue for many other species. Many eucalypts, and other genera, are also capable of regenerating vegetatively after fire, either from epicormic buds buried beneath bark in the stem tissue or from buds at the base of the stem (lignotubers). Gill has classified these adaptive responses to fire as 'seeders' that are killed by the fire, and 'sprouters' that regenerate vegetatively after fire. Most eucalypt species exercise both options of massive seed release after fire and sprouting from epicormic buds or lignotubers.

Eucalypt–Plant Interactions

Given the extent of eucalypt forest distribution, it is not surprising that a large proportion of the approximately 25 000 native vascular plant species of Australia are found in communities dominated by eucalypts. The species-richness of the 300 or so eucalypt communities varies widely from 93 species of vascular plants recorded in $128\,m^2$ in grassy woodlands in the Grampians, Victoria, to perhaps three vascular plant species in an equivalent area of mixed forest in Tasmania.

There is no real evidence of obligate associations between eucalypts and the associated plant species; indeed, evidence seems to suggest that eucalypt species have distributions that are largely independent of the distributions of the understory species at the larger scale. Nevertheless, canopy species can profoundly affect the distribution of the understory vegetation in terms of understory biomass, cover, or diversity, by either suppression or facilitation. The predominant effect of a eucalypt canopy in the Australian flora is one of suppression that produces a sparser, lower, less diverse but more xerophytic understory vegetation. These circular zones of altered growth around trees, or halos, are often conspicuous on aerial photographs and to the ground observer. Various biophysical factors have been implicated in these tree-understory patterns, including alteration in light, temperature, moisture, soil nutrient levels, litter, allelopathy, and subcanopy fauna. These effects are not always negative, however, for eucalypt canopy species may ameliorate the minimum and maximum temperatures for understory species and so reduce the combined effect of low temperature and high light intensity, i.e., cold-induced photoinhibition, on understory species, particularly in forests occurring at higher altitudes, such as *E. delegatensis* forests of Tasmania's Central Plateau.

Eucalypt–Fungal Interactions

Fungi are an integral part of all eucalypt ecosystems, with roles as pathogens, decomposers, and mycorrhizal symbionts, but relatively little is known about these important organisms. About 15 000 fungi are currently known from Australia, but based on estimates of the number of species of fungi to hosts in better-studied groups (about 10 : 1), about 250 000 species can be expected in Australia. Therefore, the 700 eucalypt species are likely to have 7000 species of associated fungi, although so far only 600 species of fungi have eucalypts recorded as the host of the type collection.

Major Fungal Parasites

Some fungal parasites of *Eucalyptus* have been studied due to their detrimental impact on forest productivity, especially species of *Phytophthora*, *Armillaria*, and canker fungi. *Phytophthora cinnamomi* is a soilborne oomycete that causes root rot and consequent dieback of many host species over a wide geographic and ecological range, but is particularly destructive in southern Australia since its recent introduction. In southwestern Australia alone, there may be as many as 2000 susceptible host species. Of the eucalypts, *Monocalyptus* species tend to be more susceptible, although the economically important plantation species *E. nitens* (*Symphyomyrtus*) is also highly susceptible. *Armillaria luteobubalina* is also a root-rotting fungus that causes widespread death and decline in native and exotic host species (including *Eucalyptus*), but is a basidiomycete and can persist in stumps and other dead wood, or form rhizomorphs and, with mycelial spread, can occupy areas of up to several hectares.

Cankers of dead bark are formed by a number of ascomycetes as the fungus invades the phloem tissue of twigs, branches, stems, and roots. Canker-causing fungi of eucalypts include species of *Botryosphaeria*, *Cytospora*, *Cryphonectria*, *Endothelia* and *Endothia*. Leaf blight fungi, such as *Mycosphaerella*, have also been studied because of their deleterious impact on forest productivity; mean damage by fungi can be as much as 30% of leaf area. Some fungi are specific to juvenile or adult foliage; some are restricted to one or other leaf surface (such as *M. molleriana* on *E. globulus*). The host-specificity of such parasitic fungal species varies widely, with *M. molleriana* found only on *Symphyomyrtus* whereas *M. cryptica* infects at least 24 species from both *Symphyomyrtus* and *Monocalyptus*. A single eucalypt leaf may be host to several fungal species with a range of interactions. A biotroph like *Ophiodothella longispora* may weaken the eucalypt host and allow the invasion of necrotrophs, such as *Fairmaniella leprosa* or *Macrohilum eucalypti*, leading to a succession of leaf decay species on a single leaf while it is still on the tree.

Mycorrhizal Fungi

Mutualistic associations between fungi and the roots of plants are widespread but, in the nutrient-impoverished soils of many eucalypt ecosystems, the increased supply of nutrients, particularly phosphorus and nitrogen, in exchange for carbohydrates, may be even more crucial to the host species. Fungi form both ectomycorrhizae and endomycorrhizae in association with eucalypts. The ectomycorrhizal habit occurs in several distinct lineages in three divisions of the Eumycota. In the basidiomycetes alone, some 470 epigeal species and 200 hypogeal species are putatively ectomycorrhizal with eucalypts, as are species of *Endogone* in the Zygomycota and *Elaphomyces*, *Muciturbo*, and *Tuber* in the Ascomycota. There is no strong evidence for specificity of ectomycorrhizal fungi among different supraspecific taxa of *Eucalyptus*.

The vesicular-arbuscular mycorrhizal (VAM) associations are a very common form of endomycorrhizal associations, possessed by 30–75% of species. Other endomycorrhizal associations, the ericoid mycorrhizae found in the Australian Epacridaceae, and the mycorrhizal fungi associated with orchids, are more specific to those groups. The VAM fungi (all zygomycetes) show low host-specificity and are also present in many ectomycorrhizal plants (13–24%), including *Eucalyptus*, where both types may be present on the one plant simultaneously, or they may vary in time or space.

An individual fungus may form mycorrhizae with one or several plants of the same or different taxa and, therefore, relationships can become complex. For example, nutrient transfer has been demonstrated between plants connected by mycorrhizal mycelium. A species of *Rhizoctonia* forms ectomycorrhizae with *Melaleuca uncinata* and also stimulates the germination of the orchid *Rhizanthella gardneri*, so it is possible that there is a transfer of nutrients from the *Melaleuca* to the orchid. In a natural ecosystem there will be many potential associations between mycorrhizal fungi and plants and the interactions certainly affect the distribution of hosts, their mycobionts, and other species at scales that vary from the individual plant to the community level.

Eucalypts, Fungi, and Animals

Mycophagy (fungus consumption) is another crucial and complex part of eucalypt forest ecosystems. Fungi comprise part of the diet of at least 37 species of Australian mammals, and are an important source of food for bettongs (*Bettongia*) and potoroos (*Potorous*) in eucalypt forest in eastern and western Australia. At least 100 species of fungi are consumed from unrelated groups in the Ascomycota, Basidiomycota, and Zygomycota; most are hypogeal (below-ground), putatively ectomycorrhizal, and dependent on mammals for spore dispersal. Sporocarp production may be linked to fire in eucalypt forests to enhance spore dispersal of ectomycorrhizal fungi by bettongs at the height of seedling recruitment (following fire). Invertebrates such as mites, collembolans, and earthworms may also be important in dispersal of fungal propagules, especially in dry climates. Macrofungi provide food and habitat for a great diversity of invertebrates, including nematodes, collembolans, mites, earwigs, millipedes, slugs, snails, moths, flies, and beetles. Some species are primary fungivores but other relationships are more complex. The ambrosia fungi in the Ascomycota, for example, are mutualistically associated with some wood-boring Coleoptera (ambrosia beetles in the Lymexelidae, Platypodidae, and Scolytinae in Australia) that attack living eucalypt trees. The ambrosia fungi cause soft rot and reduce the strength of wood, and form specialized structures and mycelium on the walls of tunnels made by the beetles. Adults and larvae feed not on the wood, but on the fungi, which are transmitted to new sites as a yeast-like single-cell state in specialized organs (mycetangia). Again, the relationships between the fungi, the host plants, and the animals are often complex and undoubtedly pivotal in shaping the eucalypt communities.

Reproductive Strategies in Eucalypts

Eucalypts generally produce large numbers of flowers, with conspicuous anthers attracting pollinators. There is extensive variation in floral traits, such as: inflorescence structure (bud number and arrangement); flower size (from 3 mm in diameter in *E. diversicolor* to 40 mm in *E. macrocarpa*); filament color and nectar production; and breeding system. The eucalypt inflorescences are produced from the current season's shoots in the outer crown, usually in groups of 3, 7, 11, 15, or more buds, that may take several months to 2 years to mature. At anthesis, the covering operculum (fused calyx and/or corolla) is shed to reveal the filaments unfolding from the outside whorl. Eucalypts are protandrous and, although the pollen is viable and available to pollinators at this stage, the stigma remains dry and unreceptive for 2–14 days after anthesis, depending on the species. Epidermal cells lining the hypanthium produce nectar from early in anthesis. The base of the ovary is divided into two or, more usually, three or four locules, with vertical rows of sterile ovulodes above fertile ovules borne on a placenta in each locule. Fertilization of the ovules occurs several days (5 in *E. regnans*, 10 in *E. woodwardii*) after the pollen grains germinate at the stigmatic surface and the pollen tubes grow down the transmitting tissue of the style.

After fertilization, the seed develops within the locules in a woody capsule. In addition to the viable seed, mature fruits also contain inviable seed (abnormal or unfertilized ovules) and chaff (the sterile ovulodes). The mean number of viable seed per capsule varies between species, individuals and seasons; the relatively large *E. globulus* capsules average 20 viable seeds per capsule (up to 100), but the average number of viable seeds in smaller capsules may be only 1–5 per capsule.

Flowering Phenology and Pollination

The majority of eucalypts produce small white or cream flowers grouped into large inflorescences, which are visited primarily by insects, a range of birds, and bats. Others develop fewer larger, colored flowers that are especially attractive to birds. Many temperate forest and woodland eucalypts rely on opportunist pollination, primarily by a diverse insect fauna, with patchy bird and mammal pollination. In contrast, many mallees and tropical woodland eucalypts appear to be adapted to pollination by nectar-seeking birds or mammals.

Specialization and coevolution with one type of pollinator (insect, bird, or mammal) undoubtedly has consequences for pollen-dispersal distances (and outcrossing rates), and flowering intensity and phenology. For example, in bird-specialist eucalypts with relatively low flowering intensity, visitors are encouraged to move between trees. Such a strategy may be associated with eucalypts with clumped, patchy, or disjunct distributions. However, a universal strategy appears to be production of many inflorescences, each presenting flowers at different phases, encouraging repeated visits by a variety of vectors.

Pollination by Insects

Insect pollinators include a wide range of taxa that depend on pollen and nectar in the adult stage, although the larval stages may be dependent on wood-boring (Buprestidae), insect predation (Ichneumonidae), or carrion-feeding (Calliphoridae). Some insect visitors to flowers are predatory or parasitic on other insects, and some forage for pollen, but the majority of species are seeking nectar. The effectiveness of these insect visitors as pollination vectors varies, however, with feeding strategies. For example, although many families of beetles contain anthophilous species, with scarab and jewel beetles identified as important pollinators of *E. leptecophylla* and *E. cylindriflora* in southwestern Australia, most beetles have gnawing mouthparts and are destructive feeders. Flies are also common and regular visitors to flowers for nectar, with half of the Australian dipteran families containing anthophilous species. Flies may be more effective pollination vectors than beetles, with larger flies carrying as many as 80 000 pollen grains. It has been estimated that medium to large calliphorid, syrphid, and tachinid flies are responsible for 11–23% of faunal pollen transfer in *E. regnans*.

The majority of Australian native bee species are largely dependent on the family Myrtaceae, including *Eucalyptus*, as their main source of floral nectar and pollen, and the medium and larger species may also be significant pollinators of tall open-forest species, such as *E. regnans*. The introduced honeybee (*Apis mellifera*) is also a common visitor to many eucalypt species (eucalypts are an important resource for the honey industry in Australia); however its effectiveness as a pollinator is not clear. Similarly, although ants are often present in eucalypt flowers, they are unlikely to be effective pollinators, and may even deter other pollinators.

Pollination by Birds

Birds may be more effective in cross-pollination than insects due to their higher energy requirements and higher rates of flower visitation. It has been estimated that more than half of the eucalypt species may be pollinated by nectar-seeking birds. Twenty-five species of honeyeaters, wattlebirds, spinebills, rosellas, lorikeets, pardalotes, and white-eyes are frequent visitors to eucalypt flowers in southern and southwestern Australia. It has been suggested that 26 of 102 Western Australia eucalypt species visited by nectivorous birds have adaptations not only to encourage bird pollination but also to limit insect access to stigmas. In these species, the flowers are large and aggregated into a ball; they are pink, red, or yellow rather than cream. This preponderance of bird pollination in south-western Australia is attributed to the large number of species with restricted distributions, climatic extremes that are often unfavorable to insect activity, but with long growing and flowering seasons providing nectar and pollen throughout the year.

Pollination by Mammals

A range of nectar- and pollen-feeding mammals visit, and may pollinate, eucalypts, including: the sugar glider (*Petaurus breviceps*); yellow-bellied glider (*P. australis*); feathertail glider (*Acrobates pygmaeus*); northern blossom-bat (*Macroglossus minimus*); Queensland blossom-bat (*Syconycteris australis*); gray-headed flying-fox (*Pteropus poliocephalus*); spectacled flying-fox (*P. conspicillatus*); red flying-fox (*P. scapulatus*), and black flying-fox (*P. alecto*). In northern Australia, *E. porrecta* and *E. confertiflora* appear to be adapted to the nocturnal visitations of the two latter species, with the majority of flowers opening after sunset and more nectar being produced after sunset. Flying-foxes appear to be important long-distance pollinators of eucalypts in a variety of eucalypts in tropical Australia, but also over considerable distances, with seasonal migration in southeastern, coastal eucalypts such as *E. tereticornis* and *E. paniculata,* and *E. maculata* in northern New South Wales.

Herbivory of Eucalypts

Eucalypts act as hosts to a wide variety of vertebrates and invertebrates, feeding not only on pollen and nectar, but on bark, foliage, flowers, seeds and exudates, as well as on each other. Because most eucalypts are evergreen (with the exception of some eucalypt species of the monsoon tropics) and retain their leaves for more than 1 year, there are quite marked differences in herbivory of eucalypts and deciduous, northern hemisphere forests. By comparison with short-lived leaves of winter-deciduous trees, leaves of evergreens generally have lower photosynthetic rates, lower nutrient contents, higher concentrations of secondary metabolites, and greater leaf thickness and specific mass. Therefore, eucalypts have foliage that is similar to that of conifers: of low nutritional quality but available over a long period. In addition, eucalypt leaves and many of the understory plants associated with them have high concentrations of lignin and carbon-based secondary metabolites, especially phenolics (including condensed and hydrolyzable tannins and a range of simpler phenol-based compounds) and terpenoids (essential oils). Collectively, these substances decrease the digestibility of proteins and cell-wall carbohydrates for vertebrate and invertebrate herbivores, although the significance of each is contentious. Some of the *Symphyomyrtus* species further reduce the digestibility of their foliage by producing cyanogenic glycosides.

For insects, the low concentrations of nitrogenous compounds and leaf toughness appear to be the most limiting factors for herbivores on eucalypts. Similarly, mammalian herbivores are limited by the availability of protein and energy in eucalypt forests. Because of the energetics of a eucalypt leaf diet, the majority of both invertebrate and vertebrate eucalypt folivores prefer young, actively growing foliage.

Herbivory by Insects

Insects have a great diversity of styles of herbivory on eucalypts: eating whole leaves, grazing on leaf surfaces, or mining their internal tissues; tunneling through bark, boring into or chewing wood; sucking sap from leaves, stems, bark, wood, or roots; and making galls. The insects occupying these niches on eucalypts differ from those in many other forest systems. For example, beetles dominate the leaf-chewing guild on eucalypts of temperate regions, whereas caterpillars dominate the leaf-chewing and mining guilds in the northern hemisphere. Similarly, psyllids are very common sap-sucking insects in eucalypt forests but aphids, which occupy the same niche in northern hemisphere forests, are totally absent. Beetles (Coleoptera, particularly the adult Christmas and other scarab beetles, Scarabaediae, and the chrysomelids, Chrysomelidae) and stick insects (Phasmatodea: Phasmatidae) can cause massive defoliation. The chrysomelid beetle, *Chrysophtharta bimaculata*, is one of the most notorious forest insect pests, attacking regrowth forests and plantations of *E. delegatensis*, *E. obliqua*, and *E. regnans*, from their earliest stages through to advanced stands, and can cause extensive defoliation. Other insects, usually caterpillars (such as the gum leaf skeletonizer, *Uraba lugens*) remove all the soft tissues from whole leaves, leaving a skeleton of the harder parts.

Psyllids or lerp insects (Psyllidae: Hemiptera) are one of the major groups of sapsucking insects found on eucalypts. The sedentary nymphs cover themselves with a starch shell (lerp) and feed by inserting their stylets into the leaf phloem. Although widespread, the psyllids apparently cause little damage at low densities, but at high densities whole leaves and canopies become necrotic and are shed prematurely, resulting in severe dieback. The white lace lerp (*Cardaspina albitextura*), for example, periodically causes severe defoliation and sometimes death of its host plants, *E. blakelyi* and *E. camaldulensis*, in south-eastern Australia.

Gall-forming insects (mostly wasps, but also flies and many psyllids) use the actively growing tissues of the eucalypt host to form protective layers that vary from simple deformations in leaf tissue to complex galls on virtually all plant parts. Wood-boring insects usually attack stressed or debilitated trees. Termites are the main wood-eating insects in eucalypts and are widespread in the tropical open woodlands. Termite invasion follows damage to the tree, usually by fire, and results in 'piping' that structurally weakens the tree and, following an intense fire, can indirectly cause mortality rates of 6–21% for some tropical open-forest eucalypt species.

Herbivory by Mammals

Many of the small arboreal marsupials and bats that feed on eucalypt nectar and pollen have been mentioned above. There are, however, many other species that eat insects, nectar, gums, and/or fruits, or any of the preceding combinations, such as the insectivorous *Antechinus* spp. There are a smaller number of leaf-eating marsupials, including: common ringtail possums (0.7–1 kg) that eat up to 50% mature eucalypt foliage; greater gliders (1–1.7 kg) that only eat young foliage; and koalas (5–13 kg) that eat *Eucalyptus* spp. leaves almost exclusively, and can survive on mostly mature foliage, when young foliage is unavailable. There are also intermediate feeders, such as the common and mountain brushtail possums (*Trichosurus* spp.) that do eat eucalypt leaves but supplement this diet with ground-story herbs and grasses, fruits, and insects. These arboreal leaf-eating mammals are relatively common in the eucalypt forests and woodlands of southeastern Australia, perhaps due to the more reliable production of young foliage, but uncommon or absent from the eucalypt forests of tropical northern Australia. There are also terrestrial mammalian herbivores in the eucalypt forests, feeding on eucalypt seedlings, roots, seeds, or other shrubs or groundcover plants or fungi. This includes the familiar marsupial kangaroos and wallabies (family Macropodidae), wombats (*Vombatus ursinus*), and bandicoots (family Peramelidae), but also placental granivorous rodents.

Impacts of Herbivory

Eucalypts are well adapted to cope with extensive defoliation by fire, drought, and herbivory, with leaf growth renewed from the naked buds in the leaf axils, from accessory buds in the leaf axils if the naked buds are damaged (as they often are), or from epicormic buds in the larger branches or the main stem of the tree if crown death is complete. In this way, most eucalypts can rapidly reestablish the leaf canopy in a single growing season. A few eucalypt species are less capable of resprouting, such as the tall ash species, *E. regnans* and *E. delegatensis* and, hence, are vulnerable to outbreaks of insect pests such as phasmatids. Death of mature eucalypts due to grazing by mammals such as koalas or common brushtail possums is usually associated with limited abundance of food trees due to clearing for agriculture or unusually high population numbers. However, grazing by brushtail possums and macropods may be important in excluding seedling regeneration by selective predation in some natural eucalypt communities and can pose serious problems for the establishment of eucalypt plantations. Strategies to reduce the impact of browsing on plantation species, such as *E. nitens*, have been tested, including: repellent sprays; coplanting with repellent species such as bitter lupins; different plantation sizes, shapes, and associated vegetation; but the principal preventive method remains the use of 1080 poison, which is currently a serious source of dispute between the forestry industry and environmental groups.

Conservation Status and Trends

The sustainable management of Australia's eucalypt forest ecosystems is a major challenge facing all sectors of Australian society. There have been dramatic changes to land use over the past two centuries since European settlement, with widespread vegetation clearance (perhaps 500 000 km^2 since 1788), grazing by introduced livestock, and consequent changes in hydrological and fire regimes affecting nearly all eucalypt forest ecosystems.

At the most fundamental level, the remaining eucalypt forests are the major source of unique terrestrial biodiversity. At more pragmatic levels, the wise management of eucalypt forests will be essential to addressing problems of greenhouse-gas pollution, degradation of water quality, widespread soil salinization and degradation that have resulted from forest clearance, poor agricultural practices of overgrazing and excessive tillage of fragile soils, and introduction of highly destructive pests.

Tenure of Eucalypt Forests

The 127 million ha of eucalypt forest in Australia are divided by tenure as follows: leasehold land 46%; private 24%; conservation reserves 13%; other crown land 8%; and multiple-use 7%.

However, the tenure over eucalypt forest varies significantly from state to state, as shown in **Table 2**. In the southeastern Australian states of Victoria and Tasmania, large proportions of the eucalypt forest (*c.* 35%) are in conservation areas with a similar proportion in multiple-use (timber-producing) forests, so that the majority of eucalypt forest is under government authority control. This is in contrast to the situation in the states with larger areas of less productive forests and woodlands (New South Wales, Queensland, South Australia, Western Australia, and the Northern Territory) where the majority of eucalypt forest is leasehold or privately owned.

As a consequence, the eucalypt forest types differ in the level of conservation, with the tall and medium open forests being relatively well reserved, in comparison to other structural types of eucalypt forest, such as the medium woodland eucalypt forests (6%) and low eucalypt forests (6% within conservation reserves), although 35% of eucalypt mallee forests are in conservation reserves.

Clearance of Eucalypt Forests

These differences in land tenure in different states and different forest ecosystems have implications for

Table 2 Tenure of eucalypt forest in Australian states ('000 ha)

	ACT	*NSW*	*NT*	*QLD*	*SA*	*TAS*	*VIC*	*WA*	*AUST*
Leasehold land	11	9470	16 313	35 581	5250	0	46	8920	75 591
Multiple-use forests	0	2496	0	2925	5	1062	3312	1600	11 400
Nature conservation reserves	106	4471	12	5000	3943	1105	3050	3805	21 491
Unresolved tenure	0	643	110	883	454	0	23	14	2127
Other crown land	0	1055	890	1131	392	80	207	9387	13 143
Private land	0	8523	15 511	10 213	822	922	1298	1639	38 928
Total native forest	117	26 658	32 836	55 734	10 866	3169	7935	25 365	162 680

ACT, Australian Capital Territory; NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; TAS, Tasmania; VIC, Victoria. Reproduced, with permission, from the National Forest Inventory May 2003. Available online at: www.affa.gov.au/content/output.cfm?&CONTTYPE = outputs&OBJECTID = D52EDDBA-23DF-485A-B1C968D1C08E79D1.

Table 3 Areas of woody vegetation cleared in states and territories in 1999 (data from National Greenhouse Gas Inventory) and 2000 (data from the Australian Conservation Foundation)

State	*Area cleared in 1999 (ha)*	*Estimated area cleared in 2000 (ha)*
ACT	0	0
Northern Territory	3320	12 700
Queensland	425 000	425 000
South Australia	3396	1600
New South Wales	30 000	100 000
Tasmania	940	17 000
Victoria	2450	2500
Western Australia	3738	6000
Total	468 844	564 800

Table 4 Area (ha) approved by the Department of Land and Water Conservation of New South Wales for clearing of native vegetation, 1996–2001

1996	*1997*	*1998*	*1999*	*2000*	*2001*
25 930	33 603	75 307	174 681	77 831	92 094

the nature of land clearance, largely because land clearance is under state government, rather than Commonwealth government control. Estimates of forest clearance across Australia vary widely, but the magnitude of deforestation is massive by any scale; it is claimed that Australia has the sixth highest land-clearing rate in the world. During the period 1990–1995, the net woody vegetation loss was 863 090 ha, or 172 620 ha $year^{-1}$, although estimates of clearing are much higher. Most of this clearing is in Queensland and New South Wales (**Table 3**). In Queensland clearing rates averaged 289 000 ha $year^{-1}$ during 1990–1995, but accelerated to 340 000 ha $year^{-1}$ in 1995–1997 and 425 000 ha $year^{-1}$ in 1997–1999. The vast majority of clearing was for pasture (86%), some cropping (10%), and small areas for forestry, mining infrastructure, and settlement (4%). This acceleration may be attributable to a rush by landowners to clear land before effective control measures are in place. In spite of changes to Commonwealth environmental law brought about by the Environment Protection and Biodiversity Act 1999 (EPBCA), the Queensland government has been reluctant to apply controls under its own Vegetation Management Act 1999 in the absence of a Commonwealth contribution to a compensation fund to landholders potentially affected.

In recent years, a number of governments in Australia have brought in legislation in an attempt to regulate the clearing of native vegetation. However, the success of such legislative controls is questionable. In a 2002 audit of the effectiveness of the Department of Land and Water Conservation (DLWC) of New South Wales in regulating land clearance since the introduction of the Native Vegetation Conservation (NVC) Act 1997, the Auditor-General was condemnatory. Amongst the findings were:

1. There are currently no objectives or targets to measure progress in conserving native vegetation. Only one of a possible 22 regional management plans has been approved since the Act commenced.
2. The DLWC does not have an adequate information system and operational capacity to regulate native vegetation in NSW efficiently and effectively.
3. The likelihood of breaches of the NVC Act is high. The number of alleged breaches is steadily increasing.

Since the commencement of the NVC in 1998, the annual clearing approvals have not decreased (**Table 4**). It should be pointed out that these figures understate the area cleared because illegal clearing and clearing under exemption are not included. Illegal clearing is a significant issue, with reported breaches of the NVC increasing steadily to more than 200 per year, with only seven prosecutions commenced out of more than 700 alleged breaches from 1998 to April 2002.

There are many implications of the changes to the eucalypt forests across Australia. The clearing of native habitat is the single most threatening process for biodiversity loss and species extinction in Australia. The loss of species in Australia over the past two centuries due to human impact is conservatively estimated at 97 plants, 17 species of mammal, and three birds. However, several hundred vertebrates, several thousand plants, and an untold number of invertebrates are threatened with extinction due to loss of habitat. The extent and rate of deforestation in Queensland are comparable to that in Western Australia and Victoria in the past, which has given rise to significant salinity problems in these states, both in terms of dryland salinity and salinization of drinking and irrigation water. The release of carbon into the atmosphere by clearing operations also contributes significantly (13% in 1996) to Australia's greenhouse-gas emission, and there is a net loss of carbon dioxide equivalent to a ratio of 3 : 1 compared with that captured by vegetation acting as a sink. Although many of these consequences of the loss of eucalypt forests have been known for decades, and have been recognized by governments and addressed in recent policy initiatives, clearing of eucalypt forests continues.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems; Reproductive Ecology of Forest Trees. **Entomology**: Bark Beetles; Defoliators; Foliage Feeders in Temperate and Boreal Forests; Sapsuckers. **Pathology**: Diseases of Forest Trees; Insect Associated Tree Diseases. **Tree Breeding, Practices**: Genetic Improvement of Eucalypts; Mycorrhizae.

Further Reading

Fox MD (1999) Present environmental influences on the Australian flora. In: Orchard AE and Thompson HS (eds) *Flora of Australia*, 2nd edn, vol. 1, pp. 205–249. Melbourne, Australia: ABRS/CSIRO Australia.

Gill AM (1997) Eucalypts and fires: interdependent or independent? In: Williams JE and Woinarski JCZ (eds) *Eucalypt Ecology: Individuals to Ecosystems*, pp. 151–167. Cambridge, UK: Cambridge University Press.

Groves RH (ed.) (1997) *Australian Vegetation*, 2nd edn. Cambridge, UK: Cambridge University Press.

Groves RH (1999) Present vegetation types. In: Orchard AE and Thompson HS (eds) *Flora of Australia*, 2nd edn, vol. 1, pp. 369–402. Melbourne, Australia: ABRS/CSIRO Australia.

House SM (1997) Reproductive biology of eucalypts. In: Williams JE and Woinarski JCZ (eds) *Eucalypt Ecology: Individuals to Ecosystems*, pp. 30–55. Cambridge, UK: Cambridge University Press.

Keith H (1997) Nutrient cycling in eucalypt ecosystems. In: Williams JE and Woinarski JCZ (eds) *Eucalypt Ecology: Individuals to Ecosystems*, pp. 197–226. Cambridge, UK: Cambridge University Press.

Kirkpatrick JB (1997) Vascular plant–eucalypt interactions. In: Williams JE and Woinarski JCZ (eds) *Eucalypt Ecology: Individuals to Ecosystems*, pp. 227–245. Cambridge, UK: Cambridge University Press.

Landsberg JJ and Cork SJ (1997) Herbivory: Interactions between eucalypts and the vertebrates and invertebrates that feed on them. In: Williams JE and Woinarski JCZ (eds) *Eucalypt Ecology: Individuals to Ecosystems*, pp. 342–372. Cambridge, UK: Cambridge University Press.

May TW and Simpson JA (1997) Fungal diversity and ecology in eucalypt ecosystems. In: Williams JE and Woinarski JCZ (eds) *Eucalypt Ecology: Individuals to Ecosystems*, pp. 246–277. Cambridge, UK: Cambridge University Press.

National Forest Inventory website. www.affa.gov.au/content/output.cfm?&CONTTYPE = outputs&OBJECTID = D52EDDBA-23DF-485A-B1C968D1C08E79D1.

Ficus spp. (and other important Moraceae)

J K Francis, Jardín Botánico Sur, San Juan, Puerto Rico, USA

Introduction

Moraceae is a family of mostly tropical trees containing 37 genera and about 1100 species. The most important genus, both in terms of numbers and benefit to humans, is *Ficus*. The family is characterized as having milky or sometimes watery latex. Leaves are mostly alternate, simple, entire, and pinnately veined. The flowers are unisexual but variable in form, as are the inflorescences. The fruits are commonly drupaceous, embedded in a fleshy receptacle forming a syncarp. The seeds are large without endosperm or small with endosperm. Although a few of the species produce timber, bark, and yield medicinal products, the greatest benefit to humans and animals is from the fruits that many produce. Except for a few of the fruit-producing species, three or four timber species, and a number of *Ficus* and other species planted for ornament and shade, members of the family are little planted or actively managed.

Taxonomy/Genetics

Note: The following treatment is based on taxonomy that predates the publication of the Angiosperm Phylogeny Group's higher-level classification of the angiosperms. Moraceae (used here in the narrow sense) is one of the ewosid families of Rosales.

Moraceae is part of the order Urticales, which is believed to have descended from a single ancestral line. Because of morphological and molecular similarity, it has been suggested that Moraceae, Celtidaceae, Cecropiaceae, and Urticaceae should be merged. The genera of Cecropiaceae appear under Moraceae in older references. Moraceae currently contains 37 genera and about 1100 species (**Table 1**).

Table 1 Details of genera and species within Moraceae

Genus	*No. sp.*	*Range*	*Life forms*
Antiaris	1	Africa, Australasia	t
Antiaropsis	1	New Guinea	t, s
Artocarpus	~50	Asia, Australia	t
Bagassa	1	America	t
Batocarpus	4	America	t
Bleekrodea	3	Melesia, Madagascar	t, s
Bosqueiopsis	1	Africa	t, s
Brosimum	13	America	t
Broussonetia	8	Asia, Madagascar	t, s, c
Castilla	3	America	t
Clarisia	3	America	t, s
Dorstenia	~105	Pan tropical	s, h
Fatoua	3	Pacific, Madagascar	s, h
Ficus	~750	Pan tropical	t, s, c
Helicostylis	7	America	t
Helianthostylis	2	America	t
Hullettia	2	Malaya	t, s
Maclura	11	North America, Pan tropical	t, s, c
Maquira	5	America	t
Mesogyne	1	Africa	t, s
Milicia	2	Africa	t
Morus	10–15	Almost worldwide	t
Naucleopsis	20–25	America	t
Parartocarpus	3	Malesia, Pacific	t
Perebea	9–10	America	t, s
Poulsenia	1–2	America	t
Prainea	4	Malaysia-New Guinea	t, c
Pseudolmedia	8–9	America	t
Scyphosyce	2	Africa	s
Sorocea	~20	America	t, s
Sparattosyce	1	New Caledonia	t
Streblus	~25	Old World	t, s
Treculia	3	Africa, Madagascar	t, s
Trilepisium	1	Africa, Indian Ocean	t
Trophis	9	America, Asia	t, s
Trymatococcus	3	America	t
Utsetela	1	Africa	s

t, trees; s, shrubs; c, climbers; h, herbs.
Information source: Kubitzki K, Rohwer JG, and Bittrich V (1993) *The Families and Genera of Vascular Plants*, vol. 2. Berlin: Springer-Verlag.

The family Moraceae consists of trees with lesser numbers of shrubs, climbers, and herbs, most of which are tropical. All (except for the genus *Fatoua*) secrete milky (sometimes watery) latex from laticifers in parenchymatous tissues in stems and sometimes leaves. Leaves are alternate or rarely subopposite, most frequently simple, entire, and pinnately veined. Stipules are present, although often fused and forming a cap over the bud. Inflorescences take various forms. Flowers are unisexual, often four-merous. Plants may be monoecious or dioecious. Although some species have dry fruits, most have drupaceous or achene fruits embedded in fleshy receptacles. The family is further divided into the tribes Moreae (*Morus*, *Broussonetia*, *Milicia*, *Maclura*, *Trophis*, *Streblus*, *Bleekrodea*, and *Fatoua*), which have 'urticaceous' stamens; tribe Artocarpeae (*Artocarpus*, *Paratocarpus*, *Triculia*, *Prainea*, *Hullettia*, *Antiaropsis*, *Sparattosyce*, *Batocarpus*, *Bagassa*, *Sorocea*, *Clarisia*, and *Poulsenia*), with generally unisexual inflorescences and seeds almost without endosperm; tribe Castilleae (*Perebea*, *Maquira*, *Castilla*, *Helicostylis*, *Pseudolmedia*, *Naucleopsis*, *Antiaris*, and *Mesogyne*), with spontaneous abscission of branches; tribe Dorstenieae (*Utsetela*, *Bosqueiopsis*, *Helianthostylis*, *Trymatococcus*, *Brosimum*, *Trilepisium*, *Scyposyce*, and *Dorstenia*) usually with uncinate hairs; and tribe Ficeae (*Ficus*), which have syconia enclosing the flowers.

The family follows various growth models. In Troll's model the architecture is built by the continual superposition of plagiotropic branches, each division alternating between main-line axis and determinate branch, and is followed by *Milicia excelsa*, in Rauh's model, a monopodial trunk grows rhythmically and develops tiers of branches and the branches are morphologically identical to the trunk, is exemplified by *Artocarpus heterophyllus*, *Ficus aurea*, and *Musanga cercropoides*. The architecture in Cook's model results when a monopodial trunk with spiral or decussate phyllotaxis adds branches phylomorphically. *Castilla* follows this model. Roux's model, followed by *Antiaris welwitschii*, *Milicia regia*, and *Perebea guianensis*, occurs when a monopodial orthotropic trunk meristem grows continuously and has plagiotropic branches that are inserted continuously. *Dorstenia* and *F. theophrastoides* grow by Corner's model in which vegetative growth of a single aerial meristem produces one unbranched axis with lateral inflorescences.

Sex determination in *F. carica*, and probably other members of the subgenus *Ficus,* is different from the XX/XY method used in most other life forms, from mosses through humans. It is believed to be determined by two pairs of alleles located on one pair of homologous chromosomes. Eleven possible combinations of dominant and recessive genes result in plants that produce caprifigs (with separate staminate male flowers and female pistillate flowers), and plants with edible figs (with only female flowers).

Members of the family have $n = 12$, 13, 14, or more (sometimes much more) base numbers of chromosomes. Some notable genera are as follows: *Dorstenia* $2n = 24$–48; *Brosimum* $2n = 26$; *Broussonetia* $2n = 26$, 39; *Ficus* $2n = 26$; *Castilla* $2n = 28$, *Artocarpus* $2n = 28$–81; *Morus* $2n =$ mostly 28 with oddities up to 308.

Ecology

Species within the family Moraceae are tropical and subtropical, with a few exceptions such as *Maclura pomifera*, *Morus alba*, *M. rubra*, and *M. serrata*, which are warm temperate. Although a wide variety of soil, topographic, and precipitation conditions make a suitable habitat, most members of the family grow in humid, fertile conditions at low to middle elevations. They vary from highly intolerant of shade to shade tolerant. Most require full or at least partial sunlight to establish themselves, grow well, flower, and bear fruit. Many Moraceae species occur in primary remnant forests while others grow in secondary forests; a few are pioneer species. One group colonizing an unusual habitat are *Ficus* species that grow in the crowns of other trees, and on rocks, cliff faces, and masonry structures.

Form, structure, and life history are usually inexorably linked with the niche each species occupies in the forest ecosystem. *Dorstenia* are perennial herbs, subshrubs, or shrubs with rhizomes or tuberous subterranean parts. They usually grow in mesic habitat in the understory of primary and secondary forests. All, or nearly all, of the Moraceae rely on animals for seed dispersal. The form and presentation of the fruits and seeds help facilitate the particular disperser. *Morus* and the small-fruited figs, such as *F. citrifolia*, present their fruits near the ends of slender branches, ideal for small birds and fruit bats. Other species, such as *Artocarpus heterophyllus*, *F. racemosa*, and *F. heteropoda*, flower and fruit on their stems and major branches (cauliflory), where the fruits are more accessible to climbing mammals and large birds. Several figs bear fruits on pendulous branches near the ground (*F. capensis*, *F. ribes*, and *F. minahassae*), at least one at the base of the trunk (*F. auriculata*), and at least *F. geocarpa* and *F. cunia* produce fruits on underground branches (geocarpic fruiting) at a distance from the parent tree, where they are uprooted by deer, pigs, and other animals. Most species of the family have small seeds that easily pass through the gut of the dispersing animal. On the other hand, the *Artocarpus* spp. have large seeds that are mostly discarded by the dispersing animal as they consume the fruit pulp.

Most Moraceae species follow the common plant life history of seeds, being deposited by dispersers on soil or superficial organic horizons, germinating, and growing into adult plants. A significant part of the genus *Ficus* develops in a different way. The seeds, which are tiny, are deposited by birds or mammals through defecation in crotches or bark crevices of trees, or in irregularities in large rocks, cliff faces, or masonry structures. They germinate during rainy periods and grow slowly, developing short roots to attach themselves and absorb moisture and nutrients. After they have grown a few leaves they begin growing a vinelike root toward the earth. The process may take a few months to several years. After the long aerial root has reached the soil, it thickens and stiffens to become the plant's stem. Cutting the vine-size roots will not kill the epiphytic plant. Additional roots to the earth may be added and lateral roots begin to surround the host tree or interlace the stone surface. Some species remain vinelike but most become trees, often very large, smothering or sometimes strangling their hosts. Some species actually have modified roots that encircle their host's trunk for the purpose of strangling them. The aerial roots that become stems eventually coalesce to form a massive trunk.

The seedless variety of *Artocarpus altilis* (breadfruit) is totally dependent on humans for long-distance transport. Once established, it suckers from the roots, sometimes as much as 30 m away from the parent tree. The variety thus reproduces and competes successfully in secondary forests that develop after farm abandonment.

The flowers of *Ficus* are pollinated by tiny wasps. The female wasps normally pass from their birth syconia, carrying pollen from male flowers that are located near the apical pore of the syconia to syconia on other trees where they oviposit in short-styled pistillate flowers. Long-styled flowers are pollinated without being parasitized. The male wasps emerge first to inseminate the females before they emerge to repeat the process. The relationship is obligately mutualistic for both the wasps and the figs. Most species of fig have their own endemic wasps. For this reason, exotic *Ficus,* which leave their endemic pollinators behind, rarely produce seed and do not become invasive. An exception to the rule, *F. microcarpa*, has naturalized in several counties in southern Florida. Members of the Moreae tribe with 'urticaceous' stamens that propel pollen into the air are wind-pollinated. Research is needed to determine how pollination is accomplished in other genera.

Silviculture

The cultivation of *Ficus*, *Morus*, and *Artocarpus* species for fruit, *Ficus* species for potted ornamentals, and *Morus alba* for silkworm fodder is well documented and beyond the scope of this silviculture treatment. Methods used for the production and establishment of seedlings for yards, streets, parks, greenbelts, and shelterbelts are similar to those used in restoration and plantation forestry. The large-seeded species and some of the small-seeded species are started from seed in nursery beds or germination trays, usually without pregermination treatments. The seedlings are then grown as bare-root or containerized seedlings by conventional methods. At least the small-seeded *Ficus*, while easy to germinate on wet peat or blotter paper, are difficult and slow to develop into plantable seedlings. They are routinely propagated vegetatively by stem or root cuttings or by air or ground layering. Field planting is done by conventional procedures. While none of the Moraceae are planted in large monocultures for timber, a few, for example *Bagassa guianensis* and *Brosimum alicastrum*, have been tested or are being cultivated in small plantations and may possibly find a place in major plantation silviculture in the future.

An alternative to monoculture plantations is enrichment planting and treatments to promote natural reproduction. *Milicia excelsa* has been produced in nurseries and outplanted. Because it is fire-sensitive, it can only be employed in enrichment planting where complete fire protection is maintained. In harvested areas in Mozambique where large *M. excelsa* were left as seed trees, reproduction occurred in the openings.

Management of *Ficus* species in natural stands is an extremely important issue but little studied and reported. One of the reasons that it is so important is that the wild figs are an important source of food (fruit) for mammals and birds in native forests, and they are dependent on those animals as dispersers of their seeds. If the principal disperser of the seeds of a species is eliminated from an area by hunting or critical habitat destruction, the *Ficus* species must eventually decline. The impact is greater because in most tropical forests, wild figs occur in low densities. The *Ficus* species, which are of low timber value, are also likely to be eliminated during timber stand improvement treatments. While killing large *Ficus* trees is difficult by cutting and girdling, and moderately difficult with herbicides, they can be eliminated with a determined effort.

Enrichment planting of *Ficus* species will probably not be much different from the establishment of ornamental figs or enrichment planting of other forest species: providing an opening with enough light for vigor of newly planted seedlings and protection from weeds and encroaching overhead shade until the planted trees show promise of reaching a codominant position in the canopy. Except for the one previously cited for *M. excelsa*, reports of successful treatments to encourage natural regeneration are not known to the author. A logical treatment for ground-seeding species would be to create openings with scattered patches of exposed soil near fruit-bearing *Ficus* trees. Treatments to encourage epiphytic species may not be possible other than the protection of potential seed trees and their animal dispersers.

Utilization

Probably the most important species in an economic sense is *F. cerica* (common fig), a low, bushy tree or large shrub. It apparently originated in western Asia, was domesticated in ancient times, and spread to the Mediterranean and to most subtropical areas of the world. Today, annual fruit production is an estimated 1 million tonnes. The fruits are eaten raw, dried, preserved, candied, made into jam, used in baking, brewed into wine, and toasted for a coffee substitute. The wood is used to some extent for boxes, small articles, and fuel. There are at least 87 other *Ficus* species whose fruits and vegetative parts are eaten by people in various parts of the world. A number are used in herbal medicine. The tissue used depends on the ailment treated. Maladies most commonly treated are skin lesions, ulcers, and other skin problems, and diarrhea and dysentery. Although used locally for lumber, crafts, and fuel, *Ficus* species do not figure in international commerce for wood. This could change with wider use of medium-density wafer board and similar products. However, great benefit is derived from many *Ficus* species as ornamentals and shade trees. A few should be noted. *F. benjamina* (benjamin fig) is one of the most common large indoor potted plants for homes and institutions. It is also grown outdoors as a street, yard, and park tree in frost-free climates. If allowed to grow freely, it may reach 30 m in height and assumes a banyan-like habit.

Ficus elastica (Indian rubber tree) is used in much the same way indoors and becomes even larger in outdoor settings. Its tapped latex was once an important source of natural rubber, but has been almost completely replaced by latex tapped from *Hevea brasiliensis*. The banyan fig (*F. benghalensis*), although an interesting curiosity, eventually covers so much area by its expanding crowns and aerial roots that become trunks that it cannot be extensively used. *Ficus microcarpa*, *F. lyrata*, and *F. religiosa* are all beautiful and manageable figs planted in parks, estates, and along streets, and loved throughout the tropics. A large number of other *Ficus* species are occasionally planted as ornamental and shade trees. *Ficus pumila*, a climber that clings to surfaces by means of adventitious roots, is used like ivy (*Hedera helix*) to cover masonry walls.

Most of the *Ficus* species are relatively common but rarely abundant in tropical forests. However, many are important sources of food (mainly the fruits) for wildlife. Over 1200 species of vertebrates have been identified that eat the fruits of *Ficus* species. Some of the *Ficus* species in India and nearby countries are used as hosts in the cultivation of *Laccifer lacca* insects, the source of shellac and certain natural dyes. A number of the *Ficus* and several species of other related genera cause contact dermatitis, especially when persons come in contact with the latex.

Other important members of the Moraceae include *Artocarpus altilis*, an important food crop in the humid tropics; it occurs in two forms. Breadfruit produces abundant 1–2-kg starchy fruits eaten like potatoes. This large (to 30 m) tree produces no seeds but reproduces aggressively by root suckers. Breadnut (the seeded form) is grown for its large edible seeds. Although once used by Pacific Islanders for canoes and surf boards, the wood is little used today. A related species is the jackfruit, *A. heterophyllus*. It produces large (up to 20 kg) cauliflorous syncarps with sweet pulp eaten raw or cooked and large seeds that are roasted or boiled. The wood finds minor local uses for furniture and the extraction of a yellow dye. Another important genus is the mulberry (*Morus*) with important representatives white mulberry (*M. alba*), black mulberry (*M. nigra*), and American mulberry (*M. rubra*). All produce delicious fruits of minor importance and are used to some extent as ornamentals. White mulberry is the principal fodder grown for silkworms (*Bombyx mori*). American mulberry wood is used for fence posts, furniture, and caskets. *Morus serrata*, native of the Himalayan area, produces valuable wood used for furniture and carvings. Osage-orange (*Maclura pomifera*), a temperate representative of the family, has been used extensively for fence posts, cattle shade, windbreaks, and conservation plantings in North America. Its neotropical relative, *M. tinctoria*, is a timber tree producing wood used for flooring, and other uses requiring toughness, and is the source of a yellow-brown dye. Two African species, *Milicia excelsa* and *M. regia*, produce valuable timber often substituted for teak.

Some members of the genus *Brosimum* produce valuable wood used locally and traded internationally. The leaves and fruits are important food for domestic and wild animals during times of drought. The seeds are edible when cooked and the sap of some of the species is drunk as a tonic. The bark of *Broussonetia papyrifera*, native or planted through Southeast Asia and the Pacific, is used to make a high-quality bark cloth for clothes, mats, wall hangings, and funerary rites. *Antiaris toxicaria* of Africa through Australia is used in the same way to make cloth, and the sap is used as an arrow poison and to treat several medical conditions. *Castilla elastica* produces a copious latex that was once tapped to make natural rubber but is of low quality and has fallen into disuse. *Bagassa guianensis* and several species of the genera *Clarisia*, *Pseudolmedia*, and *Trophis* are harvested for timber. Finally, many lesser known members of the family are used in herbal medicine.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation. **Environment**: Environmental Impacts. **Silviculture**: Natural Stand Regeneration. **Tree Physiology**: Forests, Tree Physiology and Climate. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Dry Forests; Tropical Montane Forests.

Further Reading

Berg CC (1972) *Olmedieae, Brosimeae (Moraceae)*. Flora neotropica monograph no. 7. New York: Hafner.

Bor NL (1953) *Manual of Indian Forest Botany*. London: Oxford University Press.

Burton JD (1990) *Maclura pomifera* (Raf.) Schneid. Osage-orange. In: Burns RM and Honkala BH (eds) *Silvics of North America*, vol. 2. Washington, DC: US Department of Agriculture Forest Service.

Chudnoff M (1984) *Tropical Timbers of the World*. Agricultural handbook no. 607. Washington, DC: US Department of Agriculture Forest Service.

Condit IJ (1969) Ficus, *the Exotic Species*. Riverside, CA: Division of Agricultural Sciences, University of California.

Darlington CD and Wylie AP (1956) *Chromosome Atlas of Flowering Plants*. New York: MacMillan.

Francis JK (1994) Ficus citrifolia *P. Miller. Jagüey Blanco*. SO-ITF-SM-75. New Orleans, LA: US Department of Agriculture Forest Service, Southern Forest Experiment Station.

Hallé F, Oldman RAA, and Tomlinson PB (1978) *Tropical Trees and Forests and Architectural Analysis*. Berlin: Springer-Verlag.

Kubitzki K, Rohwer JG, and Bittrich V (1993) *The Families and Genera of Vascular Plants*, vol. 2. Berlin: Springer-Verlag.

Lamson NI (1990) *Morus rubra* L. red mulberry. In: Burns RM and Honkala BH (eds) *Silvics of North America*,

vol. 2. Washington, DC: US Department of Agriculture Forest Service.
Parrotta JA (1994) Artocarpus altilis *(S. Park.) Fosb. Breadfruit, breadnut*. SO-IITF-SM-71. New Orleans, LA: US Department of Agriculture Forest Service, Southern Forest Experiment Station.
Shanahan M, So S, Compton SG, and Corlett RT (2001) Fig-eating by vertebrate frugivores: a global review. *Biological Reviews* 76: 529–572.

Mangroves

M Spalding, UNEP World Conservation Monitoring Centre, Cambridge, UK

Introduction

The term mangrove is used to define both a group of plants and also a community or habitat type in the coastal zone. Mangrove plants are trees or shrubs that normally live in the intertidal zone. Mangrove communities are those in which these plants predominate. Other terms for these communities include coastal woodland, intertidal forest, tidal forest, mangrove forest, mangrove swamp, and mangal. The word mangrove can be traced to the Portuguese word 'mangue' and the Spanish word 'mangle,' both of which are actually used in the description of the habitats, rather than the plants themselves, but still have been joined to the English word 'grove' to give the word mangrove. It has been suggested that the original Portuguese word has been adapted from a similar word used locally by the people of Senegal.

Mangrove Species

Mangrove plants are not a simple taxonomic group, but are largely defined by the ecological niche where they live. The simplest definition describes: 'a shrub or tree which normally grows in the intertidal zone and which has developed special adaptations in order to survive in this environment.' Using such a definition a broad range of species can be identified, coming from a number of different families. Although there is no consensus as to which species are, or are not, true mangroves, a core group of some 30–40 species is agreed by most authors. These 'core' species are the most important, both numerically and structurally, in almost all mangrove communities. **Table 1** provides a more complete list of mangrove species (of tree, shrub, fern, and palm), highlighting the core species.

All of these plants have adapted to a harsh environment, with regular inundation of the soil and highly varied salinities, often approaching hypersaline conditions. Soils may be shallow, but even where they are deep they are usually anaerobic within a few millimeters of the soil surface. Many mangrove species show one or more of a range of physiological, morphological, or life history adaptations in order to cope with these conditions.

Coping with Salt

All mangroves are able to exclude most of the salt in sea water from their xylem. It would appear that most species operate an ultrafiltration process at the endodermis of the roots. *Bruguiera, Lumnitzera, Rhizophora*, and *Sonneratia* species are highly efficient in this initial salt exclusion. Others, including *Aegialitis, Aegiceras*, and *Avicennia*, are less efficient and hence also actively secrete salt from their leaves. This is done metabolically, using special salt glands. Evaporation leaves salt crystals on the leaf surface which are often clearly visible (**Figure 1a**).

Anaerobic Soils

The morphological feature for which mangroves are best known is the development of aerial roots. These have developed in most mangrove species in order to cope with the need for atmospheric oxygen at the absorbing surfaces and the impossibility of obtaining such oxygen in an anaerobic and regularly inundated environment. Various types of roots are illustrated in **Figure 1**.

The stilt root, exemplified by *Rhizophora* (**Figure 1b**) consists of long branching structures that arch out away from the tree and may loop down to the soil and up again. Such stilt roots also occur in *Bruguiera* and *Ceriops* although in older specimens they fuse to the trunk as buttresses. They also occur sporadically in other species, including *Avicennia*.

A number of unrelated groups have developed structures known as pneumatophores which are simple upward extensions from the horizontal root into the air above. These are best developed in *Avicennia* and *Sonneratia* (**Figure 1c**), the former typically with narrow, pencil-like pneumatophores, the latter with secondary thickening so that they can become quite tall and conical.

Root knees are more rounded knobs which, like pneumatophores, extend upwards from the roots. In *Xylocarpus mekongensis* these are the result of localized secondary cambial growth, but in *Bruguiera* (**Figure 1d**) and *Ceriops* they are the result of a primary looping growth. In these species branching may also occur on these root knees.

Table 1 List of mangrove species

Family	*Species*[a]
Pteridaceae	*Acrostichum aureum*
	Acrostichum danaeifolium
	Acrostichum speciosum
Plumbaginaceae	*Aegialitis annulata*
	Aegialitis rotundifolia
Pellicieraceae	***Pelliciera rhizophorae***
Bombacaceae	*Camptostemon philippensis*
	Camptostemon schultzii
Sterculiaceae	*Heritiera fomes*
	Heritiera globosa
	Heritiera littoralis
Ebenaceae	*Diospyros ferrea*
Myrsinaceae	*Aegiceras corniculatum*
	Aegiceras floridum
Caesalpiniaceae	*Cynometra iripa*
	Mora oleifera
Combretaceae	***Conocarpus erectus***
	Laguncularia racemosa
	Lumnitzera littorea
	Lumnitzera racemosa
	Lumnitzera × rosea
Lythraceae	*Pemphis acidula*
Myrtaceae	*Osbornia octodonta*
Sonneratiaceae	***Sonneratia alba***
	Sonneratia apetala
	Sonneratia caseolaris
	Sonneratia griffithii
	Sonneratia lanceolata
	Sonneratia ovata
	Sonneratia × gulngai
	Sonneratia × sp
	Sonneratia × urama
Rhizophoraceae	***Bruguiera cylindrica***
	Bruguiera exaristata
	Bruguiera gymnorrhiza
	Bruguiera hainesii
	Bruguiera parviflora
	Bruguiera sexangula
	Ceriops australis
	Ceriops decandra
	Ceriops tagal
	Kandelia candel
	Rhizophora apiculata
	Rhizophora harrisonii
	Rhizophora mangle
	Rhizophora mucronata
	Rhizophora racemosa
	Rhizophora samoensis
	Rhizophora stylosa
	Rhizophora × lamarckii
	Rhizophora × selala
Euphorbiaceae	*Excoecaria agallocha*
	Excoecaria indica
Meliaceae	*Aglaia cucullata*
	Xylocarpus granatum
	Xylocarpus mekongensis
Avicenniaceae	***Avicennia alba***
	Avicennia bicolor
	Avicennia germinans
	Avicennia integra
	Avicennia marina
	Avicennia officinalis
	Avicennia rumphiana
	Avicennia schaueriana
Acanthaceae	*Acanthus ebracteatus*
	Acanthus ilicifolius
Bignoniaceae	*Dolichandrone spathacea*
	Tabebuia palustris
Rubiaceae	*Scyphiphora hydrophyllacea*
Arecaceae	***Nypa fruticans***

[a] Species in bold typeface are those that are considered 'core' species.

Buttress roots are a common adaptation of many tropical trees, but in *Xylocarpus granatum* (**Figure 1e**) and to some degree in *Heritiera* such flangelike extensions of the trunk continue into plank roots which are vertically extended roots with a sinuous planklike form extending above the soil.

The surfaces of the aerial roots are amply covered with porous lenticels to enable gaseous exchange, while the internal structure of the roots is highly adapted, with large internal gas spaces, making up around 40% of the total root volume in some species. It is further widely accepted that there must be some form of ventilatory mechanism to aid gaseous exchange. A system of tidal suction is the probable mechanism in most species: during high tides, oxygen is used by the plant, while carbon dioxide is readily absorbed in the seawater, leading to reduced pressure within the roots. As the tide recedes and the lenticels open air is then sucked into the roots.

Seeds and Seedlings

Establishment of new mangrove plants in the unstable substrates and regular tidal washing of the mangrove environment presents a particular evolutionary challenge. All mangroves are dispersed by water and particular structures in the seed or the fruit are adapted to support flotation. In a number of groups a degree of vivipary is observed which is unusual in most plants other than mangrove species. The Rhizophoraceae have developed this to its fullest extent and here the embryo grows out of the seed coat and then out of the fruit while still attached to the parent plant, so that the propagule that is eventually released is actually a seedling rather than a seed (**Figure 1f**). In a number of other groups, including *Aegiceras, Avicennia, Nypa*, and *Pelliciera*, cryptovivipary exists in which the embryo emerges from the seed coat, but not the fruit, prior to abcission.

Figure 1 Mangrove adaptations. (a) Salt crystals secreted onto the surface of a leaf of *Avicennia*; (b) stilt roots of *Rhizophora*; (c) pneumatophores in *Sonneratia*; (d) root knees in *Bruguiera*; (e) plank roots in *Xylocarpus*; (f) *Rhizophora* propagule.

Longevity of seedlings is clearly important for many species. Most species are able to survive (float and remain viable) for over a month, while some *Avicennia* propagules have been shown to remain viable for over a year while in salt water.

Mangrove Productivity

Although mangroves often form quite low forests, under ideal conditions species have been recorded growing to heights of 50 or 60 m. Unlike most other forest types there are no characteristic understory species, with the forest floor dominated by aerial roots and mangrove saplings. The biomass is dominated by the mangrove species, but there is a considerable associated productivity arising both from epiphytes and from marine algae and bacteria in the intertidal areas and in the subtidal waterways. The associated food webs link directly with both marine and terrestrial ecosystems, including an important diversity of mollusks and crustaceans, but also terrestrial insects, birds, and some mammals.

Efforts to quantify biomass and productivity have been somewhat limited. Earlier estimates have suggested typical levels of net primary production of 18–34 $kg\,C\,ha^{-1}\,day^{-1}$, but more recent studies have shown that such figures may be considerable underestimates. Productivity in a 22-year-old *Rhizophora* stand in Malaysia was measured at 155 $kg\,C\,ha^{-1}\,day^{-1}$. Even the lower productivity figures show that mangroves are highly productive, considerably more so than adjacent marine ecosystems. It has been suggested that 40% of this net primary production is surplus to ecosystem requirements. About one-third of this surplus is exported into the adjacent marine ecosystems where it plays a critical role in supporting nearshore and offshore fisheries. The carbon storage by the world's mangrove forests is also considerable, both in the living biomass and in the accumulated sediments. This is increasingly being seen as an important carbon store in calculations of global carbon budgets.

Distribution and Biogeography

As a result of their restriction to intertidal areas, mangroves are limited in global extent (**Figure 2**), and are one of the most globally restricted of all forest types. **Figure 2** clearly shows the absolute limits to mangrove distribution. Mangroves are largely confined to the regions between 30° north and south of the equator, with notable extensions beyond this to the north in Bermuda (32°20′ N) and Japan (31°22′ N), and to the south in Australia (38°45′ S), New Zealand (38°03′ S), and South Africa (32°59′ S). Within these confines they are widely distributed, although their latitudinal development is restricted along the western coasts of the Americas and Africa. In the Pacific Ocean natural mangrove communities are limited to western areas, and they are absent from many Pacific islands.

In all, an estimated 114 countries and territories have mangroves. However, for many nations the total area is very small indeed, and the total global area of these forests is only 181 000 km^2. **Table 2**

Table 2 Total mangrove area by region

Region	*Area (km^2)*	*Proportion of global total*
South and Southeast Asia	75 173	41.5%
Australasia	18 789	10.4%
The Americas	49 096	27.1%
West Africa	27 995	15.5%
East Africa and the Middle East	10 024	5.5%
Total area	**181 077**	

Data calculated from best available national sources in Spalding MD, Blasco F, and Field CD (eds) (1997) *World Mangrove Atlas*. Okinawa, Japan: International Society for Mangrove Ecosystems.

Figure 2 The global distribution of mangrove forests. Data kindly provided by the UNEP World Conservation Monitoring Centre.

provides a summary of total mangrove areas by region.

Although these statistics suggest a relatively wide distribution, the distribution of individual species within these areas is clearly far more restricted, and **Figure 3** provides a plot of mangrove biodiversity patterns. A number of points of particular interest are clearly illustrated.

1. There is a distinct region of very high mangrove diversity, sometimes referred to as the 'diversity anomaly,' centered over Southeast Asia.
2. Away from this high diversity region mangroves generally show relatively even levels of low diversity, although there is smaller peak of diversity around southern Central America.
3. There is a wide area of the central and western Pacific Ocean from 120 to 160° W where mangroves do not occur.
4. Even in the area of highest mangrove diversity there is a very rapid latitudinal decline in species numbers away from the tropics.

One further observation, which is not fully illustrated in the figures, concerns the division of the global mangrove flora into two highly distinct subregions. An eastern group (sometimes known as the Indo-West Pacific) forms one vast and contiguous block stretching from the Red Sea and East Africa to the central Pacific. This group has a totally different species composition from the western group (the Atlantic East Pacific or Atlantic–Caribbean–East Pacific), which includes both Pacific and Atlantic shores of the Americas, the Caribbean, and the shores of West Africa.

A number of these patterns are explored more fully below.

Latitudinal Patterns

Mangroves limits are closely correlated with minimum temperature requirements. There is only one genus (*Avicennia*) that survives in environments where frosts may occur, but many species appear to have their latitudinal limits set by less extreme cold temperatures: air temperatures of 5°C appear inimical to most mangrove species. Sea surface temperatures may be more important than air temperatures for some species. The 24°C mean annual isotherm appears to be the minimum water temperature tolerated by mangroves in most areas, although this minimum is closer to 27°C on the north Atlantic coasts of America and Africa, and may be much lower in areas such as southern Japan. The relatively low-latitude limits to mangroves in Peru and Angola are probably related to the cold water currents which affect these coastlines.

Eastern and Western Floras

The division of mangroves into two distinct floras is almost complete at the species level: of the species listed in **Table 1**, three genera are shared between the two regions, but only one species. In addition to having distinctive floras, the overall niche-space occupied by the two floras differs, with western mangroves restricted to higher intertidal and downstream estuarine locations than those of the eastern group.

None of these differences can be related to contemporary ecology, and they are clearly of historical origin. Mangroves have a considerable known history, with the oldest of the modern taxa, *Nypa*, being recorded from the Cretaceous (69 million years BP) and *Pellicera* and *Rhizophora* dating back to the Eocene (30 million years BP). Information on the centers of origin and subsequent distribution patterns of mangroves is still unclear, and it is likely, given their disparate taxonomic origins, that mangroves evolved independently in a number of localities. Despite this, a number of authors have suggested that the majority of mangrove species have an eastern Tethys Sea origin with dispersal north and

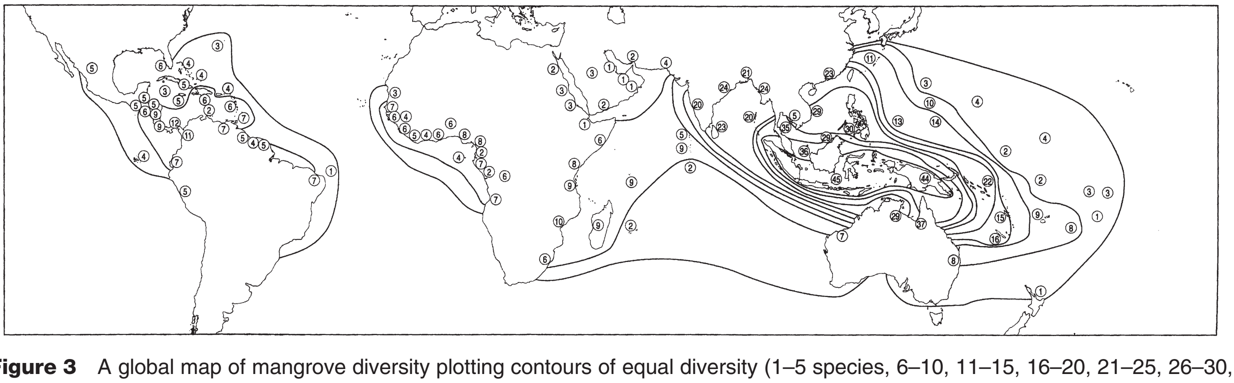


Figure 3 A global map of mangrove diversity plotting contours of equal diversity (1–5 species, 6–10, 11–15, 16–20, 21–25, 26–30, 31–35, 36–40, and 41–45). Reproduced with permission from Spalding MD (1998).

westwards (through a proto-Mediterranean) into the Atlantic and then via the Panama gap into the eastern Pacific. Whatever mechanisms may have operated, climatic conditions that were once suitable for a pan-Tethyan flora changed, and with the cooling and closure of the Mediterranean from the Tethys Sea the mangrove floras were separated. Divergence of the two communities then occurred through one or more of a number of mechanisms, including natural process of genetic drift and separation, possible extinction, and radiation. It is clear that the Atlantic Ocean and the isthmus of Panama now represent insurmountable barriers to mangrove dispersal; however, the closeness of the floras on either side of these barriers reflects the relatively short geological time since these barriers were put into place.

The Diversity Anomaly

Apart from having quite distinctive faunas, the eastern mangroves have a much greater diversity than the western group. Of the species listed in **Table 1**, only 13 are found in the western group, while 59 are found in the eastern group. This 'diversity anomaly' is reflected not only in regional maps, but also at local scales, with individual sites in the west typically having lower species counts than equivalent sites in the east. A number of theories have been propounded to explain this. It has been suggested, for example, that if most mangroves had originated in the eastern Tethys Sea the western flora may be depauperate simply as a result of being an immigrant flora. Alternatively the harsh environmental conditions during the Pleistocene, with significant temperature and sea level fluctuation, may have driven the extinction of a number of western mangroves. By contrast the Indo-West Pacific with its long and complex coastline is known to have had at least pockets of benign climatic conditions over geological timescales. These refugia may have allowed for further allopatric speciation events during periods of isolation from other areas, followed by periods of recombination with other areas as conditions ameliorated.

The relatively rapid tailing off of diversity westwards from Southeast Asia has been related to the relatively harsh climatic conditions which still prevail over much of this area, and the very large distances between more suitable localities for mangroves preventing recolonization. Similarly the gap of mangroves from the central and eastern Pacific is related to the very long distances between areas of suitable habitat. There is some evidence that mangroves may once have been more widespread in the Pacific, but if this is the case their disappearance from certain islands is probably explained by the climatic and eustatic changes of the Pleistocene.

Given the good dispersal ability of many mangrove species, distances must be very large indeed to prevent colonization, but it has also been suggested, given the relatively short time since the beginning of the last interglacial, that mangrove communities may currently be in a state of expansion.

Biodiversity Patterns at Finer Resolutions: Zonation and Succession

Numerous localized ecological factors influence the occurrence and growth patterns of mangroves. In addition to factors that affect the majority of plant species, such as water, nutrients, drainage, and soil type, significant further influence is produced by salinity and tidal influence. Considerable efforts have been made to define patterns of zonation in mangrove communities, and while such patterns do occur in many communities, the enormous variation in local conditions makes the preparation of simple summaries of 'typical' zonation patterns very difficult.

In many tidal areas the regular drying out of the soil, often coupled with patterns of restricted water circulation, or high rates of evaporation, serves to increase salinities to considerably higher levels than the surrounding seawater. This is particularly the case in areas of back mangrove where tidal flushing is less frequent and water circulation may be more restricted. It is further exacerbated in arid regions. In many areas this leads to the development of wide areas of stunted mangroves, or even bare salt pans where mangroves cannot grow. This situation is diminished or even reversed in areas where the freshwater input is more considerable, either from high rainfall or terrestrial runoff, or in some estuarine environments.

The tides also exert influences in other ways, most notably through inundation, but also through their influence on soils. Different mangrove species show quite different tolerances to inundation. Species such as *Avicennia* and *Rhizophora*, which are relatively tolerant of frequent and quite high tidal waters, typically form the most seaward zone of the mangrove system. Tides influence the soil through the delivery or removal of nutrients, and also the re-sorting of sediments. Typically finer sediments are found at higher locations in the tidal frame, while coarser sediments tend to be deposited or redistributed lower down. Once again, the complexity of interactions is highly varied between localities.

In many cases it is believed that mangrove communities may follow a succession and this has been linked to the process of terrestrial advancement (coastal progradation). It is suggested that the zonation patterns provide a model of such a succession, starting with the species more tolerant inundation and high salt levels. These are able to bind nutrients and sediments, gradually raising their position in the tidal frame such that they are then replaced by those species requiring slightly less saline and inundated conditions, and then by mangrove associates, and finally by nonmangrove species. Such a succession undoubtedly occurs in many areas, for example in parts of Southeast Asia where there is a high input of allochthonous material and where rates of coastal advancement have been recorded at 120–200 m $year^{-1}$. In other areas, however, the notion of mangroves 'creating land' is clearly not valid and mangroves show a range of responses to differing impacts of waves, climate, and sediments. In the Florida Everglades there is considerable evidence for the movement of mangrove communities both landwards and seawards, depending on sea level changes, and it may be more accurate to regard mangroves in many areas as opportunistic followers of changes in sedimentation and substrate or elevation.

Humans and Mangroves

Humans have lived in close contact with mangrove communities for millennia and in many cases have made considerable use of this association. Archaeological sites have been located that demonstrate human presence in mangrove areas in Venezuela dating back 5000–6000 years, and there is an Egyptian inscription dating back to the time of King Assa (3580–3536 BC) which mentions mangroves. Countries of the Middle East began a vigorous trade in mangrove timber from about the ninth century AD, largely for boat-building, exporting from outposts along the shores of East Africa. The European nations became involved in the utilization of mangrove bark as a source of tannins, particularly from the Americas from the sixteenth century.

The earliest record of mangrove protection dates to an edict from the King of Portugal in 1760 who restricted the cutting of mangroves for timber in Brazil unless their bark was also used for tannins. Despite such early concerns, the overexploitation of mangroves began in earnest towards the middle of the twentieth century and is continuing, and in many areas accelerating at the present time.

In many areas mangroves are highly productive and their location on the coastline places them in a zone where many other human activities have, until recently, been somewhat restricted. At the same time they often exist in close proximity to centers of human population, and can be relatively easily approached by sea or land. This makes their utilization inevitable in many areas, although the degree of sustainability of such use is highly variable.

Utilization of Mangroves

Timber and Wood Products

One of the commonest uses of mangroves is as a source of wood. Mangrove wood is often used for fuel, either directly or after conversion into charcoal. The former is widespread among artisanal communities worldwide, the latter is often for commercial purposes. Mangrove wood is also used for timber; the relatively small size of mangrove trees in many areas has meant that the primary usage of timber is the preparation of timber poles for fencing, housing construction, making of fish-traps, and other activities. Larger trees can be utilized for preparation of planking, and indeed some species have a very high value associated with their dense wood and resistance to rot, which is important for construction of houses and boats (both for local and industrial use). Further industrial use of mangrove wood is in the production of wood pulp for the paper industry, and chipboard. Large-scale commercial timber extraction or charcoal production has led to clearance of wide areas of mangroves worldwide, but there have also been some highly successful efforts to promote sustainable silvicultural practices. The Matang Mangrove Forest Reserve in Malaysia was established in 1906. With a 30-year rotation cycle this forest produces average yields of 17 tonnes ha^{-1} $year^{-1}$ of timber and fuelwood.

Fisheries

Mangroves and the associated channels that run between them are highly valuable areas of fish productivity. Numerous species inhabit mangrove areas and form the basis of artisanal and commercial fisheries, including crab, prawn, and mollusk fisheries. Mangrove areas are also widely used by a number of offshore fish species of commercial importance. These species, which include some highly profitable shrimp species, use mangrove areas for spawning or as a nursery ground, and loss of mangrove areas has severe negative impacts on fishery productivity. Cage-based fisheries have been established in many of the wider channels, and mangrove areas are widely used for the capture of juvenile prawns for transfer to aquaculture ponds. In recent years, wide areas of mangrove forest have been cut down in the development of intertidal aquaculture ponds, particularly in Southeast Asia.

Although this is a highly profitable industry, poor planning has led to the rapid and virtually irrevocable degradation of many of these ponds after only a few years. Rehabilitation of these lands is rarely undertaken, with the result that local communities lose a source of valuable natural resources, and the shrimp ponds move on to new areas.

Coastal Protection

The important role that mangroves play in the stabilization of coastal sediments and the reduction of coastal erosion has already been mentioned. This role is frequently overlooked until such time as the mangroves are removed and major storm events hit coastlines. The massive and devastating cyclones that regularly impact the coastline of the Bay of Bengal have drawn particular attention to these issues and in a number of localities around the globe there are now efforts to establish mangrove plantations precisely to stabilize sediments and reduce the impact of storm surges.

Alongside these three key areas of human importance, mangroves are regularly utilized for other purposes, a number of which are outlined in **Table 3**. It is highly difficult to place values on many of these uses and functions of mangroves. Apart from direct utilization of wood products, the link between particular products or functions and the mangrove communities which provide them is rarely made. Furthermore, for numerous communities the value in economic terms is greatly enhanced by the social value, providing a source of employment, protein, and protection for some of the world's poorest communities.

Overexploitation and Loss

Mention has already been made of the widespread loss of mangrove communities worldwide. Apart from conversion into aquaculture ponds, much of this is related to land reclamation activities for agriculture and for urban and industrial development, and large areas have also been severely degraded or removed by commercial timber companies or through overexploitation by local communities. Some further degradation or loss has been related to human-induced changes to the water regime (including upstream dams leading to reductions in sedimentation at river mouths), pollution (mangroves are particularly sensitive to oil spills), and conversion into salt pans for industrial salt production. Accurate figures for the global extent of mangrove loss are unavailable, but it is generally agreed that between 30% and 50% of the world's original mangrove cover has already gone. Reliable statistics are available for a number of countries. In Southeast Asia, for example, the loss figures for four countries are:

- Malaysia: 12% from 1980 to 1990
- The Philippines: a 60% loss from 4000 km^2 originally to 1600 km^2 by the 1990s
- Thailand: a 55% loss from 3679 km^2 in 1961 to 1676 km^2 in 1996
- Vietnam: a 37% loss from 4000 km^2 originally to 2525 km^2 by the 1990s.

These figures alone suggest a total loss of some 4% of the current global total. The four countries concerned have certainly suffered significant loss of mangrove, but they are not alone.

Sea level rise associated with global climate change must also be considered as a significant threat to mangrove ecosystems. It is important to note that the impacts of proposed changes (most models predict rises in sea level of 30–100 cm by 2100) are relatively insignificant in some areas where high levels of sediment movement and deposition will counter such rises, or where other eustatic changes, such as those associated with tectonic movements, will remove or further enhance changing sea level effects. Furthermore, mangrove species and communities are highly

Table 3 Minor or regionally restricted uses of mangroves

Honey production	An important economic activity in some countries
Fodder	For cattle, camels, and goats, notably in India and Pakistan
Recreation	Walkways, boat-based tours, and other visiting facilities have been established for tourists and local communities in some areas, notably Australia, Bangladesh, and Trinidad
Thatch and matting	Primarily from the leaves of the mangrove palm *Nypa fruticans* in Southeast Asia and from introduced populations in West Africa
Tannin extraction	Formerly widespread, this activity has become less significant as synthetic products have become available
Traditional medicine	A wide array of secondary metabolites has been recorded from mangrove plants. Products are widely used in many traditional communities, and studies are showing important anti-viral properties as well as potential uses for insect control and protection from ultraviolet light
Food	*Nypa fruticans* is widely used for the production of sugar, alcohol, and vinegar. Fruits of *Avicennia, Kandelia*, and *Bruguiera* are used as a source of food in some countries

opportunistic and will colonize new areas with some rapidity. Sea level rise remains a problem, however, as mangrove communities in many areas may become squeezed out as sea level rise forces mangrove communities landwards, but human use prevents landward migration.

Protection and Plantation

Despite the massive losses that mangrove communities have gone through in the past decades there have also been concerted efforts to protect them in some areas, and the growing realization of their value has led to widespread efforts to utilize mangroves in a more sustainable manner, and in some places large areas of mangrove plantations have now been established.

Worldwide, there are currently over 1100 protected areas with mangroves managed for conservation purposes spread between 99 countries. These cover some 10% of the global total. Although this is a far higher proportion than for many other forest types, active protection is absent from many of these areas, and the remaining unprotected sites are probably more threatened than many other forest types because of their vulnerability to human exploitation.

Increasing recognition of the various values of mangrove forests is leading to the establishment of mangrove plantation or restoration projects in many countries: for coastal defense, as a source of fuel or timber products, for fisheries enhancement, or often for a combination of these benefits. Plantation and restoration has been most widespread in Asian countries, with over 2300 km^2 in Bangladesh, Pakistan, and Vietnam.

Although the total area of such plantations remains insignificant when compared to global mangrove losses, they represent an important new development. Active management for direct economic benefits in these and other mangrove areas is growing. The Matang Mangrove Reserve in Malaysia has been managed for 100 years. Studies have shown combined benefits arising from timber and fuelwood products (notably charcoal), but also from the large nearshore fishery (directly or indirectly providing employment for over 4000 people), from aquaculture on the mud flats below the mangroves, and from tourism.

It is rare that such holistic studies have been carried out. Often the human benefits provided by mangrove fall between several sectors of the economy – fisheries, forestry, tourism, and coastal protection – and their combined benefits are not realized. Improved assessment of these benefits will undoubtedly lead to much wider-scale protection and sustainable management for mangroves globally.

Acknowledgement

Adapted with permission from Spalding MD (2001) Mangroves in Steele JH, Turekian KK and Thorpe SA (2001). *Encyclopedia of Ocean Sciences*. Published by Academic Press, London.

See also: **Ecology**: Aquatic Habitats in Forest Ecosystems. **Environment**: Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. **Resource Assessment**: Forest Resources. **Silviculture**: Treatments in Tropical Silviculture. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Tree Physiology**: A Whole Tree Perspective; Root System Physiology; Stress. Tropical Tree Seed Physiology. **Tropical Ecosystems**: Bamboos, Palms and Rattans. **Tropical Forests**: Combretaceae; Tropical Moist Forests.

Further Reading

Field CD (1995) *Journey amongst Mangroves*. Okinawa, Japan: International Society for Mangrove Ecosystems.
Field CD (ed.) (1996) *Restoration of Mangrove Ecosystems*, p. Okinawa. Japan: International Society for Mangrove Ecosystems.
Lacerda LD (2002) *Mangrove ecosystems: function and management*. Heidelberg, Germany: Springer-Verlag.
Robertson AI and Alongi DM (eds) (1992) *Tropical Mangrove Ecosystems*, Coastal and Estuarine Studies no. 41. Washington, DC: American Geophysical Union.
Saenger P (2003) *Mangrove Ecology, Silviculture and Conservation*. Dordrecht, The Netherlands: Kluwer Academic Publications.
Saenger P, Hegerl EJ, and Davie JDS (eds) (1983) *Global Status of Mangrove Ecosystems*, IUCN Commission on Ecology Papers no. 3. Gland, Switzerland: IUCN (World Conservation Union).
Spalding MD (1998) *Biodiversity Patterns in Coral Reefs and Mangrove Forests: Global and Local Scales*. PhD dissertation, University of Cambridge.
Spalding MD, Blasco F, and Field CD (eds) (1997) *World Mangrove Atlas*, p. Okinawa. Japan: International Society for Mangrove Ecosystems.
Tomlinson PB (1986) *The Botany of Mangroves*. Cambridge, UK: Cambridge University Press.

Southern Hemisphere Conifers

J C G Banks, Australian National University, Canberra, Australia

Introduction

The southern hemisphere is home to almost half of the world's conifers including a small number of tropical species that occur in both hemispheres

Table 1 World conifers, by hemispheres, families, genera and species

Taxon	World	Hemisphere		
		North	Both north and south	South
Araucariaceae				
Genera[a]	3	1	1	3
Species	40	8	3	32
Cupressaceae				
Genera[b]	20	10	1	10
Species	117	82	1	39
Pinaceae				
Genera[c]	10	10	1	
Species	192	192	1	
Podocarpaceae				
Genera[d]	11	0	2	9
Species	174	80	32	124
Taxodiaceae				
Genera[e]	11	10		1
Species	15	12		3

[a] Southern hemisphere genera: *Araucaria*, *Agathis*, *Wollemia*.
[b] Southern hemisphere genera: *Diselma*, *Fitzroya*, *Austrocedrus*.
[c] This family is represented by a single species, *Pinus merkusii*, in the southern hemisphere.
[d] Southern hemisphere genera: *Podocarpus sensu lato*, *Dacrydium*, *Phyllocladus*, *Lagostrobus*, *Saxegothaea*.
[e] The only genus of this family in the southern hemisphere is *Athrotaxis*.

(**Table 1**). All five conifer families are represented in both hemispheres with 40% of the genera south of the equator. The Cupressaceae is the most cosmopolitan of the families with 10 genera in each hemisphere, but with most species in the north. The Podocarpaceae occurs in all southern continents with significant numbers of species extending north of the equator in Africa, Southeast Asia, Central America, and the Caribbean. The Araucariaceae has a more restricted distribution found in Australasia, and north through the island chain to Malaysia, with one genus in South America. The Pinaceae and Taxodiaceae are centered in the northern hemisphere with only one and three species respectively found south of the equator. Further details on the ecology of the southern conifers is found in the reference texts. Many northern hemisphere conifers are today grown in the southern continents in plantations and/or as ornamental trees and shrubs in city parks and gardens. The major plantation species is *Pinus radiata* originating from California which supports major timber and paper industries, while other species include *P. elliottii*, *P. caribaea*, *P. patula*, and *P. pinaster*. Ecologically, these are pioneer species and when freed from their natural pests and diseases they are fast growing. Numerous ornamental cultivars, mostly from the Cupressaceae, are important components of the urban forests where they are planted for their decorative features by civic and private landholders.

Taxonomy

The focus here is on the three dominant southern families, Araucariaceae, Cupressaceae, and Podocarpaceae, with minor reference to Pinaceae and Taxodiaceae that are comprehensively covered in the article on the conifers of the northern hemisphere (*see* **Temperate and Mediterranean Forests**: Northern Coniferous Forests). The structure of the female cone can be used to recognize the southern families. In the Araucariaceae the female cone scales are spirally arranged with only one relatively large seed per cone scale to which it is fused in the genera *Araucaria* and *Agathis*, but free in *Wollemia*. In all three genera the cone disintegrates at maturity to release the seed. In Cupressaceae all the southern genera belong to the subfamily Callitroideae which has only one monospecific genus, *Tetraclinis articulata*, north of the equator. The cones in this subfamily are distinct possessing valvate scales in pairs or whorls of three; at maturity these open to release relatively small-winged seeds. In contrast the seed bearing cones in Podocarpaceae are variously reduced and in the extreme may consist of a single seed atop a fleshy, plumlike receptacle comprising the fused remnants of the cone, or with one or two seeds attached to the central axis of the 'cone.' This origin of this reduced cone was initially misidentified with the family allocated to the Taxaceae, the yews.

Araucariaceae: The Araucarias and Kauri and Wollemi Pines

The Araucariaceae consists of three distinct genera, *Araucaria*, *Agathis*, and *Wollemia*, found in an island arc from Malaysia to New Zealand and including eastern Australia with *Araucaria* extending to South America (**Figure 1**). Species occur in tropical to warm temperate rainforests in coastal to montane environments. Rainforest species are regarded as postcyclone pioneers possessing rapid growth and apical dominance. They overtop the broadleaf rainforest as emergents with the tallest species *Araucaria klinkii*, klinki pine (**Figure 2**), reaching 70 m at maturity. It is found in tropical hill rainforests in New Guinea.

Araucaria: The Araucarias

The genus *Araucaria* consists of about 19 species, two in South America and two in eastern Australia with the remainder in Oceania along the island arc from Norfolk Island to New Caledonia where several

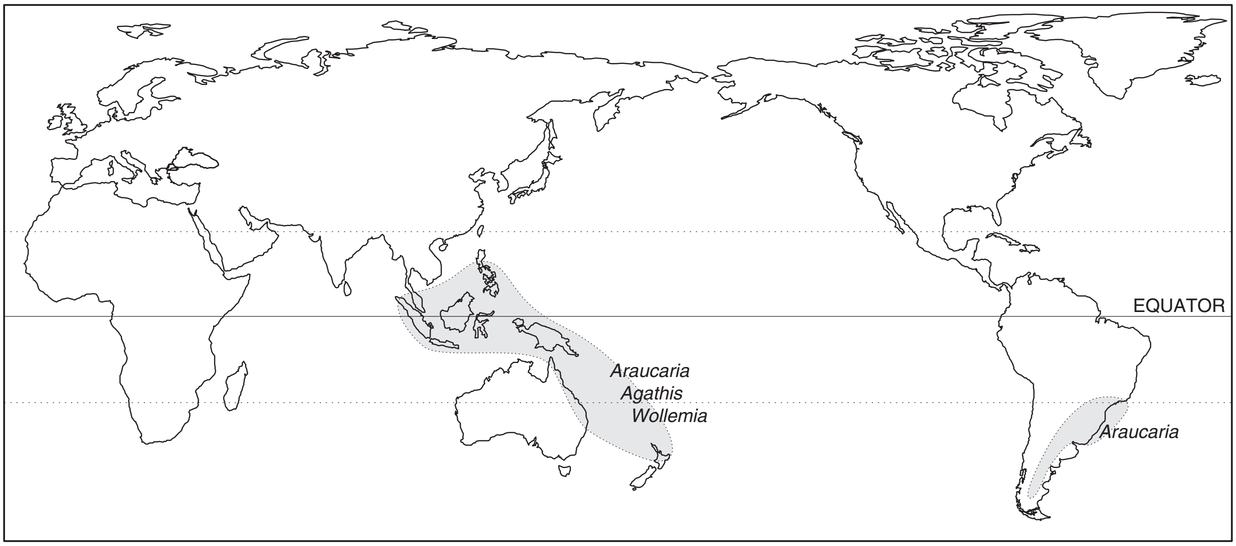


Figure 1 World distribution of Araucariaceae.

Figure 2 Klinki pine, *Araucaria klinkii*, rainforest emergents 70 m tall near Bulolo, Papua New Guinea.

species coexist on the Isle of Pines. The majority of species are maritime often occurring in pure coastline forest stands exposed to onshore salt-laden winds. To survive this hostile maritime environment the leaves are covered in a thick surface wax coat which protects them against salt damage. The significance of this feature was clearly illustrated when in the 1970s *Araucaria heterophylla*, the Norfolk Island pine, long established as a backdrop to Sydney's famous Bondi Beach, went into rapid decline. The primary cause was a new nonbiodegradable detergent that was polluting onshore winds, stripping the wax coat off the foliage and allowing salt to attack the exposed leaves.

A distinctive feature of the araucarias is that species can be readily recognized by their distinctive crown silhouettes. For example the Pacific island species *A. columnaris*, Cook's pine, has the peculiar habit of shedding its lower branches and then regenerating the lower crown from adventitious buds resulting in a dense narrow columnar crown which widens out towards the apex. Another is *A. heterophylla*, which maintains almost perfect crown symmetry with a simple two-order branching system (**Figure 3**). Similarly, the South American *A. angustifolia*, candelabra pine, and *A. araucana*, Chile pine, which both occur in pure forest stands, possess characteristic sillouettes. *Araucaria bidwillii*, the bunya bunya from eastern Australia, has the distinction of having large football-sized cones weighing 4–5 kg at maturity. *Araucaria cunninghamii*, hoop pine, is the most important araucaria plantation species providing a major softwood resource in southeast Queensland. This species exhibits some genetic variability both within and between geographic occurrences that extend from northern New South Wales to New Guinea. Tree breeding programs that began last century have significantly improved today's breeding stock for plantation use.

Figure 3 Norfolk Island pine, *Araucaria heterophylla*, showing its symmetrical crown trees at Twofold Bay, New South Wales.

Agathis: The Kauri Pines

The kauri pines are majestic trees with examples planted in urban parks in both hemispheres. The genus contains about 19 species that resemble angiosperms by having a wide-spreading crown atop massive primary branches arising from a distinct crown break. The bark is deciduous, a unique feature in the conifers with the exception of *Pinus bungeana*, the lace-bark pine from China. The bole attains massive proportions in old trees and exhibits little or no taper.

The most extensive and greatest kauri forests were in New Zealand where *Agathis australis*, known simply as kauri pine, dominated much of the temperate rainforests in the northern half of North Island. These were first seen by Capt. Cook in 1770 and noted as a potential source of spars with the first trial shipment in 1794. By 1820 timber was being exported from Whangaroa harbor. Exploitation of these forests in Northland and the Coramandel Peninsula was in full swing by the 1860s reaching its zenith by the turn of the century. Kauri timber is unsurpassed in the conifers. The wood is off-white to red and brown, resinous, straight grained, of great strength and durability and it was available in large sizes. On occasions timber was cut from buried logs, remnants of earlier forests destroyed in past volcanic eruptions. Some of these fossil logs have been dated to 30 000 years old, attesting to the timber's durability. Today only small stands remain, protected in reserves including one in Waipoura which has conserved the stand containing one of the world's largest living conifers, the Tane Mahuta or 'Lord of the Forest,' a 52-m tall tree estimated to be over 2000 years old. In eastern Australia, the three species of kauri pines are minor rainforest trees. Harvesting started in the nineteenth century and followed a similar cycle with the last cutting in the 1960s in the Ingham hinterland. Some kauri timber is still cut in small quantities in Malesia. As a plantation species in Queensland, *A. robusta*, the South Queensland kauri, was unsuccessful as it suffered severe insect defoliation when planted in pure stands.

An unusual commercial product from the kauri forests is the kauri gum, a resin that freely exudes from wounds accumulating on branches and in quantity over time beneath trees more than 1000 years old. Both fossil and fresh resin, called copal or dammar, were harvested in large quantities in New Zealand and Malesia around the end of the nineteenth century. Its principal uses were in varnishes and linoleum. Today small amounts, especially pieces with entrapped insects, are made into jewellery.

Wollemia: The Wollemi Pine

The discovery of this new monospecific genus in 1994 surprised the botanical world, as it had long been assumed that all of the world's conifers had been discovered and the major interest to conifer taxonomists was the ever-increasing number of ornamental cultivars entering horticulture. Its discovery, less than 200 km from Sydney, is described in Woodford's book devoted to the species. The scientific name given to this new taxon is *Wollemia nobilis* (**Figure 4**). The genus name is that of the national park in which it was found while the specific name alludes to its majestic form. Wollemi pine trees were found in the bottom of a deep sandstone canyon, one of many in this national park. Following intensive searching, only three stands have been located, consisting of fewer than 50 trees in total growing in small remnant stands of warm temperate rainforest that includes *Ceratopetalum apetalum*, coachwood. The pollen record shows the species to have been once widespread in southern Australia with occurrences in Antarctica and South America. Trees exceed 30 m in height and age estimates calculated from annual growth rings on a fallen tree indicates mature trees to be around 400 years old. One very distinctive feature of this new conifer is that it readily regenerates vegetatively from adventitious and basal buds. Only two widely distant conifers exhibit similar features: *Pinus canariensis*, Canary Island pine, and *Sequoia sempervirems*, Californian redwood.

Figure 4 Wollemi pine, *Wollemia nobilis*, a new conifer genus discovered in 1994 in a deep sandstone gorge in the Wollemi National Park near Sydney. Courtesy of Jaime Plaza, Royal Botanic Gardens and Domain Trust.

Cupressaceae: The Cypress Pine Family

Most species of the southern Cupressaceae are components of the cool temperate rainforests in South America, New Zealand, and Tasmania with several extending to tropical rainforests in Malesia (**Figure 5**). Species from four genera have adapted to semi-arid environments comparable to several northern cypresses and junipers, such as *Cupressus arizonica*, the Arizonia cypress, and *Juniperus monosperma*, the one-seed juniper from North America's southwest. Compared with their counterparts in the northern hemisphere very few species of the cypress pines are sources of commercial timber and then in only limited quantities, and none has attracted horticultural interest as in *Chamaecyparis, Cupressus*, or *Thuja*. Several are monospecific genera representing relic tree genera persisting under present-day environments. One is *Diselma archeri*, known only from a few isolated mountaintops in western and central Tasmania. On Mount Dundas trees of this species reach 11 m in height and 2.0 m in girth with ages in excess of 500 years. Long-lived trees can be used to provide dated tree ring chronologies from which climate signatures can be

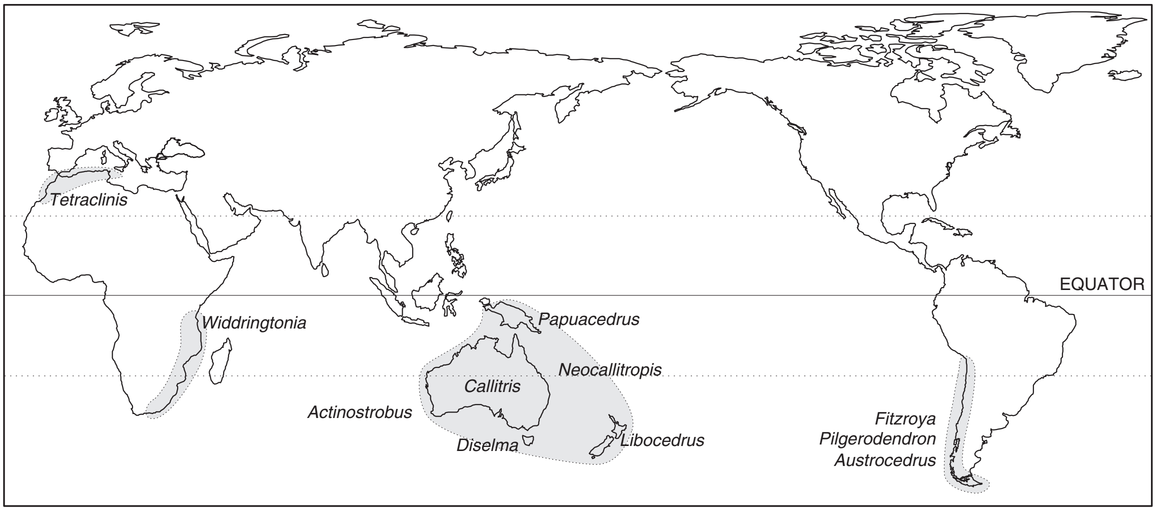


Figure 5 World distribution of Cupressaceae.

extracted for developing past climates. Pines and oaks have been used for this purpose in the northern hemisphere. In the south several Cupressaceae trees, and some from the Podocarpaceae, have proved useful for climate reconstruction. Chronologies of 1500 years have been extracted from *Fitzroya cupressiodes*, the Chilean alerce, trees that can be 50 m tall with a girth of 10 m, and similarly from *Austrocedrus chilensis*, Chilean cedar, a long-lived tree found in pure stands of xeric woodlands near the ecotone with the Patagonian steppe.

Callitris: The Australian Cypress Pines

Callitris and *Actinostrobus* in Australia and *Widdringtonia* in Africa have adapted to dry semi-arid woodlands. The most successful genus, *Callitris*, the Australian cypress pines, has three species in New Caledonia and about 12 in Australia. *Callitris intratropica*, the tropical cypress pine (**Figure 6**), is a slender tree up to 8 m tall, occasionally found in small isolated stands in the eucalypt woodlands across the summer rainfall zone of northern Australia. In contrast *C. glaucophylla*, the white cypress pine, is widely dispersed across southern Australia with major occurrences in the southeast where forests lie on the western slopes of New South Wales. It is a small to medium sized tree up to 18 m tall with a conical crown clothed in a variable but usually glaucous foliage. Interestingly, when first discovered, these forests were open woodlands of scattered white cypress pine and eucalypts from the ironbark, box, and red gum groups including *Eucalyptus crebra, E. microcarpa*, and *E. dealbata*. Following severe droughts in the late nineteenth century graziers abandoned extensive areas of these woodlands. Dense cypress regrowth then established which is the origin of today's forest stands in the Barrbine and Narrabri and Cobar districts (**Figure 7**). These are managed for their durable timber, providing about 5% of the State's total timber production.

Figure 6 Tropical cypress pine, *Callitris intratropica*, in the tropical woodlands, Kimberleys, Western Australia.

Figure 7 Regrowth forest of white cypress pine, *Callitris glaucophylla*, Pilligra State Forest, Coonabarabran, New South Wales, Australia.

Podocarpaceae: Podocarps, Plum Pines, and Yellow Woods

The Podocarpaceae comprises seven tree and two shrub genera with *Podocarpus* as the largest genus. It is divided into eight sections; these are elevated to generic status by some botanists. All genera are represented in the Australasian–Oceanic region suggesting that the family originated in this area (**Figure 8**). In total about 130 species are recognized with the majority (70%) in southeast Asia and Australasia, 20% in Central and South America, and 10% in Africa. Almost all are rainforest trees, slow growing and fire-sensitive with tree species producing strong, even-grained, easy-to-work highly valued timbers. The implications of this are that once the slow-growing virgin trees are cut out there will be no secondary timber sources; moreover it is important to conserve areas as examples of the original forest.

Podocarpus

African species of *Podocarpus* belong to the section *Afrocarpus*, most of which are called 'yellow woods' on account of the color of the timber. These include *Podocarpus latifolius*, real yellow wood, a tree growing to 30 m in height and 2 m in girth which is widely distributed in southern Africa especially in the southeast. Others are *P. falcatus* called yellow wood, also from southern Africa, and *P. dawie*, a large timber tree up to 30 m tall, from the tropical rainforests in Central Africa. In the Australasian–Oceanic region *Podocarpus* is the most widely distributed genus, with species extending to Asia including the eastern Himalayas and the southern Japanese islands. *Podocarpus nagi*, one of the most widespread species found from Burma to Fiji, is a slender tree up to 20 m in height that was much sought after as a spar tree in the days of sails. In New Caledonia *P. sylvestris*, the false kauri, has been a valued source of high-quality timber, while *Podocarpus ustus* (a smaller tree) was recognized as late as 1957 to be parasitic on another conifer *Dacrydium taxoides*. This is the only known example of parasitism in the conifers.

In tropical New Guinea the podocarps *Podocarpus archboldii* and *P. papuanus* are found in the cooler tropical environments in high-altitude primary forests between 2000 and 3000 m above sea level. In South America two species, *P. curvifolius* and *P. nubigenus*, are found in the southern Andes. Australian tree species are all rainforest trees and never very common; *P. amarus* and *P. elatus*, the black and brown pines, are large trees up to 30 m tall in lowland rainforests. In New Zealand the podocarps have in the past been important timber trees. *Podocarpus dacrydioides*, the kahitatea, is a buttressed 30 m tree of wet swamp forests, and *P. spicatus*, the matai, of the hill forests at altitudes up to 600 m above sea level. Today temperate rainforests containing residual stands of these conifers are in conservation reserves. Several species have adapted to environments outside the rainforest where they occur as small trees or shrubs. In Australia *P. spinulus* occurs in coastal sand dune woodlands in the southeast, *P. drouynianus* is a shrub in the jarrah forest in the southwest growing on poor laterite soil dominated by *Eucalyptus marginata*, and *P. lawrencei* is a small tree

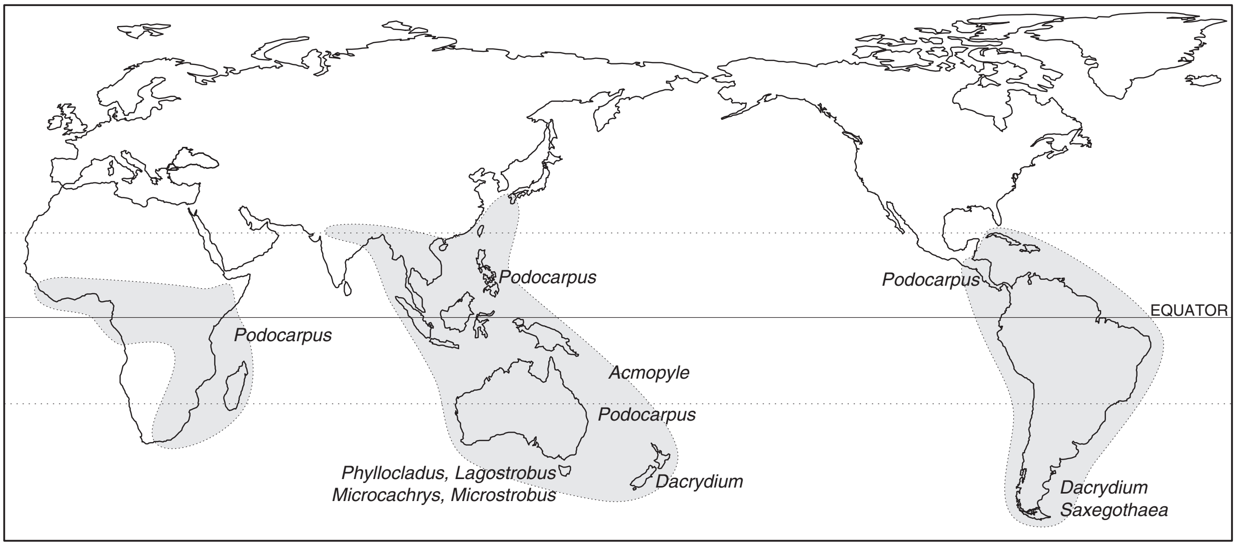


Figure 8 World distribution of Podocarpaceae.

in the subalpine forest and as scramblers in the alpine zone.

Dacrydium, Phyllocladus and *Lagostrobus*

Dacrydium, allied to *Podocarpus*, contains 20 species of which five occur in New Zealand, four in New Caledonia, and an equal number in the Indonesian island arc extending as far as Thailand. Two species are also found in New Guinea. The New Zealand species have been important elements in the virgin temperate rainforests with *Dacrydium cupressinum*, the rimu, a major timber species. It has scale leaves similar to those found in the cypress family but differing by being spirally arranged. One small species, *D. fonkii*, is found in Patagonia adding another link to the southern temperate rainforests.

The five species of *Phyllocladus* have one unique feature for the conifers: flattened branchlets, or cladodes, that take over the function of the leaves which are reduced to nonfunctional scales. *Phyllocladus asplenifolius*, the celery top pine, is a long-lived slender tree typically found in the tall wet sclerophyll forests in Tasmania. The cool temperate rainforest species *Lagostrobus franklinii*, the Huon pine, is a very slow growing long-lived species found in valley floors along stream lines and on Mt Read in the north-west. It challenges *Pinus longaeva*, the bristle cone pine, for being the oldest living conifer. The resin rich timber of Huon pine is highly prized for boatbuilding as it works easily and is durable in salt water.

Saxegothaea

This is a monospecific genus native to southern Patagonia in South America where it occurs in dense cool temperate rainforest. *Saxegothaea conspicua*, the Albert yew, is a small tree 10–12 m tall, and is regarded as a living link between *Araucaria* and *Podocarpus* having foliage resembling the former and wingless pollen and cones of the latter. It was discovered by the plant hunter William Lobb and introduced into cultivation in 1846.

Pinaceae and Taxodiaceae

Only one of the 250+ species in the family Pinaceae extends into the southern hemisphere. This is *Pinus merkusii*, the Tenasserim pine, which has natural occurrences in Burma, Cambodia, Vietnam, the Philippines, and Indonesia extending to the island of Sumatra where it is found in montane forests between 1000 and 1500 m above sea level in the Barsian Range just south of the equator. It grows in small groups of trees in the broadleaf forest and owes its survival to occasional dry-season spot fires to provide suitable regeneration gaps in the forest.

The genus *Athrotaxis* is an extreme geographic outlier of the redwood family, Taxodiaceae, reminding us that in past times this family was once widespread. Today three species are restricted to the cool montane temperate forests of Tasmania. *Athrotaxis selaginoides*, King William pine, is found in the Western Ranges and around Lake St Claire. It is a slow-growing tree, up to 30 m tall, typically occurring in small isolated stands. It is long-lived, persisting on sites that are rarely burnt by natural wildfires. At higher altitudes the smaller *A. selaginoides* is a component of the treeline forests. The third species, *A. laxifolia*, has intermediate morphology and ecologically lies between the other two species.

See also: **Mensuration**: Tree-Ring Analysis. **Temperate and Mediterranean Forests**: Northern Coniferous Forests; **Temperate and Mediterranean Forests**: Southern Coniferous Forests. **Temperate Ecosystems**: Pines. **Tree Breeding, Practices**: Southern Pine Breeding and Genetic Resources. **Tropical Ecosystems**: Tropical Pine Ecosystems and Genetic Resources.

Further Reading

Banks JCG (2000) *Interpreting Wollomi Pine Stand Dynamics*. In: Poster Proceedings, International Dendrochronology Conference 2–7 April 2000. Madoza, Argentina.

Dalimore W and Jackson AB (1966) *A Handbook of Coniferae and Ginkgoaceae, revd SG Harrison*. London: Edward Arnold.

Dargavel J, Hart D, and Libbis B (eds) (2001) *Perfumed Pineries: Environmental History of Australia's Callitris forests*. Canberra: Centre for Resource and Environmental Studies, The Australian National University.

Enright NJ and Hill RS (1995) *Ecology of the Southern Conifers*. Melbourne, Victoria: Melbourne University Press.

Jones WD, Hill KD, and Allen JM (1995) *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. *Telopea* 6: 173–176.

Mirov NT (1967) *The Genus Pinus*. New York: Ronald Press.

Rolls E (1973) *Running Wild*. Sydney, New South Wales: Angus & Robertson.

Simpson TE (1973) *Kauri to Radiata: Origin and Expansion of the Timber Industry of New Zealand*. Auckland, New Zealand: Hodder & Stoughton.

Vidakovic M (1991) *Conifers: Morphology and Variation, transl. Maja Soljan*. Hrvatske, Croatia: Graficki Zavod.

Woodford J (2000) *The Wollemi Pine: The Incredible Discovery of a Living Fossil from the Age of the Dinosaurs*. Melbourne, Victoria: Text Publishing.

Swietenia (American Mahogany)

J P Cornelius, World Agroforestry Centre, Lima, Peru
K E Wightman, Purdue University, West Lafayette, IN, USA
J E Grogan, Yale University, New Haven, CT, USA
S E Ward, Mahogany for the Future, Puerto Rico

Introduction

The *Swietenia* genus ('true' or American mahoganies) consists of three closely related species (*S. humilis*, *S. mahagoni*, and *S. macrophylla*) whose largely allopatric natural distributions are concentrated in the seasonally dry, lowland neotropics. The latter two species have also been widely planted elsewhere, particularly in tropical Asia and Oceania. The long-established, sustained demand for mahogany timber is largely due to its high stability, durability, easy workability, and beauty. It is used principally in the manufacture of high-quality furniture, flooring, doors, window frames, and decorative veneers. *Swietenia macrophylla*, the only species still with commercially exploitable natural populations, is a massively buttressed, light-demanding canopy-emergent, reaching heights of up to 70 m and diameter at breast height (dbh) of 3.5 m. It occurs principally at low densities of 0.1–3.0 merchantable trees ha^{-1}, although higher densities may occur as a result of catastrophic disturbance, e.g., hurricanes, fires, and floods. The natural ranges of *S. humilis* and *S. mahagoni* are largely deforested; the ecology of these species in natural forest is little known, but is probably similar to that of *S. macrophylla*. All three species are subject to restrictions on international trade under Appendix II of the Convention on International Trade in Endangered Species (CITES), a consequence both of general deforestation and the unsustainable exploitation to which they have been subjected. Sustained production of *S. macrophylla* in natural forests is thought to be feasible. However, due to the species' requirement for high light and relatively low competition in its early years – conditions unlikely to be met under selective logging – it will require intensive methods. The establishment of *Swietenia* plantations has been inhibited by the attacks of mahogany shoot borers (*Hypsipyla* spp.). However, accumulated experience and growing experimental knowledge indicate that, with appropriate pest management methods, mahogany can be successfully grown in plantations.

Taxonomy and Genetics

American or true mahoganies (*Swietenia* spp.) are the most valuable species of the Meliaceae, a pantropical family which includes other high-quality timber trees such as Spanish cedar (*Cedrela odorata*), andiroba (*Carapa guinanensis*), the African mahoganies (*Lovoa*, *Entandrophragma*, *Khaya*), and the Asia-Pacific red cedars (*Toona* spp.) (all of the Swietenioideae subfamily), as well as less closely related species of value, e.g., neem (*Azadirachta indica*) and pride of India (*Melia azedarach*). The genus, named after the Austrian botanist Gerard von Swieten, consists of three largely allopatric species: *S. humilis* (dry-zone, Pacific, Pacific Coast, or Mexican mahogany), *S. macrophylla* (big-leaf, Brazilian or Honduras mahogany), and *S. mahagoni* (Cuban, Dominican, West Indian, or small-leaf mahogany) (**Figure 1**). The latter, restricted naturally to the Bahamas, Cuba, Jamaica, Hispaniola, and southern Florida, is the type species. The first to enter into international trade, its rapid depletion led quickly to commercial displacement by *S. macrophylla*. This has the largest natural distribution of the three, ranging from southern Mexico (23° N) to the southern Amazon of Bolivia and Brazil (18° S). *Swietenia humilis*, the least-known species, is restricted principally to the dry Pacific watersheds of Mesoamerica from the Mexican states of Durango and Sinaloa to northern Costa Rica; although sometimes referred to as Pacific Coast mahogany, it also occurs well inland. Within and outside their natural ranges, the species are generally known as caoba (in Spanish-speaking states except Bolivia, where the name mara is used), mahogany (English-speaking states), and mogno (Brazil), i.e., without the epithets found in the technical literature. Many other names are used locally by indigenous peoples.

Biologically, the three species are rather poorly defined; the current taxonomy is maintained essentially on the basis of the largely allopatric distribution described above, coupled with general morphological differences. The species are not easily distinguished on the basis of leaf and flower morphology, and appear to hybridize readily when in proximity (e.g., *S. humilis* and *S. macrophylla* where their ranges overlap in northeastern Costa Rica; *S. macrophylla* and *S. mahagoni* as exotics in Puerto Rico). Although both common-garden experiments and preliminary studies with DNA markers confirm that the species represent distinct genetic entities, it may be that *S. humilis* and *S. macrophylla*, at least, are no more genetically distinct than regional variants of other species that range over similarly diverse conditions, e.g., Pacific and Atlantic

Figure 1 (a) Mature *Swietenia humilis* tree, Comayagua, Honduras (courtesy of JP Cornelius); (b) *S. macrophylla* saplings in 3-year-old plantations, Quintana Roo, Mexico (courtesy of KE Wightman); (c) foliage of *S. mahagoni*, Puerto Rico. Courtesy of JP Cornelius.

Central American ecotypes of *Cedrela odorata* and *Cordia alliodora* (Boraginaceae). The taxonomic significance of observed interspecific variation in chromosome number is questionable because wide intraspecific variation in chromosome number has also been reported.

The little provenance work that has been carried out (*S. macrophylla* and *S. humilis* only) suggests substantial genetic variation between widely separated provenances, but little differentiation between populations at a more local scale (e.g., within the Yucatan peninsula of Mexico). Joint consideration of randomly amplified polymorphic DNA (RAPD) studies in Mesoamerica and allozyme work in Bolivia suggests that neutral genetic variation shows a similar trend. Quantitative and molecular (allozymes, RAPDs, microsatellites) data indicate abundant genetic variation at the within-population level, as is common in tropical trees. Long-distance pollination has been demonstrated in *S. humilis*, and probably occurs in all three species, contributing to the maintenance of genetic variation even in apparently isolated populations. Sporadic tree improvement activities have been implemented, e.g., clonal seed orchards in Mexico and Fiji (*S. macrophylla*), and seedling seed orchards and progeny tests in Costa Rica, Mexico (*S. macrophylla*), and Honduras (*S. humilis*). The absence of large, sustained planting programs explains the lack of more intensive breeding activities.

Swietenia macrophylla and, to a lesser extent, *S. mahagoni*, have been widely planted outside their native ranges, particularly in Southeast Asia and Oceania; plantations established in Fiji, Indonesia, Philippines, Solomon Islands, and Sri Lanka total more than 190 000 ha. There are also increasing areas of *S. macrophylla* plantations within the natural range, particularly in southern Mexico and

Guatemala. Worldwide, however, mahogany remains a minor plantation species, with total area less than one-twentieth that of teak. In large measure, this can reasonably be attributed to the problem – real or perceived – of mahogany shoot-borer attack.

Ecology

Swietenia macrophylla

Typically, *Swietenia* are species of relatively low-altitude (≤ 1400 m), seasonally dry forests, and are largely absent from or rare in perhumid regions within their natural ranges. These factors are responsible for an interruption in the natural range of *S. macrophylla*, formed by the coast-to-coast humid and/or high-altitude belt that runs diagonally from northeastern Costa Rica to north-Pacific Panama. Similarly, *S. macrophylla*'s arc-shaped range in South America traces the seasonal tropical forests along the northern, western, and southern rims of the Amazon basin.

Big-leaf mahogany is one of the giants of the tropical forest, reaching heights of up to 70 m and diameter (above often massive buttresses) of 3.5 m. Trees of such dimensions are probably more than 400 years old and are now rarely found; across its range, the average merchantable big-leaf mahogany tree is likely to be 20–30 m tall with dbh of 60–120 cm. Young trees have narrow, shallow crowns and may remain unbranched for 6–8 m. The mature crown, composed of a few, large primary branches, tends to be irregular or umbrella-shaped. The thick bark of older trees is deeply furrowed and sometimes nearly black. The pinnately compound leaves are deciduous; trees tend to be leafless for weeks rather than months. The small, unisexual flowers emerge with the leaves, and appear to be pollinated by small bees and moths. In natural forest, trees of 14 cm dbh may flower, but only trees >30 cm with exposed crowns are likely to do so consistently. The species is monoecious and tends to be fully outcrossing, at least in relatively undisturbed conditions. It is unknown whether this is due to genetic self-incompatibility, abortion, selection against inbred zygotes, or dichogamy. Mahogany fruits are woody capsules, each containing 25–60 wind-dispersed, samaroid seeds (**Figure 2**). These measure 1–2 cm (up to 13 cm including the wing) and generally land within 50 m of the mother tree. Maximum seed production occurs in large but vigorous trees of 90–130 cm dbh, which can produce up to 800 fruit capsules in a single year. Germination of mahogany seed is maximal under shaded, closed-canopy conditions, where seedlings show remarkable persistence. Nevertheless, they will not grow vigorously without higher light levels.

Figure 2 Opened capsule and seeds of *Swietenia macrophylla*. Courtesy of KE Wightman.

Two particular patterns of frequency and abundance of big-leaf mahogany have been widely noted. First, and more rarely and locally, mahogany may form relatively dense aggregations of up to 40–50 mature trees ha^{-1}. These formations, reported particularly from the Yucatan peninsula, seem to derive from the resistance of mature mahogany trees to hurricanes and fires, both relatively common in the Caribbean region. Such catastrophic disturbances favor the species by opening the canopy and destroying seed trees and advance regeneration of other species. The copious seed rain of surviving mature mahogany trees can then lead to seedling densities of up to 1000 ha^{-1}. The annual height growth of young seedlings, which may exceed 2 m during the first 5 years, is sufficiently rapid to permit high adult stocking. The second, more common pattern is of low densities of 0.1–3.0 merchantable trees ha^{-1}, found in small aggregations. It occurs in much of Quintana Roo, Mexico, the Chimanes region of lowland Bolivia, seasonally flooded forest in the Peruvian Amazon, nonriverine, upland or terra firma landscapes in western Amazonia, and southeast Pará, Brazil, and seems to reflect absence of (recent) catastrophic disturbance. Studies demonstrate that, under spatially smaller and/or lower-intensity disturbance (resulting, for example, from flooding or tree-fall of mahogany and other large trees such as *Hura* and *Manilkara*), advance or postdisturbance regeneration of mahogany will almost always die due to lateral canopy closure or competitive effects of exploitative gap-invaders. This seems to explain the low density of mahogany in such forest: that is, conditions dictate that, of the lifetime seed fecundity of individual trees, only a small proportion – on the order perhaps of 1 in 0.25 million dispersed seeds – survives to adulthood. The survival of even this proportion is presumably facilitated by the ability of seed to germinate in closed-canopy conditions and the relative robustness and shade tolerance of mahogany seedlings.

Although mahogany is tolerant of a wide range of soil types (derived from alluvial, volcanic, metamorphic, and calcareous material) and conditions (deep, shallow, acid, alkaline, well drained, and gleyed), edaphic or hydrologic factors certainly also partly determine distribution patterns. However, the relative roles of disturbance and such factors are unknown. Physiographic associations at the population level remain poorly described and understood across the natural range. Big-leaf mahogany was first observed in riparian situations in coastal Belize. Similarly, descriptions from South America emphasize the species' association with river floodplains in the upper reaches of the western Amazon basin. From Bolivia, Brazil, Ecuador, and Peru many observers have noted highest densities on drier, firmer, and infrequently flooded soils slightly above seasonally inundated floodplains. Nonriverine associations have also been described, e.g., in interfluvial and upland ecosystems in Belize, where mahogany will even invade stands of *Pinus caribaea* on drier sites with high understory light levels.

Swietenia humilis and *S. mahagoni*

As little natural forest remains within the generally highly (human-) populated natural ranges of *S. humilis* and *S. mahagoni*, their ecology in natural conditions is to some extent a matter of conjecture. However, the close similarity between all three species suggests a similar ecological role and regeneration ecology to that of *S. macrophylla*. *Swietenia humilis* is found in farmers' fields, fence lines, riparian strips, and in some of the few remaining areas of relatively intact natural forest. *Swietenia mahagoni* is found principally in remnant stands on inaccessible terrain. Large individuals of either are rare. For *S. mahagoni*, this may be due to past exploitation (in Jamaica, a harvested specimen reached 3.7 m in diameter, and 200-year-old avenue trees in the US Virgin Islands have attained 2.0 m). Consistent with its epithet, no such *S. humilis* individuals seem to have been recorded. Common-garden provenance and species trials suggest that both *S. mahagoni* and *S. humilis* are adapted to drier conditions than *S. macrophylla*, as their respective distributions would suggest.

Conservation Status

None of the species is in imminent danger of biological extinction. Nevertheless, there is justified concern about the current conservation status of all three. *Swietenia humilis* and *S. mahagoni* are both commercially exhausted, as illustrated by current imports of *S. macrophylla* to the Dominican Republic, formerly a producer of *S. mahagoni*. They were listed in CITES Appendix II in 1975 (*S. humilis*: all parts and derivatives except seed, pollen, seedlings, or tissue cultures) and 1992 (*S. mahagoni*: logs, sawnwood, veneer, and plywood). As pioneers – considered potentially invasive in exotic locations – both species are well equipped to survive in the highly disturbed conditions where they now generally occur. However, their continued persistence is likely to depend on the nurturing of regeneration by farmers.

In parts of Central America, e.g., northern Costa Rica and adjoining parts of Nicaragua, *S. macrophylla* also is increasingly rare. In South America, particularly in Brazil and Peru, substantial stocks remain. However, intensive logging in recent decades has led to virtual local extinction over large areas of the natural range in both these countries and Bolivia. Growing concern over the impact of logging – on the species itself, on associated forest types, and on forest-dwelling indigenous peoples – led in the 1990s to a sometimes acrimonious debate, centered around successive proposals to include *S. macrophylla* in CITES Appendix II. The third such proposal was approved in November 2002, and applies to mahogany logs, sawn timber, and veneer.

Silviculture

Natural Stand Management

To date, with the exception of relatively small areas of forest certified by the Forest Stewardship Council in Mesoamerica, mahogany has been 'mined' rather than managed; with exhaustion of merchantable stems in one area, loggers have moved on to new 'deposits' in other regions or countries. Selective logging for mahogany tends to cause relatively little canopy disturbance. As discussed above, in natural, unlogged forest, rare recruitment to adulthood in tree-fall gaps may be adequate to maintain low-density populations. However, the probability of replacement arising from a specific canopy opening (e.g., one logging event) is vanishingly small, even supposing that, contrary to frequent practice, trees are not felled before seed dispersal. Consequently, sustained production of mahogany in selectively logged forests is likely to require intensive management and more complete ecological information. Recently initiated experimental management in Acre, Brazil reflects these requirements, emphasizing knowledge of local distribution patterns and population structures; retention of hollow adult trees and highly fecund individuals for seed production and maintenance of genetic structures; acceleration of diameter increment of retained trees through vine cutting and crown liberation thinnings; and artificial regeneration in treated (cleaned, burned) logging gaps with regular postharvest cleaning. Such management has the potential to increase mahogany densities substantially in 'natural' forest. In the longer term, this could permit the use of classic shelterwood regeneration systems, as has been proposed for some mahogany plantations.

Mean periodic annual diameter increments reported in the literature range from 0.36 to 0.91 cm year^{-1} in Belize over an 8-year period; an estimated 0.38–1.09 cm year^{-1} in Mexico's Yucatan peninsula, with highest increment growth by 15–30-year-old trees; 0.26–0.9 cm year^{-1} in Bolivia over a 2-year period, with fastest rates by trees 20–80 cm dbh; and 0.19–0.59 cm year^{-1} in southeast Pará, Brazil over 3 years, with increment rates declining with increasing diameter and maximum increment rates of individual trees approaching 2 cm year^{-1}. Mean rotation lengths required to grow merchantable trees from seed range from an estimated 85 years in Pará (50 cm dbh) to 122 years in Mexico (55 cm dbh), with fastest-growing trees reaching merchantable size in 50–55 years.

Plantations

The choice of species is the first decision to be faced by the potential mahogany planter. In relatively moist sites with short (2–4 months) dry seasons, *S. macrophylla* is the species of choice. Research carried out in Puerto Rico and the US Virgin Islands suggests that *S. mahagoni* or, if available, the F_1 hybrid, should be preferred to *S. macrophylla* in dry forest. Within its native range, *S. humilis* is probably the safest choice. However, consideration should be given to *S. macrophylla* in moist or irrigated sites within the range of *S. humilis*. Whatever species is used, seed should be derived from a local (or locally tested) source. *Swietenia macrophylla*, particularly, occupies an ecologically variable range, and long-distance seed transfers should be avoided. Germination capacity of fresh seed is 80–95%, although drying of seed on ventilated screens in partial sunlight for 2–3 days is recommended to reduce rot. Unopened capsules can also be dried in the sun to encourage opening. Mahogany seed is orthodox and may be stored for long periods at 4–5% moisture content and -20°C, with little or no loss of viability. If necessary, seed may also be stored in ambient conditions for 7–8 months (approximately 50% decline in viability). Seed is usually dewinged to facilitate planting, although such seed may have lower viability after storage. It should be planted flat or with the winged end pointed down. No pretreatment is necessary. Germination is hypogeal, beginning in moist soil after 2 weeks and finishing 4 weeks later. Seedlings develop a strong taproot. Planting stock can also be produced vegetatively, e.g., in nonmist propagators.

Common substrates for poly-bag production include mixtures of forest soil with sand and a variety of composted organic materials. However, results vary greatly depending on nutrient concentrations and proportions in local materials. In container nurseries, common mixtures include 50% sphagnum moss, 25% vermiculite, and 25% perlite mixed with a slow-release fertilizer. Substrates should be kept partially shaded and moist during the first weeks of germination. Seedlings are ready to plant when the base of the stem has lignified and reached a minimum diameter of 8 mm. Seedlings from 20 to 80 cm, produced after 3–6 months in the nursery, may be planted successfully. The use of bare-root stock and striplings is inadvisable because subsequent field growth may be retarded. Direct seeding in the field is a viable option, but requires high soil moisture, early competition control, and the use of abundant seed.

Plantations can be successfully established on cultivated fields (e.g., in taungya) or recently cleared areas. Weed competition must be controlled carefully but can also be managed to provide lateral shade (**Figure 1b**). This encourages height growth, reduces soil exposure, promotes biodiversity (species richness), and may reduce and/or mitigate *Hypsipyla* attack. Close spacing (2×2 m or 3×3 m) allows greater flexibility in selection of final crop trees – an important consideration when *Hypsipyla* is present – and quicker canopy closure. Wider spacing, or deployment in mixed plantations or agroforestry systems, permits biological and product diversification, intermediate income generation and may form part of the integrated management of *Hypsipyla*. Mahogany has also been successfully used in line (enrichment) planting, although this approach requires careful management of the overstory. Fertilization during the first two to four growing seasons (increasing to 200 g per plant of a complete granular fertilizer) can be effective. Well-tended plantations of any of the species on well-drained, fertile sites can easily reach average heights of 6 m in 3 years. Maximum mean annual increments for well-managed, conventionally spaced (i.e., 1111–2500 trees ha^{-1} at establishment) plantations reach 25 m^3 ha^{-1} year^{-1}. First thinning should usually take place after 5–10 years. Commercial sizes (>50 cm dbh) can be reached in 20–30 years.

Abundant regeneration has been observed in *S. macrophylla* and *S. mahagoni* plantations, suggesting that planting may be unnecessary for establishment of second and subsequent rotations. Suggested silvicultural systems include the uniform shelterwood and group selection systems. Under the latter, trees are removed in groups in order to open canopy gaps sufficiently large for continued development of new and advance regeneration. In the former, a regeneration felling is carried out 4–6 years before final felling. The resulting advance regeneration is released by the final felling of the seed trees. In either system, intensive tending would be necessary, as in natural forest.

Mahogany's relatively fast growth, ease of nursery production, and high value suit it to plantation production. However, these advantages must be weighed against the serious pest problem of the mahogany shoot-borer (**Figure 3**). The larvae of the pyralid moths *Hypsipyla grandella* (neotropics) and *H. robusta* (old tropics) feed on the pith of mahogany shoots, principally while succulent or semisucculent. *Hypsipyla* attack approaches 100% in many plantations. Unless pruned, affected trees often develop into multiple-stemmed individuals of little commercial value. Attack may also reduce growth rate because of stalling for a variable period before dormant axillary buds respond. The problem has led to widespread avoidance of mahogany and related species both by tree planters and development projects. Nevertheless, there is no doubt that mahogany can be successfully cultivated in plantations. Tree mortality due to *Hypsipyla* is very unusual, and deformations caused by *Hypsipyla* up to at least 3 m height can be relatively easily corrected by biannual or annual pruning. The length of clean stem laid down between attacks, which depends both on growth rate and speed of post-attack lateral bud break, can be increased by both genetic selection and environmental manipulation (including appropriate site selection). There is evidence that lateral shading can both reduce *Hypsipyla* oviposition and stimulate vertical growth. Finally, selective thinnings in higher density plantations can be employed to favor the best-formed trees. A combination of all these control tactics should form the basis of an integrated pest management system.

In the neotropics, mahogany plantations can also be severely attacked by leaf-cutting ants, leading to growth reduction and, in young seedlings, death or forking. Leaf-cutters may be efficiently controlled using specific insecticides. Where these are unavailable or prohibitively priced, attack may be minimized by providing alternative browsing sources (interplanted or in neighboring areas) and avoiding clean-weeding. Other pest problems, such as Ambrosia beetle (*Crossotarsus externedentatus* and *Platypus gerstaeckeri*) and termite attack in Fijian plantations, have also been noted.

Utilization

Mahogany has been one of the world's most traded timbers for the last four centuries. Currently, it is used principally in furniture manufacture, flooring, doors, window frames, and decorative veneers. Free-on-board sawnwood prices in the early 2000s have been around US\$1000 m^{-3}. At the same time, retail prices in the USA were around US\$5–6 board $foot^{-1}$, equivalent to more than US\$2000 m^{-3}. The sustained demand for mahogany is largely a result of its excellent properties: extraordinary dimensional stability, high strength (particularly for its relative lightness), workability and exquisite, subtle beauty. These qualities, combined with centuries of use, have also

Figure 3 (a) *Hypsipyla*-attacked *Swietenia macrophylla* shoot in Turrialba, Costa Rica; (b) attacked *S. macrophylla* sapling, Guanacaste, Costa Rica; note multiple leaders due to lack of post-attack pruning. Courtesy of JP Cornelius.

given rise to an associated cachet – reflected in the many different woods commercially sold as mahogany, including not only other Meliaceae, but also Dipterocarpaceae (*Shorea* spp.) and various eucalyptus – that in itself sustains demand.

Wood quality, particularly density, appears to be related to environmental conditions, particularly as they affect growth rate; faster growth appears to be related to lower density. This factor, rather than inherent genetic characteristics, may also explain an apparent tendency of both *S. humilis* and *S. mahagoni* to have higher-density wood than *S. macrophylla*. The drier conditions in the natural ranges of *S. humilis* and *S. mahagoni* are probably less conducive to fast growth than those of typical *S. macrophylla*.

Exploitation and trade have shown three distinct phases: early exploitation of *S. mahagoni* in the Caribbean; cutting and substantial commercial exhaustion of *S. macrophylla* in Mexico and Central America; exploitation from the mid twentieth century of South American sources, particularly in Bolivia, Brazil, and Peru. The exploitation history of *S. humilis* is little known. It may be that mahogany exploitation is now entering a fourth phase, as international and domestic pressures lead producing states to adopt increasingly stringent management and trade regulations.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Operations**: Nursery Operations. **Plantation Silviculture**: Forest Plantations; High Pruning; Treatments in Tropical Silviculture. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation; Overview. **Tree Breeding, Practices**: Tropical Hardwoods Breeding and Genetic Resources. **Tropical Forests**: Tropical Dry Forests; Tropical Moist Forests.

Further Reading

Chalmers KJ, Newton AC, and Waugh R (1994) Evaluation of the extent of genetic variation in mahoganies (Meliaceae) using RAPD markers. *Theoretical and Applied Genetics* 89: 504–508.

Francis JK (1991) Swietenia mahagoni *Jacq*., *West Indies Mahogany; Meliaceae, Mahogany Family*. International Tropical Forestry Report no. SM 46, pp. 1–7. Asheville, NC: US Department of Agriculture Forest Service Southern Station.

Grogan J, Barreto P, and Veríssimo A (2002) *Mahogany in the Brazilian Amazon: Ecology and Perspectives on Management*. Belém, Brazil: Imazon. Available online at www.imazon.org.br.

Lamb FB (1966) *Mahogany of Tropical America: its Ecology and Management*. Ann Arbor, MI: University of Michigan Press.

Lugo A, Figueroa Colón JC, and Alayón M (eds) (2003) *Big-Leaf Mahogany: Genetics, Ecology, and Management*. New York: Springer-Verlag.

Mahroof RM, Hauxwell C, Edirisinghe JP, *et al.* (2002) Effects of artificial shade on attack by the mahogany shoot borer, *Hypsipyla robusta* (Moore). *Agricultural and Forest Entomology* 4(4): 283–292.

Mayhew JE and Newton AC (1998) *The Silviculture of Mahogany*. Wallingford, UK: CAB International.

Negreros-Castillo P and Mize C (1993) Effects of partial overstory removal on the natural regeneration of a tropical forest in Quintana Roo, Mexico. *Forest Ecology and Management* 58: 259–272.

Newton AC, Baker P, Ramnarine S, *et al.* (1993) The mahogany shoot borer: prospects for control. *Forest Ecology and Management* 57: 301–328.

Robbins C (2002) *Mahogany Matters: The US Market for Big-Leafed Mahogany and its Implications for the Conservation of the Species*. Washington, DC: TRAFFIC North America. Available online at: http://www.worldwildlife.org/forests/attachments/mahogany.pdf.

Stevenson NS (1927) Silvicultural treatment of mahogany forests in British Honduras. *Empire Forestry Journal* 6: 219–227.

Various authors (1996) Papers arising from a meeting on 'The future for the genus mahogany in its native forests'. *Botanical Journal of the Linnean Society* 122(1): 1–87.

Veríssimo A, Barreto P, Tarifa R, and Uhl C (1995) Extraction of a high-value natural resource in Amazonia: the case of mahogany. *Forest Ecology and Management* 72: 39–60.

Weaver PL and Sabido OA (1997) *Mahogany in Belize: A Historical Perspective*. General Technical Report no. IITF-2. Asheville, NC: US Department of Agriculture Forest Service, International Institute of Tropical Forestry/Southern Research Station.

White GM, Boshier DH, and Powell W (1999) Genetic variation within a fragmented population of *Swietenia humilis* Zucc. *Molecular Ecology* 8: 1899–1909.

Teak and other Verbenaceae

P J Wood, Commonwealth Forestry Association, Oxford, UK

Introduction

The family Verbenaceae contains over 3000 species of trees, shrubs, herbs, and lianes in some 86 genera, virtually all of which are tropical or subtropical and a number of which are economically important tree species. It contains what is probably the most prized and famous of all timbers, teak (*Tectona grandis*). Other important tree genera include *Clerodendrum* and *Vitex* (Viticöideae) and *Gmelina*, *Lantana*, and *Lippia* (Verbenöideae).

Teak

Teak is arguably the most famous timber in the world (**Figure 1**). The combination of the wood's strength, durability, and stability, as well as its availability in long lengths gave it a key role not only in shipbuilding for the European empires in south and southeast Asia since the seventeenth century, but much further back in trade to Mesopotamia in the third millenium BC. In its natural habitats in India, Myanmar, Thailand, and Laos teak occurs mixed with many other species, but since the sixteenth century the species has been heavily exploited, as well as encouraged and replanted, so that today simplified monocultures of teak are the rule rather than the exception. Teak is thought to have been introduced in the fourteenth century from India to Indonesia by Hindu monks. The large-scale plundering of teak forests in the colonial era gave rise to early concerns for its regeneration and protection among some colonial administrators, so that sustained management of teak in India, Myanmar, and Indonesia probably has the longest history of any tropical tree species.

Teak occurs naturally as a component of many forest types ranging from moist to dry, though in all cases in a monsoonal climate. Like many other members of the Verbenaceae it is insect pollinated. Major phenotypic and genotypic differences have been identified in different parts of the natural distribution which have been used in tree breeding programs across the tropics, especially in south and southeast Asia.

Global areas of teak forest in 1998 were approaching 28 million ha, of which some 25 million ha were reported as natural forest (**Table 1**).

Figure 1 *Tectona grandis*.

Other Species of *Tectona*

In addition to *Tectona grandis* four other species of the genus have been identified: *T. australis*, *T. hamiltoniana*, *T. philippinensis*, and *T. ternifolia*. These are, however, of low social or commercial importance, though they form important components of different natural ecosystems.

Other Important Genera

The genus *Gmelina* is represented by over 57 species that occur mostly in the Indo-Malaysian and Australasian regions. The most commercially important species is *Gmelina arborea*, widely planted in many parts of the humid and subhumid tropics for general-purpose timber and the subject of important breeding and conservation programs. The pantropical genus *Vitex* contains several hundred species, some of which are of commercial importance.

Table 1 World teak area statistics

Country/zone	*Teak area reported, 1998 (ha × 10^3)*	*Plantations as % of teak area reported*	*Country/zone area as % of world area*
Myanmar	14 225	1.6	51
India	10 000	10	36
Thailand	2 100	4.8	7.8
Laos	22	11	<1
Indonesia	1 100	100	3.5
Other Asia	159	100	4.5
Africa	124	100	<1
Latin America	47	100	<1
Total	27 777		

Note: these figures should be regarded as a general guide only.
Source: Derived from Behagel I (1999) State of teak plantations in the world. *Bois et Forêts des Tropiques* 264(4).

The genera *Lantana*, *Lippia*, and *Clerodendron* are also pan-tropical, contain several hundred species, and are important components of many forest ecosystems. They comprise trees, shrubs and lianes. Species of *Lantana* are important weeds and *Lippia* species are important sources of medicine.

See also: **Silviculture**: Treatments in Tropical Silviculture. **Tree Breeding, Practices**: A Historical Overview of Forest Tree Improvement; Tropical Hardwoods Breeding and Genetic Resources. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia). **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

Behagel I (1999) State of teak plantations in the world. *Bois et Forêts des Tropiques* 264(4).
Champion HG and Seth SK (1968) *A Revised Survey of Forest Types of India*. Delhi, India: Government of India, Nasik Press.
Dawkins HC and Philip MS (1998) *Tropical Moist Forest Silviculture and Management: A History of Success and Failure*. Wallingford, UK: CAB International.
Kadambi K (1972) *Silviculture and Management of Teak*. Nacogdoches, TX: Stephen F. Austin State University.
Krishna Murthy AVRG (1975) *Bibliography on Teak*: Tectona grandis *Linn F.* Jughal Kishore, India: Dehra Dun.
Mathur KBL (1973) *Teak Bibliography*. Delhi: Government of India.

Tropical Pine Ecosystems and Genetic Resources

J Burley and R D Barnes, University of Oxford, Oxford, UK

Introduction

The genus *Pinus* (family Pinaceae) is one of the most widely distributed genera of trees in the northern hemisphere (**Figure 1**). The species often dominate the natural vegetation types in which they occur and provide some of the most important timber trees in the world. *Pinus* comprises approximately 100 species, of which about half occur naturally within the northern tropics. The tropical pines consist of two categories: first, those that occur naturally in the tropics, e.g., *P. oocarpa* (**Figure 2**) and, second, nontropical pines that are planted for wood production or shelter in the tropics, e.g., *P. elliottii* and *P. taeda* (**Figure 3** and **Table 1**). This definition is taken from the account of the tropical pines given in *Tree Crop Ecosystems* (Barnes *et al*., 2001; see Further Reading) and on which this contribution is based.

There are virtually no natural pine forests in the southern hemisphere (**Figure 1**). It is not surprising, therefore, that the tropical pines have been used most extensively as exotics in the southern tropics, where some 6 million ha of plantations have been established to produce structural lumber and long-fibered pulp for particleboard, kraft paper, and newsprint manufacture (**Figure 3**). Unlike other crops, it is not usually economic to modify the plantation environment artificially through fertilization or irrigation. However, the extensive gene pool of tropical pine species has made it possible to establish plantations that are many times more productive than the natural forests over a great range of environmental conditions.

Taxonomy and Variation in Natural Populations of Tropical Pines

The pines are evergreen, resin-yielding, small to very large trees, usually with a single stem and strong apical dominance. If open-grown, most branches are retained and the bole tends to be conical but, under forest conditions, lower branches are shed and clean cylindrical boles are produced. Bark varies from rough and furrowed (**Figure 4**) to smooth and scaly (**Figure 2**). All pines have mature needles in fascicles (bundles) of from one to six, enclosed in a deciduous or persistent basal sheath. The fascicles are dwarf short shoots and are important in their identification. The needles contain resin canals running along their length which vary in number and position and which are also important for species identification. Needles may possess one or two vascular bundles, upon which the two major divisions of the genus are based, viz., Haploxylon and Diploxylon. Stomata (pores for gas exchange) are borne in lines on all surfaces, varying in number between species and within subspecies and ecotypes of single species.

All pines are monoecious with male and female strobili borne on the same individual tree. The female strobilus is usually terminal or subterminal and is composed of two series of spirally arranged scales, a very small bract scale and a much larger ovuliferous scale. The latter bears two pendulous ovules on its upper surface. The mature cone shows considerable variation in size, degree of woodiness, shape and size of the individual scales, and position of the apophysis and umbo (the exposed part of the scale when the cone is closed). In the Haploxylon group of

Figure 1 World distribution of the genus *Pinus*. Reproduced with permission from Critchfield WB and Little EL (1966) *Geographic Distribution of the Pines of the World*. USDA Miscellaneous Publications.

pines (**Table 1**) the apophysis is terminal, whereas in the Diploxylon it is dorsal. The female strobilus is very important for species identification and without it an exact determination cannot usually be made. Female cone development takes from 1 year (e.g., *P. merkusii*) to 3 years (e.g., *P. leiophylla*). Pine seed is either winged or wingless (some pinyon pines).

Although the genus *Pinus* is a homogenous and natural group, its division into infrageneric and sectional groups has been the source of argument and confusion; many different schemes have been proposed. The classification adopted in **Table 1** is modified from that published by Elbert Little and William Critchfield which is based on the work of Jack Duffield who segregated groups but did not give them formal names.

Information on natural hybridization among tropical pines is scattered, incomplete, and mostly unconvincing. Many species occur sympatrically and are apparently isolated by complete or almost complete genetic barriers. There are very few published examples of natural species hybrids that have subsequently been verified by later controlled pollinations. Those that have are:

- *P. flexilis* × *P. strobiformis*
- *P. leiophylla* × *P. chihuahuana*
- *P. yunnanensis* × *P. tabulaeformis*
- *P. yunnanensis* × *P. kesiya*
- *P. pseudostrobus* × *P. montezumae*
- *P. montezumae* × *P. hartwegii*
- *P. palustris* × *P. taeda*
- *P. caribaea* × *P. oocarpa*
- *P. patula* × *P. oocarpa*

Ecology of Natural Stands of Tropical Pines

Natural Distribution

Geographic range Tropical pines occupy two disjunct areas in the western and eastern hemispheres (**Figure 1**). The smaller Latin American area has the larger number of species, and no taxon is common to both. Some species, e.g., *P. kesiya* and *P. merkusii*,

Figure 2 A natural stand of *Pinus oocarpa* at 1000 m in Honduras.

occupy enormous geographical areas in Southeast Asia. *Pinus* is almost unknown in the southern hemisphere except for *P. merkusii*, and it is absent from Africa south of the Sahara (**Figure 1**).

The folded mountain ranges and varied topography of Latin America provide an abundance of habitats and, although pines (36–40 species) are considered to have migrated south from the west and east of North America in the Tertiary period, Mexico is now recognized as a center of considerable species diversity and a secondary center of endemism. No pine has ever been recorded south of latitude 12° N in Central America and the total lack of fossil records indicates that no species of pine has ever existed in South America. In Southeast Asia, tropical pines occur in southern China,

Figure 3 Exotic pine plantations of *Pinus elliottii*, *P. patula*, and *P. taeda* at 1000–1500 m altitude in the eastern districts of Zimbabwe.

chiefly in the states of Yunnan and neighboring Szechwan, the island of Formosa (Taiwan), the whole of the former Indochina peninsular, Myanmar (Burma) and Thailand, together with the north-eastern states of India.

Altitude and climate In both geographical areas, pines commonly grow under conditions that are far from tropical. Almost all are montane, some with altitudinal ranges between 700 and 4000 m. *Pinus caribaea*, in Central America and the Caribbean, rarely grows at elevations greater than 700 m, whilst *P. merkusii* in Southeast Asia and *P. strobus* var. *chiapensis* in southern Mexico and Guatemala may be found up to 1000 m or slightly higher. These three species are the most 'tropical' of all pines and are unable to tolerate severe frost.

All the other species are submontane or montane, although one or two survive at the timberline, sometimes in permanent snow. Most seem to be adapted to a fairly narrow altitudinal range and inhabit distinct zones. Temperature appears to be the main factor controlling the altitudinal range of a species. In Latin America, however, *P. oocarpa* extends from *c*. 700 m in Central America (**Figure 2**) to 2500 m in Mexico. The lower altitude ecotypes are always frostfree, whereas the higher populations are frequently subjected to periods of severe frost. Some of the more upland pines have equally large ranges, e.g., *P. patula* and *P. tecunumanii* from 900 to 2800 m and *P. pseudostrobus* from 2000 to 3000 m. *Pinus hartwegii* is found at the highest altitude, between 2000 and 4000 m (**Figure 4**).

In Southeast Asia most of the species appear to have a greater range of altitudinal tolerance, several occurring from sea-level to 2500 m. Populations of *P. armandii* are found from sea level to *c*. 3800 m. The majority, e.g., *P. roxburghii*, are found between 1500 and 3500 m, whilst *P. densata* grows at the highest altitudes (to 4000 m).

The temperature range, therefore, over which tropical pines grow varies enormously from an annual mean of about 26°C (e.g., *P. merkusii* in Sumatra and *P. caribaea* in Nicaragua) down to treeline conditions with mean annual temperatures of 10°C (*P. hartwegii*). Mean annual rainfall also varies greatly over the areas occupied by tropical pines from as much as 10 000 mm (*P. kesiya* in the Khasi Hills, India) down to less than 600 mm (*P. caribaea* in Honduras). Almost invariably, the climate where tropical pines occur is characterized by an annual seasonal fluctuation in rainfall or temperature.

Soils Pines are able to thrive on a great variety of soils, particularly infertile, well-drained acidic soils. On richer soils, competition from broadleaved species is greater and their success in regeneration is poorer. In Central America, *P. oocarpa* tends to avoid the more alkaline soils overlying basic rocks, as does *P. caribaea* var. *hondurensis*. *Pinus caribaea* var. *bahamensis*, however, thrives on almost pure coral limestone (**Figure 5**).

Table 1 The tropical species of the genus *Pinus* classified according to Little EB and Critchfield WB (1969) (*Subdivisions of the Genus* Pinus (*Pines*). USDA Miscellaneous Publications.) and modified by BT Styles and A Farjon (Oxford Forestry Institute)

- *Pinus* subgenus *Ducampopinus* (A. Chev.) de Ferré
  - *Pinus* sect. *Ducampopinus*
    - *Pinus* subsect. *Krempfiana* Little and Critchfield
      - *Pinus krempfii* Lecomte
- *Pinus* subgenus *Strobus* Lemm. (soft or white pines)
  - *Pinus* sect. *Strobus*
    - *Pinus* subsect. *Strobi* Loud.
      - *Pinus strobus* var. *chiapensis* Martinez
      - *Pinus rzedowskii* Madrigal & M Caballero
      - *Pinus strobiformis* Engelm.
      - *Pinus ayacahuite* Ehrenberg ex Schltdl.
      - *Pinus ayacahuite* var. *veitchii* (Roezl) Shaw
      - *Pinus armandii* Franch.
      - *Pinus dalatensis* de Ferré
      - *Pinus fenzeliana* Hand.-Mazz.
      - *Pinus wangii* Hu & Cheng
      - *Pinus morrisonicola* Hayata
  - *Pinus* sect. *Parrya* Mayr
    - *Pinus* subsect. *Cembroides* Engelm. (pinyon or nut pines)
      - *Pinus cembroides* Zucc.
      - *Pinus cembroides* var. *bicolor* Little
      - *Pinus cembroides* subsp. *lagunae* (Robert Passini) DK Bailey
      - *Pinus cembroides* subsp. *orizabensis* DK Bailey
      - *Pinus maximartinezii* Rzedowski
      - *Pinus pinceana* Gord. & Glendinning
      - *Pinus nelsonii* Shaw
- *Pinus* subgenus *Pinus* (hard pines)
  - *Pinus* sect. *Pinea* Endl.
    - *Pinus* subsect. *Leiophyllae* Loud.
      - *Pinus leiophylla* Schiede ex Schltdl. & Cham.
      - *Pinus leiophylla* var. *chihuahuana* (Engelm.) Shaw
      - *Pinus lumholtzii* Robinson & Fern.
    - *Pinus* subsect. *Canarienses* Loud.
      - *Pinus roxburghii* Sarg.[a]
      - *Pinus canariensis* C. Sm.[a]
  - *Pinus* sect. *Pinus*
    - *Pinus* subsect. *Pinus*
      - *Pinus tropicalis* Morelet
      - *Pinus halepensis* Mill.[a]
      - *Pinus taiwanensis* Hayata syn. *Pinus luchuensis* Mayr
      - *Pinus massoniana* Lamb.
      - *Pinus yunnanensis* Franch.
      - *Pinus densata* Mast.
      - *Pinus merkusii* Jungh. & de Vriese
      - *Pinus kesiya* Gord.
    - *Pinus* subsect. *Australes* Loud. (southern yellow pines)
      - *Pinus caribaea* Morelet
      - *Pinus caribaea* var. *bahamensis* (Griseb.) Barr. & Golf.
      - *Pinus caribaea* var. *hondurensis* ($\mathrm{S^{V}sn^{V}scl.}$) Barr. & Golf.
      - *Pinus occidentalis* Sw.
      - *Pinus cubensis* Griseb.
      - *Pinus taeda* L.[a]
      - *Pinus elliottii* Engelm.[a]
      - *Pinus elliottii* var. *densa* Little & Dorman
      - *Pinus palustris* Mill.[a]
    - *Pinus* subsect. *Ponderosae* Loud.
      - *Pinus engelmanii* Carr.
      - *Pinus durangensis* Martinez
      - *Pinus cooperi* (CE Blanco) Farjon

Table 1 Continued

      - *Pinus montezumae* Lamb.
      - *Pinus montezumae* var. *gordoniana* (Hartweg ex Gord.) Silba
      - *Pinus hartwegii* Lindl. (including *Pinus rudis* Endl.)
      - *Pinus devoniana* Lindl. (syn. *Pinus michoacana* Martinez)
      - *Pinus pseudostrobus* Lindl.
      - *Pinus pseudostrobus* var. *apulcensis* (Lindl.) Shaw
      - *Pinus douglasiana* Martinez
      - *Pinus maximinoi* HE Moore
      - *Pinus teocote* Schiede ex Schltdl. & Cham.
      - *Pinus lawsonii* Roezl ex Gord. & Glendinning
      - *Pinus herrerae* Martinez
    - *Pinus* subsect. *Oocarpae* Little & Critchfield (closed-cone pines)
      - *Pinus patula* Schiede ex Schlechtendal
      - *Pinus patula* var. *longipedunculata* Loock ex Martinez
      - *Pinus jaliscana* Pérez de la Rosa
      - *Pinus tecunumanii* Eguiluz & JP Perry
      - *Pinus greggii* Engelm. ex Parlatore
      - *Pinus oocarpa* Schiede ex Schldtl.
      - *Pinus oocarpa* var. *trifoliata* Martinez
      - *Pinus pringlei* Shaw
      - *Pinus radiata* D. Don
      - *Pinus muricata* D. Don
      - *Pinus praetermissa* Styles & McVaugh

Authorities' names are given for precise identification. All the species listed occur in the tropics except for those followed by [a] which occur naturally only north of the tropic of Cancer but have been used operationally within the tropics.

Natural Ecosystems

Plant communities Natural pine forest ecosystems are relatively simple; species diversity is low and the number of associated taxa limited. *Pinus oocarpa* in Honduras probably forms the main forest cover over most of the country (**Figure 2**) whilst *P. caribaea* var. *hondurensis* is dominant in the savanna and lowlands of Belize, Honduras, and eastern Nicaragua. *Pinus densata* and *P. armandii* form dense forest masses in the mountains of southern China. As many as six different pines may grow together, e.g., in some forests in the state of Chiapas, southern Mexico. In both geographical areas *Quercus* species (oaks) are the broadleaved trees most commonly associated with pine, although other hardwoods can play the same role.

In Mexico and Central America at least, most pine communities are secondary fire climaxes. Irregular burning by anthropogenic fires or through lightning strikes prevents invasion by the broadleaved competitors that suppress pine growth. Fire also eliminates the build-up of seed- and seedling-eating animals, especially in the Central American *P. oocarpa* forests. The shade cast by dense pine growth suppresses the development of a significant ground flora. At the higher altitudes where rainfall is higher, temperatures lower, and fires less frequent, the pine

Figure 4 *Pinus hartwegii* in natural mixed pine forest at 2300 m in Honduras.

forest may be transitory and no longer part of a climax community and it merges with, and is finally replaced by, upper montane rainforest (**Figure 6**). A mixture of both types of forest is common in Mexico and Central America at altitudes of 2800 m and above. There is a similar transition at lower altitudes where high rainfall and fertile soils also make fire less frequent.

Mycorrhizae All pines form ectotrophic mycorrhizae with ascomycetous or basidiomycetous fungi. Fungi frequently encountered belong to genera of the Agaricales (*Amanita*, *Boletellus*, and *Suillus*); Russulales (*Lactarius*, *Russula*); Aphyllophorales (*Cantharellus*, *Thelephora*); Hymenogastrales (*Rhizopogon*); and Sclerodermatales (*Astraeus*, *Pisolithus*, *Scleroderma*). Ectotrophic associations are rare in tropical

Figure 5 Fire-maintained forest of *Pinus caribaea* var. *bahamensis* on impoverished soils over limestone rock in Bahamas.

regions, forming only in response to certain edaphic and climatic factors. Information concerning mycorrhizal fungi in these forests is very scanty (**Table 2**), mainly because the fruiting structures of the organisms are ephemeral in hot climates and because their taxonomic affinities are uncertain and difficult to ascertain.

Diseases Little is known about the pathology of most tropical pines in their native habitats. Natural forests generally contain trees of widely different ages, often consist of more than one pine species, and frequently contain a substantial component of nonconiferous shrubs and trees. In such areas, selection pressures are likely to operate against pathogens that give rise to severe epidemic diseases and in favor of pathogens that cause chronic low-level disease. This appears to be the case in the pine forests of Central America and the Caribbean islands where the trees are debilitated by mistletoes (e.g., *Arceuthobium* spp. and *Psittacanthus calyculatus*), heart rots caused by various basidiomycetous fungi, and cone rust (*Cronartium conigenum*). Other pathogens that have the potential to cause severe disease epidemics, such as the fungi *Mycosphaerella dearnessii*, *M. gibsoni*, and *M. pini*, also exist at low levels in some Central American pine forests. However, they appear to be restricted by the lack of susceptible host tissues available for infection; the very susceptible individuals and species have long since been eliminated from the forests. Similarly, heteroecious leaf and stem rust diseases also occur on the pines and alternate host plants but rarely cause severe epidemics.

Predators Six orders of insects contain significant pine pests – Coleoptera, Hemiptera, Isoptera, Lepidoptera, Orthoptera, and Thysanoptera. These pests bore into the bark, wood, shoots, cones, and seed, suck sap from stem shoot or needles, and defoliate the trees. In the undisturbed natural forest they are endemic and rarely become conspicuous. However, when the forest ecology is disturbed by climate or humans, populations can build up to epidemic levels and devastation can result. For example, in 1928 the first attacks by pine bark beetles (*Dendroctonus* spp.) were noticed in remnant trees weakened by lopping in cleared sheep pastures in highland Guatemala. Damage can also be severe at high stand density, even where this does occur naturally.

Of the larger animals, humans and their domestic or feral beasts have the most profound influence on the ecology of the natural pine forests wherever they exist. Exploitation, grazing, and clearing for agriculture all involve management or mismanagement of the natural ecosystems that leads to the progressive decline of the forest.

Ecology of Artificially Created Plantations of Tropical Pines

Exotic Distribution

Species used in plantations Of the species listed in **Table 1**, four that occur in the tropics (*P. caribaea*, *P. kesiya*, *P. oocarpa*, and *P. patula*) are widely planted as exotics for industrial plantations. Another two (*P. massoniana* and *P. merkusii*) are extensively planted in the regions where they are indigenous and a further four (*P. greggii*, *P. maximinoi*, *P. pseudostrobus*, and one 'soft' pine, *P. strobus* var. *chiapensis*) are being used commercially on special sites. Of the eight extratropical pines that have been planted as exotics in the tropics, *P. elliottii* and *P. taeda* are the most important. Exotic pines have been widely planted in environments where the biotic, climatic, and edaphic factors are frequently unlike those in their indigenous habitats. The ecology of plantations, therefore, is in marked contrast to the ecology of the natural forest.

In 1980 it was estimated that about 3 million ha of softwood plantations had been established in

Figure 6 A natural stand of *Pinus tecunumanii*, probably established after a rare fierce fire, being replaced by hardwood species at 2000 m altitude in Honduras.

76 tropical countries of Africa, America, and Asia and this had increased to 4 million by the end of the twentieth century. About 80–90% of this area were tropical pines. In 1980, *P. elliottii* was still the largest single contributor, mainly in Brazil (*c*. 30%), but by 2000 it was equaled if not surpassed by *P. caribaea* followed by *P. patula*, *P. oocarpa*, *P. kesiya*, and *P. merkusii*; all the remaining species will contribute less than 10%.

Climatic factors The most successful plantation schemes have been those where species have been used in monoculture homoclimally, i.e., in climates similar to those in which they occur naturally. Absence

Table 2 Fungi confirmed as symbionts of pine ectomycorrhizas in indigenous pine forests in the tropics

Amanita excelsa (Fr.) Kummer
Amanita flavoconia Atk.
Amanita gemmata (Fr.) Gill.
Amanita muscaria (L. ex Fr.) Hook. var. *flavivolvata* Sing.
Amanita sp. sect. Lepidella
Fistulinella conica (Rav. Apud B. & C.) Sing. var. *belizensis* Sing. & Ivory
Pisolithus tinctorius (Mich. Ex Pers.) Coker & Couch
Rhizopogon nigrescens Coker & Couch
Scleroderma texense Berk.
Suillus cothurnatus Sing.
Suillus decipiens (B. & C.) O Kuntze
Suillus granulatus (L. ex Fr.) O Kuntze
Thelephora terrestris (Ehrn.) Fr.
Xerocomus pseudoboletinus (Murr.) Sing. var. *pini-caribaeae* Sing.

Reproduced with permission from Barnes RD, Styles BT, Plumptre RA, and Ivory MH (2001) Tropical pines. In: Last FT (ed.) *Tree Crop Ecosystems*, pp. 163–192. Amsterdam: Elsevier Science.

of natural pests and diseases contributes to this success and to productivity unseen in the natural stands. There has, however, been a tendency to move species that have demonstrated excellent silvicultural characteristics in the exotic homoclime to lower and hotter areas. The physiological stress and ecological changes that occur may not be immediately apparent but, as the plantation matures, disease and pest problems develop and the natural vegetation soon destroys the pine stand structure. Less frequently, species have been moved to higher altitudes and lower temperatures than those that occur in their natural range. Although there are significant reductions in growth rate, the ecological consequences are not as striking as when species are moved to warmer climates.

Tropical pines vary in their drought-hardiness but most species will grow with mean annual precipitation as low as 800 mm. However, species cannot be moved from winter rainfall to summer rainfall areas without severe problems; for example, *P. canariensis, P. halepensis, P. muricata*, and *P. radiata* were planted operationally in the tropics but have been abandoned.

Edaphic factors With appropriate temperature and dry season, exotic tropical pines are able to exploit the full potential of the soil and become dominant even on the very best sites. Where the climate is wrong, however, fertile soils contribute to the rapid demise of exotic tropical pine forest. In such conditions, the indigenous vegetation is not a fire climax type and there are many aggressive pioneering woody species that will take advantage of the physiologically weak pines and start recolonizing the site as the first step in reestablishing wet tropical forest ecology.

The tropical pines as exotics vary in their tolerance of soils with low nutrient status (e.g., *P. kesiya* can grow on degraded sites but *P. chiapensis* requires fertile sites) and particularly in their ability to grow on poorly drained soils (e.g., *P. kesiya* is very intolerant and *P. elliottii* very tolerant). Great depths of sandy soil can have amelioratoring effects on climatic influence where rainfall is low. The most serious problems with nutrient deficiencies have been with phosphorus (e.g., *P. caribaea* in Queensland), potassium (e.g., *P. kesiya* in Madagascar), and boron (e.g., *P. caribaea* in Papua New Guinea and *P. kesiya* in Zambia).

Ecology in the Exotic Environment

Plant communities The most important biotic influences are human beings and the silvicultural practices they use to establish and maintain the pines as exotics. Initially at least, the species is nursed into its new surroundings by careful sowing, planting, and weeding techniques. On poorer soils, the pines are able to compete favorably with grass and shrubby growth but generally not with woody regrowth. On more fertile sites, it is necessary to keep woody regrowth, shrubs, and creepers cut back until the pine crop forms a canopy.

Almost invariably, when crops are harvested the area is artificially regenerated by planting. Where soil fertility is high, the second crop is often faster-growing than the first because the forest floor by that time is almost devoid of ground vegetation. On poorer sites, however, nutrient deficiencies may result in reduced production. In both cases, there are changes in the associated macro- and microflora but the long-term prognosis in this respect cannot yet be predicted. Woody weeds, both indigenous and exotic, have become conspicuous problems in pine plantations (e.g., *Acacia ataxacantha*, *Lantana camara*, and *Rubus pinnatus* in Africa).

Notwithstanding the careful cultural procedures that are used to establish exotic plantations of tropical pines, many species regenerate naturally in their new environment once they are established and some have become serious invaders of indigenous grassland and woodland, particularly where frequent fires have been preventing the local succession to climax forest communities. A good example of this is *P. patula* in the fire climax grassland and *Brachystegia* woodlands of the eastern mountainous region of Zimbabwe (**Figure** 7).

Mycorrhizae Pine plantations are usually planted on old forest or grassland sites where indigenous ectotrophic trees are absent or sparse and indigenous fungi rarely form a significant source of mycorrhizal

Figure 7 *Pinus patula* colonizing a hillside at 1800 m in Zimbabwe. Seed has been blown in from a nearby planted stand and many trees have already survived fires.

inoculum for introduced pines in areas remote from natural *Pinus* spp.

Exotic ectomycorrhizal fungi were probably introduced along with their native hosts by early settlers long before the importance of mycorrhizae was realized. However, when attempts were made to grow pines in new areas from importations of tree seeds, mycorrhizal deficiency problems were often encountered; uninfected seedlings would usually remain stunted and chlorotic in appearance and they would usually die in the nursery. Later, these problems were overcome by the introduction of fresh pine soil or the use of 'mother seedlings' in nursery beds.

The type of inoculum, its origin, the method of transportation, the method of inoculation, and possibly the identity of the recipient *Pinus* species. have had considerable influence on which fungi were successfully introduced to any given area. Usually only a few of the 23 commonly encountered fungi (**Table 3**) are observed at any one site; the range of species observed is affected by the age of the trees, the host species, and site factors, such as altitude, climate, and rotation.

Table 3 Ectomycorrhizal fungal symbionts frequently sporulating in pine plantations in the tropics

Amanita alauda Corn. & Bres.
Amanita muscaria L. (L. ex Fr.) Hook.
Boletus edulis Fr.
Cortinarius spp. (in Sri Lanka and Kenya)
Hebeloma crustuliniforme (St. Amans) Quel.
Hymenogaster spp. (in India)
Inocybe lanuginella (Schrot.) Konr. & Maubl.
Laccaria proxima (Boud.) Pat.
Pisolithus tinctorius (Mich. ex Pers.) Coker & Couch
Rhizopogon luteolus Fr. & Nordh.
Rhizopogon roseolus (Corda) Fr.
Rhizopogon rubescens (Tul. & Tul.) Tul. & Tul.
Rhizopogon villosus Zeller
Russula brevipes Peck.
Russula sororia (Fr.) Romell
Scleroderma bovista Fr.
Scleroderma citrinum Pers.
Scleroderma texense Berk.
Suillus granulatus (L. ex Fr.) O Kuntze
Suillus luteus (L. ex Fr.) SF Gray
Suillus sibirieas (Sing) Sing
Thelephora terrestris (Ehrn.) Fr.
Xerocomus spp. (in India)

Reproduced with permission from Barnes RD, Styles BT, Plumptre RA, and Ivory MH (2001) Tropical pines. In: Last FT (ed.) *Tree Crop Ecosystems*, pp. 163–192. Amsterdam: Elsevier Science.

Diseases Exotic pine plantations in the tropics and the southern hemisphere have mostly been established in areas that were naturally free from any specialized pine disease organisms. Thus the majority of disease outbreaks reported in pine plantations from these areas were, until recently, caused by nonspecialized pathogens with a wide host range able to spread from indigenous host species to exotic pines.

These pathogens usually affect the roots or heartwood of the pines. The most notable of these diseases is *Armillaria* root disease. Following felling of infected trees the roots and stumps become extensively colonized by the fungus, which then spreads to healthy trees. Most *Pinus* species are susceptible but *P. elliottii* appears to be exceptionally so. Several other nonspecialized pathogens also give rise to similar diseases in various parts of the tropics; these can lead to serious economic losses but they can usually be minimized. Since 1950 there has, however, been a gradual influx of specialized pine pathogens from the north into exotic plantations in the tropics and the southern hemisphere where some have already proved to be a serious threat to certain *Pinus* species. Dothistroma blight, caused by the fungus *Mycosphaerella pini*, is probably the most important of the pine diseases in the tropics to be caused by an exotic specialized pine pathogen. This fungus was identified as the cause of a severe needle blight of *P. radiata* in Tanzania in 1957 and has since been reported from many other countries in the tropics. Plantations of pines are obviously more prone to epidemic disease than natural forest; however, they also provide more scope for the avoidance or control of disease in addition to being vastly more productive than most natural forest areas.

Predators The first crops of exotic pines have been characteristically devoid of associated animal life but there is an increasing number of birds, insects, and mammals becoming associated with and adapted to the forests. Even-aged stands of trees provide ideal media for population explosions, particularly of insects, both native and introduced. There have now been epidemics of insect pests from all the main orders, e.g., bark beetles and aphids in southern Africa, termites in Malaysia, shoot moths in the Philippines, defoliating moths in Zimbabwe, grasshoppers in Malawi, and thrips in Kenya. The worst damage is frequently associated with mis-siting of the host species when environmental stress is thought to bring about high nutrient levels in the tree through remobilization of reserves; this makes it attractive to the pest and at the same time impairs the tree's defensive mechanisms. Epidemics may eventually be brought under control by local predators or diseases, e.g., coccinelids on aphids and various viruses on lepidopterous larvae.

Birds and mammals use pine plantations for shelter, particularly before they are pruned and thinned, but, surprisingly, a number of mammals find a source of food in pines and can become destructive. Elephants strip pine species in Africa and eat the inner bark; they find it convenient to work down the plantation rows. Eland antelope have similar habits in Zimbabwe and are very destructive in *P. patula* plantations. Pigs, wild or feral, in all parts of the world feed highly selectively on the roots of young *P. oocarpa*; it has been suggested that this is due to a specific mycorrhizal association, possibly *Rhizopogon* spp., that have edible subterranean fruit bodies. Opossums feed on the young bark of *P. taeda* in Queensland, porcupines debark *P. leiophylla* by gnawing at the base in Zimbabwe, and baboons eat the bark of several pine species in southern Africa.

Genetic Resources and Adaptation

Evidence from many national and internationally coordinated comparative trials of species, varieties, populations (provenances), and progeny in many of the large number of tropical pine species have demonstrated that significant genetic variation occurs in clinal, ecotypic, and random patterns of distribution. This stresses the importance for the forester to choose the correct original natural population for exotic plantations and to monitor the change in genetic population structure under exotic conditions.

Development of landraces The possibility of genetic differences developing between the local exotic population and the original introduced sample is dependent upon the extent of heterozygosity, the genotypes of the founder members of the exotic population, the expression of the genetic variation in the new environment, and the selection pressures encountered under local conditions.

It appears that both a reduction in genotypic variation and a changed environment may, through their effect on phenotypic expression, contribute towards the rapid changes that can take place in local exotic populations. The changes may not be possible where the species is indigenous even when it is grown under plantation conditions. Such factors as endemic disease, competition with other indigenous species, and different climatic or edaphic conditions may prohibit the expression of genes that might otherwise improve commercially important characteristics.

Despite frequently small numbers of founder individuals, there is little evidence to suggest that introduced exotic tree populations are inferior to, or much less variable than, the indigenous parent populations. In fact, adaptation can take place over surprisingly few generations and the exotic population often exhibits superiority over material that is reintroduced from indigenous stands.

Development of genetically distinct exotic populations is occurring very much more rapidly now that selection and breeding in tropical pines have started. Achievements initially have been in improvements in wood yield and in stem and branch form (**Figure 8**). These have brought a correlated response in improved physiological adaptation to the environment and, as the environments are quite different from one country to another, a large amount of variation in

Figure 8 Seventeen-year-old plantation of *Pinus patula* from first generation of bred seed in Zimbabwe.

adaptability can be preserved in the global development of a species.

Implications for Management

Plantation silviculture aims to increase uniformity in the forest and to simplify the ecology; variation increases the complexity of management. Uniformity invites biotic, climatic, and edaphic disasters. Uniformity can aggravate damage from drought and cyclone, lead to soil impoverishment and erosion, and provide ideal conditions for population explosions of plant competitors, diseases, and pests. These in turn cause wild swings in the ecology and these swings themselves can sometimes prove to be beyond control through management. In the exotic environments, it is impossible to predict or even conceive of the events that may occur and to know their consequences. Introduction of diversity in the forest through mixed ages, mixed species, rotation of species, silvicultural treatment, and genetic variation may make ecology and management more complex but it will render the crop ecosystem much more stable, robust, and self-perpetuating and provide buffers against disasters. The forester must treat crop protection as part of silvicultural planning.

See also: **Pathology**: Diseases affecting Exotic Plantation Species; Diseases of Forest Trees. **Temperate and Mediterranean Forests**: Northern Coniferous Forests; Southern Coniferous Forests. **Temperate Ecosystems**: Pines. **Tree Breeding, Practices**: *Pinus Radiata* Genetics; Breeding for Disease and Insect Resistance; Southern Pine Breeding and Genetic Resources. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Conifer Breeding Principles and Processes. **Tropical Ecosystems**: Southern Hemisphere Conifers.

Further Reading

Barnes RD, Styles BT, Plumptre RA, and Ivory MH (2001) Tropical pines. In: Last FT (ed.) *Tree Crop Ecosystems*, pp. 163–192. Amsterdam: Elsevier Science.

Birks JS and Barnes RD (1990) *Provenance Variation in* Pinus caribaea, P. oocarpa and P. patula *ssp*. tecunumanii. Tropical Forestry Papers no. 21. Oxford, UK: Oxford Forestry Institute.

Critchfield WB and Little EL (1966) *Geographic Distribution of the Pines of the World*. Washington, DC: USDA Miscellaneous Publications.

Duffield JW (1952) Relationships and species hybridization in the genus *Pinus*. *Zeitschrift für Forstgenetik und Forstpflanzenzuchtung* 1: 93–100.

Farjon A and Styles BT (1997) Pinus (*Pinaceae*). Flora Neotropica Monograph no. 75. New York: New York Botanical Garden.

Ivory MH (1980) Ectomycorrhizal fungi of lowland tropical pines in natural forests and exotic plantations. In: Mikola P (ed.) *Tropical Mycorrhiza Research*, pp. 110–117. Oxford, UK: Oxford University Press.

Ivory MH (1987) *Diseases and Disorders of Pines in the Tropics*. Overseas Research Publication no. 31. London: Overseas Development Agency.

Little EB and Critchfield WB (1969) *Sub-divisions of the Genus* Pinus *(Pines)*. Washington, DC: US Department of Agriculture Miscellaneous Publications no. 1144.

Loock EEM (1977) *The Pines of Mexico and British Honduras*. Bulletin no. 35. Pretoria, South Africa: Department of Forestry.

Mirov NT (1967) *The Genus Pinus*. New York: Ronald Press.

Perry JP (1991) *The Pines of Mexico and Central America*. Portland, OR: Timber Press.

Speight MR and Wainhouse D (1989) *Ecology and Management of Forest Insects*. Oxford, UK: Oxford University Press.

TROPICAL FORESTS

Contents

Bombacaceae

S Harris, University of Oxford, Oxford, UK

Introduction

The family Bombacaceae contains trees with some of the most enigmatic of all traits, whether it is the lightness of South American balsa wood (*Ochroma pyrimidale*), the fabled odor of Southeast Asian durian fruit (*Durio zibethinus*), or the unusual architecture of African baobabs (*Adansonia digitata*). Traditionally, the Bombacaceae have been separated as a family, distinct from the Sterculiaceae (cocoas), Malvaceae (cottons), and Tiliaceae (limes). However, detailed analyses of molecular and morphological data have concluded that a single monophyletic Malvaceae should be recognized that encompasses all of the other families. The Bombacaceae cannot be maintained as a separate family since it appears to be paraphyletic with respect to the traditional circumscription of the Malvaceae and, furthermore, the genus *Durio* and its allies are more closely related to the traditional circumscription of the Sterculiaceae.

The traditional Bombacaceae comprises some 25 genera and 250 species of tropical (primarily neotropical) trees (**Table 1**), although some generic limits are controversial. For example, the important timber species *Bombacopsis quinata* is often separated from the genus *Pachira*, whilst the widely planted ornamental genus *Chorisia* may be recognized as distinct from *Ceiba*. The majority of species are found in lowland rainforest, although some genera (e.g., *Adansonia*, *Ceiba*, *Cavanillesia*) show water-storage adaptations for survival in dry, open habitats, for example, small crowns and thick, bottle-shaped trunks.

Table 1 Distribution of genera in the family Bombacaceae

Genus	*Approx. species number*	*Distribution*
Adansonia	15	Africa, Madagascar, Australia
Aguiaria	1	Brazil
Bernoullia	2	Tropical America
Bombax	20	Old-world tropics
Camptostemon	2	Central Malesia, Australia
Catostemma	11	Northern South America
Cavanillesia	3	Tropical America
Ceiba	11	Tropical America and Africa
Coelostegia	5	West Malesia
Durio	28	Myanmar to West Malesia
Eriotheca	19	Tropical America
Gyranthera	2	Panama, Venezuela
Huberodendron	5	Tropical America
Kostermansia	1	Malaysia
Matisia	25	Tropical South America
Neesia	8	West Malesia
Neobuchia	1	Hispaniola
Ochroma	1	Tropical America
Pachira	20	Tropical America
Patinoa	4	Tropical South America
Phragmotheca	5	Tropical South America
Pseudobombax	20	Tropical America
Quararibea	35	Tropical America
Scleronema	5	Tropical South America
Septotheca	1	Peru

The hermaphrodite flowers of Bombacaceae are generally large and showy, being produced during drier periods when the trees lose their leaves. The flowers attract insects (e.g., ants in *Adansonia*), birds and mammals (particularly bats), and are generally highly outcrossed, with pollen moving large distances between trees. The fruits of Bombacaceae are often dehiscent capsules containing wind-dispersed seeds that are surrounded by cotton-like fibers, e.g., *Bombax* and *Ceiba*. *Adansonia* has an indehiscent capsule containing a sour, dry flesh that is dispersed by large mammals, whilst *Durio* seeds are surrounded by a fleshy aril, the odor of which attracts large mammals, e.g., elephants and monkeys, which may also act as dispersal agents. In the neotropics, parrots readily damage fruit capsules to retrieve the oily seeds, and this can be a problem if Bombacaceae species are being grown for their seeds.

Economically, the most important species is *Ochroma pyramidale*, which is the source of commercial balsa wood. However, other genera (e.g., *Bombax*) may also be used where light, low-quality timbers are needed. *A. digitata* is an important multipurpose African species, with a complex mythology surrounding it. Uses of *Adansonia* include fruit pulp as a drink, young leaves as a vegetable, seeds as fruits and sources of oil and tartaric acid and bark for rope and cloth. *Pachira fendleri* (synonym: *Bombacopsis quinata*) is used as a living fence in Central America and *Ceiba pentandra* is the commercial source of kapok. *Durio zibethinus* is an important fruit tree in Southeast Asia, where the fruit is said to 'smell like hell but taste of heaven.'

See also: **Tropical Forests**: Tropical Dry Forests; Tropical Moist Forests.

Further Reading

Alverson WS, Whitlock BA, Nyffeler R, Bayer C, and Baum DA (1999) Phylogeny of the core Malvales: evidence from *ndh*F sequence data. *American Journal of Botany* 86: 1474–1486.

Bayer C and Kubitzki K (2002) Malvaceae. In: Kubitzki K (ed.) *The Families and Genera of Vascular Plants*, vol. 4, *Flowering Plants*: *Dicotyledons. Malvales, Capparales and Non-Betalain Caryophyllales*, pp. 225–311. Berlin: Springer-Verlag.

Du Puy B (1996) The baobabs of Madagascar. *Curtis's Botanical Magazine* 13: 86–95.

Judd WS and Manchester SR (1997) Circumscription of Malvaceae (Malvales) as determined by a preliminary cladistic analysis of morphological, anatomical, palynological, and chemical characters. *Brittonia* 49: 384–405.

Nyffeler R and Baum DA (2000) Phylogenetic relationships of the durians (Bombacaceae-Durioneae or Malvaceae/Helicteroideae/Durioneae) based on chloroplast and nuclear ribosomal DNA sequences. *Plant Systematics and Evolution* 224: 55–82.
Wickens GE (1982) The baobab: Africa's upside-down tree. *Kew Bulletin* 37: 173–209.

Combretaceae

S Harris, University of Oxford, Oxford, UK

The Combretaceae, based on morphological and molecular data, is a monophyletic family comprising 19 genera (approximately 510 species) of subtropical and tropical trees (to 50 m), shrubs, or lianas (**Table 1**). In general, forests have a predominance of trees and lianas whilst in grasslands shrubby species are more common. Shrubby species may be suffructices, the aerial shoots of which are frequently grazed or burned, making the plants appear annual. The two most important genera are *Terminalia* and *Combretum*. *Terminalia* species are important constituents of primary and secondary forests; for example, in Malaysia the genus is common in evergreen and semideciduous rainforest, and swamp and riverine forests, whilst *T. catappa* (native to tropical Asia and Pacific region) is a common constituent of littoral forests, sandy beaches, and eroding rocky shores, often as street or garden trees rather than for commercial forestry. *Combretum* species are commonly lianas, often found in riverine habitats and on the margins of primary and secondary forests. The species of the two closely related genera (*Laguncularia*, *Lumnitzera*) are mangrove species, whilst species of the more distantly related genus *Conocarpus* are mangrove associates. For example, the adaptations of *Laguncularia racemosa* to salt-water flooding include salt glands, vivipary, and pneumatophores.

Table 1 Distribution of genera in the family Combretaceae

Genus	*Approx. species number*	*Distribution*
Subfamily Strephonematoideae		
Strephonema	6	West tropical Africa
Subfamily Combretoideae		
Anogeissus	8	Tropical Africa and Asia
Buchenavia	20	West Indies, tropical America
Bucida	8	Tropical and subtropical America, West Indies
Calopyxis	23	Madagascar
Combretum	250	Tropics and subtropics (excluding Australia)
Conocarpus	2	Tropical America and Africa, Arabia
Dansiea		Australia
Getonia	1	Indo-Malaysia
Guiera	1	North Tropical Africa
Laguncularia	2	Tropical America, West Africa
Lumnitzera	2	East tropical Africa to Pacific
Macropteranthes	3	Australia
Meiostemon	3	South-east and tropical Africa, Madagascar
Pteleopsis	9	Tropical Africa
Quisqualis	16	Old-world tropics
Terminalia	150	Tropics worldwide
Terminaliopsis	2	Madagascar
Thiloa	3	North South America

The Combretaceae are part of the Myrtales (together with Vochysiaceae, Myrtaceae, Melastomataceae, Memecylaceae, Lythraceae, and Onagraceae), a monophyletic order, of uncertain position within the Rosids, based on morphology, embryology, anatomy, and DNA sequence data. The family Combretaceae is distinguished from the other families in the Myrtales by the occurrence of characteristic hairs, unilocular, inferior ovaries with apical placentation and flattened, ribbed, or winged drupes with large fibrous seeds. However, the relationships of the Combretaceae within the Myrtales are uncertain. Traditionally, the occurrence of combretaceous hairs in some Myrtaceae has suggested a close relationship of the Combretaceae to this family, although the Combretaceae may be closely related to the Lythraceae or Onagraceae.

The flowers of Combretaceae are often clustered in globular or spicate inflorescences, and typically produce nectar to attract insects, birds, and small mammals. For example, the long tubes of *Quisqualis* flowers presumably make pollination possible only by long-tongued insects. In the majority of species, flowers are hermaphrodite and outcrossing is promoted by protogyny. However, other mating systems are found in the family; for example, *Conocarpus erectus* is dioecious, *Laguncularia racemosa* has populations of male and hermaphrodite individuals and *Terminalia* species have male and hermaphrodite flowers on the same individual.

Combretaceae fruits of savanna and grassland species are often winged and adapted for wind dispersal, whilst forest species often have wingless fruits which are either fleshy and animal-dispersed or spongy and water-dispersed. Mangrove species (e.g., *Laguncularia*) have viviparous fruits that germinate on the parent plant. Combretaceae fruits can be important for species identification in some genera (e.g., *Terminalia*), whilst in others, flowers are important (e.g., *Combretum*).

The majority of Combretaceae produce poor-quality timber, although *T. ivorensis* and *T. superba* are internationally important timbers and have been grown in West African plantations; others (e.g., *Lumnitzera* in Malaysia and *T. arjuna* in India) have important local timber uses. The family produces important ornamentals (e.g., *Quisqualis indica*, *Combretum grandiflorum*) and widely planted pantropical street trees (e.g., *T. catappa*). The fruits of some *Terminalia* species (known as myrobalans) are important in tanning, whilst other combretaceous species are important as local foods, dyes, and medicines.

See also: **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Dry Forests; Tropical Moist Forests.

Further Reading

Conti E, Litt A, Wilson PG, *et al.* (1997) Interfamilial relationships in myrtales: molecular phylogeny and patterns of morphological evolution. *Systematic Botany* 22: 629–647.

Exell AW (1954) Combretaceae. In: Van Steenis CGGJ (ed.) *Flora Malesiana Series 1,4*, pp. 533–589. Jakarta: Noordhoff-Kolff.

Exell AW and Stace CA (1972) Patterns of distribution in the Combretaceae. In: Valentine DH (ed.) *Taxonomy, Phytogeography and Evolution*, pp. 307–323. London: Academic Press.

Sazima M, Vogel S, do Prado AL, *et al.* (2001) The sweet jelly of *Combretum lanceolatum* flowers *(Combretaceae)*: a cornucopia resource for bird pollinators in the Pantanal, western Brazil. *Plant System Evolution* 227: 195–208.

Tan F, Shi S, Zhong Y, Gong X, and Wang Y (2002) Phylogenetic relationships of Combretoideae (Combretaceae) inferred from plastid, nuclear gene and spacer sequences. *Journal of Plant Research* 115: 475–481.

Wickens GE (1973) *Flora of Tropical East Africa: Combretaceae*. London: Crown Agents.

Lauraceae

S Harris, University of Oxford, Oxford, UK

Introduction

The Lauraceae is a family (about 50 genera and about 3000 species) (**Table 1**) of mainly subtropical and tropical trees (except the genus *Cassytha* which is an herbaceous parasite), and is most diverse in the American and Asian tropics, although many species occur in Australia and Madagascar. Some genera range into the temperate region, e.g., *Sassafras* in North America, *Lindera* in Japan, and *Beilschmiedia* in New Zealand. The family is primarily found in lowland and montane rainforest, and can occupy a wide range of elevations from sea level to páramos in South America. In some habitats the Lauraceae is one of the most common trees families, for example, in the foothills and at mid-elevations in the Andes and as dominants in the relict laurel forests of the Canary Islands and Madeira.

Classification

Morphological and molecular data indicate that the Lauraceae is a monophyletic family, although classification with the family is less clear. Despite its ecological importance in tropical ecosystems, the Lauraceae is poorly known, since material is difficult to collect, the flowers are inconspicuous, and fruits and flowers are needed for accurate identification of most species. This creates problems for the delimitation of both genera and species, and thus absolute statements about generic distribution are difficult to make, particularly for genera that have widely disjunct distributions (e.g., *Apollonias* between India and the Canary Islands).

Traditional Lauraceae classifications have placed the parasitic genus *Cassytha* in its own subfamily (Cassythoideae), and treated the remaining genera as a second subfamily (Lauroideae). Within the Lauroideae, morphological characters (e.g., flower and wood anatomy) have been used to define three tribes: (1) Laureae (e.g., *Laurus*); (2) Perseeae (e.g., *Persea*); and (3) Cryptocaryeae (e.g., *Beilschmiedia*). However, molecular analysis of the family suggests that *Cassytha* should be placed with either *Hypodaphnis* or *Neocinnamomum*, and that the Lauroideae tribes, as currently defined, are not monophyletic.

Reproduction

Lauraceae flowers are insect-pollinated, usually with modified stamens that secrete either odor or nectar, and individual trees are hermaphrodite, monoecious, or dioecious. In addition to dioecy, there are mechanisms to promote outcrossing, including the occurrence of two flower types with different daily patterns of stigma receptivity and pollen presentation, as found in *Persea americana*. The Lauraceae

Table 1 Distribution of genera in the family Lauraceae

Genus	*Approximate number of species*	*Distribution*
Actinodaphne	100	Asia
Aiouea	20	Central and South America
Alseodaphne	50	Tropical Asia
Anaueria	1	Amazonia
Aniba	40	Tropical America
Apollonias	2	Canary Islands; India
Aspidostemon	15	Madagascar
Beilschmiedia	250	Pantropical
Brassiodendron	2	Pacific islands; Australia
Caryodaphnopsis	15	Asia; Central and South America
Cassytha	20	Pantropical
Chlorocardium	2	South America
Cinnadenia	2	Southeast Asia
Cinnamomum	350	Tropical and subtropical Asia; Australia; Pacific islands
Cryptocarya	350	Pantropical
Dahlgrenodendron	1	South Africa
Dehaasia	35	Asia
Dicypellium	2	East Amazonia
Dodecadenia	1	Southern Himalaya
Endiandra	100	Asia; Australia; Pacific islands
Endlicheria	40	Tropical America
Eusideroxylon	1	Malesia
Gamanthera	1	Costa Rica
Hexapora	1	Malaysia
Hypodaphnis	1	West Africa
Iteadaphne	2	Southeast Asia
Laurus	2	Mediterranean Europe; Canary Islands; Azores
Licaria	40	Tropical America
Lindera	100	Asia; Australia; North America
Litsea	400	Asia; Australia; Pacific islands
Mezilaurus	20	Tropical South America
Nectandra	120	Tropical and subtropical America
Neocinnamomum	6	South China; North Vietnam
Neolitsea	100	Asia
Nothaphoebe	40	Asia, mainly Malaysia and Indonesia
Ocotea	350	Tropical and subtropical America; Madagascar; Africa; Canary Islands
Paraia	1	Amazonia
Parasassafras	2	Bhutan; Myanmar; China
Persea	200	Tropical to temperate America and Asia; Canary Islands
Phoebe	100	Asia
Phyllostemonodaphne	1	Southeast Brazil
Pleurothyrium	45	Central and South America
Potameia	30	Madagascar; Asia
Potoxylon	1	Borneo
Povedadaphne	1	Costa Rica
Ravensara	30	Madagascar
Rhodostemonodaphne	20	Tropical South America
Sassafras	3	North America; China
Systemonodaphne	1	Guianas; Amazonia
Umbellularia	1	North America
Urbanodendron	3	Southeast Brazil
Williamodendron	3	Central and South America

usually have a unilocular ovary that produces a single-seeded drupe. The fruit may be free of the fruit stalk or partially or entirely enclosed by the receptacle.

Lauraceae fruits are primarily dispersed by specialist frugivorous birds, particularly bell birds, fruit pigeons, quetzals, and toucans, with approximately 80% of the diet of some species comprising lauraceous fruits. In the majority of cases the whole fruit is swallowed and the seed then regurgitated a short distance from the parent tree. Nonspecialist birds are important dispersers in temperate regions, whilst mammals (e.g., squirrels and monkeys) and fish may also be important dispersers.

Economic Uses

Historically, the Lauraceae is a very important economic family, especially the genus *Cinnamomum*, as a source of spices, e.g., cinnamon (*C. verum*), cassia bark (*C. cassia*) and laurel (*Laurus nobilis*), perfume oils, e.g., rosewood oil (*Aniba roseodora*) and sassafras oil (*Ocotea odorifera*), and pharmaceuticals, e.g., camphor (*C. camphora*). However, the most internationally important product produced today is the avocado fruit (*Persea americana*). Lauraceae wood is widely used locally, although a few are internationally important as high-quality timbers for furniture making or for resistance to salt water, e.g., greenheart (*Chlorocardium rodiaei*), Borneo ironwood (*Eusideroxylon zwageri*), and Queensland walnut (*Endiandra palmerstonii*). Some species (e.g., *Ocotea bullata*), once internationally important, are now protected because of past over-exploitation.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Medicinal, Food and Aromatic Plants**: Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Tree Physiology**: Physiology of Sexual Reproduction in Trees. **Tropical Forests**: Tropical Moist Forests; Tropical Montane Forests.

Further Reading

Chanderbali AS, van der Werff H, and Renner SS (2001) Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. *Annals of the Missouri Botanical Garden* 88: 104–134.

Kubitzki K and Kurz H (1984) Synchronized dichogamy and dioecy in neotropical Lauraceae. *Plant Systematics and Evolution* 147: 253–266.

Renner SS (1999) Circumscription and phylogeny of the Laurales: evidence from molecular and morphological data. *American Journal of Botany* 86: 1301–1315.

Rohwer JG (1993) Lauraceae. In: Kubitski K, Rohwer JG, and Bittrich V (eds), *The Families and Genera of Flowering Plants*, vol. 2, *Flowering Plants: Dicotyledons – Magnoliid, Hamamelid and Caryophyllid families,* pp. 366–391. Berlin, Germany: Springer-Verlag.

Rohwer JG (2000) Toward a phylogenetic classification of the Lauraceae: evidence from *mat*K sequences. *Systematic Botany* 25: 60–71.

Snow DW (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13: 1–14.

van der Werff H and Richter HG (1996) Toward an improved classification of Lauraceae. *Annals of the Missouri Botanical Garden* 83: 409–418.

Lecythidaceae

S A Mori, New York Botanical Garden, New York, USA

Introduction

The Lecythidaceae is a pantropical family of trees found in the tropics of Central and South America, southeast Asia, and Africa, including Madagascar (**Table 1**). The family is divided into five subfamilies: (1) the Planchonioideae, with six genera, the best known of which is *Barringtonia*, and 59 species in tropical Asia, Malaysia, northern Australia, the Pacific Islands, and Madagascar; (2) the Foetidioideae, with a single genus, *Foetidia*, and 17 species in Madagascar, Mauritius, and East Africa; (3) the Napoleonaeoideae, with two genera, *Crateranthus* and *Naopoleonaea*, and 11 species in West Africa; (4) the Scytopetaloideae, with a single species, *Asteranthos brasiliensis*, in the Negro and Orinoco river basins of Brazil and Venezuela and six genera and as many as 21 species in Africa; and (5) the Lecythidoideae of the western hemisphere. This article focuses on the New World species of Lecythidaceae.

New World Lecythidaceae range from Veracruz, Mexico (*Eschweilera mexicana*) to Paraguay (*Cariniana estrellensis*). The Caribbean harbors only *Grias cauliflora*, a species found in Jamaica, Central America, and northwestern South America. Several species of *Eschweilera* occur on Trinidad and Tobago, but these islands are South American, both geologically and in their floristic affinities.

Neotropical Lecythidaceae are best known for the Brazil nut of commerce (*Bertholletia excelsa*); for the cannon-ball tree (*Couroupita guianensis*), which is planted as a botanical curiosity in tropical and subtropical botanical gardens; and because species of the family are often ecological dominants in Amazonian forests.

Taxonomy and Genetics

In tropical America, there are 10 genera and 202 known species of Lecythidoideae and a single species, *Asteranthos brasiliensis*, of the African centered Syctopetaloideae. The largest genus is *Eschweilera* with 85 species followed by *Gustavia* (41), *Lecythis* (26), *Couratari* (19), *Cariniana* (15), *Grias* (7), *Corythophora* (4), and *Couroupita* (3). *Allantoma lineata*, *Asteranthos brasiliensis*, and *Bertholletia excelsa* belong to monotypic genera.

Molecular studies have demonstrated that the Lecythidaceae are monophyletic if members of the

Table 1 Subfamilies and genera of Lecythidaceae according to Morton *et al.* (1998)

Subfamily	*Region*	*Genera*	*Number of species*
FOETIDIOIDEAE	Madagascar, Mauritius, and east African tropics	*Foetidia*	17
LECYTHIDOIDEAE	New World tropics	*Allantoma*	1
		Bertholletia	1
		Cariniana	16
		Corythophora	3
		Couratari	19
		Couroupita	3
		Eschweilera	85
		Grias	7
		Gustavia	41
		Lecythis	26
NAPOLEONAEOIDEAE	African tropics	*Crateranthus*	3
		Napoleonaea	8
PLANCHONIOIDEAE	African and Asian tropics	*Abdulmajidia*	2
		Barringtonia	41
		Petersianthus	2
		Chydenanthus	2
		Careya	4
		Planchonia	8
SCYTOPETALOIDEAE	African tropics and *Asteranthos* in Amazonia	*Asteranthos*	1
		Brazzeia	3
		Oubanguia	3
		Pierrina	1
		Rhaptopetalum	10
		Scytopetalum	3

Scytopetalaceae are included. The relationship of *Asteranthos brasiliensis* with the Scytopetalaceae is supported by similarities in embryology, the presence in both of ruminate endosperm, and molecular affinities.

Ongoing molecular studies of neotropical Lecythidaceae indicate that not all of the genera are monophyletic. *Cariniana*, *Eschweilera*, and *Lecythis*, for example, include several clades that may have to be segregated as separate genera. Other genera, for example *Corythophora, Couratari*, *Couroupita*, *Grias*, and *Gustavia*, form natural groups as they are currently defined.

Ecology

New World Lecythidaceae are often dominant in lowland forests on well-drained soils between 19° N and 25° S latitudes. They rank as the first or second most important family of trees in frequency, density, and dominance in the vicinity of Belém, Brazil; the third most important at La Fumée Mountain, French Guiana; and one of the most important in central Amazonian Brazil.

A 100-ha plot established for the study of Lecythidaceae as part of the Biological Dynamics of Forest Fragments Project in central Amazonian Brazil about 80 km north of Manaus illustrates the ecological importance of Lecythidaceae in Amazonian forests. In this plot, there are 7791 trees of Lecythidaceae equal to or greater than 10 cm in diameter at 1.37 m (dbh, diameter at breast height). Among these trees are 38 different species, or nearly 19% of all of the species of Lecythidaceae known from the Neotropics. In each hectare, there are 45 to 149 individuals and 11 to 24 species. In this forest, where there are about 285 species of trees in all families in this size class per hectare, the Brazil nut family accounts for 12% of the individuals and 6% of the species of trees.

Species of the Brazil nut family diminish in importance at elevations above 1000 m, in periodically flooded forests, and in extremely dry habitats such as the *llanos* of Colombia and Venezuela and the *caatinga* of northeastern Brazil.

Nearly all neotropical Lecythidaceae are trees of either the understory, canopy, or emergent layers. The tallest, for example the forest-dwelling *Cariniana micrantha* and *Couratari stellata*, may reach 55–60 m in height. These genera, both dispersed by the wind, possess species of smaller stature when they are found in more open habitats; for example, *Couratari pyramidata* of the *cerrado* of central Brazil. The smallest is *Eschweilera nana*, a species that often possesses an underground trunk adapting it to survive the frequent fires of the *cerrado*. Individuals of *E. nana* may only reach several meters in height.

Trees of *Bertholletia excelsa* in the 140–150 cm dbh size class have been estimated by radiocarbon dating to be only 270 years old. One of the oldest known trees from the Neotropics is an individual of *Cariniana micrantha* radiocarbon dated at 1400 years old.

Species of Lecythidaceae are not common in secondary vegetation because they are extremely vulnerable to fire. If a forest is cut down and not subjected to fire, many Lecythidaceae will sprout from the cut stumps and flower and set fruit from the new branches. However, if fire follows cutting most Lecythidaceae are killed; hence old slash-and-burn fields throughout the Neotropics harbor few species and individuals of Lecythidaceae. Species of Lecythidaceae are generally indicators of undisturbed habitats.

Pollination Biology

The Brazil nut family provides examples of plant–animal coevolution. The flowers, fruits, and seeds are morphologically and anatomically adapted to the animals that pollinate their flowers and the animals, wind, and water that disperse their seeds.

Adaptation of Lecythidaceae for pollination has taken place, for the most part, in the male part of the flower. There are two types of flowers, radially and bilaterally symmetrical and three different rewards offered to pollinators – fertile pollen, sterile pollen, and nectar (**Figure 1**). Radially symmetrical flowers, such as those of *Gustavia superba* (**Figure 2**), offer only fertile pollen as a reward; consequently the pollinator reward and the pollen that effects

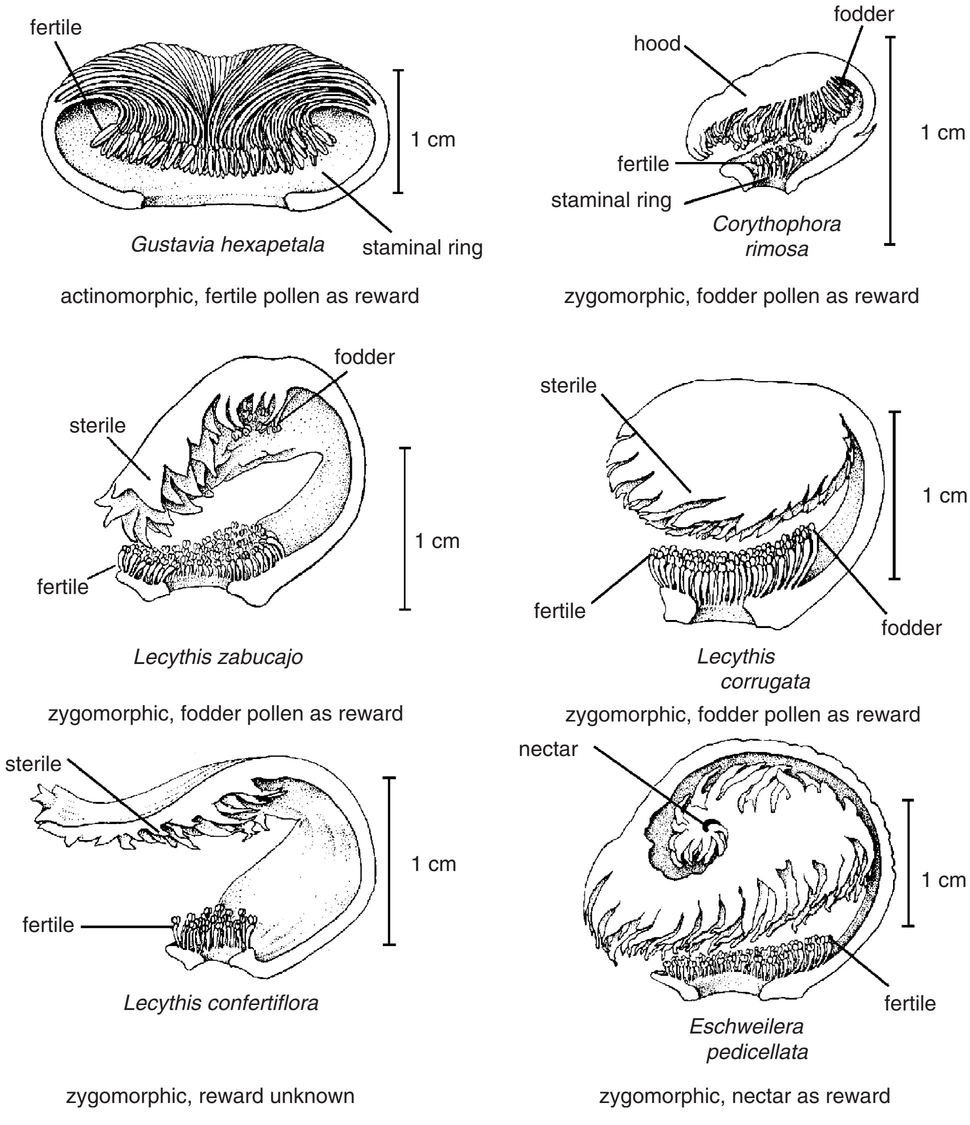


Figure 1 Examples of flower symmetry and pollinator rewards of Neotropical Lecythidaceae. Adapted with permission from Mori SA (1989) Diversity of Lecythidaceae in the Guianas. In: Holm-Nielsen LB, Nielsen IC, and Balslex H (eds) *Tropical Forests*, pp. 319–332. London: Academic Press. Illustration prepared by Bobbi Angell.

Figure 2 Radially symmetrical flowers of *Gustavia superba*. The pollinator reward in this species is nondifferentiated pollen. Photograph © SA Mori.

Figure 3 Bilaterally symmetrical flowers of *Lecythis pisonis*. The pollinator reward in this species is fodder pollen. Photograph © CA Gracie.

fertilization are morphologically and physiologically identical. Female bees visit the flower without restriction, collect pollen that is subsequently eaten by their larvae, and pollen is haphazardly deposited on their bodies. When the bees move to a flower of another tree, the pollen is deposited onto the stigma of that flower and eventually effects fertilization.

In contrast, species of Lecythidaceae with bilaterally symmetrical flowers offer two types of rewards, differentiated pollen and nectar. *Lecythis pisonis* (**Figure 3**), the *sapucaia* of the Amazon and the coastal forests of eastern Brazil, is a bilaterally symmetrically flowered species with both sterile and fertile pollen in the same flower. The fertile pollen is located in the staminal ring and sterile pollen is found in the staminal hood. Large, female bees, often of the genus *Xylocopa*, land on the staminal hood to collect sterile pollen from the hood. While collecting this pollen, the bee is dusted on the head and back with fertile pollen from the staminal ring. Experiments have demonstrated that the pollen purposely collected by the bee never germinates while that accidentally deposited onto the head and back always does. It is the latter pollen that is brushed off the head and back of the bees onto the stigmas of subsequent flowers visited that effects fertilization.

Eschweilera pedicellata (**Figure 1**) is a bilaterally symmetrically flowered species that offers nectar as a reward to the pollinators which are usually robust male and female euglossine bees. Both sexes visit flowers of this kind of Lecythidaceae because the nectar reward is utilized as an energy source for adult bees. In this type of flower, the staminal hood usually closes the flower; moreover the hood is internally coiled and nectar is produced at the apex of the coil (**Figure 1**). The nectar is secreted from vestigial stamens that no longer bear anthers.

Although the most important pollinators of Lecythidaceae are bees, at least two species (*Lecythis barnebyi* and *L. poiteaui*) and perhaps a third (*L. brancoensis*) are pollinated by bats, and some species of *Grias* are suspected to be pollinated by beetles. The bat-pollinated species have nocturnal flowers, display their flowers at the periphery and above the canopy, and emit an aroma dominated by sulfur-bearing compounds that is similar to rotting cabbage, all features of flowers visited by bats. The putative beetle-pollinated species of *Grias* emit aromas dominated by fatty acids similar to those produced by other beetle-pollinated plants.

Dispersal Biology

Neotropical species of the Brazil nut family have fruits that either do not open (indehiscent) or open via a lid at maturity (dehiscent). The seeds of different species are dispersed by animals, the wind, or water.

Several examples will give an idea of the wide variation in dispersal systems found in the New World Lecythidaceae. Species of *Gustavia* and *Grias* possess indehiscent fruits with the seeds often surrounded by a pulp eaten by animals, including humans. For example, *Grias neuberthii* has a fleshy mesocarp surrounding a fibrous endocarp, and, in that regard, is similar in structure, but not shape, to a peach. The fruits are sold in western Amazonian markets for their edible mesocarp. The endocarp, however, facilitates flotation of the fruit once the mesocarp has been eaten by animals, and it appears that this species may be secondarily dispersed by water currents.

In *Couroupita guianensis* (**Figure 4**), the mature fruits fall from trunk and crack open upon impact with the ground to expose a bluish-green, foul-smelling pulp, in which are embedded numerous, small seeds. In the Brazilian Amazon, peccaries have been reported to eat the pulp and swallow the seeds and it is presumed that the seeds pass through the peccaries' digestive tracts and subsequently germinate some distance from the mother trees, thereby effecting seed dispersal. The pulp is often fed to domestic pigs and poultry and seeds have been reported to germinate in the feces of these animals. This is the only genus of Lecythidaceae known to have numerous, long hairs arising from the seed coat. It is hypothesized that these hairs protect the seeds from digestive juices as they pass through the peccaries' digestive tracts.

Bertholletia excelsa, the Brazil nut of commerce, has a very specialized dispersal system. At maturity the fruits drop to the ground with the seeds trapped inside because the size of the fruit opening is smaller in diameter than the size of the seeds (**Figure 5**). Rodents, especially agoutis (*Dasyprocta* spp.) gnaw through the woody fruit walls by enlarging the small opening of the lid, chew through the thick and bony seed coat to consume the embryos of some of the seeds, and cache other seeds for future consumption. Some of the cached seeds are forgotten, and it is these that germinate 12–18 months later to form the next generation of trees. The fruits are so rot resistant that after the seeds have been removed by animals, they accumulate water and serve as breeding sites for an assemblage of anuran and insect species.

The largest fruited species of Lecythidaceae is *Lecythis pisonis* (**Figure 5**). After fertilization by carpenter bees (*Xylocopa* spp.), the fruits reach the size of a human head after nearly a year of development. This species, distributed in the Atlantic forests of eastern Brazil and in eastern Amazonia, opens via a lid that drops when the seeds are mature. The fruit opens while still in the tree crown and the seeds remain attached to the inner fruit wall by a funicle, which, in turn, is surrounded by a fleshy, white outgrowth called an aril. Bats, including *Phyllostomus hastatus*, remove the seeds with the attached aril on the same night that the fruits open. After the aril

Figure 4 The indehiscent fruits of *Couroupita guianensis*. Peccaries eat the pulp of the fruits of this species. Photograph © CA Gracie.

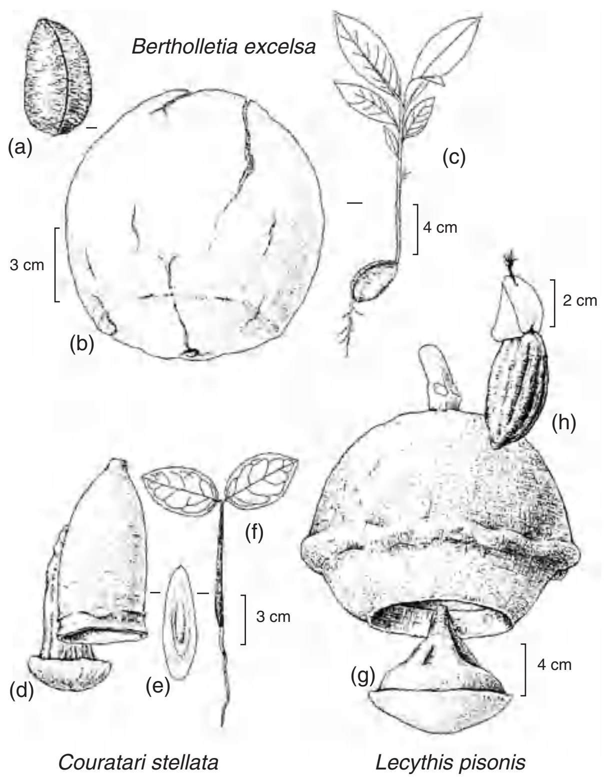


Figure 5 Fruits, seeds, and seedlings of *Bertholletia excelsa* and *Couratari stellata* and fruit and seed of *Lecythis pisonis*. Adapted with permission from Mori SA (1989) Diversity of Lecythidaceae in the Guianas. In: Holm-Nielsen LB, Nielsen IC, and Balslex H (eds) *Tropical Forests*, pp. 319–332. London: Academic Press. Illustration prepared by Bobbi Angell.

is eaten, the bats drop the intact seeds either in flight or under their roosts.

All species of *Cariniana* and *Couratari* (**Figure 5**) are dispersed by the wind. The woody, cylindric fruits open to release seeds that are either winged at one end in *Cariniana* or winged all around the seed in *Couratari*. Species of these genera are either very tall forest trees or smaller trees of open habitats; consequently seeds falling from the fruits are exposed to the wind. The seeds of these genera are very light and possess embryos with leaflike cotyledons that enable the seedlings to begin photosynthesis immediately upon germination of the seeds, thereby compensating for the lack of nutrients in the seeds.

Water dispersal, although relatively uncommon, takes place in two different ways. In some species, the seeds fall from the fruit, float on the water because of the corky seed coats, and are carried away by currents. A common Amazonian tree found in periodically inundated forest, *Eschweilera tenuifolia* (**Figure 6**), is dispersed in this fashion. In *Lecythis rorida*, the entire fruit falls into the water and floats away with the seeds inside. The morphologically most similar species to *L. rorida* is *L. chartacea*, a species that normally grows in nonflooded forest away from the river. *Lecythis chartacea* has fruits that open at maturity to reveal seeds subtended by an aril that is most likely sought after by animals that, in turn, disperse the seeds. The seeds of *L. rorida* lack an aril, which would serve no purpose in water dispersal.

The woody fruits of Lecythidaceae are viewed as a way to protect the seeds from predispersal predation. The thick and woody fruit walls of *Cariniana micrantha*, however, do not deter brown capuchin monkeys (*Cebus* spp.) from opening the lids just before the fruits would naturally open and eating the seeds. The monkeys tear the fruits from the branches, knock them against the larger limbs and trunk, consume seeds, and then drop the fruits with a few remnant seeds to the ground. In one year, 99.5% of the entire seed production of a tree in central Brazilian Amazon was destroyed by brown capuchins.

Figure 6 Trees of *Eschweilera tenuifolia* growing in periodically inundated forest on the Rio Negro, Brazil. The seeds of this species drop into the water and are carried away by currents. Photograph © SA Mori.

Silviculture

The methodology for growing Brazil nuts in large plantations has been developed by the Brazilian agricultural research institution, EMBRAPA, in Belém and a great deal of literature exists about starting plantations from seeds and about grafting high-yield clones onto established root stocks. Nevertheless, most of the Brazil nuts reaching the international market are still gathered from wild trees, perhaps because native pollinators are not as abundant in the disturbed habitats of plantations as they are in more mature forests.

Utilization

The Brazil nut is the economically most important species of Lecythidaceae. Brazil nuts are gathered only from *Bertholletia excelsa*, a species of nonflooded forest native to Guyana, Surinam, Amazonian Colombia, Venezuela, Peru, Bolivia, and Brazil. Brazil nut trees are cultivated as a curiosity in tropical botanical gardens and sporadically in experimental plantations outside of the original range of the species. The edible seeds of the Brazil nut, along with the latex of rubber (*Hevea brasiliensis*) are often cited as the most important products of extractive reserves in Amazonia and these products are heralded as a way to conserve tropical diversity while at the same time sustaining human populations.

Brazil nut trees flower during the dry season into the wet season and are only found naturally in regions with a 3–5-month long dry season. Toward the end of the rainy season, the leaves of Brazil nut trees begin to fall. As the dry season approaches, new growth flushes of leaves and inflorescences are produced at the apex of the current growth. The flowers open shortly below daybreak and the petals and attached androecium fall in the afternoon of the day they open. Robust nonsocial or semisocial bees of *Bombus*, *Centris*, *Epicharis*, *Eulaema*, and *Xylocopa* are the pollinators. Both sexes of these bees visit the flowers for nectar. Although the Brazil nut is mostly self-incompatible, a small amount of self-compatibility does occur; therefore, the bee pollinators are usually essential for carrying pollen from one tree to the next as most of the fruit set results from their visits.

Brazil nuts are an economically important crop because the seeds are retained within the fruit when the fruit falls to the ground. The fruits, which weigh from 0.5 to 2.5 kg and contain 10 to 25 seeds, are easily harvested from the ground. A few other species, such as *Lecythis pisonis* (**Figure 5**), produce seeds equally as good to eat and as nutritious as the Brazil nut. However, they appear only sporadically in local markets because the fruits open and the seeds are carried away by bats before they can be harvested. These species are generally harvested by climbing the tree and cutting the entire fruit shortly before the fruit would naturally dehisce, a system that does not lend itself to the easy gathering of massive numbers of seeds by human collectors. Two closely related species, *L. minor* and *L. ollaria*, also yield edible seeds, but the seeds sometimes accumulate selenium, and, if too many of them are eaten, hair and even finger nails may be temporarily lost as the possible result of mild selenium poisoning.

A few species of *Gustavia* and *Grias* are grown in backyard gardens for the pulp surrounding the seeds that can be eaten raw or cooked. The best known are *Gustavia speciosa*, known as *chupa* in Colombia and *chopé* in Peru, and *Grias neuberthii*, the *sacha mangua* of Peru.

For the most part, the Brazil nut family is not known for high-quality timber. However, species of *Cariniana* have long straight boles and excellent timbers. The best known are *albarco* (*C. pyriformis*) of northwestern South America and the *jequitibás* (*C. estrellensis* of eastern Brazil and *C. legalis* of southwestern Amazonia and eastern Brazil). Brazil nut trees also produce high-grade timber, but they are protected by law because of their greater value as producers of edible seeds.

Only minor medicinal properties have been reported for the family. The most significant chemical use of Lecythidaceae is as an arrow poison derived from *Cariniana domestica*. The poison, extracted from the bark, kills small animals by disrupting their blood-clotting mechanisms thereby causing excessive bleeding when the animals are hit by poisoned arrows.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest. **Silviculture**: Managing for Tropical Non-timber Forest Products; Treatments in Tropical Silviculture. **Tropical Forests**: Tropical Moist Forests; Tropical Montane Forests.

Further Reading

Appel O (1996) Morphology and systematics of the Scytopetalaceae. *Botanical Journal of the Linnean Society* 121: 207–227.

Caldwell JP (1993) Brazil nut fruit capsules as phytotelmata: interactions among anuran and insect larvae. *Canadian Journal of Zoology* 71: 1193–1201.

Camargo PB de, Salomão R de P, Trumbore S, and Martinelli LA (1994) How old are large Brazil-nut trees (*Bertholletia excelsa*) in the Amazon? *Scienta Agricola, Piracicaba* **51**, 389-391.

Jacobs JW, Petroski C, Friedman PA, and Simpson E (1990) Characterization of the anticoagulant activities from a Brazilian arrow poison. *Thrombosis and Haemostasis* 63(1): 31–35.

Kerdell-Vargas F (1966) The depilatory and cytotoxic action of coco de mono (*Lecythis ollaria*) and its relationship to chronic seleniosis. *Economic Botany* 20: 187–195.

Knudsen JT and Mori SA (1996) Floral scents and pollination in Neotropical Lecythidaceae. *Biotropica* 28: 42–60.

Mori SA (1992) The Brazil nut industry: past, present, and future. In: Plotkin M and Famolare L (eds) *Sustainable Harvest and Marketing of Rain Forest Products*, pp. 241–251. Washington, DC: Island Press.

Mori SA and Prance GT (1990) *Lecythidaceae*, Part II, *the Zygomorphic-Flowered New World Genera* (Couroupita, Corythophora, Bertholletia, Couratari, Eschweilera, and Lecythis), *With a study of the secondary xylem of Neotropical Lecythidaceae by Carl de Zeeuw*. Fl. Neotrop. Monographs, vol. 21. New York: The New York Botanical Garden.

Mori SA, Becker P, and Kincaid D (2001) Lecythidaceae of a central Amazonian lowland forest: implications for conservation. In: Bierregaard RO Jr., Gascon C, Lovejoy TE, and Mesquita RCG (eds) *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*, pp. 54–67. New Haven, CT: Yale University Press.

Moritz A (1984) Estudos biológicos da castanha-do-Brasil (*Bertholletia excelsa* H.B.K.). *EMBRAPA, Centro de Pesquisa Agropecuária do Trópico Umido, Documentos* 29: 1–82.

Morton CM, Mori SA, Prance GT, Karol KG, and Chase MW (1997) Phylogenetic relationships of Lecythidaceae: a cladistic analysis using *rbc*L sequence and morphological data. *American Journal of Botany* 84: 530–540.

Morton CM, Prance GT, Mori SA, and Thorburn LG (1998) Recircumscription of the Lecythidaceae. *Taxon* 47: 817–827.

Müller CH (1981) Castanha-do-Brasil; estudos agronômicos. *EMBRAPA, Centro de Pesquisa Agropecuária do Trópico Umido, Documentos* 1: 1–25.

Oliveira AA de and Mori SA (1999) A central Amazonian *terra firme* forest. I. High tree species richness on poor soils. *Biodiversity and Conservation* 8: 1219–1244.

Peres CA (1991) Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in central Amazonia. *Biotropica* 23: 262–270.

Prance GT and Mori SA (1979) *Lecythidaceae*, Part I, *The actinomorphic-flowered New World Lecythidaceae*

(Asteranthos, Gustavia, Grias, Allantoma, and Cariniana). Fl. Neotrop. Monographs, vol. 21. New York: The New York Botanical Garden.

Tsou C-H (1994) *The Embryology, Reproductive Morphology, and Systematics of Lecythidaceae*. Memoirs of the New York Botanical Garden, vol. 71. New York: New York Botanical Garden.

Monsoon Forests (Southern and Southeast Asia)

K K N Nair, Kerala Forest Research Institute, Peechi, Kerala State, India

Introduction

Tropical forests are of two major types – rainforest and monsoon or seasonal forest, close to the equatorial region. Monsoon forests are also known as mixed forests, along the borders or part of tropical rainforests in southern and southeastern parts of Asia. The forest type is characterized by a dry period of 3–5 months, when plant growth is limited by water stress, whereas in typical tropical rainforests this phenomenon does not exist. In general, monsoon forests are more nanic in stature than typical rainforests and many tree species in the forest formation remain leafless during the dry season; this is otherwise known as deciduous species. Because of this, more sunlight reaches the understory, promoting the growth of rich heliophilous ground flora, in addition to several lianas. However, woody epiphytes are comparatively few in number in monsoon forests, compared to rainforests. The monsoon vegetation of South and Southeast Asia is subject to much degradation, especially due to fire in the drought season, as well as shifting cultivation and several other factors. In order to conserve the forest type and its biodiversity, protected areas have been established in almost all countries in the region.

Definition and Terminology

In the early twentieth century, based on climatic and vegetational parameters, monsoon forests were described as more or less deciduous or leafless during the dry season and tropophilous in nature, i.e., alternating in hygrophilous and xerophilous characters, regulated by the monsoon climate. In typical rainforest areas of the Asian continent there is evenly distributed and heavy rainfall throughout the year, whereas in certain countries within the continent (Cambodia, India, Myanmar, Sri Lanka, Thailand and Vietnam), rainfall is seasonal with an annual dry period of about 3–5 months. In those countries, monsoon forests are quite common, apart from the evergreen and semievergreen rainforests. Due to the dry period and consequent deciduous nature of many tree species constituting the upper story of the vegetation, the subcanopy flora is fairly rich with woody climbers, shrubs, and herbaceous ground flora. At the same time, because of the dry climate and the deciduous nature of the forest formation, monsoon forests are poor in biomass content as compared to rainforests. Monsoon forests are also subjected to seasonal fire, promoting the development of savannas or grasslands, containing thorny or unarmed, stunted trees and shrubs. Because of the complex nature of monsoon forests, they are also designated as mixed forests, and vegetation types like moist and dry deciduous forests, savannas, scrubs, and thorn forests all belong to this category. Often, tropical rainforests merge or penetrate into monsoon forest formations, especially along water courses and wet habitats and the continuity of the two forest types is also restricted by repeated fire, resulting in the formation of savannas, which separate the two forest types. Such extensions of rainforests into monsoon forests are called gallery forests. **Figure 1** shows different categories of tropical forests in South

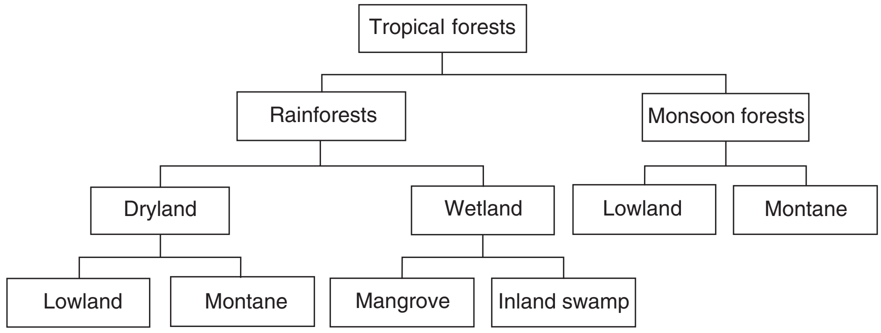


Figure 1 Categories of tropical forests in South and Southeast Asia.

and Southeast Asia. It may be noted that both rainforests and monsoon forests are distributed in lowlands and high mountains, and it is the climate which plays the major role in the development of the two different forest types within the same phytogeographical region.

Based on the duration of the dry period, monsoon forests may be open-canopy deciduous woodlands, closed-canopy thorn forests, scrubs, grasslands, or desert formations. Within the forest type, there are also different localized formations, varying in physiognomy and species composition, depending mainly upon soil, topography, and climate.

Monsoon Forest Environment

In tropical South and Southeast Asia, monsoon forests are mostly developed in rain shadow areas where there is seasonal drought for 3–5 months. During this period, average rainfall seldom exceeds 100 mm and, consequently, dry-weather conditions prevail there. As a result, the vegetation becomes tropophilous in character with deciduous and thorny plants dominating the formation. There are also local variations in monsoon climate. In Myanmar, the forest formation is distributed in areas receiving 400–800 mm rainfall; wherever precipitation exceeds 800 mm, rainforests are more common.

The soil types harboring the monsoon forests differ in different countries of the region. In peninsular India, they are developed in loamy, rocky, and similar uncharacteristic soil types, poor in nutrient content and water retention. However, in the north-eastern part of the country and also Bangladesh, sal *Shorea robusta* – dominated forests are common in alluvial soils along the deltas. In Cambodia, Laos, Myanmar, and Vietnam, both alluvial and dry and rocky soils harbor the vegetation type. In China and Southeast Asian countries (e.g., the Philippines), the forest formation is more common on limestone soils, as in the case of China.

Distribution and Extent of Monsoon Forests

In South and Southeast Asia, monsoon forests are distributed in Bangladesh, Cambodia, China, India, Indonesia, Laos, Myanmar, Philippines, Sri Lanka, Thailand, and Vietnam (**Figure 2**). The estimated area occupied by this forest type in different countries and the percentage of the area of total forest cover are given in **Table 1**. Brunei, Java, Kalimantan, Peninsular Malaysia, Sabah, Sarawak, Singapore, Sumatra, and Taiwan, do not have significant areas of monsoon forests. Among the different countries with monsoon forests, Sri Lanka has the greatest percentage (88%) of total forest area. This is followed by India (70%), China (66%), Cambodia (42%), and Vietnam (34%). Indonesia is predominantly under rainforest with less than 3% of total forest area classified as monsoon

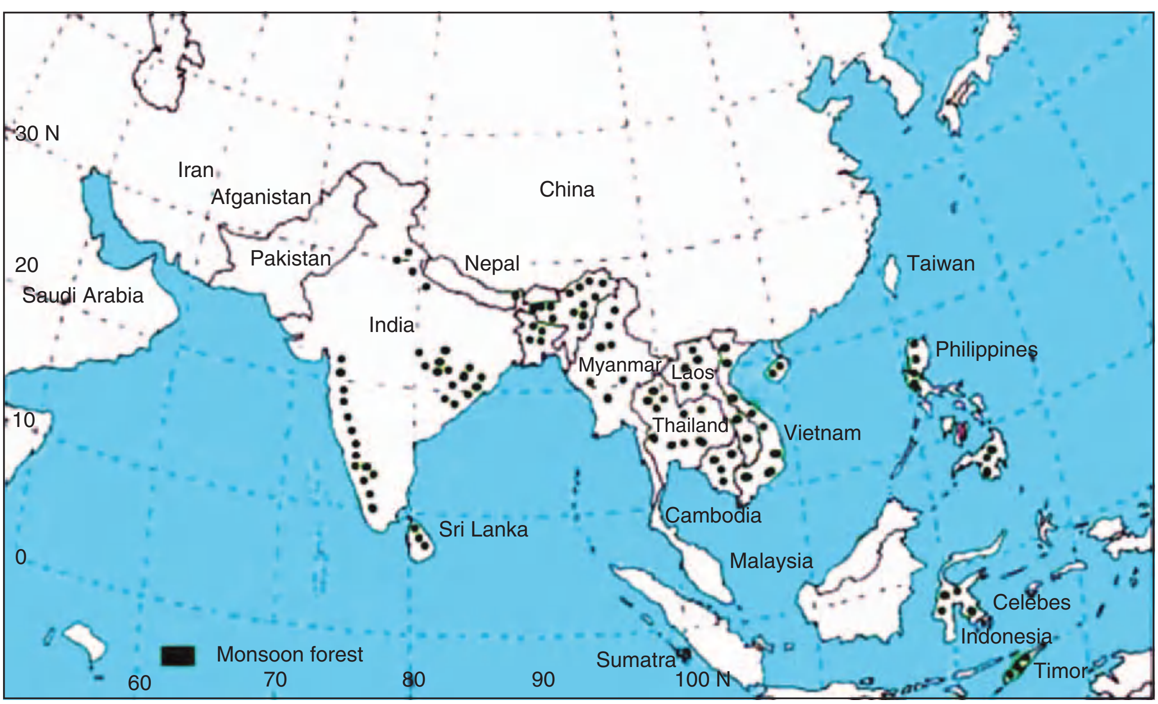


Figure 2 Distribution of monsoon forests in South and Southeast Asia.

Table 1 Total forest area, monsoon forest area and its percentage in different South and Southeast Asian countries

Country	*Total forest area (km²)*	*Monsoon forest area (km²)*	*Percentage*
Bangladesh	14 042	645	4.6
Cambodia	113 250	47 750	42.16
China	24 200	17 050	70.5
India	228 330	158 950	69.6
Western Ghats	38 610	18 410	47.6
NE India	82 490	38 780	47.0
Andaman and Nicobar Islands	6840	3620	52.9
Other parts	100 390	98 140	97.8
Indonesia	1 179 140	30 740	2.8
Lesser Sunda Islands	14 590	13 690	93.8
Sulawesi	11 240	8120	72.2
Moluccas	56 070	8930	15.9
Laos	124 600	25 810	20.7
Myanmar	311 850	88 460	13.4
Philippines	66 020	15 280	23.1
Sri Lanka	12 260	10 820	88.3
Thailand	106 900	31 500	29.5
Vietnam	5680	19 510	34.4

forest. This is because Java, Kalimantan, and Sumatra, are devoid of this forest type, even though about 90% of the total forest area of the Lesser Sunda Islands is covered by monsoon vegetation. With regard to China, even though 70% of the total forest area of the country is occupied by monsoon vegetation, only a very limited part of it is located in South Asia. In the case of Bangladesh, mangrove forests are well represented, with approximately 4.6% of the total forest area occupied by the much-degraded monsoon vegetation. The Pacific island of Papua New Guinea, beyond the limit of Southeast Asia, is also very poor in representation of monsoon forests, with less than 1% of the total forest area of the country belonging to this vegetation type. On the whole, approximately 57% of the total forest area in different countries of South and Southeast Asia comprises monsoon forests.

In Sri Lanka in the Indian Ocean, more than 88% of total forest area is occupied by monsoon forests. Tropical rainforests of the evergreen and semievergreen types, common in neighboring peninsular India, are rather restricted to the southwest corner of the island, where annual rainfall ranges between 4000 and 5000 mm and the altitude exceeds 1000 m above msl. The monsoon vegetation of Sri Lanka is distributed in the northern, northwestern, and eastern rain shadow parts of the country (**Figure 3**). Degraded thorn and scrub forests are common here. Human interventions in the forest area have drastically transformed the original vegetation of the country and the establishment of tea plantations is one of the major reasons for this. Remnants of mangrove forests are also represented in the island (about 10% of the total forest area).

Figure 3 Distribution of monsoon forests in Sri Lanka.

Southern and northeastern parts of India and the Andaman and Nicobar Islands contain monsoon forests, often sharing or merging their borders with the rainforests (**Figure 4**). In peninsular India, monsoon forests are distributed along both the western margins and eastern side of the Western Ghats, where rainfall is very meager or absent for a few

Figure 4 Distribution of monsoon forests in mainland India.

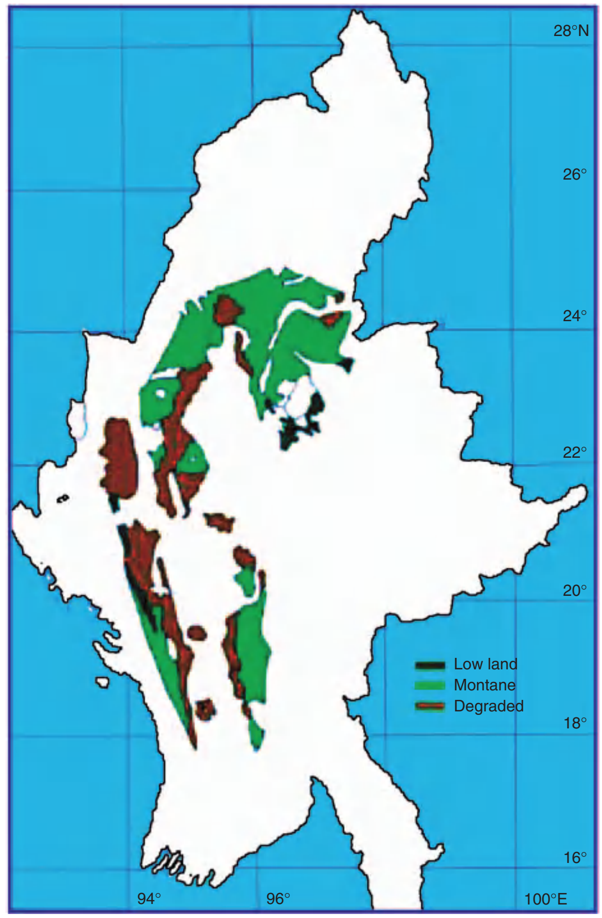


Figure 5 Distribution of monsoon forests in Myanmar.

months. In the northeastern part of the country, bordering Bangladesh and Myanmar, monsoon sal forests are common, often restricted or degraded by the Jhum or shifting cultivation. In the case of the monsoon forests of the southern part of India, degradation is taking place mainly due to encroachments and conversion of forest areas for nonforestry purposes, as well as the unregulated exploitation of timber and nontimber resources, of both plant and animal origin. The monsoon forests of Bangladesh are a continuation of the forest type in northeastern India and are restricted to the inland plains of the country, mainly distributed in the Madhupur tract. Also, relicts of the forest type occur in Dhaka, Mymensingh, and Tarigail forest tracts in the northern part of the country. Sal forests dominated by *Shorea robusta* trees characterize the vegetation type in Bangladesh, which at present is in a highly degraded condition. The major forest type of the country is the Mangals (mangrove forests), distributed along the estuaries and seashores.

Rainforests dominate the vegetation types of Myanmar, distributed along the west-facing slopes of the south–north running mountains, in the western and eastern frontiers of the country, either as evergreen or semievergreen formations. In the rain shadow Irrawadhy plains, on the western side of Myanmar, the characteristic vegetation type is dry deciduous woodlands, dominated by dipterocarp trees, interspersed by thorn forests. Surrounding this zone, monsoon forests are distributed along the eastern flanks of Arakan Yoma and the Chin Hills (**Figure 5**). In the Shan Plateau also, the forest type is distributed towards the east of Salween and towards the south, covering the hills bordering Thailand. Adjoining Myanmar, in the southern part of the mainland of the People's Republic of China, monsoon forests are distributed in areas of limestone substratum, in southern Guangxi. The Island of Taiwan close to the Chinese mainland is devoid of monsoon forests and rainforests are quite prevalent there. However, in the island of Hainan, within the South Asian region, monsoon forests are well represented. Moreover, approximately 70% of the total forest area of China is comprised of monsoon forests; the remaining 30% is composed of lowland and montane rainforests (**Figure 6**). However, most of the monsoon forest areas of mainland China fall in central Asia and not in the southern part of the continent.

In Indochina, along the eastern side of the Mekong river and in the northern part of Tonle Sap, extending to the border of Thailand and the Laos PDR, monsoon forests are distributed in

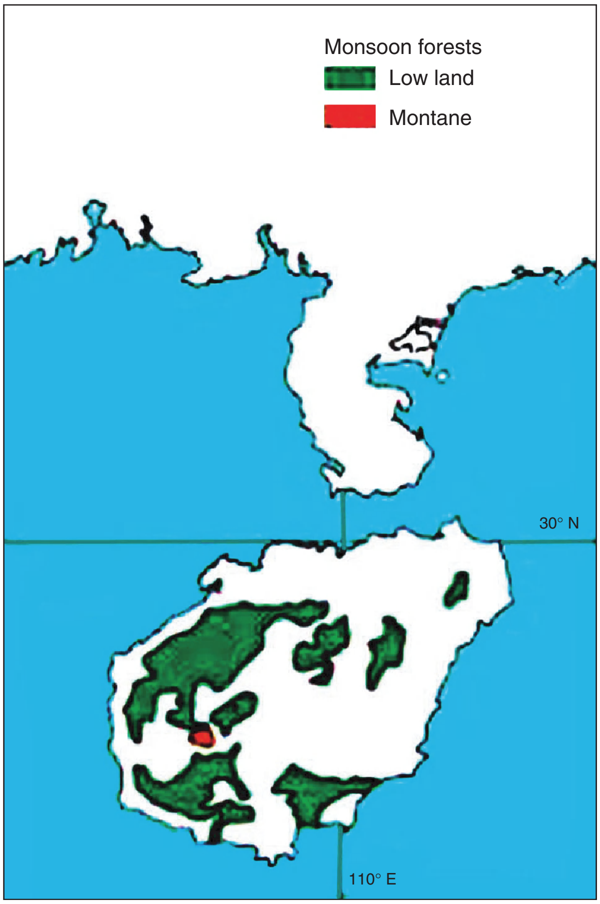


Figure 6 Distribution of monsoon forests in Hainan (PR China).

Cambodia (**Figure 7**). A variety of dense, dry, deciduous and semideciduous woodlands represents the forest formation of the country. The monsoon forests of Cambodia are in a badly devastated and degraded state due to shifting agriculture and fire which transformed the vegetation into open savannas and woodlands. In Laos PDR, monsoon forests are distributed in areas north and west of Mekong and are characterized by the dominance of teak trees of high timber value (**Figure 8**). In the past, more than 50 000 km^2 of the forest area of the country was occupied by monsoon forests, covering the drier parts where 5–6 months of dry weather prevail. However, more than 70% of the natural forests of Laos are constituted by rainforests of both evergreen and semievergreen types which, in many areas, are replaced by monsoon forests due to human and other disturbances, including shifting cultivation. In Vietnam, dipterocarp-dominated lowland evergreen forests are more common in the southern parts of the country, whereas monsoon forests are distributed towards its northern side (**Figure 9**). Almost 45% of the total forest area of Vietnam comprises monsoon forests, where deforestation is a serious problem consequent to migration of people, plantation forestry, and war damage. The rich mangrove wealth of the country, including the *Melaleuca* forests, was also devastated during the much-prolonged Vietnam war and only their remnants remain at present, along the banks of the Red river. Application of the devastating herbicide Agent Orange was highly detrimental to the natural forests of the country, for both mangroves and land vegetation.

Towards the southeastern part of the Asian continent, namely Thailand, monsoon forests are common in the northern parts, bordering Myanmar. However, the adjoining peninsular Malaysian region is predominantly covered by typical rainforests of both evergreen and semievergreen types. At present, the monsoon teak forests of Thailand are in a highly degraded condition (**Figure 10**). Dry deciduous woodlands with species of dipterocarp also occur in the northern and eastern parts of the country. Heath forests, limestone vegetation, freshwater swamps, and beach forests are other vegetation types of Thailand, apart from the complex and very varied montane rainforests, dominated by genera of temperate plants like *Castanopsis, Lithocarpus*, and *Quercus*. The Himalayan species *Betula alnoides* is also common in the rainforests of Thailand.

In the Lesser Sundas, Sulawesi and Malacca near to Irian Jaya, which is the southeastern limit of the Asian continent, about 30 000 km^2 of monsoon forests are distributed. However, in Java, Kalimantan, Sumatra, and also Irian Jaya, the forest type is not very prevalent. In the northeastern part of Java, monsoon forests were seen in the past, in a highly disturbed state. In the Lesser Sunda Islands, monsoon forests and grasslands are restricted to the south-facing sides of the mountain, where sandalwood (*santalum album*) forests are common, similar to that of the dry deciduous forest tracts of southern peninsular India (**Figure 11**). In Sulawesi, the forest type is fairly well represented in the southern part and in Irian Jaya eucalyptus forests and grasslands are more common. Beyond the Southeast Asian limit, in the Pacific Islands of Papua New Guinea, less than 1% of the total forest area is occupied by the monsoon forests; this is the eastern limit of the forest type of the world. In the chain of the Philippine islands, the northernmost Luzon Island contains monsoon forests along the centrally located Mount Data, running in a north–south direction. Also, in Zambales, along the Carapello mountains, towards the western side of the island, disturbed patches of this forest type occur. In southernmost Mindanao also, degraded monsoon forest patches are common towards its western side (**Figure 12**). Both lowland and montane types of forest formations are common

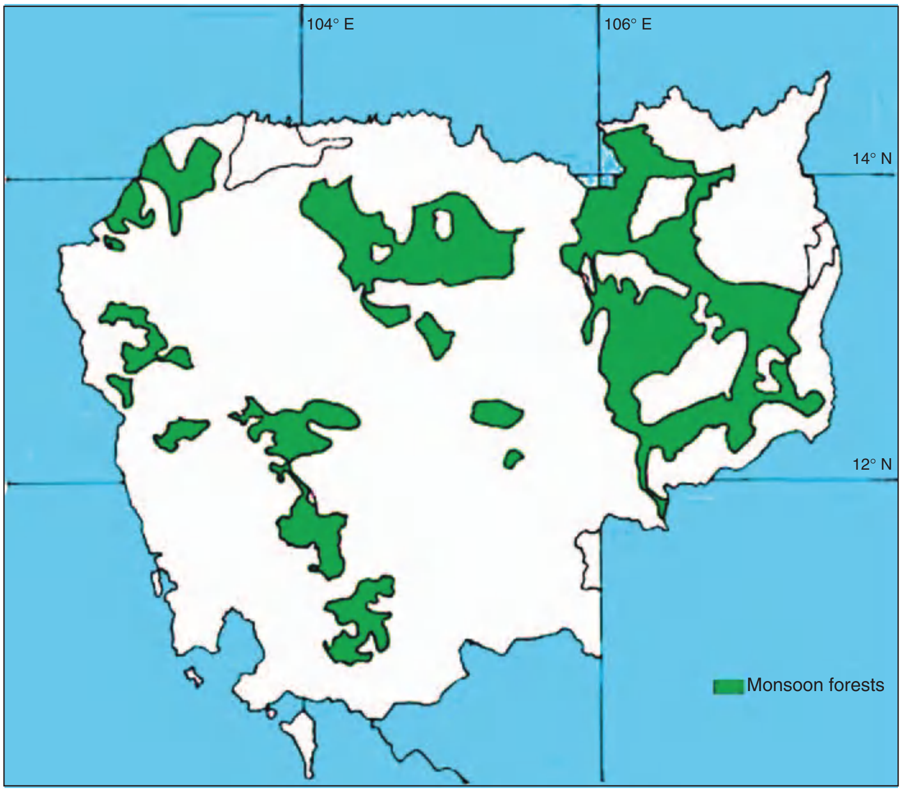


Figure 7 Distribution of monsoon forests in Cambodia.

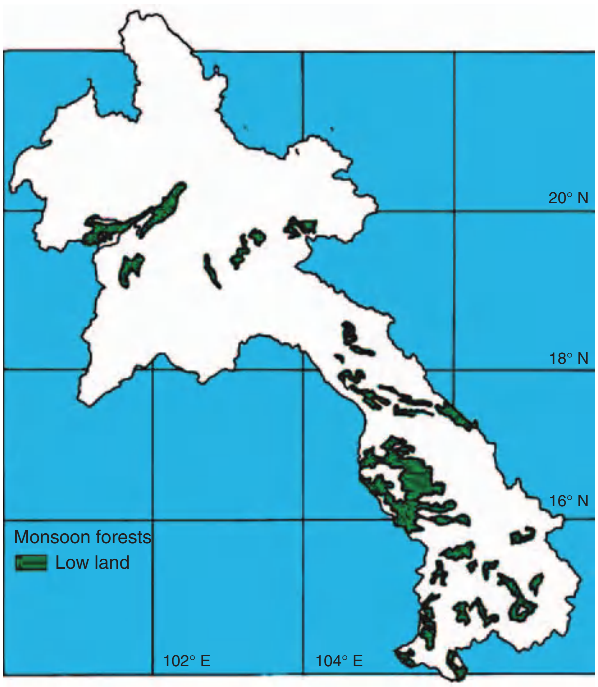


Figure 8 Distribution of monsoon forests in Laos.

in these islands, dominated by two species of pine (*Pinus kesiya* and *P. menkusii*). Forests of Molave are also, in general, monsoon formations, developed in well-drained limestone soil, behind the beach or mangrove formations. The forest type here is characterized by the preponderance of *Vitex* trees belonging to the teak family (Verbenaceae).

Structure and Composition of Monsoon Forests

In South and Southeast Asia, both lowland and montane monsoon forests occur. Also, there are different local formations within the forest type, depending on topography, climate, and soil. The structural and floristic composition of the monsoon forests of South and Southeast Asia differs greatly from the adjoining rainforests of the region. If lofty trees of dipterocarps dominate the rainforests of Southeast Asia, this type of tall tree is less frequent and more stunted in nature in the monsoon forests there. The typical tree species in the monsoon forests of Southeast Asia belong to genera such as *Acacia, Albizia, Borassus, Butea, Caesalpinia, Cassia, Corypha, Dalbergia, Dichrostachys, Feronia, Garuga, Homalium, Lannea, Melia, Schleichera, Stereospermum, Tectona,* and *Tetrameles*. Australian plants, including species of *Banksia, Eucalyptus*, and *Grevillea*, are also common in the monsoon forests of the Lesser Sunda Islands. *Santalum album* and *Melaleuca leucodendron* are other Australian elements found

Figure 9 Distribution of monsoon forests in Vietnam.

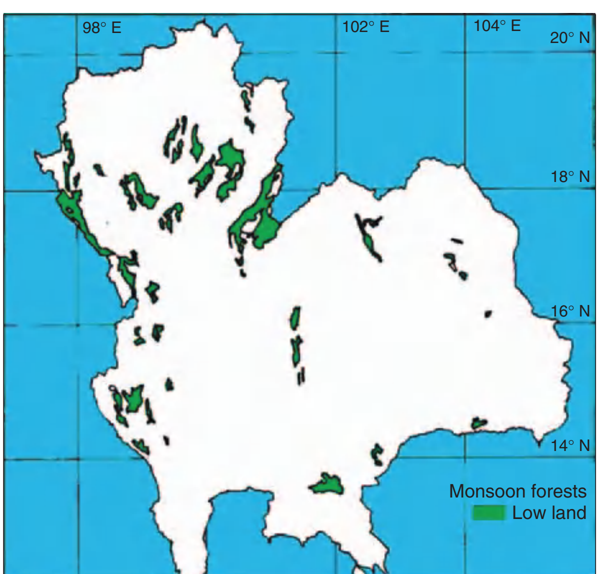


Figure 10 Distribution of monsoon forests in Thailand.

in the monsoon forests of the Lesser Sunda Islands and the former is also common in peninsular India. There are also several endemic species in the monsoon forests, e.g., species of *Semicardium* in Malaysia and *Dalbergia* in peninsular India. However, many plants in the monsoon forests in South and Southeast Asia enjoy wider ranges of distribution from India to Australia or even beyond, as in the case of the tamarind tree (*Tamarindus indica*), distributed in both African and Asian continents. In the monsoon forests of the region, there are also plant species which prefer wet conditions, e.g., fern species belonging to the genera *Dicranopteris* and *Gleichenia,* and the moss flora on the mountains clothed with monsoon forests. However, drought-resistant species dominate the forest type and, apart from the cultivated sugarcane which needs only seasonal dryness, several drought-hardy members of the family Fabaceae are quite prevalent in the forest formation. Due to the highly fragmented nature of monsoon forests, stemming from climatic and degradation factors, many plant groups characteristic of the forest type show regional or national breaks in their total range of distribution, resulting in the phenomenon called disjunctive distribution. For the same reason, many endemic plants are also common in the forest type. Extensions of many species beyond their regional range is mainly due to the fact that the forest type itself was of much greater extent in the past, favoring the distribution of xerophytic plants between countries or regions such as India in South Asia and Indonesia in the southeastern part of the region. Euphorbiaceous plants (e.g., species of *Blackia, Melanolepis*, and *Phyllanthus*) are also common in the seasonal dry parts of Southeast Asia, including Kalimantan. Therefore seasonal drought is one of the major factors that influence the distribution of plants, especially those species characteristic of the monsoon forests.

In South Asia, moist deciduous forests are prevalent in India, especially in the northeastern and peninsular regions. The forest type is also common in Myanmar, western Thailand, and in the central part of the Philippines. The formation has its characteristic teak (*Tectona grandis*) trees in Myanmar and Thailand, in association with species of *Lagerstroemia, Pterocarpus*, and *Terminalia*. In Myanmar, depending on the altitude, upper moist deciduous forests are identified on the flat plains above flood level, composed of species like *Homalium tomentosum, Tectona grandis*, and *Xylia dolabriformis*. The lower-level moist deciduous forests of the country, developed in rich soils, are in a devastated state, mainly due to the cultivation of paddy (rice). Unlike the upper moist deciduous forests, low-level

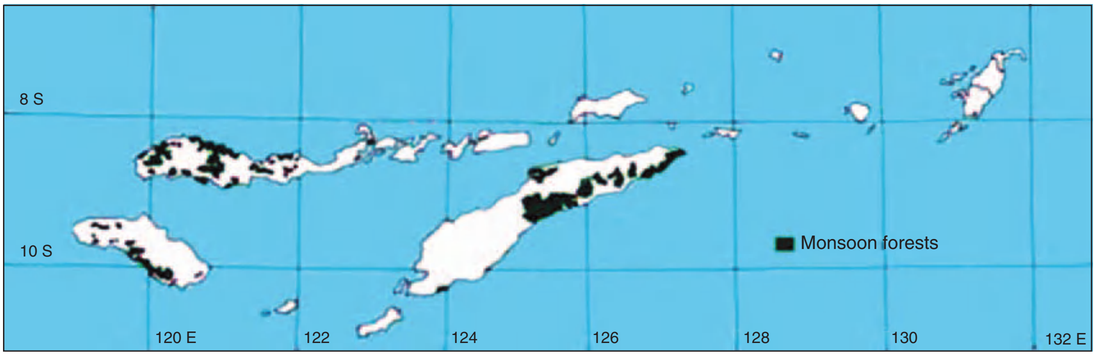


Figure 11 Distribution of monsoon forests in Lesser Sunda Islands and adjacent islands (Indonesia and East Junor).

Figure 12 Distribution of monsoon forests in the Philippines.

Figure 13 Moist deciduous forests of India.

monsoon forests, in general, are devoid of bamboo species, even though the climbing bamboo *Oxytenanthera* is common to both formations. In the southern part of Myanmar, moist deciduous riverine forests and moist clay-soil forests of quite different floristic compositions are distributed. In the Indian subcontinent and Sri Lanka, moist deciduous forests dominate all other monsoon forest types, even though, in Bangladesh, mangrove forests are more widely distributed. Teak forest is a very notable formation of the monsoon forest type, which is very important economically, because of the timber value of the dominant species. Teak forests are also quite prevalent in the central part of India, whereas, towards the peninsular and North-eastern part of the country, the representation of the species is much less (**Figures 13** and **14**). The *Albizia–Xylia–Pterocarpus* association is more common in the south and *Shorea–Schima* trees are quite prevalent in the northeastern parts of the country. In the Andaman Islands, it is the *Pterocarpus–Terminalia–Canarium* association that is characteristic of the monsoon forests. In Sri Lanka, dry-zone evergreen forests are widespread and these are also found in the eastern part of the Deccan peninsula (India), in fragments. In southeastern Indochina, species of *Chloroxylon, Drypetes, Feronia,* and *Manilkara*, dominate the monsoon forests with associated scrub composed of species of *Bauhinia*, *Cassia,* and *Dichrostachys*. *Acacia* thorn scrub is also common there, in heavily disturbed areas. The monsoon forests of Sri Lanka are also characterized by a high degree of endemism and is the major habitat of the Asian elephant. However, more than 75% of the forest type of the island is in a highly degraded state, and a network of protected areas has been established to preserve the forest formation and its biodiversity.

Figure 14 Buttressed trees in monsoon forests.

Biodiversity, Endemism, and Conservation

South and Southeast Asian countries are very rich in biodiversity and endemism. They are also the centers of origin of many cultivated plants and domesticated animals. Forests of the region contain gigantic trees like dipterocarps and terminalias on the one hand and rich and diverse shrub and herbaceous ground flora on the other. Reputed timber trees such as teak, rosewood, and sal, medicinal and other nontimber forest produce plants of arborescent or herbaceous habit, while plants yielding paper and handicraft raw material including bamboos and canes, horticultural plants like orchids and ferns, epiphytic species of both flowering and nonflowering plant groups, creepers, herbaceous and woody climbers form part of the forest type in the region. The Asian elephant, lion, tiger, panther, mountain goat, monkeys, birds, insects, reptiles, and thousands of other terrestrial and arboreal fauna represent the rich and diverse faunal heritage of the monsoon forests of the region. In South and Southeast Asia, India, Indochina, and Malesia are the main biodiversity-rich regions, and specific floristic and faunistic accounts are also available for almost all the countries in the region.

There are no separate estimates available on the biodiversity of the different ecosystems (monsoon forests, rainforests, and savannahs) in the region. **Table 2** gives details of total numbers of plant and animal species in different countries of South and Southeast Asia and also which are threatened with extinction or genetic impoverishment. It may be

Table 2 Total and endangered plant and animal species in different countries of South and Southeast Asia

Country	*Plants*		*Animals*	
	Total	*Endangered*[a]	*Total*	*Endangered*[a]
Bangladesh				
Cambodia	770	0	1334	41
India	15 000	3120	4735	172
Indonesia	11 217	184	6359	416
Laos	347	1	2487	57
Malaysia	12 082	371	3215	76
Myanmar	2211	6	2935	75
Philippines	8481	320	2531	135
Sri Lanka	7456		3658	
Thailand	3497	355	3705	79
Vietnam	1130	297	3155	85
Total	62 191	4654	34 114	1136

[a] Endangered implies threatened with extinction or genetic erosion and impoverishment.

Table 3 Details of protected areas in different countries of South and Southeast Asia

Country	*Total area* (km^2)	*Protected area* (km^2)	*Annual deforestation percentage*
Bangladesh	13 570	688	
Cambodia	181 000	32 671	1
India	3 268 090	49 434	
Indonesia	1 919 445	345 118	0.7
Laos	236 725	27 563	1
Malaysia	332 965	15 274	1.2
Myanmar	678 030	1735	0.3
Philippines	300 000	14 540	1.5
Sri Lanka	64 740	8193	
Thailand	514 000	70 711	2.5
Vietnam	329 565	9951	1.2

noted here that all the animal and plant groups are not covered in such estimates; angiosperms among plants, and amphibians, birds, fishes, mammals, and reptiles, among animals are the groups on which more exhaustive data are available for most countries in the region. Moreover, such estimates do not reflect the actual species content of the monsoon forests *per se,* and the data given in **Table 2** provide only an overall picture with regard to the biodiversity status of different South and Southeast Asian countries.

Due to various disturbances to the ecosystem and the habitats of species in the region, several plant and animal taxa, and especially those confined to one country, phytogeographical region or ecological niche, are now listed in one of the threatened categories such as rare, endangered, threatened, or vulnerable recognized by various national and international institutions. In **Table 2**, country-wise details on the representation of such taxa in the region are given and many more such species are likely to be added to the list, once their population status is assessed. It may be noted that monsoon forests of the region, rich in timber and nontimber plants and edible and game animals, have suffered the greatest loss in biodiversity, mainly due to the proximity and accessibility of the forest type to human habitations and suitability of the area for agriculture and plantation establishment, as well as from fire and other natural and anthropogenic causes. Also, the food and other habits of people living in the region have influenced the conservation status of the floral and faunal wealth of the region. In order to protect biodiversity, countries in South and Southeast Asia have established conservation areas like wildlife sanctuaries, national parks, biosphere reserves, World Heritage Sites, Ramsar sites, Man and Biosphere sites. Details of the extent of protected areas in relation to the total forest area of different countries in the region are given in **Table 3**. Also, the annual deforestation data given for various countries indicate the pace of loss in biodiversity. Available data point to the fact that deforestation is occurring faster in Laos, Philippines, Thailand, and Vietnam than in Cambodia, Indonesia, and Myanmar, all of which are neighboring countries. Moreover, in the South Asian countries of Bangladesh, India, and Sri Lanka, the deforestation rate will be greater due to various factors, including increases in population and the consequent escalation in demand for land, plant, and animal resources.

The International Union for the Conservation of Nature and Natural Resources (IUCN) has prepared *The Red Data Book* on plant and animal species throughout the world, identifying those belonging to different threatened categories. This is mainly intended to promote a conservation program for such species in order to save them from total extinction. Also, the protected-area network in South and Southeast Asian countries, established in representative ecosystems, including the monsoon forests, can facilitate the preservation of dwindling populations of many such species, in addition to the overall conservation of the ecosystem.

See also: **Biodiversity**: Endangered Species of Trees. **Ecology**: Human Influences on Tropical Forest Wildlife. **Health and Protection**: Forest Fires (Prediction, Prevention, Preparedness and Suppression). **Tropical Ecosystems**: *Ficus* spp. (and other important Moraceae); Acacias; Dipterocarps; Mangroves; Teak and other Verbenaceae. **Tropical Forests**: Combretaceae; Tropical Dry Forests; Tropical Moist Forests; Tropical Montane Forests; Woody Legumes (excluding Acacias).

Further Reading

Anonymous (1962) *Types of Forests of Thailand*. Bangkok: Royal Forest Department, Ministry of Agriculture.

Ashton PS and Ashton M (1976) *Classification and Mapping of South-East Asian Ecosystem. Transactions of the Fourth Aberdeen-Hull Symposium in Malaysian Ecology*, Series no. 17. Hull, UK: University of Hull.

Burtt Davy J (1938) *Classification of Tropical Woody Vegetation Types*. Oxford, UK: Imperial Forestry Institute.
Champion HG and Seth SK (1968) *Revised Survey of the Forest Types of India*. New Delhi, India: Manager of Publications, Government of India.
Collins NM, Sagyer JA, and Whitmore TC (eds) (1991) *The Conservation Atlas of Tropical Forests: Asia and Pacific*. London: Macmillan.
Edward MV (1950) *Burma Forest Types*. Indian Forest Records (new series). Silviculture 7(2). Dehra Dun, India: Forest Research Institute.
Holmer CH (1958) The broad pattern of climate and vegetation distribution in Ceylon. In *Proceedings of a Symposium on Humid Tropics Vegetation, Kanly*. Paris: UNESCO.
IUCN (1988) *The Red Data Book*. Switzerland: IUCN.
Kurz S (1877) *Forest Flora of British Burma*, 2 vols. Calcutta, India: Bishen Singh, Dehra Dun.
Lane-Poole CE (1925) The forests of Papua New Guinea. *Empire Forestry Journal* 4: 200–234.
Richards PW (1982) *The Tropical Rainforests*. Cambridge, UK: Cambridge University Press.
Schimper AFW (1903) *Plant Geography Upon a Physical Basis*. London: Oxford University Press.
Spencer JE (1966) *Shifting Cultivation in South-Eastern Asia*. Berkeley, CA: University of California Press.
UNESCO/ UNEP (1978) *Tropical Forest Ecosystems*: *A State of Knowledge Report*. Paris, France: UNESCO/ UNEP.
van Steenis CGGJ (1957) Outlines of vegetation types in Indonesia and some adjacent regions. *Proceeding of a Pacific Science Congress* 8(4): 61–97.
Vidal J (1960) *Végétation du Laos*, 4 vols. Toulouse, France: Sonladowe.
Whitmore TC (1984) *Tropical Rainforests of the Far East*, 2nd edn. Oxford, UK: Clarendon Press.

Myristicaceae

J P Janovec, Botanical Research Institute of Texas, Fort Worth, TX, USA
R García, St Louis, MO, USA

Introduction

The Myristicaceae is a pantropical family of trees found in Central and South America, Africa, Madagascar, India, and Asia. The family consists of 20 genera and at least 500 species. Floristic and ecological studies have revealed that the Myristicaceae rank among the top five to ten most common and important tree families throughout the majority of the lowland moist tropical forests of the world, where the family has significant ecological importance. Fruit of the Myristicaceae, particularly the lipid-rich aril surrounding the seed in some species, are important as food for birds and mammals of tropical forests. Numerous species are valued by humans as sources of food, medicine, narcotics, and timber, including *Myristica fragrans*, the source of nutmeg and mace, the spices of commerce.

Throughout the geographical range of Myristicaceae, aromatic leaves, often stellate pubescence, a unique arborescent architecture (**Figure 1**), and sap the color of blood (**Figure 2**) are characteristics that strongly enhance recognition of this family in the field. Species of this family are usually dioecious. Flowers are tiny and found in paniculate inflorescences, with filaments of stamens fused into a column, giving rise to either free or fused anthers (**Figures 3** and **4**). Fruits are one-seeded, dehiscent or indehiscent, and are notable for the typically red arillate covering around the seed.

Taxonomy and Genetics

There are about 500 species of Myristicaceae in 20 genera, restricted to individual continents (**Table 1**). Nutmeg trees first appeared in the earliest botanical works dealing with the East Asian region, and in 1742 Linnaeus established the genus *Myristica*, which remained a broad concept and the only genus in the family until 1856. Warburg produced the first

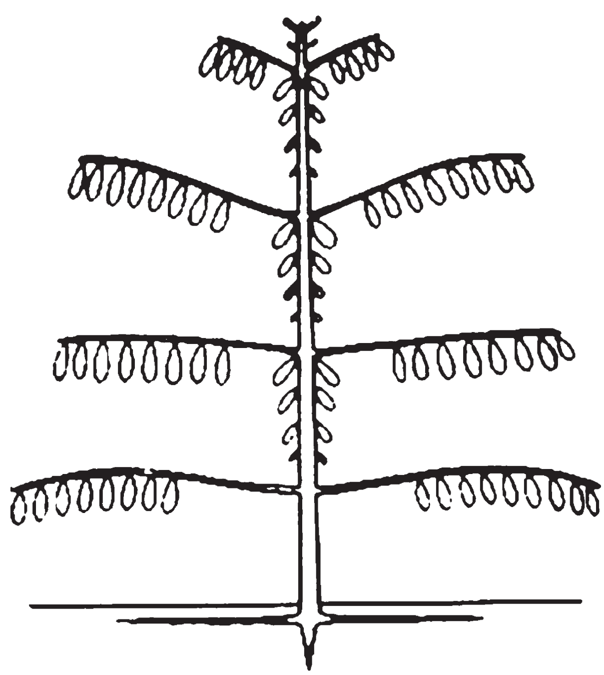


Figure 1 Massart model of tree architecture typical of the Myristicaceae. Modified with permission from Hallé F, Oldeman RAA, and Tomlinson PB (1978) *Tropical Trees and Forests: An Architectural Analysis*. Berlin: Springer-Verlag.

Figure 2 Blood-red sap exuding from trunk of *Compsoneura excelsa* in the Osa Peninsula of Costa Rica. Courtesy of John Janovec.

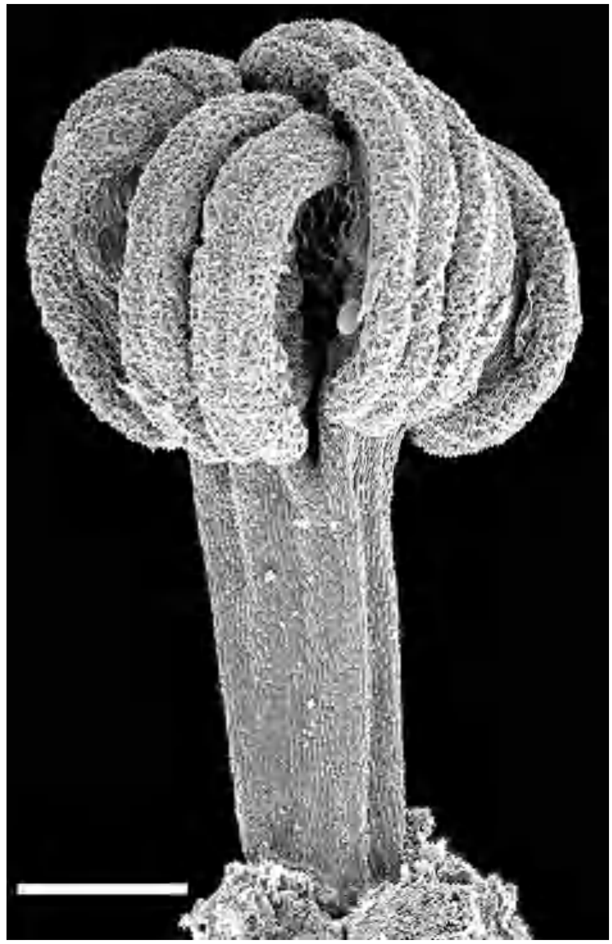


Figure 3 Androecium of *Compsoneura capitellata* from the Peruvian Amazon, showing an elongated column of fused filaments giving rise to anthers. Scale bar = 250 μm. Courtesy of John Janovec.

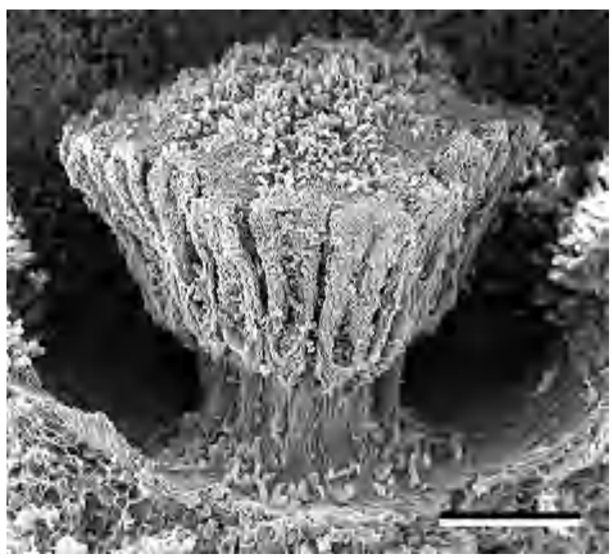


Figure 4 Androecium of *Compsoneura trianae* of western Colombia, showing a reduced column of fused filaments which give rise to a group of anthers fused to central connective tissue. Scale bar = 250 μm. Courtesy of John Janovec.

and last major global treatment and the first phylogenetic tree of the Myristicaceae, and divided the sections of *Myristica* into many of the genera currently accepted. All modern authors include the Myristicaceae within an ancestral lineage of dicotyledonous flowering plants which includes families such as the Magnoliaceae, Canellaceae, Winteraceae, and Annonaceae. Analyses of nucleotide sequences from the chloroplast gene *rbc*L have generated support for this placement. Attempts have been made by Sauquet *et al*. to reconstruct the intergeneric phylogeny within the Myristicaceae. Basic studies of species diversity are needed within each genus to better understand relationships, character evolution, and classification of the family.

Various authors have overviewed the geohistorical setting of Central and South America, so far as it is known. Africa and South America began to separate during the Jurassic approximately 140 million years

Table 1 Genera and species of Myristicaceae

Region	*Genus*	*Number of species*
Tropical America	*Bicuiba*	1
	Compsoneura	25, in progress
	Iryanthera	24 +
	Osteophloeum	2
	Otoba	8
	Virola	45 +
Indo-Asia	*Endocomia*	4
	Gymnacranthera	7
	Horsfieldia	100
	Knema	90
	Myristica	170
	Paramyristica	1
Africa and Madagascar	*Cephalosphaera*	1
	Coelocaryon	4
	Pycnanthus	7
	Scyphocephalium	4
	Staudtia	2

before present (BP). By about 90 million years BP, the two continents were completely separated and life on each took its own course. The center of origin for the Myristicaceae may well be South America, or in a geohistorical context, West Gondwanaland of the early Tertiary or late Cretaceous (about 100–70 million years BP). With this in mind, and since the family is present on all Gondwanaland-based continents that currently have tropical forest (South America, Africa, Madagascar, India, Southeast Asia), it can be hypothesized that the Myristicaceae had diversified before the separation of South America and Africa.

From the point of complete separation (about 90 million years BP), the neotropical Myristicaceae evolved on the South American land mass independently from members of the family which currently occur in Africa or elsewhere on the Gondwanan geoplex. It is truly hard to tell what pathways were taken during such a long period of time. However, the genera of the Myristicaceae have evolved in three major regions (Americas, Africa–Madagascar, and India–Asia).

Ecology

Floristic and ecological studies have revealed that the Myristicaceae rank among the ten and often five most common and thus important tree families in lowland moist tropical forests of the world. In the American tropics, the Myristicaceae is one of the eleven families – along with Fabaceae, Lauraceae, Annonaceae, Rubiaceae, Moraceae, Sapotaceae, Meliaceae, Arecaceae, Euphorbiaceae, and Bignoniaceae – that contribute about half of the species richness of any lowland forests and this pattern is present in some samples of Africa and Asia as well.

The center of diversity of the Myristicaceae in the Neotropics is the Amazon basin, represented by *Virola* with a few species reaching Central America. The genus *Otoba* has its center of diversity and endemism in the Chocó region of northwestern South America. *Otoba* has five species in this area and additional species in Panama and another widespread in Amazonia. *Myristica* has its center of diversity in the Malayan peninsula and New Guinea, and *Knema* is dominant in Borneo. In many forests of South America the Myristicaceae are very conspicuous and form an important element of its rich flora. Some pacific tropical forests in Colombia are dominated by *Otoba gracilipes*, *Virola reidii*, and *V. sebifera*. In an inventory of various types of Amazonia terra firme forests in Peru, *Iryanthera juruensis, I. macrophylla, I. paraensis, I. polyneura, I. tricornis, I. ulei, Virola calophylla*, and *V. pavonis* were the most common species. The importance index values in this study showed that the Myristicaceae was largely higher than the other tree families with a preference of well-drained terra firme soils. More recently, Myristicaceae was found to have exceptional numbers of common species in Manu National Park (Peru) and Yasuni National Park (Ecuador).

Although most species of the family in neotropical forests occur on rich soils, some are restricted to higher-stress habitats. For example, *Virola pavonis* is one of the most important species on the nutrient-poor white sand soils around Loreto, Peru. *Virola surinamensis* is common to swampy areas of lowland Amazon forests where it forms associations with the palm *Maurita flexuosa*. Aerial or stilt roots are one of the adaptations to anoxic, inundated soil exhibited by this species (**Figure 5**). *Virola steyermarkii* is reported endemic for the montane tepui forests in Venezuelan Guayana.

The family is poorly represented at higher elevations. In an analysis of the floristic composition and diversity of Amazonia and the Guiana Shield, it was found that Myristicaceae occurs in high density in terra firme forests of western Amazonia. This diminished in Central Amazonia, eastern Amazonia, and the Guiana Shield, suggesting an increase in the abundance and diversity of the family from the Guianas toward Western Amazonia. This difference may be due in part to richer soils present at western Amazonia in comparison to other sites where a different suite of poor-soil-tolerant plants dominate: Chrysobalanaceae, Burseraceae, and Lecythidaceae among others. In a study of several 1-ha forest plots in Amazonia and Central America, the

Figure 5 Aerial or stilt roots of *Virola surinamensis* growing in a *Mauritia flexuosa* palm swamp of the Peruvian Amazon. Courtesy of John Janovec.

late Alwyn Gentry found that Yanamono and Mishana forest preserve areas in northern Amazonia of Peru presented a higher representation in Myristicaceae than Central America. In La Selva (Costa Rica) and Barro Colorado Island (BCI, Panama) forest plots, Myristicaceae is not one of the most diverse tree families.

Many xeromorphic features (thick cuticle, a dense tomentum, sunken stomata) are present in Myristicaceae in spite of its present-day humid tropical forest distribution. This may be indicative of a wider ecological amplitude than the current distribution. The presence and type of pubescence are useful for differentiating the genera in the family; this character has been used since the pioneering studies of this family prior to 1900. It has been hypothesized that the hairs function as protection against herbivory and regulate the physiology of the water in the plant.

Most species of Myristicaceae are trees occupying the middle-story of canopy in the forests. For example, *Virola surinamensis* is a large tree, attaining 30 m in height and 1 m in diameter at breast height (dbh), generally with a straight, cylindrical trunk above the buttressed roots. Other species in the family reaching or exceeding the canopy are: *Virola duckei*, *V. pavonis, Otoba glycicarpa*, and *Osteophloeum platyspermum*. Most *Iryanthera* and *Compsonera* species are treelets or medium-sized trees.

Figure 6 Fruit of *Compsoneura mexicana* from Belize, showing the two-parted dehiscent orange fruit at maturity and the red aril covering a black-mottled seed. Courtesy of John Janovec.

One of the most noteworthy features of the Myristicaceae is its branching architecture corresponding to the Massart model (**Figure 1**). This branching pattern may enable the family to better survive the dynamic conditions of tropical forests. This is especially important during younger stages of growth and establishment for efficient use of forest resources, to allow recovery from traumatic events, and for adjustment to environmental changes in the struggle to reach the canopy.

The small, pale flowers common in the family are presumed to be pollinated by small insects. *Myristica fragans* is pollinated by small nocturnal beetles. Both the male and female flowers are strongly scented and pollen is the only reward. *Compsoneura sprucei* (= *C. mexicana*) has been reported to be pollinated by thrips, based on studies in Costa Rica. In the Asian tropics, *Myristica myrmecophylla* has an association with ants that may play a role in pollination.

The principal dispersers of the family are thought to be birds because of the attractive arillate seeds (**Figure 6**). But this assumption has been challenged in recent studies showing that spider monkeys act as principal dispersers of *Virola calophylla* in the southern Peruvian Amazon. In the Old World, rodents occasionally act as dispersers. Observations in Belize suggest that rodents may act as secondary dispersers, which may account for the camoflauge mottling found on seeds of *Compsoneura mexicana* (**Figure 7**), which are difficult to see in the leaf litter on the forest floor.

Figure 7 Black mottled seeds of *Compsoneura mexicana* from Costa Rica. Courtesy of John Janovec.

Silviculture

As a family primarily of trees, many species of Myristicaceae have been studied in experimental plantations. In Brazil, *Virola surinamensis* has been studied with silvicultural methods. However, few of these studies have been adopted by the industry and an unfortunate consequence is that much of the lumber is coming from the forests. In the Peruvian Amazon it is becoming more common to see timber from *cumala*, the vernacular name for species of Myristicaceae. Some of the more valuable species are: *Otoba glycicarpa*, *Virola pavonis*, *V. duckei*, and *Osteophleum platyspermum*. Seeds remain viable for a limited period of time and germinate in damp, shady environments offered only by tropical old growth forest. Seed germination trials conducted using *Compsoneura* and *Virola* seeds from Central America showed that some seeds can take up to 6 months to germinate in a greenhouse setting.

Utilization

Economically, the most important species, *Myristica fragrans*, is Asiatic and is widely cultivated as the source of nutmeg (the ground seed) and mace (the dried aril). This species is also cultivated in areas of Central America and the Caribbean. Some species are used in the timber industry, such as *Virola surinamensis* in Brazil, and *Otoba gracilipes*, *V. reidii*, and *V. sebifera* in Colombia. In the American tropics, species of the Myristicaceae have been valued as sources of food, medicine, and narcotics. Amazonian Indians utilize the dried sap and ground inner bark of numerous Myristicaceae species (*Osteophloeum platyspermum*, *Virola calophylla*, *V. cuspidata*, *V. duckei*, *V. elongata*, *V. pavonis*, *V. sebifera*, and *V. surinamensis*) to make hallucinogenic snuffs used in spiritual ceremonies and as medicine in the treatment of various ailments. In the Venezuelan Guayana region, the wood of *Iryanthera lancifolia* is used for lumber and the reddish sap of *Virola surinamensis* is used to seal wounds. *Virola surinamensis* is also valued as timber, especially in the plywood industry. Some species yield essential oils and fats that have been used in perfumery and in making candles. It has been suggested that nutmeg produces hallucinations when ingested by humans, but this has been criticized as a myth.

See also: **Ecology**: Reproductive Ecology of Forest Trees. **Medicinal, Food and Aromatic Plants**: Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Tree Physiology**: Tropical Tree Seed Physiology. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Moist Forests; Tropical Montane Forests.

Further Reading

Armstrong JE and Drummond BA III (1986) Floral biology of *Myristica fragrans* Houtt., the nutmeg of commerce. *Biotropica* 18: 28–32.

Beccari O (1884) *Malesia*, vol. II, 1, 2. Genoa, Italy: R. Istituto Sordo-Muti.

Bennett BC and Alarcon R (1994) *Osteophloeum platyspermum* and *Virola duckei* (Myristicaceae): newly reported as hallucinogens from Amazonian Ecuador. *Economic Botany* 48(2): 152–158.

Del Valle JI (1996) Practicas tradicionales de producción y ordenamiento territorial. In: Del Valle JI and Restrepo E (eds) *Renacientes del Guandal: Grupos Negros de los Rios Satinga y Snaquianga*, pp. 443–473. Bogotá: Universidad Nacional de Colombia.

Gentry AH (1979) Transfer of the species of *Dialyanthera* to *Otoba* (Myristicaceae). *Taxon* 28: 417.

Gentry AH (1982a) Patterns of neotropical plant species diversity. *Evolutionary Biology* 15: 1–84.

Gentry AH (1982b) Phytogeographic patterns as evidence for a Chocó Refuge. In: Prance GT (ed.) *Biological Diversification in the Tropics*, pp. 112–136. New York: Columbia University Press.

Gentry AH (1990) Floristic similarities and differences between southern Central America and Upper and Central Amazonia. In: Gentry AH (ed.) *Four Neotropical Rainforests*, pp. 141–160. New Haven, CT: Yale University Press.

Hallé F, Oldeman RAA, and Tomlinson PB (1978) *Tropical Trees and Forests: An Architectural Analysis*. Berlin: Springer-Verlag.

Jimenez-Rojas EM, Londoño-Vega AC, and Vester HFM (2002) Descripción de la arquitectura de *Iryanthera*

tricornis, *Osteophloeum platyspermum* y *virola pavonis* (Myristicaceae). *Caldasia* 24(1): 65–94.
Kühn U and Kubitzki K (1993) Myristicaceae. In: Kubitzki K, Rohwer JG, and Bittrich V (eds) *Flowering Plants: Dicotyledons: Magnoliid, Hamamelid, and Caryophyllid Families*, pp. 457–467. Berlin: Springer-Verlag.
Nogueira BMM (1992) Anatomia foliar de *Virola* Aublet (Myristicaceae). *Boletin du Museu Paraense Emilio Goeldi-Botanica* 8(1): 57–142.
Pitman NCA, Terborgh JW, Silman MR, *et al.* (2001) Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82(8): 2101–2117.
Rodrigues WA (1980) Revisão taxonomica das especies de *Virola* Aublet (Myristicaceae) do Brazil. *Acta Amazonica* 10(1): 1–127. (Suppl.)
Russo SE (2003) Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136(1): 80–87.
Schultes RE and Raffauf RF (1990) *The Healing Forest*. Portland, OR: Dioscorides Press.
Schultes RE and Smith EW (1976) *Hallucinogenic Plants: A Golden Guide*. New York: Golden Press.
Ter Steege H, Sabatier D, Castellanos H, *et al.* (2000) An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology* 16: 801–828.
Van GC and Cox PA (1994) Ethnobotany of nutmeg in the Spice Islands. *Journal of Ethnopharmacology* 42(2): 117–124.
Warburg O (1897) Monographie der Myristicaceen. *Nova Acta Academica Leopold-Caroliniana* 68: 1–680.
Wilde WJJ O de (2000) Myristicaceae. *Flora Malesiana Seed Plants* 14: 1–634.

Tropical Dry Forests

S J Van Bloem and P G Murphy, Michigan State University, East Lansing, MI, USA
A E Lugo, US Department of Agriculture Forestry Service, Río Piedras, Puerto Rico, USA

Introduction

Tropical dry forests occur in nearly every tropical country. This forest type provides critical habitat for large mammals and migratory birds, and patches of dry forest can support a high proportion of endemic plant and animal species, as well as being highly valued for agricultural and production forestry uses. Consequently, conservation and understanding of these forests need emphasis, yet conservationists and scientists still frequently overlook this ecosystem.

Distribution and Definition

Dry forests comprise 42% of all tropical forests – the largest proportion of any forest type. They can be found as large continuous tracts, particularly in India, Mexico, eastern South America, northern Australia, and Africa, or in smaller, more local areas. Smaller tracts grow in rainshadows of tropical islands, Central America, and western South America (**Figure 1**). Coastal environments support dry forest when elevation is too low to generate rainfall from orographic uplift of ocean air masses.

Tropical dry forests occur in frost-free areas where annual precipitation is 500–2000 mm, mean annual biotemperature is $>17^{\circ}C$, and potential evapotranspiration exceeds precipitation (**Figure 2**). Rain falls in one or two seasons each year, depending on the latitude of the forest, and forests experience 3–10 dry months (<50 mm rainfall) each year. The most important characteristic is the highly variable length of the dry season, seasonal distribution of rainfall, and amount of rainfall. Perhaps the only real constant from site to site is the occurrence of a dry season. Savannas often grow under the same climatic conditions as dry forests, but sparse tree cover and frequent fire in savannas allow grass to dominate.

Typically, dry forests have a closed canopy, but this may not be the case in the driest parts of their range, or if disturbance is prevalent. Due to their variability in climate and appearance, many names are applied to dry forests. These include: deciduous forest, semideciduous forest, semi-evergreen forest, woodland, and dry seasonal forests. Local names are also used: caatinga in Brazil, miombo in southern Africa, and chaco in parts of South America. Southeast Asia has a specific type of dry forest – deciduous dipterocarp forests – dominated by about six species of Dipterocarpaceae.

As a consequence of prolonged dry seasons, tropical dry forests are less complex than wet or temperate forests (**Table 1**). They have one to three canopy layers and short canopies with relatively low leaf area index (3–7) and leaf biomass (2–7 tonnes ha^{-1}). In mature forest, the stems can still be quite narrow, with common diameters in the range of 3–15 cm, and stem densities can exceed one stem per square meter. Trees are frequently multistemmed. Among dry forests, most structural features vary by two to ten times (**Table 1**), with the upper limits overlapping the lower limits in wetter forests, leading to inconsistencies in the scientific literature when classifying forest types. Climate features such as the amount of rainfall or the length of the rainy season can explain canopy height and biomass, but other structural characteristics,

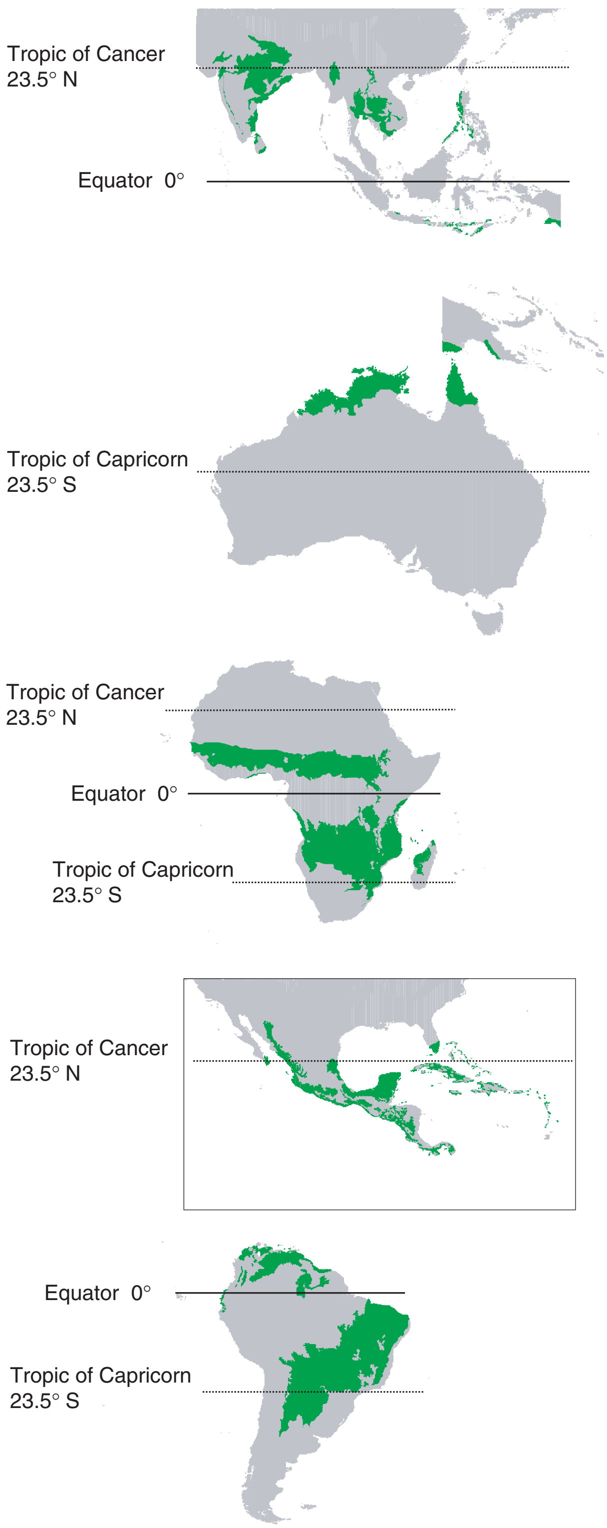


Figure 1 Global potential distribution of tropical dry forests. Highlighted areas are predominantly dry forest, but moist or open forest is interspersed in some areas. Dry forest is also found in many small tropical island nations, including American Samoa, Comoros, Cook Islands, Fiji, French Polynesia, Guam, Kiribati, Marshall Islands, Mauritius, New Caledonia, Palau, Reunion, Solomon Islands, and Vanuatu.

particularly stem density, are often the result of disturbance (see below).

Components of Tropical Dry Forest

Plants

Seasonally dry forest communities worldwide contain a variety of important plant species. Trees valued for lumber include teak (*Tectona*), mahogany (*Swietenia*), sal (*Shorea robusta*), and African mahogany (*Khaya*). Commercially important fruit trees include tamarind (*Tamarindus indica*), mango (*Mangifera indica*), and cashew (*Anacardium occidentale*). Agroforestry projects have planted *Leucaena leucocephala* and *Prosopis juliflora* (mesquite) to improve soils via nitrogen fixation. *Casuarina equisetifolia* (Australian pine) and *Eucalyptus camaldulensis* are native to Australian dry forest and have been introduced in many areas for soil stabilization and wood production. In addition to these species, many others are used for firewood, construction wood, food, and medicinal purposes.

Deciduous trees are usually most common in dry forests, but evergreen species become more important at both the upper and lower limits of the rainfall gradient (**Figure 2**). The frequency of growth forms depends on climate and disturbance. Cacti and euphorbs frequent drier locations while the diversity of lianas and other vines increases with greater rainfall and following disturbances that open canopy gaps. Dry forests have more understory species than tree species but their abundance and biomass is quite low, except in open woodlands.

The high variety of growth forms and numerous physiological adaptations provide tolerance to drought conditions. Dry forest species can maintain metabolism under lower soil and leaf water potentials than temperate or moist tropical species. Dry forests average higher ratios of root to shoot biomass than moist or temperate forests. Though data on root biomass are scarce, 35–49% of root mass is below 10 cm depth as compared to 5–21% in wet forests. In dry forests, maximum root : shoot ratios range from 0.4 to 1.0. In moist forests they rarely exceed 0.25. Cacti and some deciduous tree species store water in succulent stems. The amount of water stored cannot maintain leaves, but supports flower and fruit development prior to the onset of the rainy season.

Water use is influenced by leaf habit (evergreen vs. deciduous), leaf morphology, and wood density. Compared to wetter forests, more dry tropical trees have wood specific gravity greater than 1.0. Dense-wooded and evergreen species have narrow xylem that resists cavitation under dry conditions but

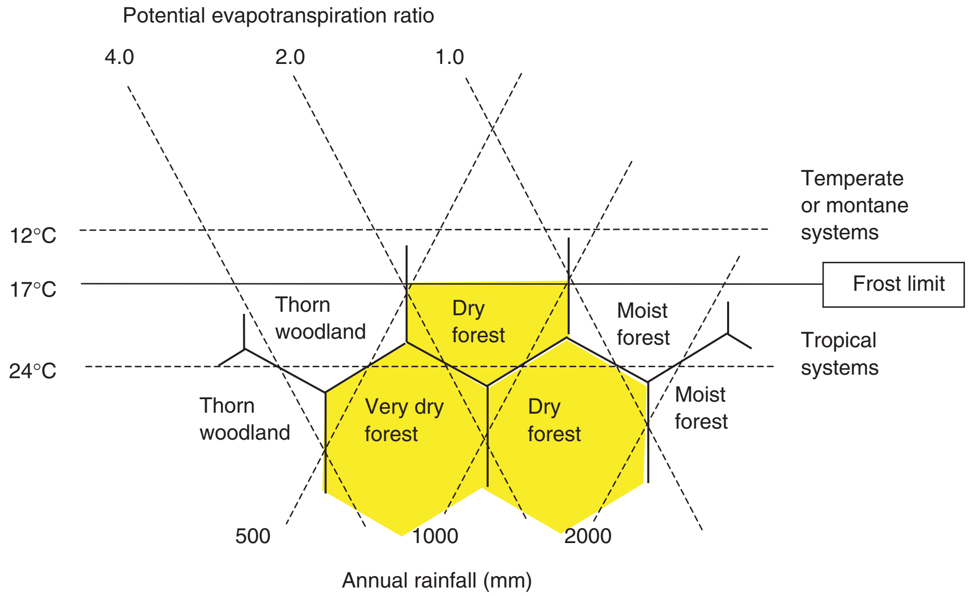


Figure 2 Climate characteristics that define tropical and subtropical dry forest life zones according to the Holdridge life zone classification system. The temperature values represent an adjusted biotemperature. PET ratio is annual potential evapotranspiration divided by annual precipitation.

transports water less efficiently. Light wooded and deciduous species have wider xylem that is more prone to cavitation and greatly reduces water conductance as the dry season progresses, but transports water more efficiently and responds faster to light rains at the onset of the rainy season. Thus, the ability to reduce cavitation during drought is traded for more efficient water conductance. Deciduous species avoid dry season water loss by shedding leaves, usually at the onset of the dry season, while the sclerophyllous leaves of evergreen species have thick cuticles and smaller internal air pockets that resist desiccation. Sclerophylly may increase in plant populations growing under drier conditions, or experiencing nutrient limitation caused by insufficient soil moisture for nutrient uptake and transport. Sclerophyllous trees frequently exhibit high nutrient use efficiency, suggesting nutrient limitation, even when soil nutrient pools are relatively high. Thus, the leaf habit of evergreen species aids in drought tolerance, while deciduousness leads to drought avoidance.

During the rainy season, dry forest trees, regardless of their particular responses to drought, exhibit many physiological similarities. For example, both drought-deciduous and evergreen dry forest species have similar values for carbon assimilation and stomatal conductance. These values equal those found in moist forest trees. When scaled by growing-season days, both dry and wetter forests have similar growth rates, suggesting they all have equally efficient productivity during favorable seasons. This may be expected because trees (with the exceptions of bamboo, arborescent cacti, and some euphorbs) all use C_3 photosynthesis, regardless of their habitat.

Phenology is closely related to the dry season in many cases, but there is a variety of patterns. Most deciduous species lose leaves at the onset of the dry season, but a few are wet-season deciduous (e.g., *Faidherbia albida* and *Jacquinia pungens*). Some species flower and fruit just before the rainy season commences, before leafing out, while others wait until after the rains have begun. Dry forest species generally flower and fruit for shorter periods than moist forest species. Often plants flower for less than 6 weeks – frequently for only the first few days following an isolated rain event or the first significant rain breaking a drought period. As annual rainfall increases on either a regional or local scale, the prevalence of species with wind-dispersed seeds decreases. In general, most species exhibit some pattern of seasonality.

Animals

Larger bodied vertebrates include elephants, large ungulates, and large felines in dry forests of Africa and Asia, jaguar in the neotropics, and monkeys in many mainland areas. In general, reptiles and birds comprise a substantial portion of dry forest fauna. In addition to the many bird species that reside in dry forests year round, dry forests in the neotropics and Africa are essential wintering grounds for many temperate species. For this reason, much of the

Table 1 Structural and functional characteristics of mature tropical dry forest

	Chandraprabha, India	*Varanasi, India*	*Ping Kong, Thailand*	*Lubumbashi, Democratic Republic of Congo*	*Chamela, Mexico*	*Guanacaste, Costa Rica*	*Rancho Grande, Venezuela*	*Veri Mer, Guyana*	*Guánica, Puerto Rico*	*North Andros Island, Bahamas*	*Wet forests*
Climate											
Annual rainfall (mm)	1050	800	1200	1273	707	1750	1140	1520	860	1300	> 2000
Dry months	6–8	> 6	3–4	5	6–8	6	4	3	6		< 4
Mean annual temperature (°C)	26	25	25	20	24.9	25			25.1	25	> 17
T/P[a]	2.5	3.1	2.1	1.6	3.5	1.4			2.9	1.9	< 1.0
Vegetation											
Basal area ($m^2\,ha^{-1}$)	15–20	30.6	35.4	20–40	23.6	21.6–41.6	36.2	48.9	17.8	23	20–75
Canopy height (m)	15–20	18	10–29	14–22	10–15	10–20	20	25	9	8	20–84
Stem density (number ha^{-1})[b]	1055 (3.0)	644 (3.0)	713 (4.5)	1465 (?)	8400 (2.5)	1950–4370 (2.5)	6000 (2.5)	4000 (2.5)	12000 (2.5)	7957 (2.5)	
Total biomass (tonnes ha^{-1})	95	240	78–291	150–320	105–120				98		269–1186

[a] Temperature/precipitation × 100, used as an indicator of potential evapotranspiration.
[b] Minimum stem size (cm) in parentheses.
Data from Murphy PG and Lugo AE (1986) Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88; Proctor J (1989) *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*. Oxford: Blackwell Scientific Publications; Quigley MF and Platt WJ (2003) Composition and structure of seasonally deciduous forests in the Americas. *Ecological Monographs* 73: 87–106; Smith IK and Vankat JL (1992) Dry evergreen forest (coppice) communities of North Andros Island, Bahamas. *Bulletin of the Torrey Botanical Club* 119: 181–191.

international conservation effort in dry forests results from concern for migratory songbirds and raptors. The relatively isolated and compact area of dry forest in western Mexico has had particular emphasis because it is the winter home for the migratory birds from the North American west coast.

Like dry forest plants, animals (both vertebrates and insects) synchronize their activities, such as reproduction, to the seasonality of their habitat. Many species enter a period of decreased activity in the dry season and some change their diets based on seasonal availability or quality of prey. For example, when living in dry forest, the northern tamandua will eat ants in the rainy season, then switch to termites in the dry season, when the termites have a higher moisture content than the ants. Aside from behavioral adaptations to seasonality, many animals have water conserving physiological adaptations as well, such as the production of dry feces.

As in other systems, animals influence plant populations. A wide variety of insects act as pollinators and specialized plant–pollinator systems are common. Vertebrates and termites disperse seed. The former transport seeds stick to their skin or fur, by caching, or in feces. Some species of termites harvest fleshy fruits to provide material for decomposition by symbiotic fungi, which the termites 'farm.' The termites usually throw unused seeds from the fruits out of the nest.

Herbivores include vertebrates and insects, particularly leaf-eating caterpillars, beetles, and leaf-cutting ants. In the neotropics, insects are the main herbivores but this may be an artifact of hunting that has reduced vertebrate populations (e.g., deer). Generally, deciduous dry forests incur greater herbivory than evergreen dry forests. Herbivory tends to be greater in the first half of the rainy season, but not because younger leaves have more nutrients or fewer secondary chemicals. Instead, herbivory decreases as the rainy season progresses, as parasite and predator populations increase, or as larval herbivorous insects mature and stop eating plants. On average, herbivory decreases leaf area from 10% to 17%. Leaf loss due to herbivory appears to decrease fruiting, fecundity, and seed viability in plants but is poorly understood. In addition, about 10% of dry forest plants incur high rates of seed predation, with some species losing nearly 100% of their seeds each year.

Termites play a vital role in dry forest dynamics. Some termite species construct majestic, meters-tall mounds that provide habitat for a suite of other animal species and, in Africa, create locally dry areas with unique tree species composition. Other species of termites live in smaller arboreal or subterranean nests. Many vertebrates and insects exploit termites as an important food source. The ability of termites to collect and process tons of dead plant material every year makes them essential to nutrient cycling in a system where many vectors of decomposition slow or cease in the dry season. Termites hasten decomposition by cutting up litter and move nutrients from place to place in the forest. They also improve soil quality by bringing up leached clay minerals from underground to build their nests.

Soil and Microbes

Dry forest soils vary widely and may be of volcanic, alluvial, or limestone origin – many are lateritic. Soil moisture content falls below field capacity for most of the year. Even during the rainy season, soil moisture drops below field capacity if rains do not occur at frequent intervals. Although leaching is less than in wetter areas, the soils are highly weathered due to their age. Similar to wet forests, the majority of dry forest soils have low nutrient supplies, particularly for phosphorus. Soils from calcareous parent material frequently have high total nutrient concentrations, but an average pH above 7.8 binds phosphorus to calcium and makes it unavailable to plants. Acid soils have high concentrations of iron and aluminum which also bind phosphorus. Conversely, some dry forest soils, particularly younger ones, have high amounts of organic matter and available nutrient pools, leading to high productivity. These soils develop mollic horizons and are found in parts of the neotropics and India. They frequently become converted to agricultural lands. The Brazilian caatinga and some forests on rocky, calcareous soil have a climate favorable for moist forest development, but the soils drain quickly, resulting in edaphically dry habitats.

Shallow or infertile soils tend to support evergreen forests, while deciduous forests generally grow on better soils. Organic matter can build up as humus in such thick litter layers that some soils have been called dryland peats. Soils with lateritic or calcareous crusts provide little habitat for grasses and herbs, supporting greater biomass in trees which can access subsurface moisture reserves.

Research on the soil microbial community of dry forests has lagged behind that in temperate or tropical wet forests, but some patterns have emerged. Like much of the rest of the living community in dry forests, microbial activity decreases greatly in dry seasons. However, termites compensate somewhat for the loss of microbial contribution to decomposition and nutrient cycling in the dry season (see above). As in other ecosystems, symbioses exist between plants and nitrogen-fixing bacteria or mycorrhizae.

Biodiversity

Diversity of dry forest plants and animals tends to be lower than in tropical moist forests, but greater than in temperate forests. Dry forests share a high proportion of their plant families and genera with moist forests, but few species overlap. Little is known about insect diversity. Larger, more mobile animals reside in both habitats, but smaller animals with limited dispersal ability or range tend to be unique to dry forests. Dry forests contain many locally and regionally endemic species of plants and animals, proportionally more than wet forests. Of the 25 hot spots identified by Conservation International as critically important for preserving biodiversity, nine contain tropical dry forest. A general trend of higher diversity in dry forests nearer the subtropics than the equator is well demonstrated in the western hemisphere. Bolivian and western Mexican forests have higher diversities of plants, reptiles, and amphibians than dry forests located at lower latitudes (**Table 2**). Subtropical African dry forests are also more diverse, with the southern region having more species than the northern.

Plant species diversity does not correspond to precipitation in dry forests, but does increase as the ratio of potential evapotranspiration (PET) to precipitation decreases. Low abundance and diversity of epiphytes further distinguish most dry forests from moist forests. Leguminous trees frequently dominate in all regions. Euphorbiaceae, Sapindaceae, and Rubiaceae are commonly found in neotropical dry forests, while Myrtaceae are common in the West Indies, Combretaceae in Africa, and Dipterocarpaceae in some Asian dry forests. The most common lianas belong to Bignoniaceae. Cacti are common in drier neotropical forests, but decrease in abundance as precipitation increases.

Lower animal diversity in dry forests can be explained in part by lower habitat diversity. Dry forests lack niches for frugivorous and semiaquatic species found in moist forests. Dry forests that border wetter forests have greater diversity as some species retreat to adjacent moist areas during the dry season. Seasonal migration of animals between forest types is common in all regions of the world.

Function of Tropical Dry Forest

Functional traits of dry and wet forests differ much less than structural differences. For example, aboveground net primary productivity (ANPP) ranges from 6–16 tonnes $ha^{-1} year^{-1}$ in dry forests and 10–22 tonnes $ha^{-1} year^{-1}$ in wet forests. Only tree growth rates separate distinctly between the two forest types. Diameter growth in dry forests averages

Table 2 Species diversity for tropical dry forests

Species diversity[a]	*Caatinga, Brazil*	*Chamela, Mexico*	*Bolivia*	*Central America*	*West Indies*	*Zambezian Area, southern Africa*	*Thailand and India*
Plants by area		94.3 (0.1 ha)	83 (0.1 ha)	67 (0.1 ha)	52 (0.1 ha)		76 (1.0 ha)
Trees by area	10–47 (0.1 ha)	80 (0.1 ha)	53 (0.1 ha)	51 (0.1 ha)	34–54 (0.1 ha)	95 (0.1 ha)	10–31 (0.2 ha) 42–50 (1.0 ha)
Endemic plants		16%		6%		Up to 35%	
Mammals (endemic species in parentheses)	86 (2)	70 (26)	110 (22)		(29%)[b]		(22%)[b]
Birds (endemic species in parentheses)	<200 (2)	270 (25)	409 (4)		(22%)[b]		(12%)[b]
Reptiles and amphibians (endemic species in parentheses)	47 (1)	173 (74)	80 (low)		(85%)[b]	? (24)	(50%)[b]

[a] Values are numbers of species unless indicated as a percentage.
[b] Regionally endemic species, may be found in either dry or moist forest.
Data from Bullock *et al.* (1995); Proctor (1989).

1–2 mm year^{-1} and occurs in one or two pulses per year. In wet forests, diameters increase 2–5 mm year^{-1} and usually grow continuously. The longer, wetter rainy season explains greater growth rates. The overlap in productivity highlights the success of dry forest species in adapting to seasonally xeric conditions.

Characteristics of nutrient cycling in tropical dry forests suggest that many sites are somewhat more fertile than moist forest. N : P ratios in dry forest leaves ($\sim$15 : 1) have lower averages than in moist forest ($\sim$28 : 1), but still exceed plants with well-balanced nutrient supply (10 : 1). Leaf N in dry forests is lower and leaf P similar to moist forests of moderate fertility. Nutrient use efficiency for nitrogen (NUE) and phosphorus (PUE) varies widely among dry forests. Many sites appear to have sufficient nutrient supplies (NUE < 130, PUE < 1600) but other dry forests exhibit phosphorus limitation (**Table 3**).

Dry forests accumulate and store nutrients in surface litter. The residence time can be about 3.5 years for N and over 5 years for P. Microbes alternately immobilize and release these nutrients. Rapid wetting of soils from the first rains burst microbial cells (plasmoptysis), leading to the greatest nutrient release at the onset of the rainy season. This type of release occurs throughout the rainy season because rainfall events are irregularly spaced. Isolated rains after the beginning of the dry season can also cause a nutrient pulse. Where soil microbes immobilize large amounts of nutrients, trees rely on greater amounts of retranslocation before leaf fall to meet nutrient demands.

Dry forest trees associate with either ectomycorrhizae (ECM) or vesicular–arbuscular mycorrhizae (VAM) or both. Mycorrhizae increase water uptake and access forms of phosphorus and nitrogen chemically unavailable to plants. In some forests, such as the dry dipterocarps, ECM species constitute only 10–15% of all plant species, but contribute 30–75% of basal area. The presence of legumes as dominant plants in many dry forests results in the potential for the improvement of soil fertility by N fixation. Limited research suggests that N-fixing trees predominate in areas with low N but can be limited by low available P. ECM are dominant in the driest areas, and both VAM and ECM are common in soils with low P, but patterns in their distribution across soils of varying N concentrations have not been clearly identified.

Disturbance

Disturbance is an important factor in tropical dry forests. Hurricanes bring destructive winds and

Table 3 Nutrient contents in leaves and litterfall and nutrient use efficiencies for a variety of tropical dry forests

Site	*Leaf*			*Leaf litterfall (kg ha^{-1})*				
	N : P	*%N*	*%P*	*N*	*P*	*Biomass*	*NUE*	*PUE*
Puerto Rico	26	1.64	0.064	44	0.7	4337	97	6056
Chamela, Mexico	11	2.96	0.28	52	2.5	2310	44	926
India	15	1.95	0.13				79	1059
Belize	15	1.50	0.10	153	9.2	12 600	82	1369
Congo	20	2.20	0.11	224	7	12 400	55	1700
Australia	27	1.66	0.06	134	12	9000	67	750
Ivory Coast				123	4	9600	78	2400
Tanzania				142	8	8800	62	1100

N, nitrogen; NUE, nitrogen use efficiency; P, phosphorus, PUE, phosphorus use efficiency.
Data from Bullock *et al.* (1995); Proctor (1989); Lugo AE and Murphy PG (1986) Nutrient dynamics in a subtropical dry forest. *Journal of Tropical Ecology* 2: 55–72; Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65(1): 285–298.

floods to some areas, fires affect others, and prolonged or unusually severe droughts threaten all forests. The frequency and intensity of these disturbances can have important effects on dry forest structure and function. High winds from hurricanes result in defoliation and breakage of trees, with long-term consequences for forest structure. Return intervals for hurricanes range from 5 to 100 years. Mature dry forests in the hurricane-prone West Indies tend to have shorter canopies, higher stem densities, and a greater proportion of multiple-stemmed trees than dry forests outside of the hurricane belt.

Fire is a difficult feature to interpret in dry forests. In most locations, even in Africa, fire is not a frequent or severe aspect of the ecosystem. Lightning occasionally starts fires in dry forests, but they are low intensity, small scale, and usually doused by rains. Sparse understory and grass cover limit the intensity of the ground fires that burn leaf litter about every 5–10 years, returning some proportion of nutrients to the soil as ash, while losing others to the atmosphere. Forest floor heterogeneity caused by termite mounds, rock outcrops, and crusty surfaces inhibit the ability of fires to spread. During the last 50 000 years, humans have probably caused the vast majority of fires in dry forest in order to clear land, hunt animals, and burn fallow to encourage new growth for livestock. Frequent burning transforms forests into savanna, shrub, and open woodland – ecosystems more correctly associated with fire. Conversely, humans prevent burning in other forests that naturally would experience ground fires. This alters natural disturbance patterns and can lead to very destructive crown fires sparked by the build-up of litter and underbrush during long fire-free periods.

Dry forests have a particularly long history of human disturbance because they occur in climate regions that are pleasant to live in and favorable for grazing and agriculture. The dry season provides respite from rain and humidity, and reduces populations of agricultural and human pests. Livestock survive well in dry forest areas, and the relatively small trees are easy to clear for agricultural fields. Because of the desirability of dry forest climates, human population densities in these areas exceed 100 km^{-2} globally and are expected to double every 20–25 years.

Human disturbance in dry forests is primarily related to land use change and extractive activities. As in other ecosystems, there are some examples of sustainably managed dry forests, depending on political, economic, and population pressures. Large-scale logging operations affect dry forest primarily in continental locations. Some dry forest species are suitable for plantations but others grow poorly because of infestation by pests (e.g., shoot-boring insects on mahogany in monoculture). Trees are cut for firewood or charcoal production in most regions. Firewood accounts for 80–90% of dry forest harvest. Many trees coppice – an advantage when used for firewood. Unfortunately fuelwood is not regrowing quickly enough to sustain demand in many areas of Africa. The long-term effects of extraction depend on the amount and pattern of biomass removed and the degree of soil disturbance or compaction that accompanies tree harvests.

Conversion of forests to agricultural, industrial, or residential areas completely removes forest cover and disrupts roots and soil structure. Traditionally, shifting agriculture has been practiced in dry forest regions in a sustainable manner, but increasingly short fallow periods prevent re-establishment of the forest. Grazing and agriculture increase nutrient loss from the system by erosion. Grazing reduces forest biomass because cattle reduce understory growth while compacting the soil and accelerating erosion. Approximately 32% of the area that once was dry forest remains, with continuing annual losses of 0.7–1.5%. The highest deforestation rates occur in Africa, even though population densities in dry forests there are only one-fifth of those in Asia. This trend continues in most areas, but in some locations where economies have turned from agriculture to manufacturing, land is reverting back to forest. This is the case in Puerto Rico, Cuba, and the Gambia.

Response to Disturbance

The ability of dry forest to tolerate disturbance, whether natural or anthropogenic, depends on disturbance type, frequency, duration, and severity. The forest that regrows following disturbance may resemble the original, or differ greatly in terms of function and composition. In general, dry forests exhibit a high rate of resilience, defined as the rate at which a forest stand recovers from large, infrequent disturbance. Compared to other forests, succession in dry forests progresses quickly, and in some cases this can lead to expansion into other systems. In Mexico, clearing of large tracts of rainforest resulted in a drier environment that was subsequently recolonized by dry forest.

Dry forests in Puerto Rico have provided a location to compare response to natural and anthropogenic disturbances. The forest recovered similarly from the effects of a recent hurricane and small-scale tree cutting for charcoal production in the past. Both resulted in patchy loss of <25% of trees, while soil systems remained intact. Stem density increased after each disturbance, as broken trees grew from coppice sprouts. After 45 years, cut areas regained an average of 87% of mature forest structure. Post-hurricane forest will probably take about 25 years to fully recover. Neither disturbance changed the species pool. Conversely, forest recovery from abandoned agricultural and residential uses has taken much longer. After 45 years, abandoned agricultural areas had only recovered an average of 71% of mature forest structure, while residential sites were 58% recovered. The disruption of root systems had a large effect – root biomass was half or less that in mature forests and coppice growth was minimal. These areas have shifted from being dominated by native species to the invasive species *Leucaena leucocephala*, although native Puerto Rican species have begun reappearing after 40 years.

Recovery following forest conversion to agriculture or housing illustrates how a disturbance can cause a system to shift toward monodominance by a single, invasive tree species. Conversion of African dry forests to grass-dominated savanna by fire results in both a new species composition, and also dominance by a different growth form. Both of these anthropogenic disturbances have resulted in new ecosystems with different structure, though the *Leucaena* system more closely resembles the original dry forest than does the savanna.

The occurrence of multiple disturbances can have major consequences for dry forests. In the Mexican Yucatan, 10% of trees died following a hurricane, but fires subsequently burned through a portion of the forest resulting in 85% mortality, among the highest mortality rates recorded for a dry forest. On the other hand, when a hurricane hits a forest within a year following the previous hurricane, damage is usually light, as the susceptible trees have already been removed.

Characteristics of dry forests that help confer resilience include a high concentration of nutrients below ground or in litter, high root : shoot ratios, and the ability to coppice. When trees are lost, nutrient pools support regrowth and roots access nutrients and minimize erosion. Mycorrhizae and high nutrient use efficiency of dry forest trees help to keep nutrients from being leached. Dry forest trees have adapted to their natural disturbances, allowing forests to withstand drought and regrow following wind, fire, and insect damage. Dry forests absorb human activities that mimic natural disturbances but when no natural disturbance analog exists, dry forests may shift toward other systems or become susceptible to invasion by exotic species.

Conservation and the Future of Tropical Dry Forests

Loss of forest lands occurs as a function of human population density or energy use. Given the demands of increasing human population size and energy requirements from developing economies, this trend will continue in the dry tropics. On the other hand, some conservation efforts have succeeded. In Puerto Rico and India, plantations have reclaimed degraded agricultural land and fostered the regrowth of dry forest. More countries have committed to increasing forest area in parks and reserves, and about 5% of dry forests worldwide are protected. Most conservation projects fail when the needs of the local citizenry are not considered, but conservation efforts in Guanacaste, Costa Rica, have shown that local citizens can benefit from protecting dry forest. Efforts in Guanacaste have also demonstrated methods by which invasive species can be controlled and eliminated when they are detrimental to the system – this has proven to be a difficult task in any ecosystem. Future efforts in conservation should focus on taxonomically diverse locations, such as

Bolivia, western Mexico, and southern Africa, and explicitly include benefits for local citizens.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Natural Disturbance in Forest Environments. **Environment**: Environmental Impacts; Impacts of Elevated CO_2 and Climate Change. **Operations**: Small-scale Forestry. **Soil Development and Properties**: Nutrient Cycling. **Tree Physiology**: Mycorrhizae; Stress. **Tropical Ecosystems**: Acacias; Dipterocarps; Eucalypts. **Tropical Forests**: Combretaceae; Tropical Moist Forests.

Further Reading

Bellefontaine R, Gaston A, and Petrucci Y (2000) *Management of Natural Forests of Dry Tropical Zones*, FAO Conservation Guide no. 32. Rome: Food and Agriculture Organization of the United Nations.

Bullock SH, Mooney HA, and Medina E (1995) *Seasonally Dry Tropical Forests*. Cambridge: Cambridge University Press.

FAO (2001) *Global Forest Resources Assessment 2000*, FAO Forestry Paper no. 140. Rome: Food and Agriculture Organization of the United Nations.

Holdridge LR (1967) *Life Zone Ecology*. San José, Costa Rica: Tropical Science Center.

Janzen DH (1986) *Guanacaste National Park: Tropical, Ecological and Cultural restoration*. San José, Costa Rica: Editorial Universidad Estatal a Distancia.

Mueller-Dombois D and Fosberg FR (1998) *Vegetation of the Tropical Pacific Islands*. New York: Springer-Verlag.

Murphy PG and Lugo AE (1986) Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88.

Proctor J (1989) *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*. Oxford: Blackwell Scientific Publications.

Tropical Moist Forests

L G Saw, Forest Research Institute Malaysia, Kepong, Kuala Lumpur, Malaysia

Distribution of the Tropical Moist Forests

The tropical moist forests are limited by the tropics of Cancer and Capricorn (**Figure 1**). However, the distribution is not evenly dispersed across the Americas, Africa, and Asia, often being restricted by the climatic conditions surrounding the land area. The largest area of tropical forest is found in the Neotropics (4×10^6 km^2). The neotropical forests occur in three parts: the Amazon and Orinoco basins are the largest area, followed by a block which lies across the Andes on the Pacific coasts of Ecuador and Colombia, extending northwards through Central America as far as Veracruz in southernmost Mexico. The Atlantic coast of Brazil has a third area of rainforest, a strip less than 50 km wide on the coastal mountains, extending from Bahia in the north to Rio Grande do Sul in the south. The area has now been reduced to about 12% of its original extent.

The second largest block of tropical moist forests occurs in eastern tropics and is estimated to cover 2.5×10^6 km^2. Centered in the Malay archipelago, it includes all of the Southeast Asian countries into the Pacific islands and in a narrow coastal strip in Queensland, Australia. In Australia, the forest extends in small pockets into New South Wales but is mainly restricted to the wettest sites with most fertile soils. In the Malay peninsula, the forests extend into Myanmar, Thailand to the southern Himalayas in upper Myanmar, Assam, and southern China. Africa has the smallest block of the tropical moist forests, with an area of about 1.8×10^6 km^2. Centered in the Congo basin, this block extends from the high mountains at its eastern limit westwards to the Atlantic ocean, with outliers in East Africa. It extends as a coastal strip into West Africa and woodlands reach the coast at the Dahomey Gap. There are tiny patches of rainforest on the east coast of Madagascar and in the Mascarenes.

Environment of the Tropical Moist Forests

A number of interacting environmental features influence the distribution of vegetation, e.g., climate, temperature, and moisture. Tropical moist forests occur in climates where the mean temperature of the coldest month is more than 18°C. This excludes some tropical montane areas, although an alternative definition includes forests where the difference between the mean temperatures of the warmest and the coldest months is less than 5°C. Another important characteristic of tropical climates is that the diurnal range of mean daily temperature exceeds the annual range. The amount of rainfall and its distribution through the year defines different tropical climates. Rainforests develop where monthly rainfall exceeds 100 mm and short dry spells last only a few days or weeks. Where there are regular dry periods (60 mm rainfall or less), monsoon forests or tropical seasonal forests develop. Superficially, both forest formations appear similar but they have very different species compositions: tropical moist forests are species-rich with a heterogeneous physiognomy, whereas monsoon forests are relatively species-poor and have a simple structure, often containing

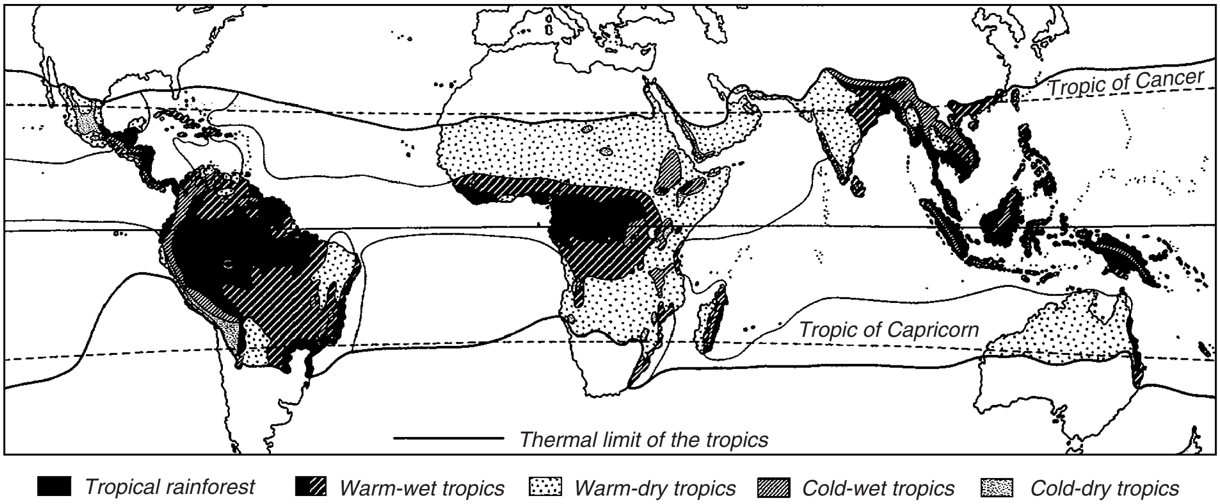


Figure 1 Distribution of tropical rainforest within hygrothermal zonations. Modified, with permission, from Lauer W (1989) Climate and weather. In: Lieth H and Werger MJA (eds) *Ecosystems of the World*, vol. 14B, *Tropical Rain Forest Ecosystems*. Amsterdam: Elsevier.

deciduous canopy trees. Tropical moist forests occur in ever-wet or perhumid climates.

Forest Formations

The structure and the species physiognomy of the major tropical moist forests are similar. This has often been described as forest formations. A forest formation is recognized by a particular combination of vegetation structure and physiognomy regardless of flora. Different species in the three areas have evolved similar responses to particular environments. The forest formations occupy different physical habitats, which are mostly sharply bounded; where this is not so there is a merging zone.

The formations develop from three interacting environmental factors: climatic, edaphic, and soil water influences (**Table 1**). Temperature regimes are more-or-less constant throughout the year in the tropical moist forests; the amount and distribution of rainfall in a region often determine the kind of major formation that develops. Seasonality of rainfall patterns has a tremendous demarcating effect on the type of formation developing. For example, in the extreme north of peninsular Malaysia in the states of Perlis and Kedah, a pronounced 2–3-month dry period results in a semievergreen rainforest that is predominantly Myanmarese and Thai. Here, deciduous trees form a good proportion of the forest. A short distance south in the state of Perak, the vegetation is lowland evergreen rainforest. Similarly, in the African rainforests, the percentage of contribution of deciduous trees rises as the climate becomes drier, as one moves north or south of the equator. A further factor that influences climate is the change in temperature regimes as elevation changes. Lowland evergreen rainforest is often restricted to elevations below 1200 m above sea level; beyond that, montane and subalpine forests develop. After climate, the substrate upon which the vegetation develops defines other forest formations. For example, soil water availability will restrict the type of plant community. In dryland areas, the climatic forest types develop in normal (mainly oxisols and ultisols) soils. However, with different availability of nutrients, other very distinctive formations develop. In podzolized sands, heath forest develops and other specialized formations are found over limestone, ultrabasic rocks, and quartzite rocks.

Where the water table is high and under maritime influence (i.e., salt water, swells) beach, mangrove, and brackish water forests may develop. Under inland freshwater swamp, depending on the degree of inundation, freshwater swamp and freshwater periodic swamp forests develop. An example of the kind of forest formations developing in Borneo indicates the dominance of particular species (**Figure 2**).

Dryland Forests

Tropical Lowland Evergreen Rainforest

This is the most luxuriant of all plant communities, and is dense evergreen forest 45 m or more tall, characterized by large numbers of tree species. Gregarious dominants are uncommon and usually two-thirds or more of the canopy individuals and two-thirds or more of the upper-canopy trees are of

Table 1 Forest formations of tropical moist forests. Reproduced with permission from Whitmore TC (1990) *An Introduction to Tropical Rainforest*. Oxford University Press

Climate	*Soil water*		*Soils*	*Elevation*	*Forest formation*
Seasonally dry	Strong annual shortage				Monsoon forests (various formations)
	Slight annual shortage				Semievergreen rainforest
Ever-wet (perhumid)	Dryland		Zonal (mainly oxisols, ultisols)	Lowlands	Lowland evergreen rainforest
				Mountains	
				(750) 1200–1500 m	Lower montane forest
				(600) 1500–3000 (3350) m	Upper montane rainforest
				3000 (3350) to treeline	Subalpine forest
			Podzolized sands	Mostly lowlands	Heath forest
			Limestone	Mostly lowlands	Forest over limestone
			Ultrabasic rocks	Mostly lowlands	Forest over ultrabasics
	Water table high (at least periodically)	Coastal saltwater			Beach vegetation
					Mangrove forest
					Brackish water forest
		Inland fresh water	Oligotropic peats		Peat swamp forest
			Eutropic (much and mineral) soils	$\pm$Permanently wet	Freshwater swamp forest
				Periodically wet	Freshwater periodic swamp forest

species individually contributing no more than 1% of the total number in the Neotropics and Asian blocks of the lowland rainforest. This formation is conventionally regarded as having three tree layers, although the layers may grade into each other: (1) upper layer of individual or grouped giant emergent trees sometimes >70 m; (2) main stratum at about 24–36 m; and (3) smaller, shade-tolerant trees below that. Ground vegetation is often sparse, and mainly of small trees and understory palms; herbs are uncommon. Some of the biggest trees have a clear bole of 30 m and reach 4.5 m girth, and may be deciduous or semideciduous, without affecting the evergreen nature of the canopy as a whole. Boles are usually cylindrical. Buttresses are common. Cauliflory and ramiflory are common. Leaves are often large and pinnate or variously dissected. Big woody climbers are frequent. Shade and sun epiphytes are occasional to frequent. Among the three regions of tropical lowland rainforests, the African block is less typical, as described above. Although the great majority of understory trees in the African forests are evergreen, a substantial proportion of the taller trees can be deciduous. Further, there can be a dominance of a single species in the canopy.

In this formation, tree diversity is the richest in the world. It is usual in this formation for tree diversity exceeding 150 species for trees (≥ 10 cm diameter at breast height) per hectare. In one particularly rich forest in Yanamomo, Peru, over 280 species per hectare have been recorded. More recently, large ecological plot studies have shown diversity of 817 species per 50 ha and 1171 species per 52 ha recorded for trees ≥ 1 cm diameter at breast height, in Malaysia. In comparison in more seasonal forest areas of India, Panama, and Thailand, the diversity was less than half of the Malaysian totals, ranging from 68 species to 305 species per 50-ha plot.

Floristic Composition of Lowland Evergreen Rainforests

Among the three blocks of evergreen rainforests, the African forest is less diverse, for example, the tree

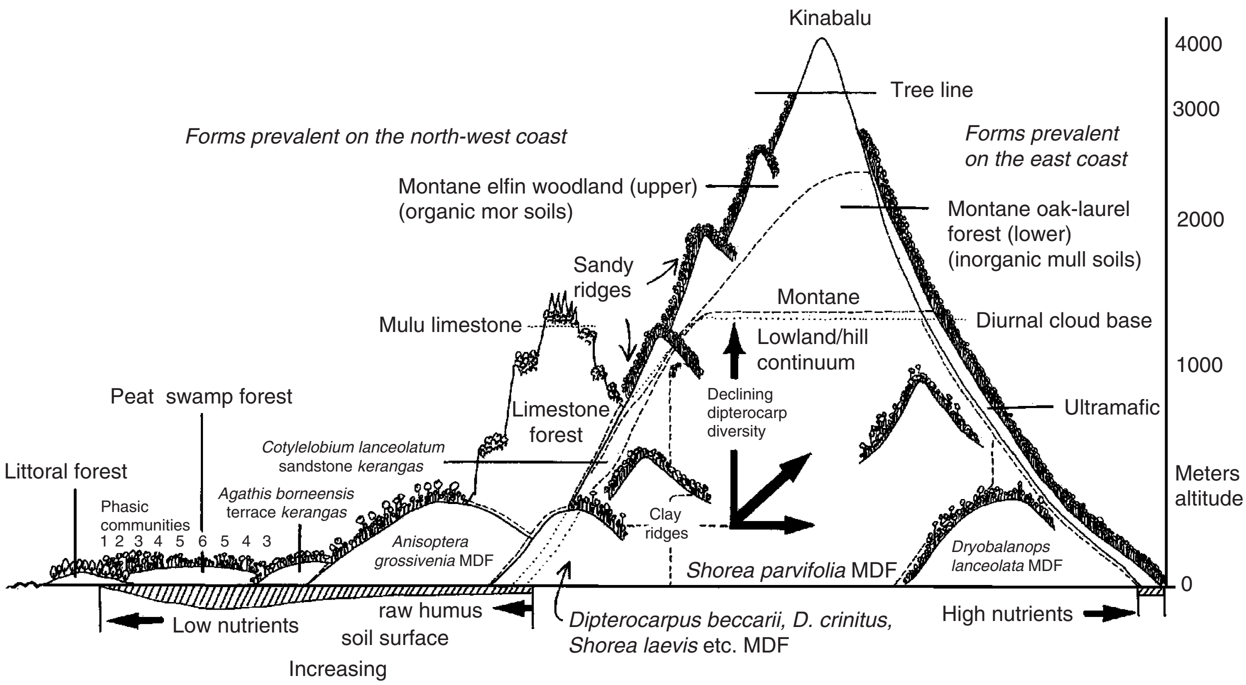


Figure 2 Diagram of the major floristic associations in Bornean forests. MDF, mixed Dipterocarp forest. The bold arrows indicate declining dipterocarp diversity with changes in nutrients levels in the soil, and altitude. Reproduced with permission from Ashton PS (1995) Biogeography and ecology. In: Soepadma E and Wong KM (eds) *Tree Flora of Sabah and Sarawak*, vol. 1. Kuala Lumpur, Malaysia: Forest Research Institute Malaysia.

diversity of the various lowland evergreen forests in the Ivory Coast is much lower than that in Malaysia and Surinam. By African standards, these Ivory Coast forests are floristically rather rich, yet they contain about a quarter of the number of tree species per unit area found in Malaysia. There have been many speculations over the poverty of the African forest flora. It has been suggested that forest flora was once much richer than today but has been reduced by progressive aridity since the Miocene, and especially by a series of severe dry episodes during the Quaternary. The African rainforest shares similar richness in legume species with the South American and in the absence of Dipterocarpaceae, a family so typical of Southeast Asian forests. However, it is particularly poor in palm species in its understory species. In contrast with rich bromeliad flora of South America, Africa has only one bromeliad species (*Pitcairnia feliciana*). Major families shared with South America include Euphorbiaceae, Meliaceae, Moraceae, and Sapotaceae. These probably represented old families which were present on both continents before rifting. A number of leguminous trees, including *Brachystegia laurentii*, *Cynometra alexandri*, *Gilbertiodendron dewevrei*, *Michelsonia microphylla*, and *Scorodophloeus zenkeri* may dominate the canopy of the lowland African forests as single species.

The flora of the eastern block, in particular, the Malesian region is rich with about 42 000 species of vascular plants. The flora of the Malesian region is also not homogeneous. There are marked differences from island to island. However, there are two floristic elements, one centered on the Sunda shelf and the other on the Sahul shelf. A strong zoogeographical boundary runs through these shelves, sometimes called Wallace's line. Dipterocarpaceae is probably the most important single distinction between the forests west and east of Wallace's line. Dipterocarpaceae west of Wallace's line dominates the rainforests in Malesia as upper-canopy or emergent trees like no other tree families. Species are also very diverse, particularly on the island of Borneo. Other groups that are centered on the Sunda shelf include some palm genera such as *Daemonorops*, *Iguanura*, and *Pinanga*, Magnoliaceae, and *Artocarpus* (Moraceae). Conifers are more abundant east of Wallace's line, more in the mountains, but some species may form dense stands in lowland forests. These conifers all belong to two families, Araucariaeae and Podocarpaceae. Among the palms, *Gronophyllum*, *Gulubia*, *Hydriastela*, *Metroxylon*, and *Siphokentia*, are confined to the east side of Wallace's line. The family Proteaceae is centered on the Sahul shelf, except for *Heliciopsis* which has a Sundaic focus. Other plant groups, e.g., *Syzygium* (Myrtaceae), are equally abundant on both sides of Wallace's line. The north eastern Australian rainforests have similar affinity to New Guinea Island and with floristic composition of the Sahul shelf. With its present drier climate, some genera endemic to this rainforest include *Backhousia*, *Blepharocarya*, *Buckinghamia*, *Cardwellia*, *Castanospermum*, *Ceratopetalum*, *Doryphora*, *Flindersia*, *Musgravea*, and *Placosperma*.

As in the eastern block of rainforest, the neotropical rainforest is complex and not homogeneous. Floristic composition varied with the different forest types. Principally, in the *terra firme* forest Leguminosae is the most abundant family in terms of genera and species and the Lecythidiaceae in numbers of individuals. Other important families with larger-sized trees include Burseraceae, Celestraceae, Meliaceae, Myrtaceae, and Sterculiaceae. The understory, may include Euphorbiaceae, Myrtaceae, Palmae, and Rubiaceae. Some common genera include *Bertholletia*, *Eschweilera*, *Goupia*, *Parkia*, *Tabebuia*, *Tetragastris*, and *Vouacapoua*. The absence or presence of palms and lianas is sometimes indicative of the forest type in the rainforests of the Neotropics. Some of the common palms found in the forest include *Euterpe precatoria*, *Jessenia batuaua*, *Maximiliana regia*, *Oenocapus distichus*, and *Orbignya barbosioana*.

Heath Forest

Heath forest occurs on soils developed from siliceous parent material, which are inherently poor in bases and highly acidic, and of coastal alluvium or weathered sandstone origin. Such soils become podzolized. In some substrate, particularly those under sandstones, the soils become temporarily waterlogged, particularly during the rainy season. The streams draining from such forests are tea-colored owing to the presence of organic colloids that leached out from the soils. They are usually acid (pH <5.5), and with a low oxygen content. The most extensive heath forests are found in the upper reaches of Rio Negro and Rio Orinoco in South America. In Brazil, they are known as campina, campinarana, caatinga Amazonica, or campina rupestre. In the Far East, there are also large areas of heath forest in Borneo (called kerangas), less extensively in peninsular Malaysia, Sumatra, and New Guinea. African heath forests are less extensive areas and are found in coastal sands in Gabon, Cameroon, and Ivory Coast.

This forest is strikingly different from the lowland evergreen forest in having a very different flora, structure, and physiognomy. Depending on the depth of the heath soils and variability of water supply, the vegetation varies from low scrublands comprising sedges, grasses, and stunted gnarled trees to near-lowland rainforest formation. Characteristically, the forest is dominated by pole-sized trees, where the main story is formed by large saplings and small poles and forms a tidy and orderly stand. The canopy is low, uniform, and usually densely closed with no trace of layering. Single emergents may occur but often in areas with deeper soils. There are more trees with small leaves, many species with sclerophyllous leaves; deciduous species are absent. Big woody climbers are rare, but slender, wiry, independent climbers are frequent. Myrmecophytes are abundant, especially in the more open and stunted heath. Amongst the herbs are insectivorous plants, e.g., *Drosera, Nepenthes,* and *Utricularia*.

When the sandstone formation extends into higher elevations, the montane flora extends to the lower elevations. In many respects, the upper montane and heath forest have many features of structure and physiognomy in common.

Limestone Forest

The total extent of limestone is small and is often found in the lowlands. The largest areas are found in the Far East. They are absent in the humid tropics of Africa and are rare in Latin America, except in the Caribbean region. A distinctive feature of the limestone hills is the karst landscape. In the Far East, it occurs in Central Sumatra, peninsular Malaysia, Borneo (mainly in Sarawak and in small areas in Sabah), Java, the Lesser Sunda Islands, Celebes, the Moluccas, and New Guinea.

There are a diversity of habitats and soils within the limestone hills that sometimes support very specific animal and plant species. The alluvial soils at the base of the limestone hills, although derived from other rocks, are under the influence of run-off water and erosion from the limestone. The soils are often more fertile and more base-rich and often the vegetation is an extension of the adjacent forest. The second zone is the base of cliffs and ravines in the hills, sometimes with small scree slopes of limestone boulders. Here a few species may dominate, for example, in peninsular Malaysia the palm *Arenga westerhoutii* sometimes completely dominates the slope. The third zone is the limestone slope with its dense, irregular forest with trees clinging precariously, their roots penetrating to great depths in crevices. Sheer cliffs may bear scattered shrubs and a characteristic herb flora. In peninsular Malaysia and Borneo, Gesneriaceae with species adapted to desiccation are prominent, and *Cycas* and some *Pandanus* are often seen clinging to crevices of cliffs. The final zone is the summits of the limestone hills. It is a peculiar habit. It has a deep mat of peat-like humus, held together by tree roots and anchored to the limestone pinnacles underneath. It often contains many epiphytic plants and plants specializing in the drier and harsher environment; orchids and ferns may be common.

Limestone flora often contains many endemic plants. For example, the palm genus *Maxburretia* is completely restricted to the limestone hills of the Malay peninsula, each species being endemic to specific limestone hills. Similar examples, although not as restrictive, can be seen in many genera of Gesneriaceae, e.g., *Boea*, *Chirita*, *Monophyllaea*, and *Paraboea*.

Beach Vegetation

Two kinds of beach vegetation are recognized. One occurs on accreting coasts where new sand is deposited and plant cover is often of low herbaceous creeping plants (the *pes caprae* association). Species found in this habitat are often pantropical. At the inland margin of the sand beach, the second vegetation forms; in the Far East, for example, the *Barringtonia* association is found here. Inland it merges with the lowland rainforest. Its composition is very uniform throughout Malesia and many species extend from the coast of Africa through Malesia far into the Pacific. Many species have seeds or fruits adapted to water dispersal. The trees are sometimes loaded with epiphytes, particularly orchids, ferns and asclepiads (*Hoya* and *Dischidia*).

Swamp Forests

Mangrove Swamp Forest

Mangrove forest develops where there is coastal sedimentation of mud; mangroves are the usual initial colonizers. The mud is invaded by the tide twice daily, but the pneumatophore shoots of pioneer species of *Avicennia*, followed at a later stage by the many-stemmed stools of *Rhizophora*, trap sediment very efficiently (sometimes up to several meters a year). The vegetation is simple in structure, 5–25 m in height depending on the community, with comparatively even and unbroken canopy, a very poor understory layer which is frequently absent, and poor in species. The principal tree species are restricted to such habitats, and are frequently characterized by special root formations such as stilt roots (*Rhizophora*) and pneumatophores (*Avicennia*, *Bruguiera*, *Sonneratia*, and *Xylocarpus*). The vegetation is often very simple, with few species dominating the whole stand. There is also a distinct succession from the seaward front to the landward side. Mangrove forest is found throughout the tropics. The mangroves of Madagascar and eastern shores of Africa have a strong Asian affinity while those of the Atlantic shores of the USA and West Africa share similar floristic affinities.

In the Far East, on the edge of the mangrove and the upper tidal limit of estuaries, there is a forest with a number of distinctive species, amongst which *Nypa fruticans* is important and forms extensive pure stands, mainly along water courses in river estuaries.

Peat Swamp Forest

In parts of Sumatra, Malaya, Borneo, and west New Guinea a physiological setting exists which favored the formation of peat. Since sea level rose at the end of the last Ice Age, rivers deposit silt as levees and on flood plains. Swamps form behind the levees and became less saline and over time under anaerobic conditions peat develops from the accumulated litter. The process continues until the present day. Peat is semiliquid and low in nutrients because the only input is from rainfall. Peat reaches 13 m thick in the most developed domes, a formation that is better understood in Southeast Asia where the domes occur in large areas, particularly in east Sumatra, Malaya, Borneo, and New Guinea. Less in extent are the peat swamp forests found in the USA and Africa.

Structurally and floristically, the peat swamp forest is not a uniform formation. In Borneo, for example, there exists a catena of at least six types of phasic communities which are moderately sharply distinct in structure, physiognomy, and flora. In general, the forest has a three-layered tree structure. Most of the tree families of the lowland forest are found in the peat swamp forest. However, there are species that specialize in such environments. Palms are poorly represented; those that occur are either swamp specialists or species restricted to this formation (e.g., *Cyrtostachys renda*, *Korthalsia flagellaris*).

Freshwater Swamp Forest

The soil surface of land covered by the freshwater swamp forest formation is regularly to occasionally inundated with mineral-rich fresh water of fairly high pH (nonacidic). There may be peat present in the soil but one key difference of this formation from the peat swamp forest is that in the latter, rain is the only source of water reaching this forest, which is nutrient-poor. Freshwater swamp occurs throughout the tropics, where the river system runs into low-lying areas and regular flooding produces the condition for this formation to develop. As with the peat swamp forest formation, this is a varied formation, often dependent on the degree of inundation and the kind of parent material in which the vegetation develops. The Amazon, which has annual floods and is influenced by tides to some 600 km inland, has very extensive and diverse freshwater permanent and periodic swampy forests. Igapó is applied to black and clear water areas and várzea muddy water inundation. Várzea is formed by flooding with muddy water rivers such as the Amazonas and the Madeira, and igapós on sandy soil and clear water. The várzeas have soils that are more fertile. The Zaire basin is about one-third occupied by swamp forests. The greatest extent of this formation in Asia is where the biggest rivers are, e.g., in Indo-China, Thailand, and Myanmar (Mekong and Irrawaddy), and in New Guinea (Fly and Sepik). In recent years, much of this habitat has been destroyed due to conversion to agriculture.

Global Trends in Rainforest Areas

Increasing human population in the last hundred years has had a profound impact on the tropical rainforests. In many tropical societies, land-use patterns have shifted from a low-impact traditional use of forestlands to a more intensive industrial use. Tropical forests are being altered at a rapid pace in one of two different ways. Some areas are converted to other uses; others are logged but left to regenerate. Land conversion poses the greatest threat. There are major differences between regions in the rate at which tropical moist forests are disappearing. In Southeast Asia, the major conversion has been from planned conversion of forest areas to industrial agriculture plantation crops such as rubber and oil palm. More recently, areas have also been converted to tree plantation crops to produce pulp. Most often *Acacia mangium* is planted. In the neotropics, large areas have been converted to pastures for cattle farming. Industrial tree crops are also planted in large areas, often using species of *Acacia mangium*, *Eucalyptus*, and tropical pines. These are examples of planned conversion often initiated by government policies. Forest conversion also comes about that is not centrally planned. In many countries, peasant farmers moved into rainforest, usually to practice shifting cultivation, and often illegally. These people often moved into new forest areas following commercial logging. Forests are also destroyed for dams and mines.

Harvesting timber from the forest will alter the nature and dynamics of the rainforests. Commercial logging in tropical rainforests can take a number of forms, almost all of which involve the removal of selected trees rather than the clear felling of whole stands. This is different from temperate forestry operations where clear felling is much more common. In the past, such practices, i.e., selective felling, were not intensive and often forests regenerated. In peninsular Malaysia, for example, under the Malayan Uniform System, it was possible to return to harvest a forest area after about 60 years of first harvesting. Changing market forces and more mechanized logging operations in recent years have now increased logging intensities. This has resulted in the slow recovery of logged-over forests. However, many countries are now considering better ways of managing the forests. Studies have indicated that when properly managed, forests, can provide both services and products for the present and the future.

To conserve the rainforests, increasingly, many tropical countries are looking into sustainable forest management (SFM) practices. Tropical rainforests are a renewable resource, which can be utilized while retaining their diversity and richness. Bringing such principles into forest management has become a strong challenge for many developing countries in the tropics.

See also: **Tropical Ecosystems**: Bamboos, Palms and Rattans; Dipterocarps; *Ficus* spp. (and other important Moraceae); Mangroves. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Montane Forests.

Further Reading

Ashton PS (1995) Biogeography and ecology. In: Soepadmo E and Wong KM (eds) *Tree Flora of Sabah and Sarawak*, vol. 1. Kuala Lumpur: Forest Research Institute.

Hamilton A (1989) African forests. In: Lieth H and Werger MJA (eds) *Ecosystems of the World*, *vol. 14B*, *Tropical Rain Forest Ecosystems*. Amsterdam: Elsevier.

Lauer W (1989) Climate and weather. In: Lieth H and Werger MJA (eds) *Ecosystems of the World*, *vol. 14B*, *Tropical Rain Forest Ecosystems*. Amsterdam: Elsevier.

Pires JM and Prance GT (1985) The vegetation types of the Brazilian Amazon. In: Prance GT and Lovejoy TE (eds) *Key Environments*: *Amazonia*. Pergamon Press. Oxford: UK.

Prance GT (1989) American tropical forests. In: Lieth H and Werger MJA (eds) *Ecosystems of the World*, *vol. 14B*. *Tropical Rain Forest Ecosystems*. Amsterdam: Elsevier.

Richards PW (1996) *The Tropical Rain Forest*. Cambridge, UK: Cambridge University Press.

Stocker GC and Unwin GL (1989) The rain forests of northeastern Australia: their environment, evolutionary history and dynamics. In: Lieth H and Werger MJA (eds) *Ecosystems of the World*, *vol. 14B*, *Tropical Rain Forest Ecosystems*. Amsterdam: Elsevier.

Webb LJ and Kikkawa J (1990) *Australian Tropical Rainforests*. Victoria, Australia: CSIRO.

Webb LJ and Tracey JG (1981) The rainforests of northern Australia. In: Groves RH (ed.) *Australian Vegetation*. Cambridge, UK: Cambridge University Press.
Whitmore TC (1984) *Tropical Rain Forests of the Far East*, 2nd edn. Oxford, UK: ELBS/Oxford University Press.
Whitmore TC (1989) Southeast Asian tropical forests. In: Lieth H and Werger MJA (eds) *Ecosystems of the World, vol. 14B*, *Tropical Rain Forest Ecosystems*. Amsterdam: Elsevier.
Whitmore TC (1990) *An Introduction to Tropical Rain Forest*. Oxford, UK: Clarendon Press.
Whitmore TC and Sayer JA (eds) (1992) *Tropical Deforestation and Species Extinction*. London: Chapman & Hall.
Wyatt-Smith J (1955) *Manual of Malayan Silviculture for Inland Forest*. Malayan Forest Records no. 23, vol. 1. Kuala Lumpur: Forest Research Institute.

Tropical Montane Forests

M Kappelle, Utrecht University, Utrecht, The Netherlands

Introduction

Mid and high-elevation regions near the equator such as are found in the Andes and on Papua New Guinea support tropical montane forests (TMF), which range from relatively dry woodlands to extremely wet forests. TMF forms a major component of several of the world's biodiversity hotspots (e.g., Meso-America and the northern Andes), as it represents an extremely species-rich system, which is highly endangered due to human interference. The most important and diverse of all TMF types is the tropical montane cloud forest (TMCF). This conspicuous ecosystem filters global air masses in such a way that they seize and incorporate water and nutrients from mist and fog into their cycles. It may be even richer than the tropical lowland rainforest (TLRF) when diversity is measured as species density on a per-unit-area basis. TMCF is well known for its important fresh-water resources, which feed the many rivers passing through major mountain cities in the Andes such as Bogotá and Quito, which in turn depend on these resources to supply their human populations with sufficient drinking water. However, today these fragile forests are among the most endangered ecosystems worldwide, due to destructive anthropogenic forces causing forest loss and habitat fragmentation, ultimately leading to species extinction and loss of environmental goods and services which are vital to the regional and local human populations.

The present article presents a brief overview of TMF, emphasizing its most important representative, the TMCF type. A bioclimatic definition is presented and its overall aspects are discussed. Subsequently, its geographic distribution and main determinants are treated. Details on climate, soils, and topography are elaborated. Furthermore, past trends in forest cover are dealt with. This is followed by a detailed discussion of the TMF structure, species composition, dominance, and dynamics as a result of disturbances. Regional subtypes and boundaries with other forest types are listed. Next, the ecological/environmental and sociocultural importance of this specific forest ecosystem is analyzed. Past and current TMF use practices are assessed and some sustainable forest management systems identified. Finally, threats to the survival of species and the integrity of the ecosystem as a whole are evaluated and current and future conservation strategies discussed. Such an analysis ultimately permits the setting of priorities in conservation and sustainable development for the benefit of the peoples living in and depending on TMF systems.

Definition

Forests on Tropical Mountains

TMF is latitudinally restricted to the tropics and may only be found, in its strict sense, at northern and southern latitudes between the tropics of Cancer and Capricorn. In a wider sense, TMF reaches a northern latitude of 23° in Mexico and a southern latitude of 25° in Argentina. Within this latitudinal range, TMF is altitudinally restricted to montane elevations. This is the most difficult part of the elaboration of a concise definition, for scholars have not been able to define the altitudinal limits of the montane belt unanimously. In general, as a rule of thumb, it is assumed that montane forests occur between 500 and 4000 m above sea-level. However, there are places on earth, especially on volcanic islands, where montane forests may occur at 300 m elevation (e.g., in the Caribbean), while there are sites in certain tropical mountain chains such as in the South American Andes where small pockets of montane forests occur in wind-protected valleys at elevations over 4000 m. In the latter case, these montane forests are better known as tropical subalpine forests (TSF) as they often occur just below – or amongst – the treeless, tropical alpine grasslands and shrublands.

Tropical Montane Cloud Forests

In contrast, TMCF – the cloudy version of TMF – was well defined a decade ago. Specialists now agree that TMCF differs significantly in composition and structure from rainforests in tropical lowlands (TLRF). It typically occurs as a narrow altitudinal belt in tropical highlands where the atmospheric environment is characterized by persistent, frequent, or seasonal cloud cover at vegetation (or ground) level, i.e., the tree crowns are regularly bathed in mist and fog ('canopy wetting'). Although little is known about the hydroecological effect of the mist-forming, enveloping, and wind-driven clouds on the hydrological input in this ecosystem, it has been widely recognized that the frequent cloud and mist presence causes a considerable increase in atmospheric humidity within the forest interior – a phenomenon presently known as 'horizontal precipitation.'

Characterizing Tropical Montane Forests

Limiting climatic factors such as horizontal precipitation (cloud stripping), a reduced photosynthesis due to reduced solar radiation, a periodic water shortage (vapor deficit), strong diurnal temperature oscillations, a general reduction of the evapotranspiration rate, exposure to strong winds, and a limited nutrient uptake, are the most important environmental factors which determine the large array of differences in forest structure and composition when cloudy TMF is compared to TLRF. Some of these striking differences include a particular, often elfin-like physiognomy characterized by a reduced tree stature, an increased tree stem density, frequently gnarled trunks and branches of stunted trees with dense crowns and small-sized, sclerophyllous and coriaceous leaves. At first sight, the branches of trees and shrubs appear typically draped with pendant mosses covered with water droplets and filmy ferns. In fact, a complex mosaic-like assemblage of vascular and nonvascular epiphytes (orchids, bromeliads, ferns, mosses, liverworts, algae, lichens, and fungi) blankets the surface of host trees and shrubs (**Figure 1**).

The epiphytes contribute to an enormous extra above-ground biomass which may retain a significant quantity of additional water from clouds (i.e., the above-mentioned process of cloud stripping). All these diagnostic features, together with the forest's low productivity and low nutrient cycling rates, characterize the general structure and functioning of the TMCF and hence the most typical of all TMF varieties.

Figure 1 Epiphytic communities of vascular and nonvascular plants on tree branches in Colombian tropical montane forests at elevations of (a) 1980 m, (b) 2550 m, and (c) 3370 m, studied by Jan H.D. Wolf. Courtesy of Gerard Oostermeijer.

Distribution

Geographical Distribution

TMF as well as TMCF occurs between 500 and 4000 m altitude on all three tropical continents (Africa, America, and Asia) and in equatorial

Oceania. The majority of TMF sites are found between 1200 and 2800 m elevation. They are found from central Mexico (Eje Neovolcánico Transversal) south-eastward along the Central American mountain chains (Guatemala, Costa Rica), and further south along the Andes to northern Argentina (Salta-Tucumán). They appear especially well developed in the northern Andes (Venezuela, Colombia, Ecuador, and Peru), on both the eastern and western flanks of their cordilleras. In Central Africa they occur in mountainous countries like Uganda (Bamenda Highlands, Rwenzori Mountains), and in East Africa along the so-called Eastern Arc (e.g., Mount Kilimanjaro, Mount Kenya) and at the drier Ethiopian highland plateaux. Further to the east, they are encountered on the higher parts of Southeast Asia (e.g., Mount Kinabalu in Sabah, East Malaysia; Kalimantan and Irian Jaya in Indonesia; Philippines; Papua New Guinea). They inhabit the mountaintops of many oceanic islands where exceptionally wet, marine, equatorial conditions prevail, as is the case in the Caribbean region (Jamaica, Puerto Rico) and the Pacific Ocean (Fiji, Hawaii; **Figure 2**).

The Massenerhebung Effect

It is well known that TMF formations occur at higher elevations on taller mountains. The upper limit of lowland forest may be brought down to varying degrees below the temperature-determined uppermost limit when the fog characteristic of TMF environment occurs at lower levels. This little understood phenomenon is known as the Massenerhebung or telescope effect, first described for the Alps in Europe. Apparently, the compression and depression of the forest belts on small mountains, such as on tropical islands (e.g., Hawaii) and along coasts, seems mainly associated with a lowering in the level at which cloud habitually forms. More specifically, the altitudinal distribution of TMCF is related to the cloud level itself, which in turn is dependent upon the humidity at the foot of a mountain. The greater the humidity is at the mountain's base, the lower the cloud level occurs (**Figure 3**).

Climate

The average temperature in TMF and cool-humid TMCF depends principally on elevation, as temperature decreases with increasing altitude. Average annual temperatures range from 8°C at 3400 m to 20°C at 1000 m. Average annual rainfall is correlated with slope orientation and fluctuates between 500 and 10 000 mm, although yearly precipitation generally ranges from 1000 to 3000 mm. Ascending air masses bring increased precipitation to mountain slopes (windward slopes; e.g., under the influence of trade winds in the Caribbean) unless they are sheltered from the wind (leeward slopes; rain shadow). As has been said, the net precipitation or throughfall in TMCF is significantly enhanced beyond rainfall contribution through direct canopy interception of cloud water (horizontal precipitation), a process also known as cloud stripping. It is therefore not surprising that TMF is particularly rich in epiphytes, which obtain water directly from the perhumid atmosphere.

Soil

TMF soils are quite different from tropical lowland soils. On tropical mountains, the often reddish-brown loamy lowland soils on flat plains become replaced by more yellowish, acid and peaty soil types with organic upper horizons on steep slopes in rugged terrain. TMF soils are frequently water-logged and suffer from podsolization, a soil-forming process, which causes the leaching of nutrients (lixiviation) from upper soil horizons to lower levels. These nutrient-poor, water-saturated soils may experience an anaerobic environment, which in turn originates impeded root respiration, a reduction in below-ground bioactivity, and lower decomposition levels. The final result is the accumulation of humus in the topsoil (histosols) and/or loss of nutrients at top- and mid-soil levels (podsols). However, on a number of mountains (e.g., volcanoes) nutrient-rich soil types may prevail (andosols), as intrusive rocks intermingled with marine sediments become exposed and weathered. Soil characteristics in TMCF appear to correlate strongly with plant community distribution.

Present Forest Cover

Over the last few decades TMF and particularly TMCF has suffered greatly from human interference. Large-scale deforestation for timber, fuelwood, and charcoal production in combination with forest conversion to pastureland has caused uncontrolled habitat fragmentation and severe land degradation. Today, TMF covers an estimated 200 million ha throughout the tropics. This is only 30% of the 700 million ha of the globe's tropical montane landmass. Throughout the 1980s the annual TMF deforestation rate was 2.5 million ha. TMCF makes up less than 1% of the world's closed canopy forests, while in the neotropics it presently covers only 65–75 million ha, about a third to half of which occurs in Colombia. Further research using high-resolution satellite imagery is urgently needed to assess precisely the area currently covered by TMF and TMCF in particular.

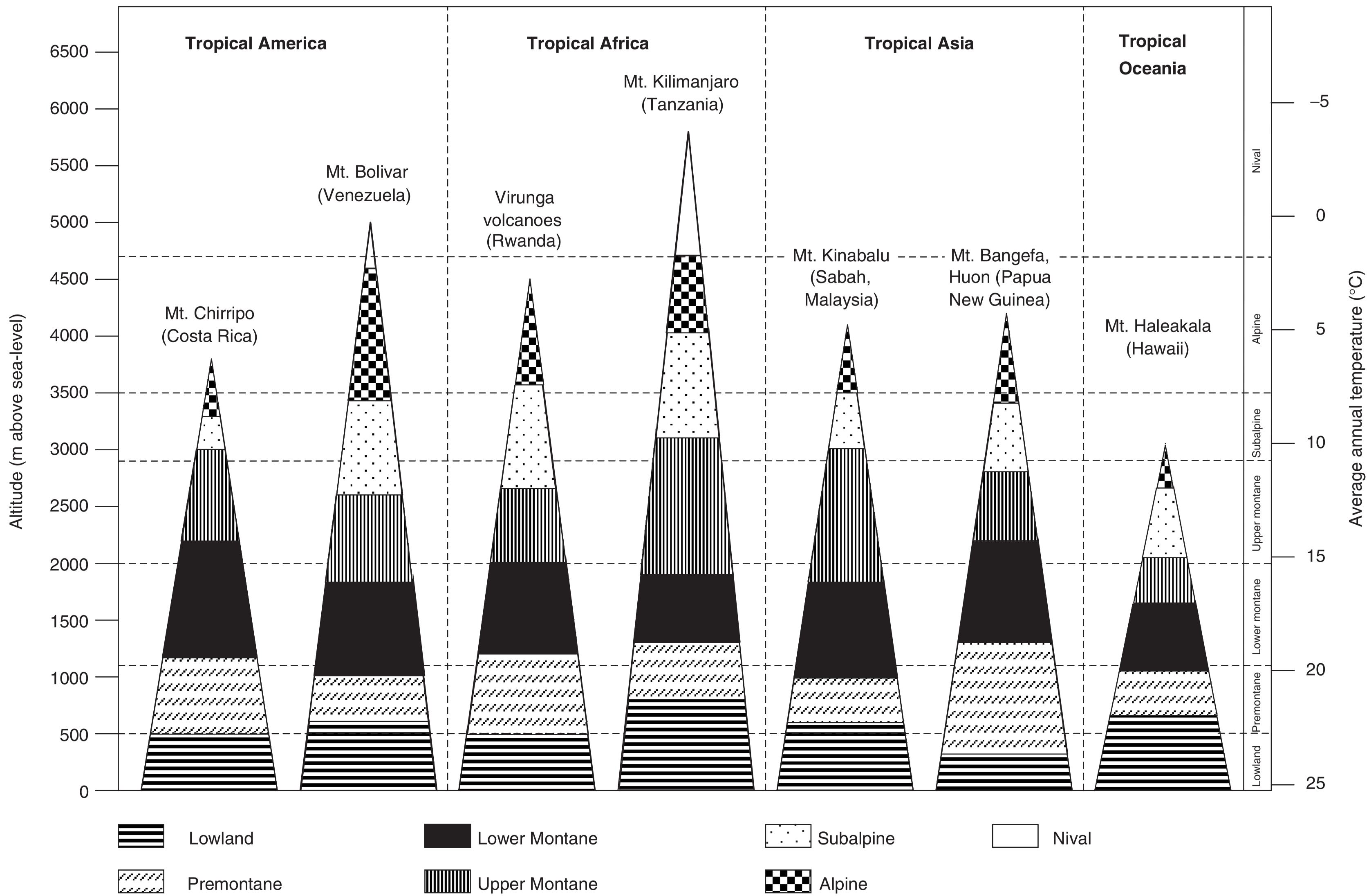


Figure 2 Altitudinal vegetation zonation on selected mountains on all tropical continents. The tropical montane forest (TMF) is strictly found in the lower and upper montane belts, but may occur locally in adjacent zones of the premontane and subalpine belts. The transitional subalpine belt (just below the upper TMF tree line, separating the TMF from alpine scrub) is regionally and locally also known as the ericaceous belt, while the transitional premontane belt (separating the lowland forest from TMF formations) has also been named as the (foot) hill zone or submontane belt.

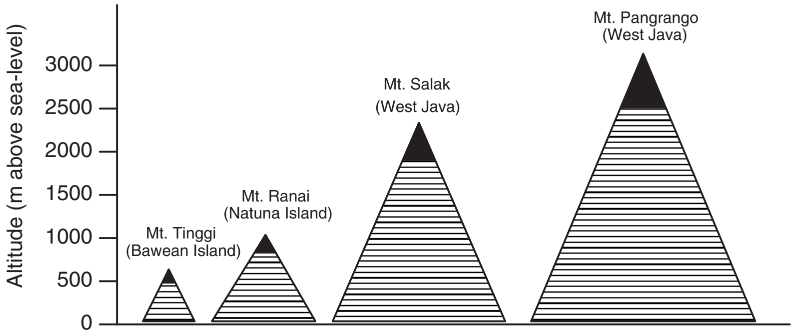


Figure 3 The Massenerhebung or telescope effect of tropical vegetation zonation, exemplified by the occurrence of mossy montane forest at contrasting altitudes on different-sized mountains in South-East Asia. (Adapted with permission from Bruijnzeel LA and Hamilton LS (2000) *Decision Time for Cloud Forests*. Paris: WWF, IUCN, and UNESCO.)

Table 1 Characters of structure and physiognomy used to define the principal tropical lowland and montane rain forest formations

Formation	*TLF (evergreen)*	*TLMF*	*TUMF*
Canopy height	25–45 m	15–33 m	1.5–18 m
Emergent trees	Characteristic, to 60 (80) m tall	Often absent, to 37 m tall	Usually absent, to 26 m tall
Pinnate leaves	Frequent	Rare	Very rare
Principal leaf size class of woody plants[a]	Mesophyllous	Mesophyllous	Microphyllous
Buttresses	Usually frequent, and large	Uncommon, and small	Usually absent
Cauliflory	Frequent	Rare	Absent
Big woody climbers	Abundant	Usually none	None
Bole climbers	Often abundant	Frequent to abundant	Very few
Vascular epiphytes	Frequent	Abundant	Frequent
Nonvascular epiphytes	Occasional	Occasional to abundant	Often abundant

[a] Leaf sizes according to the 1934 Raunkiaer Leaf Sizes Classification System.
TLF, tropical lowland forest; TLMF, tropical lower montane forest; TUMF, tropical upper montane forest.
After Whitmore TC (1984) *Tropical Rain Forests of the Far East*. Oxford, UK: Clarendon, with permission.

Description and Major Features

Forest Formations along an Altitudinal Gradient

When climbing a high tropical mountain, one passes through nearly all climatic and vegetation zones of the world over a relatively short distance. It is therefore no surprise that tropical mountains are extremely rich in species and ecosystems. One may observe a series of forests with different structure, physiognomy, and composition. As the late Tim Whitmore clearly stated, one of the most striking features is the change from mesophyll-dominated forest with an uneven billowing canopy surface to a lower, more even, often pale-colored, microphyll-dominated canopy, of more slender trees, usually with gnarled limbs and very dense subcrowns. At mid-elevation in the northern Andes, the transitional tropical premontane forest (TPMF; 500–1200 m above sea-level) and its adjacent lower montane forest (TLMF; 1200–2400 m) occur with a broad ecotone against the 30–40-m-tall lowland forest formation (TLF; **Table 1**).

At higher elevations, closer to the upper forest line, upper montane forest (TUMF; 2400–3600 m) occurs. The change from frequent cloud cover at vegetation level in TLMF to more persistent cloud cover in TUMF is one of the major factors determining the common boundary between both TMF belts at 2200–2600 m altitude. TUMF is often only 10–25 m tall or less, and its shorter version is sometimes called 'dwarf forest,' 'elfin forest,' 'montane thicket' or – when nonvascular epiphytic plants abound – 'mossy forest.' Its trees may be swathed in bryophytes (mosses, liverworts) and filmy ferns.

On the highest peaks TUMF is replaced by a shorter, much more gnarled formation, stunted by the wind, with even tinier, often xeromorphic leaves (nanophylls). This formation is known as subalpine rainforest (TSF), and has been observed at such geographically disjunctive places as Costa Rica, Ecuador, and New Guinea. The upper tree line (also known as the timber line) on the tallest mountains can be found around 4000 m elevations, although this line is often depressed by human-set fire. Above the tree line occurs a treeless, alpine, cold, wet and misty biome, often dominated by giant stem rosette plants belonging to genera such as *Espeletia, Lobelia*, and *Senecio*, shrubs, forbs, bunch grasses, bamboos, sedges, mosses, liverworts, and beard-like lichens. This biome or ecosystem is regionally known as the paramo (Latin America), the afroalpine (Africa), or tropic-alpine (southeast Asia) ecosystem. It is a tundra-like, peaty system extending up to the rocky snowline at about 4500 m elevation, above which the nival belt extends with its mountain glaciers and snowy summits.

Structure and Physiognomy

The structure of the average high-elevation TMF and TMCF has a dwarfish appearance. Small, flattened, sometimes bonsai-like trees display curved trunks due to soil creep on steep slopes. They occur clumped together in an almost impenetrable setting. Twisted branches with thick (pachyphyllous), hard (sclerophyllous), tiny (microphyllous to nanophyllous) leaves, located in thick bunches on dense subcrowns are heavily loaded with woody and herbaceous epiphytes. Without doubt, the abundance of epiphytes causes an enormous increase in aboveground forest biomass and may act as a sponge, retaining water from clouds and fog.

Maximum canopy tree heights range generally from 7 m at 3400 m elevation (Peru) to 20 m at 1000 m (Monteverde, Costa Rica). Stem densities (diameter at breast height (dbh) > 5 cm) are higher in TMF than at lower elevations in TLF and may fluctuate between 500 stems per hectare at 2700 m elevation in Colombia and Costa Rica and 1000 stems per hectare at 3300 m in Ecuador. If all stems over 2.5 cm dbh are included, a total of 1600 stems per hectare may be recorded (Peru). In the case of 15–35-year-old secondary TMF at 500–3000 m altitude, values of 2500–3500 stems per hectare (dbh > 2.5 cm) seem normal (Costa Rica, Puerto Rico). However, TMF structure data may differ significantly over different slopes (windward versus leeward), along different rainfall gradients, and at different altitudes (temperature variations).

Next to the generally more elfin TMF formations, other TMF types exist in which huge, 35–55-m-tall trees prevail. An example is the tropical montane fagaceous-bamboo forest type found in Central and South America as well as in certain parts of Southeast Asia. In Costa Rica this TMF type is dominated by different species of white and black oak (*Quercus*) in its canopy and *Chusquea* bamboo in its 3–6-m-tall understory. Similar fagaceous-dominated TMF is observed in Andean Colombia where oak trees (*Quercus, Trigonobalanus*) are accompanied by *Chusquea* and *Neurolepis* bamboos, in Indonesia (Sumatra, Kalimantan, Java), where *Castanopsis* and *Lithocarpus* trees form dense stands, as well as on Papua New Guinea, where *Nothofagus* trees spread shade over an understory of climbing *Nastus* bamboos. Other fagaceous–bamboo-dominated montane forests are distributed over more subtropical regions, such as parts of Chile (*Nothofagus* trees with *Chusquea* bamboos), the Himalayas (*Quercus* trees with *Arundinaria* bamboos), and Japan (*Fagus* trees with *Sasa* bamboos).

In Costa Rican TMF at 2500 m elevation (Talamanca mountains), giant oaks (*Quercus*) grow in large quantities and show dbh over 2 m. Below the tall, epiphyte-blanketed oak crowns appears a subcanopy layer with a large number of 10–25-m-tall tree species from both temperate and tropical origin. Temperate plant genera and species begin to appear in TMF at 2000 m elevation. Examples in Costa Rica are alder (*Alnus*), oak (*Quercus*), and willow (*Salix*). Here, values of basal area are among the highest found in tropical forests worldwide: at several places, a basal area value higher than $50\,m^2\,ha^{-1}$ was measured. Values of 25 (Ecuador) to 40 (Puerto Rico) $m^2\,ha^{-1}$ are more likely for TMF between 1000 and 3000 m above sea-level.

Besides the more common and widespread moist TMF formations (including wet, rain, and cloud forests) discussed so far, there occur in some places seasonally dry tropical montane woody vegetation types (woodlands, bushlands, thickets, shrublands, and other xeromorphic communities). This is especially the case in sections of Africa but also in northern Meso-America (e.g., in Mexico and some parts of Guatemala), where conifers such as the pine tree *Pinus hartwegii* dominate the forest structure and intense droughts and fire appear to be the most frequent disturbance factors.

Biological Diversity and Endemism

TMF species-richness decreases with latitude, with lower per-unit-area values for countries around the tropics of Cancer and Capricorn (e.g., Argentina, Mexico) and highest near the Equator (Costa Rica, Indonesia, Papua New Guinea, Peru). At the same time, TMF species diversity is highest at mid-elevation and decreases towards subalpine elevations (**Figure 4**).

In the neotropics, the northern Andes appear to be a center of speciation, from which originated the radiation of numerous species into the peripheral TMF areas at higher latitudes. Endemism is low at the generic level but high at the species level. Some plant genera such as found in the orchids (e.g., *Epidendrum*) and piperoids (e.g., *Peperomia*) are extraordinarily rich in species. About a decade ago, a new tree family restricted to the neotropical TMF was found

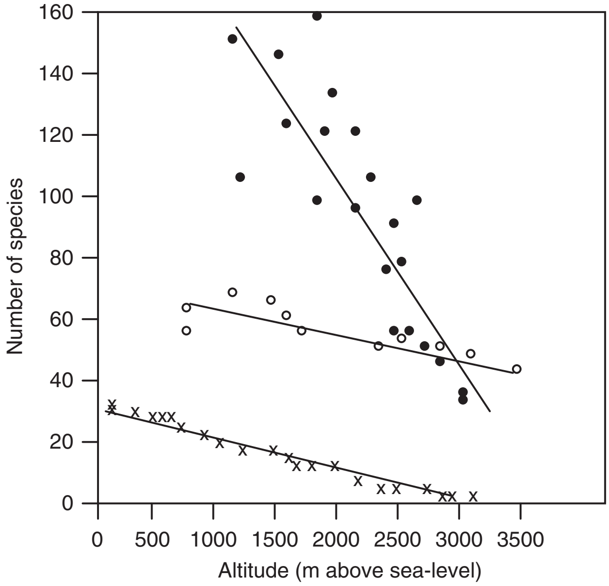


Figure 4 Species-richness in tropical montane forests plotted as a function of altitude, with regression lines. Closed circles represent tree species (diameter at breast height ≥ 2.5 cm) in 0.1 ha plots in Andean forests (data from Gentry AH in Churchill SP, Balslev H, Forero E, and Luteyn JL (eds) (1995) *Biodiversity and Conservation of Neotropical Montane Forests*. New York: New York Botanical Garden); open circles represent numbers of syntopic bird species in Andean Peru, and crosses represent rodents in montane New Guinea (birds and rodents according to Rahbek C in Körner C and Spehn E (eds) (2002) *Mountain Biodiversity: A Global Assessment*. New York: Parthenon).

(Ticodendraceae, Costa Rica). A major reason for these high levels of endemism is the fact that many TMF sites are situated on mountain tops where species populations became isolated from their metapopulations at the end of the ice ages when Pleistocene climatic fluctuations took place. They could therefore evolve into new, locally restricted (endemic) species.

Plant Growth Forms, Species Richness, and Composition

If we take a look at the main plant families and genera making up the average neotropical TMF, we may encounter a large number of broad-leaved canopy trees, subcanopy trees, understory shrubs, a series of ground herbs, some hemiepiphytes, and a few giant native coniferous trees (needle-leaved gymnosperms; **Table 2**).

A very important life form in these forests is the tree fern, which has been considered diagnostic for TMCF. These woody, stemmed, 2–7-m-tall pteridophytes with their enormous leaf rosettes occur in almost all TMCF types around the world. Other conspicuous understory elements include large monocotyledons such as understory bamboos, often-dwarfish palms and colorful heliconias. Bright-green, pteridophytic *Selaginella* species and terrestrial mosses (Polytrichaceae) preferring damp, cool climates may carpet the forest floor. Woody climbers are few, but herbaceous vines may abound.

Vascular epiphytes are extremely diverse and include an almost infinite number of orchids, bromeliads, ferns (including the filmy ferns of the genus *Hymenophyllum*), aroids, ericads, cyclanths, gesneriads, and piperoids. Whereas the number of flowering epiphytes decreases with increasing altitude (lower temperatures), pteridophytic plant groups such as ferns and club mosses (Lycopodiaceae) become more abundant. Epiphytic bryophytes, including mosses (Musci) and liverworts (Hepaticae), are ubiquitous and cover the trunks, branches, and twigs of trees and shrubs. In addition, a diverse set of epiphytic and epilithic yellow, red, brown, green, and white-colored foliose, fruticose, and crustose lichens complete the rich spectrum of TMF life forms.

Animal Diversity

Faunal diversity is also striking. The diversity among birds and amphibians is especially remarkable. Recent research results show that the highest avian biodiversity in South America is found at the transition between Amazon TLF and TMF in the adjacent eastern slopes of the Andes. The Convention on International Trade in Endangered Species (CITES) and The World Conservation Union (IUCN)-listed, endangered spectacled bear (*Tremarctos ornatus*) known from the Andes in South America and the mountain gorilla (*Gorilla gorilla beringei*, with 620 individuals in 2000) inhabiting the Virunga volcanoes on the border of the Democratic Republic of Congo, Uganda, and Rwanda in Africa are probably the best-known 'flagship' mammals still living in TMF, although with populations hunted down, in an ever-decreasing habitat. Other species still to be found in TMF and TMCF include a tapir, large cats (puma, jaguar, ocelot), several deer, marsupials, monkeys, rodents, rabbits, mice, and a fair number of bats, among many others. Studies on TMF arthropods (insects, spiders) have only just begun and species numbers have to be estimated. In most cases, little is known about the distribution, natural history, and population ecology of TMF animal species and further attention from scholars is urgently needed.

Disturbance Regimes

TMF and especially TMCF in the neotropics are often affected by natural disturbance regimes, including factors such as storms and hurricanes. Storm-induced landslides are a common phenomenon on steep slopes in TMF areas and may cause local forest disturbance.

Table 2 Most important vascular plant families and genera observed in neotropical montane forests (data from the author)

Life form	*Family*	*Genus*
Needle-leaved trees	Pinaceae	*Pinus*
	Podocarpaceae	*Podocarpus*, *Prumnopitys*
Broad-leaved trees	Annonaceae	*Guatteria*
	Betulaceae	*Alnus*
	Boraginaceae	*Cordia*
	Brunelliaceae	*Brunellia*
	Caprifoliaceae	*Viburnum*
	Clethraceae	*Clethra*
	Cunoniaceae	*Weinmannia*
	Ericaceae	*Comarostaphylis*, *Vaccinium*
	Escalloniaceae	*Escallonia*
	Euphorbiaceae	*Alchornea*, *Croton*, *Hieronyma*, *Sapium*
	Fabaceae	*Inga*, *Pithecellobium*
	Fagaceae	*Quercus*
	Flacourtiaceae	*Abatia*, *Casearia*, *Xylosma*
	Lauraceae	*Cinnamomum*, *Nectandra*, *Ocotea*, *Persea*
	Loganiaceae	*Buddleia*
	Magnoliaceae	*Magnolia*, *Talauma*
	Meliaceae	*Guarea*, *Trichilia*
	Monimiaceae	*Mollinedia*, *Siparuna*
	Moraceae	*Cecropia*, *Ficus*, *Pourouma*
	Myrtaceae	*Eugenia*, *Myrcia*, *Myrcianthes*
	Sabiaceae	*Meliosma*
	Symplocaceae	*Symplocos*
	Theaceae	*Cleyera*
	Winteraceae	*Drimys*
Trees, shrubs	Actinidiaceae	*Saurauia*
	Aquifoliaceae	*Ilex*
	Celastraceae	*Crossopetalum*, *Maytenus*
	Chloranthaceae	*Hedyosmum*
	Melastomataceae	*Clidemia*, *Miconia*, *Topobea*
	Myrsinaceae	*Ardisia*, *Myrsine*, *Parathesis*
	Rosaceae	*Polylepis*, *Prunus*, *Rubus*
	Rubiaceae	*Elaeagia*, *Faramea*, *Hoffmannia*, *Palicourea, Psychotria*, *Rondeletia*
	Solanaceae	*Acnistus, Cestrum, Solanum*
Trees, hemiepiphytes	Araliaceae	*Dendropanax*, *Oreopanax*, *Schefflera*
	Clusiaceae	*Clusia*, *Tovomita*, *Vismia*
Shrubs, herbs	Asteraceae	*Eupatorium*, *Diplostephium*, *Senecio*
	Hypericaceae	*Hypericum*
	Piperaceae	*Peperomia*, *Piper*
	Urticaceae	*Phenax*, *Pilea*, *Urera*
Herbs	Acanthaceae	*Dicliptera*, *Hansteinia*, *Justicia*
	Campanulaceae	*Burmeistera*, *Centropogon*
	Scrophulariaceae	*Calceolaria*, *Castilleja*, *Hemichaena*
Parasitic shrubs	Loranthaceae s.l.	*Dendrophthora*, *Gaiadendron*, *Phoradendron*, *Struthanthus*
Palms	Arecaceae	*Ceroxylon*, *Chamaedorea*, *Geonoma*
Bamboos	Poaceae	*Aulonemia*, *Chusquea*
Climbers	Asteraceae	*Liabum*, *Mikania*
	Alstroemeriaceae	*Bomarea*
	Dioscoreaceae	*Dioscorea*
	Hydrangeaceae	*Hydrangea*
	Passifloraceae	*Passiflora*
	Vitaceae	*Cissus*

continued

Table 2 Continued

Life form	*Family*	*Genus*
Tree ferns	Cyatheaceae	*Alsophila*, *Cyathea*, *Lophosoria*
	Dicksoniaceae	*Culcita*, *Dicksonia*
Ferns	Adiantaceae	*Adiantum*, *Cheilanthes*, *Eriosorus*
	Aspleniaceae	*Asplenium*
	Blechnaceae	*Blechnum*
	Dryopteridaceae	*Dryopteris*, *Polystichum*
	Elaphoglossaceae	*Elaphoglossum*
	Grammitidaceae	*Ceradenia*, *Grammitis* s.l.
	Hymenophyllaceae	*Hymenophyllum*, *Trichomanes*
	Polypodiaceae	*Campyloneurum*, *Polypodium*
	Pteridaceae	*Pteris*
	Thelypteridaceae	*Thelypteris*
	Vittariaceae	*Vittaria*
Fern-allies	Lycopodiaceae	*Huperzia*, *Lycopodium*
	Selaginellaceae	*Selaginella*
Vascular epiphytes	Araceae	*Anthurium*, *Monstera*, *Philodendron*
	Ericaceae	*Cavendishia*, *Macleania*, *Psammisia*, *Satyria*
	Bromeliaceae	*Pitcairnea*, *Puya*, *Tillandsia*, *Vriesea*
	Cyclanthaceae	*Asplundia*, *Sphaeradenia*
	Gesneriaceae	*Alloplectus*, *Solenophora*
	Orchidaceae	*Cattleya*, *Epidendrum*, *Malaxis*, *Maxillaria*, *Stelis*, *Telipogon*

Studies conducted in the TMF of the Luquillo mountains in Puerto Rico demonstrate the importance of disturbance, both natural and anthropogenic, in controlling both the structure and functioning of these forests. On a smaller scale, the same is true for tree fall gaps caused by the natural death of senescent TMF trees. However, many successional plant species, pioneers as well as late-secondary elements, appear to be well adapted to the sudden occurrence of natural gaps, which they may colonize within a short period of time. A whole gamut of fast-growing pioneer herbs and soft-wooded shrubs may fill a gap within a few weeks or months, particularly in the wet season, although full recovery following a large-scale disturbance may take decades or up to a century or more. A study of TMF recovery taking place after a period of clearing, burning, and years of grazing in Costa Rica resulted in a conservative estimate of 65–85 years as the theoretically minimum time needed for recovery of the terrestrial structure and floristic composition of the forest. An additional 50 years may be necessary for a natural recovery of the full epiphytic biomass and flora present before the disturbance took place (**Figure 5**).

Conservation and Utilization

Forest Conversion and Habitat Loss

TMF has suffered a long history of transformation by human beings. Particularly in the Andes, TMF conversion took place long before the arrival of the Hispanic culture some 500 years ago. Near Bogotá, Colombia, large groups of gatherers and hunters lived in the TMF altitudinal belt some 12 500 years before the present time, while indigenous artifacts in the TMF zone at the flanks of the Llalo volcano in Ecuador date from some 14 000 years before now. Intensive maize agriculture started in the Colombian Andes some 2500–3000 years ago.

The current situation of TMF is alarming, as it has become one of the most threatened tropical ecosystems worldwide. Over the centuries, as mountain roads were constructed, TMF has been cleared to harvest timber, fuelwood, and charcoal, and cut and burned for crop and grazing land. The loss of about half of the Mexican TMF, and especially its mesophyllous TMF, is just one of many striking examples. In Colombia, only 10–20% of the original TMF cover (i.e., as present in pre-Columbian times) remains today. Due to habitat fragmentation, endemic bird and frog species concentrated in TMF may become threatened with extinction. In Central American TMF the dwindling resplendent quetzal (*Pharomachrus mocinno*) has become the flagship bird species in conserving remnant TMF fragments. The golden toad (*Bufo periglenes*) – now believed to be extinct due to climate change (e.g., loss of cloud cover) and habitat loss – has become the symbol of the destructive human impact on TMCF worldwide. Moreover, invasive alien species have become an

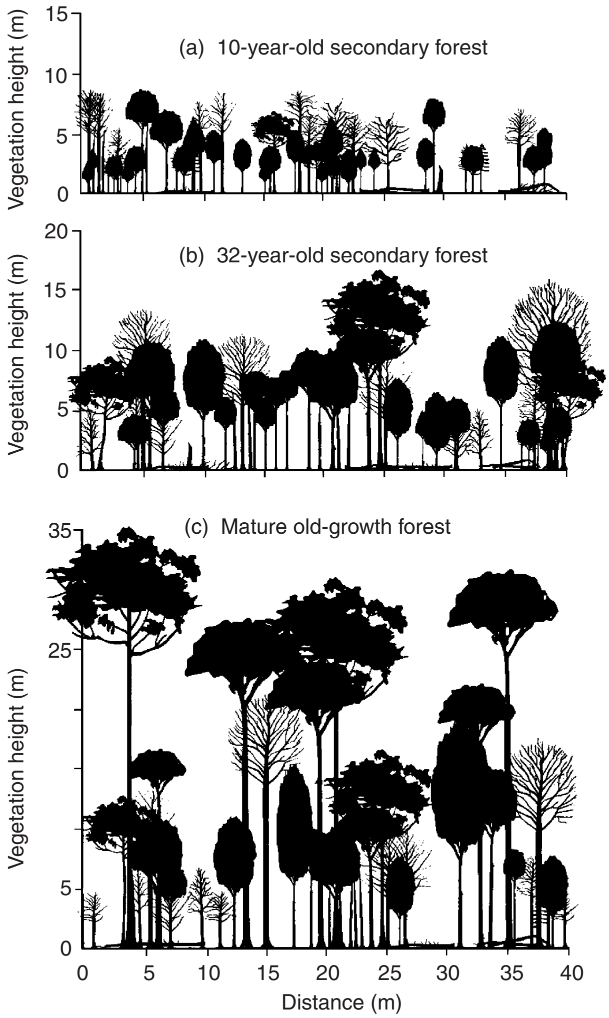


Figure 5 Schematic lateral profiles of three successional stages of tropical montane oak-bamboo forest at 2700–2900 m elevation in Costa Rica (Talamanca mountains). (a) 10-year-old secondary forest (following clearing, grazing, and abandonment); (b) 32-year-old secondary forest (following clearing, grazing, and abandonment); (c) over-250-year-old mature forest (data from the author).

increasing threat to native and often endemic plant and animal species (e.g., the African kikuyu grass which was introduced in tropical montane America).

Sustainable Forest Management

It appears to be extremely difficult to manage TMF in a sustainable way, due to the unfavorable conditions in climate (high rainfall), topography (steep slopes in rugged, highly dissected terrain) and soils (fragile, susceptible to erosion). Moreover, TMF has an important hydrological function, especially in the upper watersheds where water resources are accumulated which serve as drinking and irrigation water for human communities and as generators of hydroelectricity for households. Once mountain roads are constructed and the TMF has been removed, these hydrological services vital to people living down-slope are almost irrevocably lost. Soil erosion and landslides take place and may lead to the ultimate rise of badlands, which cannot be used by humans. Down-slope, runoff of sediment-loaded water (e.g., mud flows) may cause uncontrolled flooding, affecting mid-elevation and lowland villages. Many slopes in areas formerly covered by TMF have been converted into badlands and are now one of the best examples worldwide of how we have mismanaged nature and its natural resources.

Therefore, it is of utmost importance to develop sustainable ways of TMF use. Currently, numerous projects directed at sustainable forest management are underway worldwide. A successful example in TMF areas is the growth and use of secondary forests on previously grazed but now abandoned pasturelands where once old-growth, mature TMF grew. These naturally regenerated, restored forests are subsequently used in a selective way by coppicing and controlled fuelwood extraction, as elements of agroforestry systems or as bird-watching sites to be visited by ecotourists.

Valuation of Traditional and Potential Uses of Biodiversity

On all tropical continents (America, Africa, Asia, and Oceania), TMF products and services have extensively been used for many centuries and probably millenniums, to maintain local human populations. Traditionally, but also in modern times, rural communities have gathered numerous timber and nontimber forest products from TMF, including food, fodder, fiber, fuel, medicine, dyes, gums, oils, antioxidants, spices, poisons, ornamental plants and pets. Examples are found among populations in Central America, the Andes, the African Eastern Arc, the Himalayas, Western Ghats, Indonesia and Papua New Guinea.

An ethnobotanical survey of traditional knowledge in a Costa Rican TMF revealed the use of almost 25% of all 590 species of plants by a local farming community for medicinal, food, ornamental, and construction purposes or as sources of combustibles, dye, fodder, gum, oil, and poison. Indeed, among the planet's TMF species are many wild relatives of some of the world's major food plants (e.g., wild potato and tomato plants in the Andes, avocado trees in Central America, and coffee shrubs in Africa). The preservation of their genetic resources in protected areas is essential to society.

TMF harbors species of plants, animals, and microorganisms, many of which are endemic and/or threatened, and many of which are not yet known to science. They may have a potential in future medicine and may only be revealed after being discovered and screened by biodiversity prospecting and biochemical analysis. These species only flourish if they can maintain minimum viable populations in minimum-sized habitats where ecological integrity is guaranteed. Therefore, it is of utmost importance to conserve and, where necessary, restore their habitat in today's fragmented TMF landscape mosaic.

Conservation and Sustainable Development

At present, only about one-third (23 million ha) of the neotropical TMCF area has some kind of protected status. If we are to preserve a large part of TMF's variety of life as expressed in its genes, species, and ecosystem types in the long term, we will need to elaborate a conservation strategy in which not only networks of protected core areas, buffer zones, and corridors form a fundamental component, but also participatory planning strategies in which different local and regional stakeholder groups and decision-makers are involved, in order to establish a broad-based, consensus-oriented conservation framework. This is particularly vital as a prerequisite for long-term conservation and sustainable use, for it is the recognition of the overall set of environmental goods and services offered by TMF to the local and regional peoples – and thus strategies including compensation payments to forest-owners for these goods and services – which will make its conservation economically necessary, sociopolitically feasible, and ecologically successful.

See also: **Biodiversity**: Biodiversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation. **Harvesting**: Forest Operations under Mountainous Conditions. **Health and Protection**: Diagnosis, Monitoring and Evaluation. **Hydrology**: Hydrological Cycle; Impacts of Forest Management on Water Quality; Soil Erosion Control. **Landscape and Planning**: Landscape Ecology, the Concepts. **Medicinal, Food and Aromatic Plants**: Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Resource Assessment**: Forest Change. **Silviculture**: Natural Regeneration of Tropical Rain Forests; Treatments in Tropical Silviculture. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation; Overview. **Tree Physiology**: Forests, Tree Physiology and Climate. **Tropical Forests**: Tropical Moist Forests.

Further Reading

Blyth S, Groombridge B, Lysenko I, Miles L, and Newton A (2002) *Mountain Watch: Environmental Change and Sustainable Development in Mountains*. Cambridge, UK: UNEP-WCMC.

Bruijnzeel LA and Hamilton LS (2000) *Decision Time for Cloud Forests*. IHP humid tropics programme series no. 13. Paris: WWF, IUCN and UNESCO.

Churchill SP, Balslev H, Forero E, and Luteyn JL (eds) (1995) *Biodiversity and Conservation of Neotropical Montane Forests*. New York: New York Botanical Garden.

Convention on Biological Diversity (CBD) (2002) *Mountain Biological Diversity: (1) Status and Trends of, and Threats to, Mountain Biological Diversity; (2) Measures taken for the Conservation and Sustainable Use of Mountain Biological Diversity.* Reports UNEP/CBD/SBSTTA/8/5-6. Montreal, Canada: Secretariat of the Convention on Biological Diversity.

Grubb PJ (1971) Interpretation of the 'Massenerhebung' effect on tropical mountains. *Nature* 229: 44–45.

Hamilton LS, Juvik JO, and Scatena FN (eds) (1995) *Tropical Montane Cloud Forests*. Ecological studies no. 110. New York: Springer-Verlag.

Hurni H, Wachs T, Ives J, *et al.* (eds) (1980–2003) *Mountain Research and Development*. United Nations University (UNU) and International Mountain Society (IMS). Berne, Switzerland: University of Berne.

Kappelle M, Brown AD (eds) (2001) *Bosques Nublados del Neotrópico*. (Cloud Forest of the Neotropics.) Santo Domingo de Heredia, Costa Rica: World Conservation Union (IUCN) and Instituto Nacional de Biodiversidad (INBio).

Körner C and Spehn E (eds) (2002) *Mountain Biodiversity: A Global Assessment*. New York: Parthenon.

Messerli B and Ives JD (eds) (1997) *Mountains of the World: A Global Priority.* New York: Parthenon. [Spanish version: Sarmiento F (ed.) (2002) *Montañas del Mundo: Una Prioridad Global con Perpsectivas Latinoamericanas*. Quito: Ediciones Abya-Yala.]

Myers N, Mittermeier R, Mittermeier CG, daFonseca GAB, and Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Nadkarni NM and Wheelwright NT (eds) (2000) *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. Oxford, UK: Oxford University Press.

Pounds JA, Fogden MPL, and Campbell JH (1999) Biological response to climate change on a tropical mountain. *Nature* 398: 611–614.

Price MF and Butt N (eds) (2000) *Forests in Sustainable Mountain Development: A State-of-Knowledge Report for 2000*. IUFRO research series no. 5. Wallingford, UK: CAB International.

Stadtmüller T (1987) *Cloud Forests in the Humid Tropics*. Turrialba, Costa Rica: United Nations University (UNU) and Centro Agronómico Tropical de Investigación y Enseñanza (CATIE). [Spanish version: Stadtmüller T (1987) *Los Bosques Nublados en el Trópico Húmedo*. Costa Rica: Turrialba. United Nations University (UNU) and Centro Agronómico Tropical de Investigación y Enseñanza (CATIE).]

Vitousek PM (ed.) (1998) The structure and functioning of montane tropical forests: control by climate, soils and disturbance. Special issue. *Ecology* 79(1): 1–72.

Whitmore TC (1984) *Tropical Rain Forests of the Far East*. Oxford, UK: Clarendon Press.

Woody Legumes (excluding Acacias)

S Harris, University of Oxford, Oxford, UK

Introduction

The Fabaceae (or Leguminosae) is the second largest family of flowering plants. Furthermore, no family, except perhaps the Poaceae, has a wider geographical distribution in a broader range of habitats. Legumes are distributed throughout every continent, except Antarctica, and in almost every habitat from the freshwater lakes of Amazonia, through the tropical and subtropical forests of the New and Old Worlds to the deserts of Central Asia and the arctic-alpine vegetation of the temperate region. The reason for the ecological success of the family has been suggested as the ability to form root nodules with nitrogen-fixing bacteria, although not all Fabaceae fix nitrogen. Together with their ecological diversity, the Fabaceae have habits that range from annual herbs through lianas to shrubs and very tall trees (at approximately 88 m, the tallest tropical angiosperm is the Southeast Asian tree *Koompassia excelsa*). In tropical and subtropical regions, legumes are primarily woody, whilst in temperate regions they are herbaceous. It is the herbaceous legumes that have the most obvious economic value to humans (particularly the genera *Phaseolus* and *Glycine*). However, the economic value of woody legumes is also immense, particularly in the tropics, and ranges from timber, fuelwood, and forage production to sources of resins, toxins, and dyes. The present article, which focuses on the woody legumes (excluding the genus *Acacia*), will provide an overview of Fabaceae systematics together with information on their ecological and reproductive diversity. Finally, the utility of woody legumes is reviewed.

Systematics

The Fabaceae comprises approximately 640 genera and 18 000 species, which have traditionally been divided into three morphologically distinct subfamilies (Mimosoideae, Caesalpinioideae, Papilionoideae) (**Table 1**), although some classification systems have also recognized these subfamilies as families. Molecular and morphological data strongly support the monophyly of the Fabaceae, although the monophyly of only two (Mimosoideae, Papilionoideae) of the three subfamilies is supported. Subfamily Caesalpinioideae is paraphyletic, with some genera more closely related to the Mimosoideae and some to the Papilionoideae than they are to each other. The three subfamilies have disproportionate distributions of species with the tree habit; more than 80% of subfamilies Caesalpinioideae and Mimosoideae are trees, whilst less than 40% of the Papilionoideae are trees. Furthermore, the Caesalpinioideae and Mimosoideae are primarily tropical whilst the Papilionoideae are primarily temperate.

Each subfamily is divided into tribes (**Table 2**); the Papilionoideae contains the largest number of tribes, of which fewer than half contain tree species. Molecular data indicate that temperate herbaceous lineages are more recently derived from woody tropical lineages, although it is unclear how many origins of the herbaceous habit have occurred. Furthermore, within the Papilionoideae, *Swartzia* and the tribe Sophoreae appear to be basal groups.

The Fabaceae contains some of the largest and most diverse genera in the plant kingdom, e.g., *Acacia*, *Astragalus*, and *Mimosa*. Furthermore, these genera may contain high numbers of endemic species, for example, *Mimosa* in central Brazil.

Table 1 Characteristics of the three subfamilies in the Leguminosae

	Mimosoideae	*Caesalpinioideae*	*Papilionoideae*
Genera/species (approximate)	64/2950	153/2175	425/12 150
Habit	Trees or shrubs, some herbs	Trees or shrubs, some herbs	Herbs or shrubs, some trees
Leaves	Usually bipinnate	Usually pinnate or bipinnate	Pinnate to trifoliate, occasionally unifoliate
Corolla	Actinomorphic. Petals just touching. Not showy	Usually zygomorphic. Petals overlapping, upper petal usually innermost. Usually showy	Mostly zygomorphic. Petals overlapping, upper petal outermost. Showy
Stamens	Ten to many. Showy	One to 10. Usually not showy	Ten. Not showy
Pollen	Monads, tetrads, polyads	Monads	Monads
Pleurogram	Present	Usually lacking	Lacking
Root nodule occurrence	60–70%	25–30%	>95%

Table 2 Distribution of woody taxa among the Fabaceae tribes; only those tribes containing trees are shown

Tribe	*Habit*	*Distribution*	*Example genera*
Caesalpinioideae (four tribes total)			
Caesalpinieae	Trees or shrubs, rarely herbs	Primarily tropical	*Erythrophleum* *Caesalpinia* *Parkinsonia*
Cassieae	Trees or shrubs, rarely herbs	Tropical and subtropical	*Ceratonia* *Dialium* *Senna*
Cercideae	Trees or shrubs	Mainly tropical, one genus north temperate	*Cercis* *Bauhinia*
Detarieae	Trees; some suffrutices	Tropical	*Cynometra* *Afzelia* *Brachystegia*
Mimosoideae (five tribes total)			
Parkieae	Trees	Tropical	*Parkia* *Pentaclethra*
Mimoseae	Trees or shrubs, rarely herbs	Tropical and subtropical, rarely temperate, most numerous in tropical South America and Africa	*Mimosa* *Prosopis* *Entada*
Acacieae	Trees or shrubs, rarely herbs	Mainly tropical and subtropical	*Acacia* *Faidherbia*
Ingeae	Trees or shrubs	Mainly tropical	*Inga* *Calliandra* *Albizia*
Papilionoideae (31 tribes total)			
Swartzieae	Trees, rarely shrubs	Tropics	*Swartzia* *Mildbraediodendron*
Sophoreae	Trees or shrubs, rarely herbs	Tropics	*Sophora* *Myroxylon* *Ateleia*
Dipteryxeae	Trees	Neotropics, mainly Amazonia	*Dipteryx* *Pterodon*
Dalbergieae	Trees or shrubs	Tropics, mainly tropical America	*Dalbergia* *Macherium* *Pterocarpus*
Millettieae	Trees or shrubs	Mainly tropical	*Derris* *Lonchocarpus* *Millettia*
Robinieae	Trees, shrubs or herbs	Temperate and tropical New World, *Sesbania* pantropical	*Sesbania* *Gliricidia* *Robinia*
Psoraleeae	Small trees or shrubs, rarely herbs	Widespread, rarely tropical	*Psoralea*
Amorpheae	Small trees, shrubs or herbs	New World	*Amorpha* *Dalea*
Carmichaelieae	Small trees or shrubs	New Zealand	*Carmichaelia*
Brongniartieae	Trees or shrubs	New World	*Brongniartia*
Podalyrieae	Small trees or shrubs	South Africa	*Podalyria*
Genisteae	Small trees, shrubs, or herbs	Worldwide	*Genista* *Ulex*

Ecology

The morphological diversity of legumes reflects ecological diversity, where species occupy habitats as diverse as the deserts of Central Asia, estuarine tropical forest to temperate and alpine forests. However, it is in the tropical habitats that the greatest diversity of tree legumes is found. Legumes are important ecosystem components wherever they are found, although some habitats are dominated by tree legumes, for example, the miombo woodlands of southern Africa. In other cases, legumes may be infrequent; for example, despite the value of the timber, large-scale commercial exploitation of *Ormosia* species in Southeast Asia is limited because the low density of individuals makes selective harvesting uneconomic.

In addition to their dominant role in some natural habitats, woody legumes may also be important components of pioneer and secondary forest vegetation, for example, *Mimosa* species in the neotropics. Furthermore, changes in human activities (e.g., pasture management) may cause considerable changes in legume domination. Another major effect of humans on the distribution of woody legumes has been the intercontinental movements of species, for example, neotropical species being moved to Africa and Asia. The consequences of such movements have been unpredictable; some species can be highly productive in part of the introduced range whilst destructive in other parts of the range, for example the high value of *Leucaena leucocephala* as a fodder in Australia but its major role as a weed in Hawaii.

Legumes generally form symbiotic relationships with the bacterial genus *Rhizobium*, producing root nodules and fixing atmospheric nitrogen, although this is not always the case, particularly in the Caesalpinioideae (**Table 1**). In addition to root nodules, legumes may also have mycorrhizae.

Reproductive Biology

In legumes, the pollination unit is either the inflorescence or the flower, and pollen is usually released as monads (single cells), although in the Mimosoideae pollen is also often released as tetrads or polyads (groups of pollen grains). Mechanisms to promote outcrossing in legumes include: (1) protogyny, where the stigma is receptive to pollen before pollen in the same flower is released; (2) andromonoecy, where male and hermaphrodite flowers occur on the same plant; and (3) self-incompatibility, where successful fertilization is determined by the genotype of the pollen. Rarely are legumes dioecious (e.g., *Ateleia*). The structure of the legume inflorescence suggests that the majority of species are pollinated by insects, including Coleoptera, Diptera, Hymenoptera, and Lepidoptera, although others are pollinated by mammals (e.g., *Parkia*) and nectarivorous birds (e.g., *Erythrina*). However, some legumes (e.g., *Ateleia herbert-smithii*) are wind-pollinated. In addition to sexual reproduction, vegetative reproduction may also be important in both natural (e.g, *Albizia*) and artificial (e.g., *Gliricidia sepium*) ecosystems.

Seed dispersal in legumes is usually by gravity or mechanical means. Many genera have elastically dehiscent fruits, whilst others may be dispersed by water (e.g., *Entada*) and wind (e.g., *Centrolobium*, *Pterocarpus*). However, mammals (e.g., for *Inga*, *Tamarindus*) and birds (e.g., for *Pithecellobium*) may play an important role in seed dispersal. Humans are an important means of long-distance dispersal of legume seed, whether it is seed for establishing plantations (e.g., *Calliandra*), cultivation of ornamentals (e.g., *Delonix regia*), movement of multipurpose species (e.g., *Gliricidia sepium*), or transport by their livestock (e.g., *Mucuna*).

Many legume seeds have hard seed coats (particularly Caesalpinioideae and Mimosoideae) and need to be scarified before they will germinate. Scarification may occur naturally by passage through animal guts, although for plantation establishment it is necessary to use other treatments (e.g., damaging the seed testa or treatment with boiling water). Many legume seeds may be lost through predation of the developing ovules by beetle larvae (Bruchidae) at the early stages of fruit development.

Utilization

Timber

The morphological and ecological diversity of legumes are reflected in their wood properties, ranging from hard, durable woods (e.g., *Xylia*) to soft, perishable woods (e.g., *Erythrina*). Potentially, therefore, legume woods are suitable for all purposes, from building (e.g., *Koompassia*) to boat construction (e.g., *Copaifera*, *Pterocarpus*) and carving (e.g., *Dalbergia*). For example, legumes provide some of the most highly prized woods for the manufacture of fine furniture, marquetry, and veneers, including the rosewoods (*Dalbergia*) of South America and Southeast Asia, Jichimu (*Ormosia*) of China, and *Afzelia* of Africa and Southeast Asia. Trade in some species has threatened natural populations (e.g., *Pericopsis mooniana* in Southeast Asia and *Dalbergia latifolia* in India), whilst the properties of some genera have influenced how they are extracted from forests. For example, the wood of *Cynometra* species is so dense that trunks sink in water and hence they must be moved over land rather than floated down rivers.

Tannins and Resins

The pods of *Caesalpinia* species (e.g., *C. brevifolia*, *C. coriaria*, *C. spinosa*) and the bark of *Robinia pseudoacacia* are important sources of vegetable tannin (used in leather and adhesive manufacture). Species of *Hymenaea* and *Copaifera* are important sources of resin for the manufacture of high-quality varnishes, particularly as copals.

Human Food and Ornamentation

Tree legumes are minor sources of human foods, particularly in their native areas; for example, the immature pods of *Leucaena* species are used as a vegetable in Mexico and *Prosopis juliflora* pods are used for the manufacture of flour, syrup, and coffee substitutes (**Figure 1**). Some species (e.g., the pulp of *Tamarindus indica* fruits) have both local and international markets. The fruits of *Ceratonia siliqua* are an important source of edible gum (locust gum) and are used as a cocoa substitute. Tree legumes can also be important sources of nectar for honey production (e.g., *Robinia*, *Calliandra*) or habitats for bees (e.g., *Koompassia*). Brightly colored legume seeds (e.g., *Erythrina*, *Ormosia*, *Adenanthera*) are often used in ethnic jewelry whilst *Dipteryx* seeds are a source of perfume.

Fodder

Legume trees are important food components of animal diets in natural populations, whilst there are significant economic uses of the foliage and green pods as livestock fodder of many genera (e.g., *Calliandra*, *Gliricidia*, *Leucaena*, *Prosopis*, *Ulex*). In the case of *Leucaena*, a nonprotein amino acid called mimosine is found which at high concentrations may result in reduction in weight gain, hair loss, and abortion in nonruminant animals. Furthermore, fodder species may also have additional uses, e.g., fuelwood and charcoal. Legumes may also be important shade trees in some agroforestry systems, e.g., *Inga* species as shade trees for coffee production in South America.

Ornamentals, Dyes, Poisons, and Medicines

Legume species are planted throughout the tropics as street trees, e.g., *Delonix regia* and *Albizia lebbeck*, whilst others (e.g., *Laburnum*, *Robinia*, *Wisteria*) are important temperate ornamentals. Indigo (*Indigofera tinctoria*; Asia) and logwood (*Hymantoxylum campechianum*; Mexico) provide two of the most important plant-derived dyes, whilst historically other important dyes have been isolated from the genera *Caesalpinia* and *Genista*. *Derris elliptica* and *Lonchocarpus* species are used as fish poisons in South America but have recently attracted attention as environmentally friendly insecticides. Numerous traditional products are derived from legume trees. For example, *Erythrophleum suaveolens* bark is used as an ordeal poison throughout Africa. The seeds of *Sophora secundiflora* (mescal bean) are used by native North Americans to induce hallucinations, although the psychoactive alkaloid (cytisine) is very toxic. Many legume genera (e.g., *Cassia*) yield both locally and internationally important medicines.

Weediness

Many woody legumes have become serious weeds, particularly in the tropics. Genera introduced for forestry purposes may have unforeseen weedy

Figure 1 Examples of inflorescences from the three legume subfamilies. (A) *Leucaena greggii*, a mimosoid legume; (B) *Bauhinia* sp., a caesalpinoid legume; (C) *Pterodon pubescens*, a papilionoid legume.

consequences, e.g., *Leucaena leucocephala*, *Parkinsonia aculeata*, *Prosopis juliflora* and *Robinia pseudoacacia*, whilst changes in management practice may make previously valuable species potential weedy species, e.g., *Ulex europaeus* in Scotland. The weediness of woody legumes means that their use in agroforestry and amenity situations must be considered very carefully.

See also: **Biodiversity**: Biodiversity in Forests. **Ecology**: Reproductive Ecology of Forest Trees. **Genetics and Genetic Resources**: Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics. **Landscape and Planning**: Landscape Ecology, Use and Application in Forestry. **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest; Forest Biodiversity Prospecting; Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Tree Breeding, Practices**: Tropical Hardwoods Breeding and Genetic Resources. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Dry Forests; Tropical Moist Forests.

Further Reading

Allen ON and Allen EK (1981) *The Leguminosae: A Source Book of Characteristics, Uses and Nodulation*. London: Macmillan.

Bruneau A, Forest F, Herendeen PS, Klitgaard BB, and Lewis GP (2001) Phylogenetic relationships in the Caesalpinioideae (Leguminosae) as inferred from chloroplast *trn*L intron sequences. *Systematic Botany* 26: 487–514.

Crisp MD and Doyle JJ (1995) *Phylogeny*. Kew, UK: Royal Botanic Gardens.

Duke JA (1981) *Handbook of Legumes of World Economic Importance*. New York: Plenum Press.

Herendeen PS and Bruneau A (2000) *Advances in Legume Systematics*, part 9. Kew, UK: Royal Botanic Gardens.

Hughes CE (1994) Risks of species introductions in tropical forestry. *Commonwealth Forestry Review* 73: 243–252.

Hughes CE (1998) *Leucaena: A Genetic Resources Handbook*. Oxford, UK: Oxford Forestry Institute.

National Research Council (1979) *Tropical Legumes: Resources for the Future*. Washington, DC: National Academy of Sciences.

Pasiecznik NM (2001) *The Prosopis juliflora–Prosopis pallida Complex: A Monograph*. Coventry, UK: Henry Doubleday Research Association.

Pickersgill B and Lock JM (1996) *Legumes of Economic Importance*. Kew, UK: Royal Botanic Gardens.

Polhill RM and Raven PH (1981) *Advances in Legume Systematics*, part 1. Kew, UK: Royal Botanic Gardens.

Stirton CH and Zarucchi JL (1989) *Advances in Legume Biology*. St Louis, MI: Missouri Botanical Garden.

U

URBAN FORESTRY *see* LANDSCAPE AND PLANNING: Urban Forestry.

W

WINDBREAKS AND SHELTERBELTS

B Gardiner, Forest Research, Roslin, UK

Historical Background

The use of trees for personal shelter or for the shelter of livestock is as old as the history of humanity although this has tended to be opportunistic. Planting for shade around habitation or along roads has a long and established history, but only recently have there been systematic efforts to improve climatic conditions through tree planting. Over the last 200 years there has been a much more systematic approach to the use of trees to shelter agricultural crops and human habitation as part of the European agricultural reforms of the eighteenth, nineteenth, and twentieth centuries, particularly in Germany. Part of the motivation has been the expansion of agriculture onto land previously not used for crop production. This has included the prairies of North America, the steppes of Russia and the Ukraine, and the heathlands of Denmark. More recently shelterbelts have been planted extensively in parts of China, Japan, New Zealand, and Australia. In addition, shelter from trees and the way they modify microclimate is a critical component of agroforestry systems and is of particular importance in the drier tropics and subtropics.

Shelter Basics

The principal aim of planting trees for shelter is to modify the local microclimate. Trees can provide shelter from the wind, precipitation, blowing snow, and the sun. They are also effective at capturing dust and pollution (see Further Reading section for recent reviews of current knowledge).

Wind is the flow of air in response to atmospheric pressure differences, and modifying this flow is the principal way in which shelterbelts are used to affect microclimatic conditions. Modifying the airflow not only affects wind speed but also turbulence intensity, temperature, humidity, and soil erosion. At the same time the shelterbelts may affect the amount of sunlight falling on adjoining fields and heat loss due to radiation.

Shelterbelts and windbreaks present a porous obstacle to the approaching airflow, creating an increase in pressure ahead of the belt and a decrease behind (**Figure 1**). The high pressure slows the

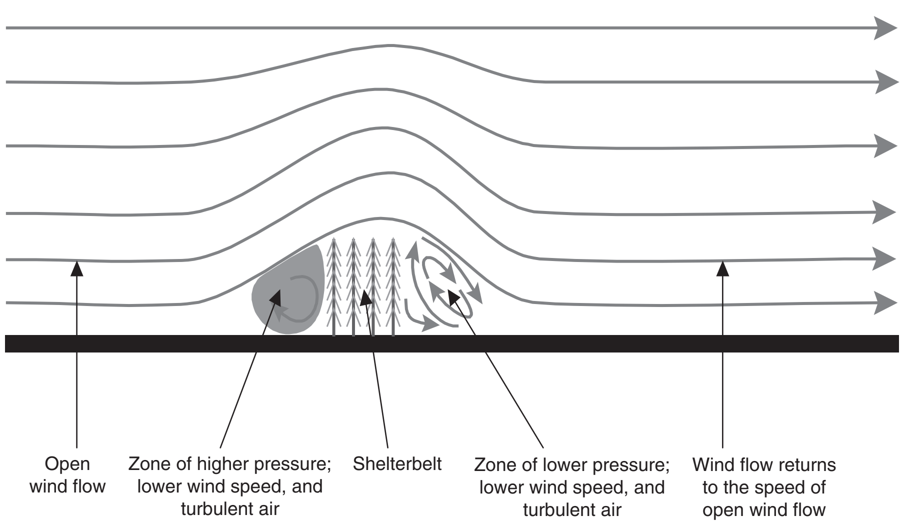


Figure 1 Flow pattern over shelterbelt or windbreak. Crown Copyright 2004.

approaching flow down and forces it to be deflected upward in a region referred to as the displacement zone (**Figure 2**). Above the top of the shelterbelt the wind is accelerated and the increased wind shear leads to an increased production of turbulence. Some of the approaching flow filters through the shelterbelt with a reduced velocity due to the drag provided by the trunks, branches, and foliage. If the shelterbelt is extremely dense then almost no air penetrates through the wood and a stagnant slow circulating eddy is formed behind the shelterbelt. The more open the shelterbelt is, the weaker this feature becomes until it disappears completely and the wake zone begins immediately behind the shelterbelt. The wake zone is the region in which fast-moving air displaced above the shelterbelt begins to mix with the slower-moving air that has filtered through the shelterbelt. Downstream of the shelterbelt, within the wake zone, the wind speed gradually increases until it is the same as the wind speed upwind. The wake zone is the main area where there are microclimatic benefits of shelter.

Microclimatic Benefits

A summary of the main microclimatic changes associated with shelterbelts is given in **Table 1**.

The wind speed is reduced ahead of and behind the shelter. However, turbulence levels may be increased in the cavity zone, which can lead to increased lodging and abrasion damage to crops. Within the shelterbelt itself the wind speed of the flow through the trees is generally reduced. However, if the wood has a very open understory squeezing of the flow between the canopy and the ground may increase the wind speed under the canopy.

The daytime temperature and relative humidity are generally increased in the cavity and wake zones. However, close to and within the shelterbelt there may be shading from the sun, which will reduce the temperature. This may be a disadvantage if solar heating is important, but if crop scorching or sunburn to animals is a consideration it may be of benefit. Within the shelterbelt the night-time temperatures will be raised because the canopy reduces radiation transfer to the atmosphere. However, the night-time temperature may be reduced in the cavity zone if the belt is very dense because it will restrict mixing of cold air near the ground with warmer air above.

Within the wake zone the reduced wind speed and turbulence leads to a reduction in the movement of gases to and from the ground. This means that moisture levels are higher and there is reduced water

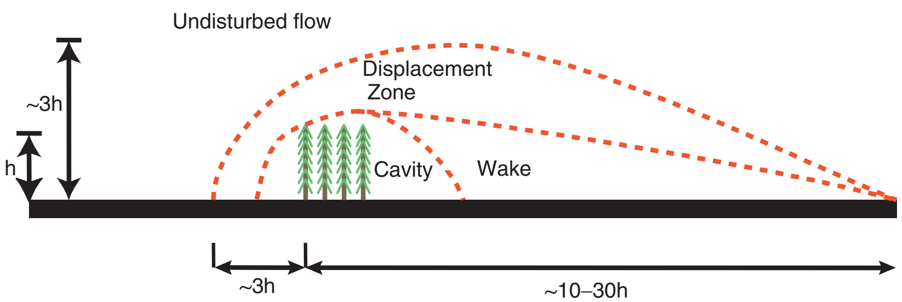


Figure 2 Description of flow zones in vicinity of shelterbelt or windbreak. Crown Copyright 2004.

Table 1 Changes in microclimatic conditions in different areas adjacent to a shelterbelt. Crown Copyright 2004

Area	*Increased*	*Reduced*
Displacement zone	Windspeed above shelterbelt Turbulence	Windspeed at ground level Sunlight close to shelterbelt
Inside shelterbelt	Windspeed (only for very open shelterbelt) Nightime temperature	Windspeed Daytime temperature Sunlight
Cavity zone	Turbulence Daytime temperature Humidity Lodging and abrasion Waterlogging on wet soils	Wind speed Night-time temperature Sunlight close to shelterbelt
Wake zone	Daytime temperature Humidity Carbon dioxide	Windspeed Turbulence Erosion Water loss

loss from the soil. Close to the shelterbelt, within the cavity zone, this may lead to waterlogging if the soil is particularly wet or to increased plant growth if the soil is prone to drought. The reduced wind speeds also lead to reduced soil erosion.

Factors Controlling Shelterbelt Performance

Height

The height of the shelterbelt, together with its porosity, is the most important factor controlling performance of a shelterbelt. The area ahead of and behind the shelterbelt over which it is effective is a direct function of shelterbelt height. The higher the shelterbelt the larger is the area of shelter.

Porosity

In simple terms, porosity is a measure of how open the shelterbelt is and how easily the air can flow through it. The porosity of the shelterbelt directly influences the intensity and area of shelter produced by the shelterbelt. Porosity is affected by planting density, canopy distribution, species mix, shelterbelt width, and time of year.

A dense shelterbelt will result either from closely spaced trees and shrubs or a large width of woodland or a combination of both factors. Shelterbelts tend to have lower porosities when they are young. With time the porosity tends to increase as the trees grow and mortality occurs. In addition, a shelterbelt of deciduous trees may have a low porosity in summer but a much higher porosity in winter.

In a dense shelterbelt the majority of air is forced over the trees by the high pressure ahead of the shelterbelt. So little air passes through the shelterbelt itself that the flow separates and a cavity zone and a large drop in pressure is created behind the wood. This low pressure causes the high-speed wind above the shelterbelt to return quickly to the surface giving a short region of shelter but with very reduced wind speeds.

A medium-density shelterbelt allows much more air to flow through the belt. This reduces the chance of flow separation behind the wood so that the cavity zone may not exist and the wake zone begins immediately. The pressure changes across the shelterbelt are also less severe than with the dense belt and, therefore, the return of the faster-moving air towards the ground is more gradual. The result is the maximum area of shelter that any shelterbelt can provide but the intensity of the microclimatic changes are less dramatic.

An open shelterbelt has a limited area of shelter and the reduction in wind speed downwind may be minimal. If the lower part of the shelterbelt canopy is completely open it is possible actually to increase the wind speeds within and just downwind of the wood compared to the open field values.

Width

Width is generally not of such direct importance as height except in the way it affects porosity. A two-row shelterbelt is as effective as a six-row belt provided they both have the same porosity and it also uses less land. In extremely windy climates the leading rows of trees may be stunted in their growth and, therefore, a wider shelterbelt will be necessary to obtain the required height.

Very wide shelterbelts (width $>2\times$ height) do not provide more shelter than a narrow belt because they behave very similarly to a dense shelterbelt and wind speeds recover very quickly in their lee. Furthermore, the turbulence intensity over wide shelterbelts is greater and can lead to problems of lodging and plant abrasion.

However, an advantage of wider shelterbelts is that it is much easier to replace them when they get old and trees begin to die while at the same time retaining some shelter. With a narrow shelterbelt there will inevitably be a period of little shelter when the belt is replaced.

Length

To be effective, the shelterbelt must be longer than the length of the area requiring shelter. This is due to the triangular shape of the sheltered zone behind the shelterbelt. The air speeds up around the edge of the shelterbelt resulting in higher wind speeds and turbulence levels at the ends of shelterbelts. Behind the shelterbelt this high-speed turbulent air begins to encroach into the sheltered wake zone in an identical manner to the air that was displaced over the shelterbelt.

Orientation

The orientation of the shelterbelt to the wind affects the area provided with shelter. The greatest area of protection is provided when the wind strikes the shelter at right angles but this is reduced when the wind strikes at a smaller angle. Therefore, the shelterbelt is ideally located when it is perpendicular to the wind direction of particular concern (the long axis of the shelterbelt should be at right angles to the wind). However, it is possible to construct shelterbelts that provide protection from more than one direction.

Another effect of orientation is on porosity. A narrow shelterbelt is most porous to the wind when the wind strikes it at right angles. As the angle is reduced the porosity decreases because the effective width of the shelterbelt is increased. The effect is more marked with wide shelterbelts.

Openings

Any opening in a shelterbelt has the same effect as the ends of the shelterbelt by increasing the wind speed and turbulence through the gap. The wind speeds within the opening may be significantly higher than the upwind values. If an opening is required for access then it should be angled through the shelterbelt or a 'dog-leg' included.

Profile

The ideal profile for a shelterbelt is generally straight-sided. This provides the maximum shelter for the minimum use of ground. A profiled edge will tend to deflect more air over the shelterbelt and allow less to flow through the trees. The result is to produce a sheltered area very similar to that achieved with a dense shelterbelt.

Types of Shelter

Clearly the benefits of shelterbelts have to be balanced against the disadvantages. To ensure benefits are maximized careful shelterbelt design is required. Poor design can lead to a potential benefit becoming a disadvantage. In **Table 2** a summary of the type of shelterbelts to use for different purposes is presented. In general, semipermeable shelterbelts (porosity 40–60%) are used where a large area of moderate shelter is required. Typical enterprises are

Table 2 Shelterbelt types, their impact on windspeeds and their application. Crown Copyright 2004

Shelterbelt type	*Features (porosity/height/length)*	*Porosity profile*	*Area of windspeed reduction*	*Reduction of open windspeed*	*General application*
Windbreak	Semipermeable As tall as possible As long as necessary	60–40%	20–30 times height of the wood	20–70%	Crops Improved pasture
Windshield	Close to impermeable As tall as necessary As long as necessary	$<40\%$	Up to 10 times height of the wood (maximum shelter at 3–5 times the height)	Up to 90%	Lambing/calving areas Feeding areas Farm buildings
Hybrid	Impermeable understory; canopy semi-permeable As tall as possible As long as necessary	$<40\%$ understory 60–40% canopy	5 times (approx.) height of the understory 20–30 times height of the canopy	Up to 90% 20–70%	Where a combination of applications suit both windbreak and windshield shelterbelt types

Table 3 Benefits and disadvantages of shelterbelts for crops. Crown Copyright 2004

Benefits	*Disadvantages*
Increased ambient temperature leading to improved germination and growth rates	Competition with crops for light, moisture, and nutrients leading to reduced crop yields close to belts
Reduction of moisture loss and control of snow drifting	Increase in lodging due to increased turbulence
Reduction of mechanical damage leading to improved crop quality	Reduction in pollination for certain crops
Increased soil organic matter by production of leaf litter	Land taken out of production
Trapping or recycling nutrients	Waterlogging of soil close to dense belts
Reduction of soil erosion	High costs of establishment and management
Reduction of crop lodging	
Promotion of mineralization of soil nitrogen	
Retention of heat in the soil and air thereby extending the growing season	
Reduction of soil acidification in certain soil types	
Improvement of pollination efficiency for certain crops	
Control of spray drift	
Reduction of infiltration of water to groundwater systems preventing the rise of saline water tables	

Table 4 Benefits and disadvantages of shelterbelts for livestock. Crown Copyright 2004

Benefits	*Disadvantages*
Increased yield of pasture and root crops used for feed	Overcropping close to shelterbelt
Earlier grass growth in spring	Spread of disease by concentration of animals close to shelter
Reduced heat loss leading to increased animal productivity (milk production and weight gain)	Increase in insect pests in low wind speed region behind dense belts
Reduced mortality of newborn animals and shorn sheep	Reduction in air temperature on clear nights behind belts
Increase in range of breeds that can be utilized	
Shade provision reducing overheating and sunburn	
Increased animal welfare by provision of protection from wind, rain, snow, and sun	
Increased fertility due to better condition and provision of more comfortable conditions	
Reduction in heat loss on clear nights if animals able to move under trees	
Shelter for wildlife and game animals (deer, pheasants, etc.)	

Table 5 Benefits and disadvantages of shelterbelts for buildings and roads. Crown Copyright 2004

Benefits	*Disadvantages*
Reduced heat loss during cold weather leading to energy efficiencies	Land use
Shading in summer providing a reduction in requirements for air conditioning	Damage to buildings by the roots of trees planted too close
Improved conditions in the vicinity of buildings such as lower wind speeds and increased temperatures	Shading by trees reducing the heating benefits of the sun
Reduction in building damage from driving rain and diurnal temperature fluctuations	Increased snow build-up from poorly designed or positioned snow belts
Increased animal comfort in barns sheltered by trees	
Roads kept free of snow drifts	
Visual screening of buildings and roads	
Reduction in noise levels	
Capture of pollution such as dust, soot, spray, and gases	

the protection of crops and improved pasture. Dense shelterbelts (porosity $<40\%$) are used where intense shelter is required over a short distance, such as for the protection of lambing and calving and buildings. In some cases it is beneficial to have some of the features of both a semipermeable and a dense shelterbelt. This can be achieved with a hybrid shelterbelt in which the upper part of the belt is relatively open and the bottom of the belt is made dense by planting shrubs or slow-growing shade-tolerant trees.

Generally shelterbelts should be kept as narrow as possible. This is partly to minimize the land used but also to maintain the effective area downstream. Wide forests are found to be very ineffective at providing a large area of shelter. However, where snow retention is the objective, a wider wood can provide a larger area of snow accumulation. (Snow accumulation is useful in protecting roads from drifting or helping to stop snow blowing off farmlands where it accounts for a significant part of the total precipitation, such as the northern prairies of the USA). It has been found that multiple shelterbelts have no cumulative benefit but rather the increased turbulence behind upwind belts can slightly reduce the effectiveness of subsequent shelterbelts.

Shelterbelt Use

Shelter of Crops

Shelter can provide positive and negative benefits to crops as summarized in **Table 3**.

Shelter of Livestock

Much less work has been carried out on the benefits of shelterbelts for livestock in comparison to crops (see **Table 4**).

Shelter of Buildings and Roads

The benefits of shelter for buildings and roads are summarized in **Table 5**.

See also: **Hydrology**: Snow and Avalanche Control. **Afforestation**: Species Choice.

Further Reading

Bird PR (1998) Tree windbreaks and shelter benefits to pasture in temperate grazing systems. *Agroforestry Systems* 41: 35–54.

Brandle JR and Hintz DL (1988) Windbreak technology: Proceedings of an International Symposium on Windbreak Technology. *Agriculture, Ecosystems and Environment* 22–23: 598.

Caborn JM (1957) *Shelterbelts and Microclimate*. Forestry Commission Bulletin no. 29. Edinburgh, UK: HMSO.

Caborn JM (1965) *Shelterbelts and Windbreaks*. London: Faber & Faber.

Gregory NG (1995) The role of shelterbelts in protecting livestock: a review. *New Zealand Journal of Agricultural Research* 38(4): 423–450.

Hislop AM, Palmer HE, and Gardiner BA (1999) Assessing woodland shelter on farms. In: Proceedings of *Farm Woodlands for the Future* Conference, September 1999, Cranfield University, Silsoe, UK.

Kort J (1988) Benefits of windbreaks to field and forage crops. *Agriculture, Ecosystems and Environment* 22–23: 165–190.

Nageli W (1964) On the most favourable shelterbelt spacing. *Scottish Forestry* 18: 4–15.

Nuberg IK (1998) Effect of shelter on temperate crops: a review to define research for Australian conditions. *Agroforestry Systems* 41: 3–34.

Palmer H, Gardiner B, Hislop H, Sibbald A, and Duncan A (1997) *Trees for Shelter*. Forestry Commission Technical Paper no. 21. Edinburgh, UK: Forestry Commission.

Shaw DL (1988) The design and use of living snow fences in North America. *Agriculture, Ecosystems and Environment* 22–23: 351–362.

Song ZM (1991) A review of the development of shelterbelt system in China. In: Shi KS, Deng JF, Ding YY, Li WC, and Chen ZD (eds) *Development of Forestry Science and Technology in China*, pp. 64–70. Beijing: China Science and Technology Press.

WOOD FORMATION AND PROPERTIES

Contents

Formation and Structure of Wood

A Zink-Sharp, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

Introduction

Close examination of a piece of wood with a microscope reveals a minute cell structure that usually escapes casual observation. Remarkably, it is this minute cell structure that is responsible for many of the physical properties and characteristics of a piece of wood. All materials exhibit some degree of dependence on the fine structure of their components; however, this tendency is very pronounced with wood. An understanding of the appearance, properties, and potential of wood for use requires complete comprehension of both the physical properties and the fine structure. Knowledge of the formation processes is also required for complete awareness because wood is produced in a biological environment and the tree is subject to varying growth conditions. The formation of wood and its anatomical structure on the micro- and macroscopic scale are described in this section. Chemical and physical properties are described elsewhere (*see* **Wood Formation and Properties**: Physical Properties of Wood; Mechanical Properties of Wood.

Tree Growth and Wood Formation

Features of Woody Plants

Woody tissue is formed in a variety of plants, but it is the wood in trees that is of interest here. Characteristics of all woody plants include the following:

- possess vascular tissue that is specialized conducting tissue consisting of xylem (wood) and phloem (inner bark)
- are perennial and live for a number of years

- have a persistent stem that endures from year to year and does not die back
- have a means of secondary thickening of the stem by subsequent growth in diameter.

The basic structural and physiological unit of plants is the cell. Wood is a collection of various kinds of cells that are typically elongated and consist of an outer cell wall encompassing a hollow cell cavity. Wood cells are the result of secondary diameter thickening of tree stems. They exhibit an orderly arrangement that is characteristic of tree species, and each type of cell has a specific function.

Basic Processes in Tree Growth

Tree growth parallels the seasons in many parts of the world. It begins in the spring, slows in midsummer, and usually stops entirely in the autumn. A well-defined sequence of activities takes place during each growth season. Growth is activated when temperatures warm to an average of about 6° or 7°C and growth hormones are produced in the buds. At about the same time, water and dissolved minerals begin to move up the stem from the roots to the buds, then the buds swell due to formation and growth of cells, and soon thereafter, leaves emerge from the buds. The process of photosynthesis now begins in the leaves. During photosynthesis, water and carbon dioxide from the atmosphere are combined in the presence of chlorophyll and sunlight to make several different types of sugar.

Products of photosynthesis include oxygen that is released to the air and basic sugars, such as glucose, mannose, galactose, xylose, arabinose, and other five- and six-carbon sugars. The glucose units produced during photosynthesis are used to form cellulose, a linear, long-chain polymer with a degree of polymerization ranging as high as 30 000 monomer units. Glucose and the other five- and six-carbon sugars and sugar derivatives are used in synthesizing lower molecular weight hemicelluloses. These are branched polymers, with degrees of polymerization only in the hundreds. The tree transports the sugars to growth regions at branch and root tips and to the growth region that sheaths the main stem where they will be used to fuel cell formation and development.

New cells are formed in trees in growth areas called meristematic regions. There are two meristems involved in height and diameter growth, the apical meristem and the vascular cambium. Apical meristems are responsible for growth in height. They are composed of specialized dividing cells found at branch tips. As new cells are formed at the branch tips, the apical meristems are pushed outward, where they continue to divide and form new cells. In this manner, branches lengthen, the crown expands, and the tree gets taller and broader. Height growth begins just after the leaves emerge and is rapid at first, but slows as the growth nutrients are diverted to other regions in the tree.

Trees expand in diameter through cell enlargement and repeated cell division in the vascular cambium. This meristematic region is a thin layer of cells that lies just underneath the inner bark. It completely sheaths the entire tree and consists of specialized cells that divide to form new phloem (inner bark) to the outside and new xylem (wood) cells to the inside. Each growing season, the vascular cambium forms new layers of wood and inner bark over the entire surface of the stem and the branches. The result is an increase in stem and branch diameter (**Figure 1**).

Diameter growth in trees found in temperate zones occurs in two stages. This in turn results in two growth zones familiar to us as annual tree rings. These two growth zones are the earlywood and latewood portions of a tree ring. Cell formation during the early spring is rapid and focused on quantity. As a result, the earlywood cells form a large portion of an individual growth ring, and the cells themselves are often thin-walled and large in diameter. Toward the late summer, cell formation slows and a different scheme is used to produce new cells. Cells formed late in the growing season make up the latewood portion of tree rings. Usually there are fewer latewood cells produced per ring than earlywood, and they are thicker walled and smaller in diameter.

Growth rings or annual rings are characteristic of all temperate zone trees but this is not the case in trees growing in tropical regions where growth can be continuous year round. In this case, the wood may

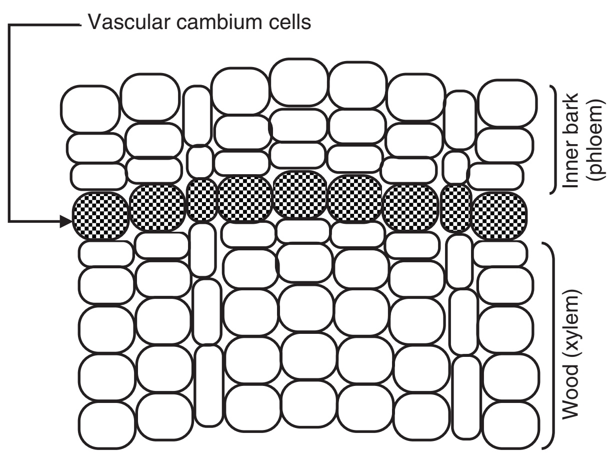


Figure 1 Diagram of a cross-section through the vascular cambium of a tree. Division of the cambial cells results in diameter expansion of the tree stem.

appear not to have any growth rings at all. Some notable exceptions are teak (*Tectona grandis*), padauk (*Pterocarpus* spp.), Honduras rosewood (*Dalbergia stevensonii*), Brazilian tulipwood (*Dalbergia fructescens* var. *tomentosa*), and sapele (*Entandrophragma cylindricum*), among others. In these woods, growth rings appear distinct due to specialized cell types and cell structure rather than two stages of growth annually.

Growth in trees is rapid in early spring but starts to decline as the end of the growing season draws near (approximately mid-July to October in the northern hemisphere). Eventually all growth stops when the meristem regions become dormant. The exact mechanisms that trigger initiation of dormancy are unknown, but there are common processes that occur. Production of growth hormones decreases and growth inhibitors accumulate. This combination results in a reduction in growth rate and eventually halting of growth. The factor that is thought to lead most reliably to dormancy is reduction in the photoperiod (length of day).

Formation and Development of Wood Cells

As mentioned earlier, wood cells in the stems of trees originate through division of the vascular cambium cells. This division can occur in one of two directions – parallel to the cambial ring or perpendicular to it. Division parallel to the ring is called periclinal and results in formation of a pair of cells – a new cambium cell and either a new xylem or phloem cell. Anticlinal division is division perpendicular to the ring and creates a pair of vascular cambium cells that provide for increasing the circumference of the cambium as the tree stem enlarges. The two types of division can take place in the same cambium cell, but do not occur simultaneously. **Figure 2** illustrates a highly idealized vascular cambium dividing periclinally to form two new cells. One of the cells becomes a new cambium cell and the other begins to mature into a new wood or bark cell. If the newly formed cell is to the outside of the cambium, it will become a bark cell, and if it is toward the inside, a wood cell.

Within a few days of formation, the new wood cell undergoes a sequence of changes involved in the maturation process. The shape of the cell changes, it increases in diameter, most cells elongate, and all cells enlarge. A newly formed wood cell consists of a thin, membrane-like wall called a primary wall and a fluid-filled center. A secondary wall is added to the inner surface of the delicate primary wall once the new cell reaches full size and shape. The secondary wall is constructed using macromolecules (cellulose, hemicelluloses, and lignin) that are synthesized from biopolymers found in the fluid-filled center of the developing cell. Progressive layers are added to the cell wall from the inside. Eventually the fluid filling is expended and the cell has a thickened, rigid wall and a hollow center. Cell formation and maturation continues during the growing season, with the vascular cambium producing new wood and bark cells as rapidly as the conditions allow. Earlywood cells are formed first in the early spring, and those formed later are the latewood cells. Cell formation and maturation continues until growth is terminated at the end of the growing period.

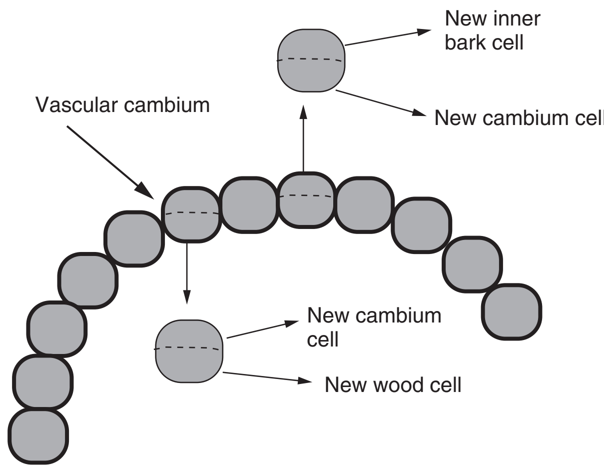


Figure 2 A highly simplified diagram of the vascular cambium dividing periclinally to form new cambial cells and new wood or bark cells.

Microscopic Structure

Chemical Structure

At the chemical element level, wood cell walls are made of carbon, hydrogen, and oxygen. Percentages vary with species, but average carbon content is 49%, hydrogen is about 6%, and oxygen is 44%, based on dry wood weight. There are other chemical elements found in wood but in very minor quantities. As mentioned above, carbon, hydrogen, and oxygen are combined in the fluid-filled center of a developing cell to synthesize macromolecules of cellulose, hemicellulose, and lignin. Cellulose and hemicellulose together make up the polysaccharide fraction of wood substance. Cellulose accounts for roughly half the dry weight of wood substance. Cellulose is a high molecular weight, linear polymer synthesized from the glucose produced during photosynthesis. Cellulose is present in all the higher plants, many of the algae, and some of the fungi. In a wood cell wall, cellulose occurs in both a crystalline and a noncrystalline (amorphous) form. Hemicelluloses are also formed using sugars produced during photosynthesis. In general, hemicelluloses are branched carbohydrate polymers that constitute from 35% to 50% of the total dry weight of wood substance. Lignin is not a polysaccharide but rather a complex, high molecular weight amorphous polymer built upon phenylpropane units. Lignin content varies from 15% to 35% of the dry weight. Percentages of the various chemical components differ with tree species and growth conditions.

The three macromolecule groups – cellulose, hemicelluloses, and lignin – are incorporated together to assemble the cell walls. An extremely efficient incorporation scheme is employed by wood cells for fabrication of their walls that is sometimes referred to as the 'reinforced matrix process.' Molecular chains of crystalline cellulose aligned lengthwise are encased in a shell of hemicellulose to construct a long filament. This core of cellulose and hemicelluloses is then surrounded in an amorphous matrix of lignin. In this manner, the lignin matrix is reinforced with cellulose and hemicellulose filaments. These filaments are usually called microfibrils, but just fibrils by some.

Cell Wall Structure

Microfibrils The basic building-block of wood cell walls is the cellulose microfibril. As mentioned above, the core of a microfibril is composed of groups of cellulose crystallites encased in hemicelluloses. During cell wall formation, microfibrils are encased in an amorphous matrix of lignin. Individual microfibrils are approximately 10–12 nm wide and about 5–6 nm thick. A typical wood cell wall consists of several layers of microfibrils in parallel aggregates. As seen in the next section, orientation of the microfibril aggregates varies within and across layers. Microfibrillar orientation greatly affects the properties of wood on all scales of structure and properties, however mechanical properties and the relationship between wood and water are most significantly impacted.

Cell wall layers A wood cell wall is not homogeneous in structure or chemical content. It is a rather complex, layered composite consisting of an outer primary wall and from one to three secondary inner layers. All wall layers, however, are composed of cellulose microfibrils embedded in the lignin matrix. The layers are continuous, but when a wood cell wall is viewed on the cross section with an electron microscope, it is possible to distinguish discrete layers within the cell wall. **Figure 3** is a drawing of a wood cell and the cell wall in cross-section. The outermost layer, the primary wall, is the first formed layer; it is high in lignin and pectin, it is very thin – on the order of 0.1 μm in thickness, and it has a random, netlike microfibril orientation. Once the cell reaches full, mature size, the secondary cell wall layer develops. Thickness of the secondary wall is highly variable, it is dense and rigid, and it consists of highly ordered layers of microfibrils aligned in nearly parallel aggregates. The number of secondary wall layers depends on cell type and to some extent, growing conditions. Cell walls that have the most advanced layer structure have three secondary layers, designated S_1, S_2, and S_3 (**Figure 3**).

Orientation of the microfibril aggregates varies from layer to layer in a cross laminate pattern (**Figure 4**). Microfibrils in the S_1 layer are oriented in parallel clusters that are roughly perpendicular to the cell axis. The S_2 layer microfibrils are nearly parallel to the cell axis, and the orientation in the S_3 is again nearly perpendicular to the cell axis. As mentioned, the cell wall is a continuum but discrete layers can be

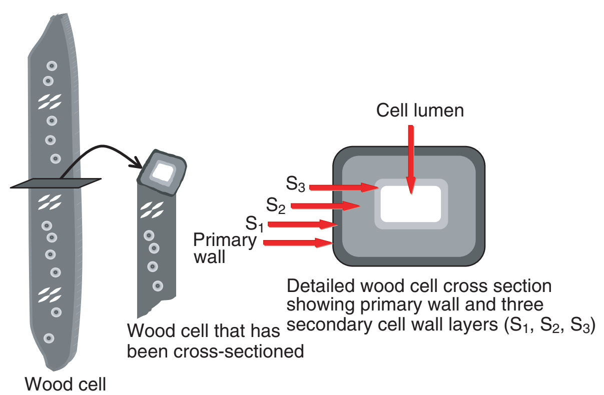


Figure 3 Diagram of a wood cell and the cell wall in cross-section.

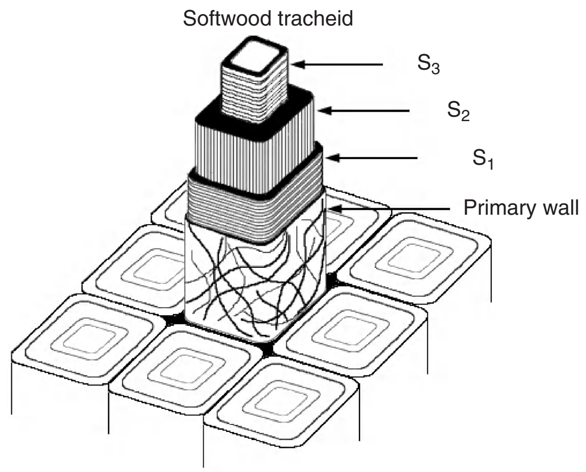


Figure 4 Diagram of cell wall layers and microfibrillar orientation within the layers.

identified in microscopic images. This wall structure is typical of almost all wood cells found in the needle-bearing trees (gymnosperms) and many of the cells found in the wood of the broadleaf trees (angiosperms).

Cell Types and Features

Due to the way in which wood cells are formed in the cambium and performance requirements of the tree, stem wood cells resemble tapered, rigid tubes in function and appearance. They are systematically assembled in tree stems in patterns that are reflective of tree type. Their cross-sectional shape varies from round to hexagonal, and their length varies from less than 1 mm to as long as 7 mm in certain trees. The majority have their long axis parallel to the tree stem, but up to 30% are oriented radially in the stem.

Trees are found in two botanical classifications based on seed type, the angiosperms and the gymnosperms. Angiosperms have seeds encapsulated inside an outer fruit, and gymnosperms have exposed seeds. In practice however, angiosperms are more commonly called hardwoods and gymnosperms, softwoods. While in general there are many similarities between the two groups, the fine structure and features are significantly different. The differences are found in the amount of cell diversity and in the arrangement schemes. **Figure 5** reveals these differences in fine cell structure. In the softwood (**Figure 5a**) the microstructure is fairly uniform and one cell type dominates the cross-section, the softwood tracheid. Tracheids occupy over 90% of softwood volume and are formed in uniform radial alignments. They average 3–5 mm in length and vary from 0.03 mm to 0.45 mm in diameter. Tracheids are rectangular to hexagonal in cross-section and are tapered at their ends. The ribbons of cells running vertically in **Figure 5a** are called wood rays. They are composed of a group of radially oriented cells called ray cells and are responsible for radial transport of fluids in the tree stem. Wood rays in softwoods are practically indistinguishable because they are almost always one cell wide, i.e. uniseriate. They occupy approximately 7% of the volume of softwood stems. Aside from the two cell types visible in **Figure 5a** (tracheids and ray cells), there is really only two other noticeable differences in cell structure: tracheid diameter and wall thickness. Tracheids formed early in the growing season in softwood trees found in temperate zones, i.e., the earlywood, are larger in diameter and have a thinner cell wall than those formed later in the growing season.

Pines (*Pinus* spp.), Douglas-fir (*Pseudotsuga* spp.), larches (*Larix* spp.), and spruces (*Picea* spp.) genera have a specialized feature called resin canals. These are basically a space between cell corners that has been surrounded by specialized resin-secreting cells, as seen at the arrows in **Figure 5b**. Resin canals are oriented both longitudinally and radially in those genera that normally exhibit them. They can be found also in other softwood trees that have been injured in some way. Resin canals that result from injury are called traumatic resin canals and are almost exclusively longitudinal in orientation.

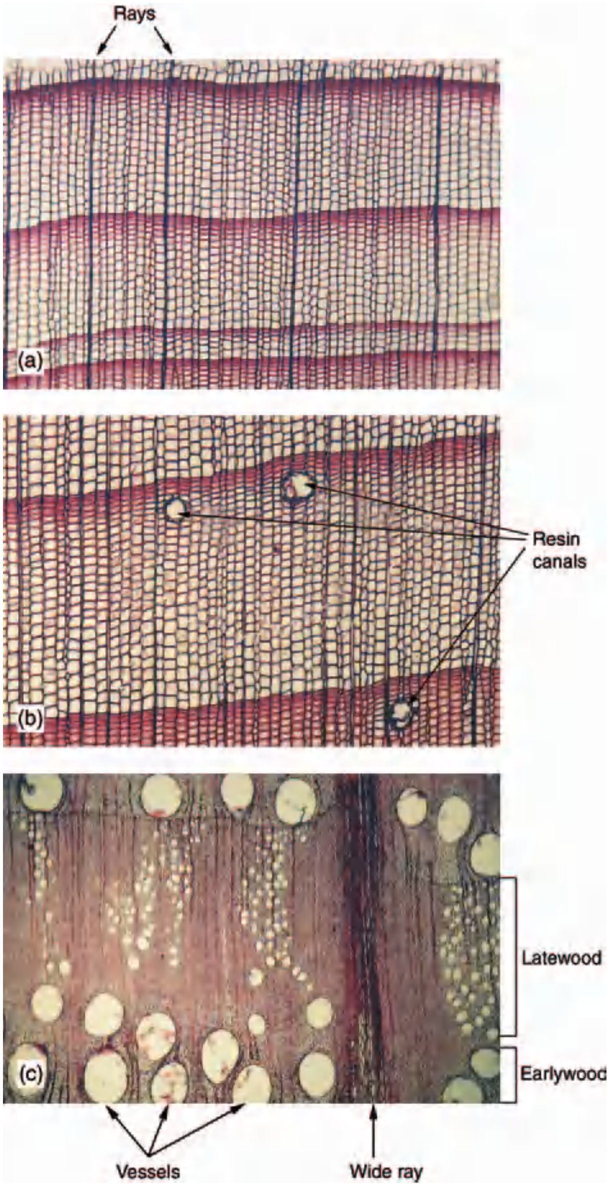


Figure 5 Differences in fine structure of cross-sections of wood as seen with a light microscope. (a) Nonresinous softwood, redwood (*Sequoia sempervirens*) (magnification × 80); (b) resinous softwood, red spruce (*Picea rubens*) (magnification × 100); (c) hardwood, white oak (*Quercus alba*) (magnification × 80).

Figure 5c illustrates the increased complexity of a hardwood in cross-section. Cell structure, features, and arrangements are considerably more diverse.

The uniform radial alignment found in softwoods is absent and there are very large-diameter cells mixed with smaller, thicker walled cells, and multiseriate rays mixed with uniseriate rays. The ray on the right of the micrograph is an example of the very wide rays found in oak (*Quercus*). Not all hardwoods exhibit these extremely wide rays, but almost all have rays that are many cells wide. The very large diameter, round cells on the bottom of **Figure 5c** are specialized transport cells called vessels. There are two groups of vessels visible in **Figure 5c** indicating the earlywood and latewood portion of the growth ring. Vessels are unique to the hardwoods and function as vertical fluid passageways for the trees. They are perforated at the ends with a variety of perforation types that vary from a simple opening to intricate, lacey patterns. Vessels occupy from 5% to 60% of total cell volume of hardwoods. Several other longitudinal cell types surround the vessels and rays in hardwoods. They are fibers, parenchyma cells, and hardwood tracheids. Tracheids and fibers serve as vertical transport and support for the tree and parenchyma serve primarily as nutrient storage. Fibers account for 20–70% of total hardwood cell volume, parenchyma from 1% to 33%, and hardwood tracheids from 27% to 70%. Each type of tree is characterized by a fine structure specific to it, so the actual percentages of any one cell type are almost entirely dependent on tree type.

Vessels in cross-section are sometimes referred to as pores. The difference in pore diameter within a growth ring is used to further classify hardwoods into ring porous, semi-ring porous, or diffuse porous subgroups. **Figure 6** illustrates the subclassification scheme based on porosity within a growth ring. Vessels within a growth ring of a ring porous wood exhibit very large differences in diameter in the earlywood versus the latewood portion of the ring (**Figure 6a**). Semi-ring porous woods exhibit earlywood vessels that are just slightly larger than the latewood vessels (**Figure 6b**). **Figure 6c** illustrates a diffuse porous wood in which the difference in vessel diameter is barely noticeable. Diffuse porous wood is the predominate growth pattern in the world and ring porous woods are usually found only in the temperate zone. Of course, there are a few notable exceptions; for example, teak and Brazilian tulipwood are ring porous woods that grow in tropical regions.

All cell elements regardless of tree or cell type display openings in the side walls, called pits, that allow for passage of fluids and water vapor between individual cells as well as radially in the tree stem. Pits possess microscopic features specific to tree and cell type. For example, the shape and pattern of pits between hardwood vessel elements, called intervessel pitting, can sometimes be used to distinguish one tree from another, and the pitting that occurs where wood rays cross and connect to softwood tracheids is indicative of genus. Pits vary from simple openings in the cell wall to an intricate valved structure in softwood tracheids.

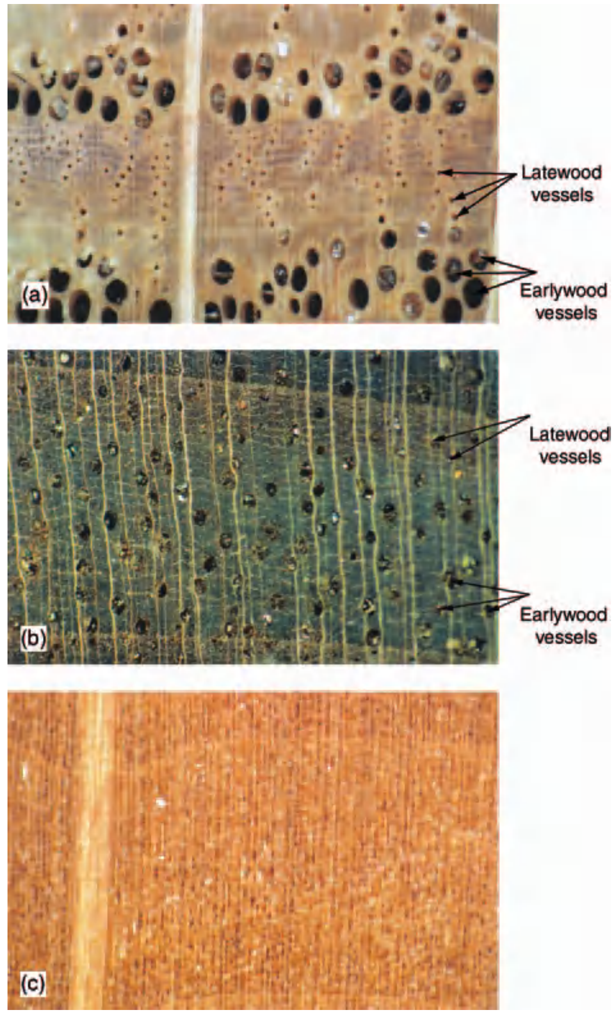


Figure 6 Classification scheme based on variation of vessel size across a growth ring. Magnification × 10. (a) Ring porous hardwood, red oak (*Quercus rubra*); (b) semi-ring porous hardwood, black walnut (*Juglans nigra*); (c) diffuse porous hardwood, red alder (*Alnus rubra*).

Three Surfaces to Microscopic Structure

Microscopic observation of slices or thin sections taken from a piece of wood reveals different anatomical structure depending on the direction of the original sectioning. An example of a section taken across the tree stem axis is a cross-section and, when viewed in a microscope, appears as in **Figure 7a**. A slice taken parallel to the tree axis and the wood rays is a radial–longitudinal slice (**Figure 7b**); observe the many pit openings along the tracheids.

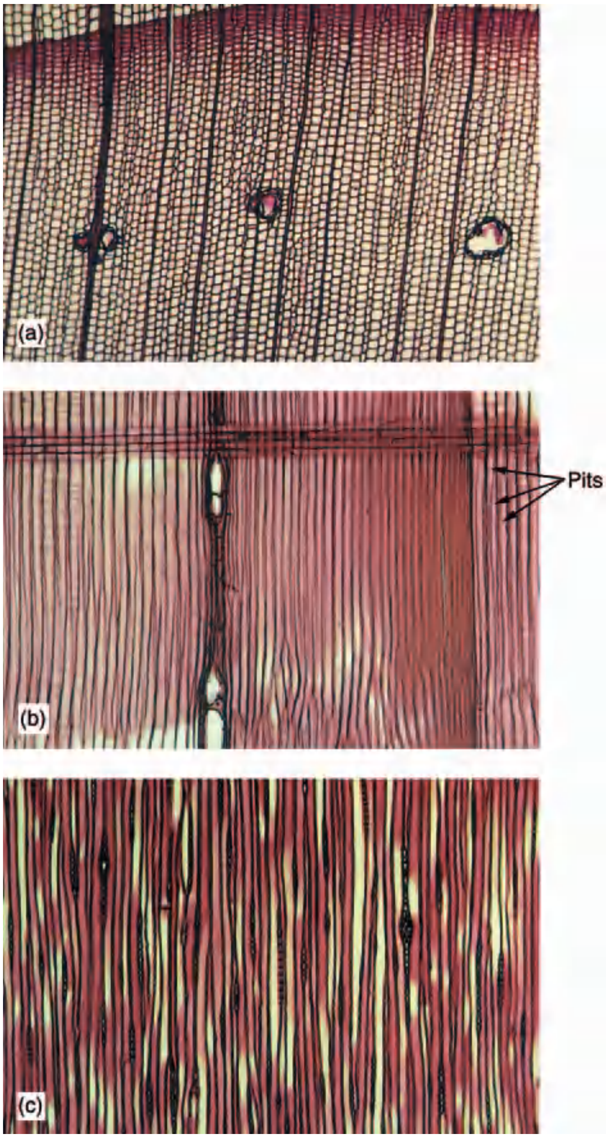


Figure 7 Microscopic images of the three surfaces of a softwood cube, southern yellow pine (*Pinus* sp.). Magnification × 100. (a) Cross-section; (b) radial surface; (c) tangential surface.

Figure 7c is the tangential section made from a cut parallel to the tree axis and a growth ring. Notice how the same piece of wood appears considerably different depending on which surface is being viewed. These differences have arisen from directional differentiation and the way in which the cells were created. Cell formation by the tree's vascular cambium results in elongated, pseudocircular cells that are arranged in a more or less radial ordering within rings around a central axis. Formation and elongation of radial cells perpendicular to the tree's axis further adds to patterning within a wood block.

There are many other, even finer structures and features in wood cells that are not described here. With an electron microscope and a great deal of time it has been possible to observe the extremely fine microscopic features of wood cells. Space simply does not allow a thorough description of the microscopic features (more information may be found in the books listed in the Further Reading section).

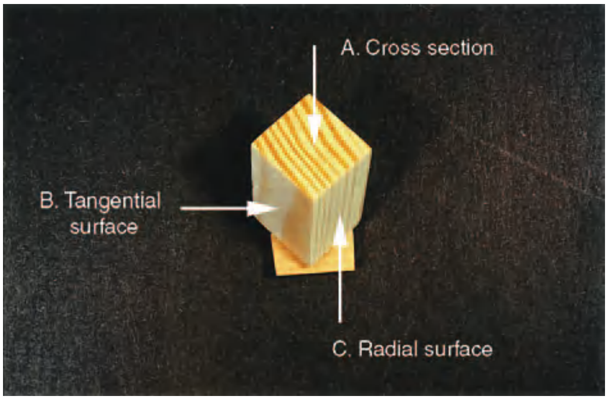


Figure 8 Photomacrograph of a southern pine cube illustrating the different macroscopic features of the three surfaces.

Macroscopic Structure

Anatomical structure visible without the aid of a microscope or hand lens can be thought of as macroscopic structure. Cell formation and directional differentiation have resulted in fine structure differences that translate into macroscopic structure and property differences as well. Examples are structural directions, growth rings, heartwood and sapwood, and ray patterns, among others.

Three Structural and Property Directions

Informal observation of a piece of solid wood reveals different surface characteristics depending on the surface being viewed. Microscopic cell structure is responsible for the three images visible in that single piece of wood. **Figure 8** illustrates surface features of each of the three faces of a wood block that has been cut parallel to both the rays and the growth rings. The surface on the top of the cube is the cross-section, the left face is the tangential surface, and the right face is the radial surface. Not only are the visual features different, the physical properties differ with, and are dependent on, the fine cell structure directions. Lumber grading, processing parameters, wood identification, physical property characterization, and dimensional stability are but a few of the areas in which knowledge of the surface and wood anatomy direction is important.

Growth Ring Structure

Growth rings are more or less distinct in trees depending on the degree of cell differentiation within an individual growth ring. **Figure 9a** indicates that growth rings are more easily distinguished in softwoods due to the usually marked difference in cell diameter and cell wall thickness in the earlywood and latewood growth regions. Ring porous hardwoods also exhibit distinct growth rings (**Figure 9b**), but growth rings are less easy to determine in the diffuse porous woods (**Figure 9c**). Physical and mechanical properties also differ within growth rings due to the cell structure differences. In general the latewood regions exhibit superior mechanical properties, higher density, more shrinkage, and darker color than the earlywood regions.

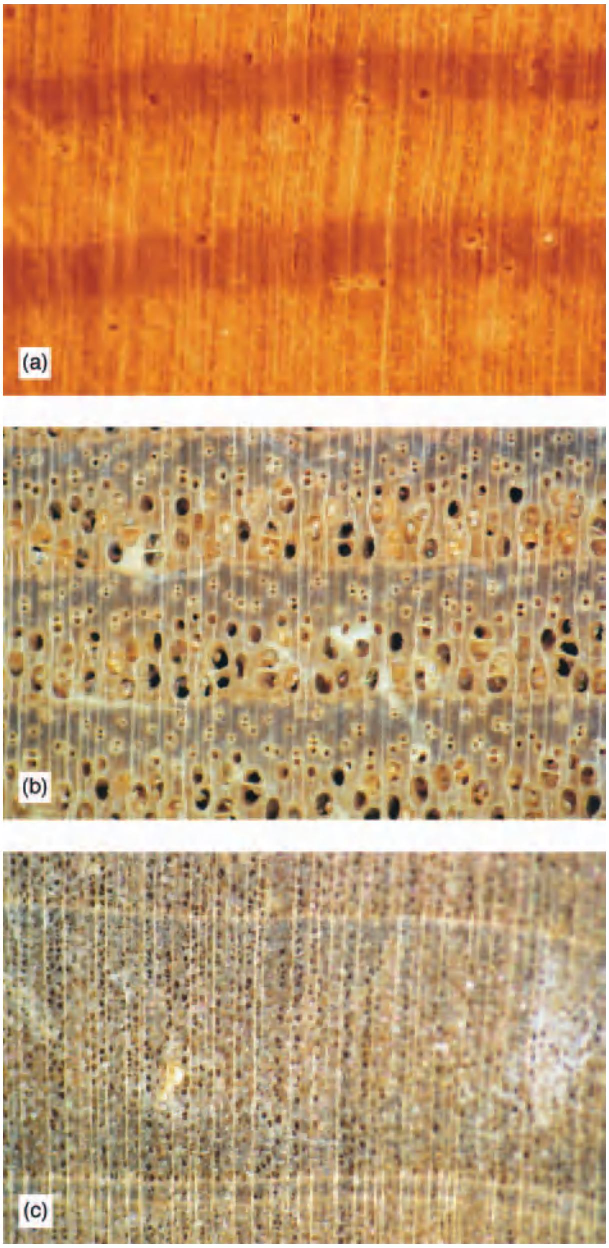


Figure 9 Photomacrographs showing distinct versus indistinct rings. Magnification × 10. (a) Softwood with distinct growth rings, southern yellow pine (*Pinus* spp.); (b) ring porous hardwood with distinct growth rings, black ash (*Fraxinus nigra*); (c) diffuse porous hardwood with indistinct growth rings, yellow-poplar (*Liriodendron tulipifera*).

Heartwood and Sapwood

Figure 10 illustrates two visibly different regions in a tree stem disk. The outer rim is lighter in color and is called the sapwood, and the inner, darker region is called heartwood. In twigs and very small, young trees, the entire xylem (wood) portion is involved in sap conduction upward and this wood portion is fittingly named 'sapwood.' As the tree ages, the entire sapwood portion is not needed to transport fluids to the leaves, so at the center of the tree, the cells cease to conduct, lose their nutrients, and eventually die. This transformation from living, conducting cell tissue to empty, dead cells is responsible for cells being converted into 'heartwood.' The transformation is accompanied by production of chemical compounds in the cell wall called extractives, disappearance of living nuclei, and reduction in nitrogen, starch, and sugar content. Notice however, there is no change in cell structure, i.e., cell structure in sapwood and heartwood is essentially the same, it is the chemical content that has been altered. Heartwood is usually darker in color than sapwood because some extractives in the cell walls of heartwood are usually, but not always, dark in color. In addition, extractives give heartwood increased durability, odor, and taste.

Rays

Also visible in **Figure 10** are wood rays extending from the vascular cambium inward toward the pith of the tree. As mentioned, wood rays in

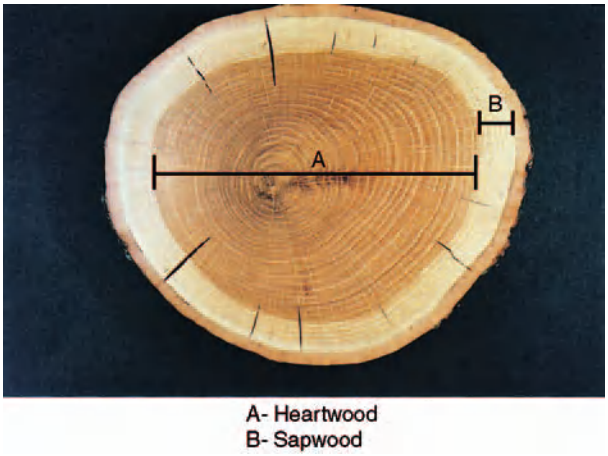


Figure 10 Photograph of a tree disk showing heartwood, sapwood, and rays of oak (*Quercus* sp.).

softwoods are very fine and essentially nondistinct macroscopically, but the rays in many hardwoods are very distinct and make dramatic patterns in finished products. Because the cells in wood rays have their long axis oriented perpendicular to the longitudinal cells, they reflect light differently and can also make unusual patterns on radially cut surfaces. The wood rays tend to form a plane of weakness within the otherwise longitudinally aligned cell structure, but at the same time, are thought to reduce radial shrinkage.

Juvenile and Reaction Wood

Juvenile Wood Features

Wood formed at the apical meristem (branch tips) and later incorporated into the main tree stem by diameter growth in the vascular cambium is significantly different from the outer stem wood. Because this wood is formed at growth shoots and at very early stages of stemwood formation, it is called 'juvenile wood.' It is also known as core, pith, or crown wood. It is formed in a cylindrical column around the pith and depending on species, is the first 5–20 growth increments in the tree stem. **Figure 11** illustrates the location of juvenile wood at the center of the tree stem disk. All trees have some portion of juvenile wood, but it is especially prevalent in plantation grown softwoods and where fast growth has occurred. Cell structure, chemistry, and wood properties all differ in juvenile wood when compared to mature wood. Cell length, cell wall thickness, and percentage of latewood per ring are lower in juvenile wood. This combination of structural features results in lower density. The S_2 microfibril angle is increased (more horizontal) over mature wood as is the percent of lignin in the cell walls.

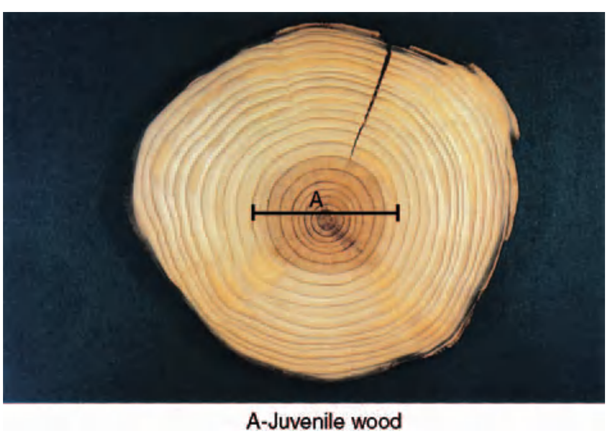


Figure 11 Photograph of a tree disk with juvenile wood, Table-mountain pine (*Pinus pungens*).

In general, juvenile wood is considered inferior to mature wood in terms of mechanical and physical properties. It is weaker, less stiff, more prone to warp, and is more problematic to process into paper and fiber products. Differences in the cell structure and chemistry of juvenile wood are again responsible for macroscopic features. There are select circumstances or situations in which juvenile wood is considered acceptable, and perhaps even, preferable. Low-density wood-based composites and some paper products would be examples of products in which juvenile wood performs acceptably and with consistency.

Reaction Wood

Wood formed in leaning stems is also significantly different from wood formed in nonleaning stems. Collectively this wood is called 'reaction wood.' When found in leaning softwood stems, it is called compression wood, and tension wood in leaning hardwoods. Compression wood is formed on the lower side of leaning softwood stems or branches and tension wood is usually on the upper side of

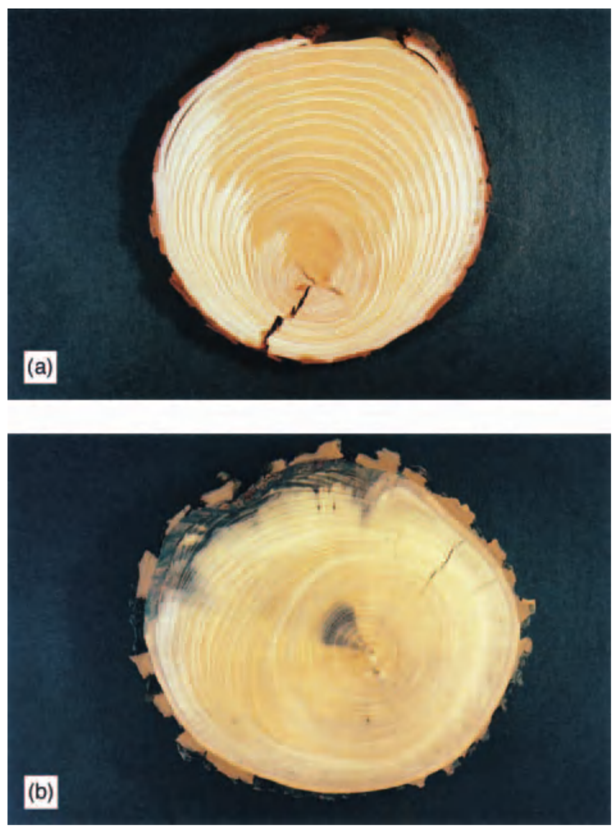


Figure 12 Photographs of cross-sections of reaction wood found in leaning tree stems. (a) Eccentric rings and discoloration of compression wood in spruce (*Picea* sp.); (b) eccentric rings of tension wood cross-section in ash (*Fraxinus* sp.).

leaning hardwood stems or branches. Characteristics of compression wood include eccentric growth rings, a high percent of latewood per ring, higher density, intercellular spaces, helical checking of the cell walls, a large microfibril angle in the S_2, and a higher lignin content. It is often 'dull' looking or darker in color. **Figure 12a** illustrates the eccentric rings and darkening of compression wood. Tension wood has eccentric growth increments, fuzzy cut surfaces, a gelatinous almost pure cellulose layer that may replace part of the cell wall, a higher percent of thick-walled fibers, and an increased cellulose content. Macroscopic features such as eccentric rings of tension wood of ash are shown in **Figure 12b**. Wood on the opposing side of the reaction wood is also 'unusual' in that it does not possess the same features of wood in the nonleaning stem portion. As with juvenile wood, the physical properties of reaction wood are reflective of the fine structure and chemistry and are considered inferior to those of mature wood.

See also: **Tree Breeding, Practices**: Biological Improvement of Wood Properties; Genetics and Improvement of Wood Properties. **Wood Formation and Properties**: Chemical Properties of Wood; Mechanical Properties of Wood; Physical Properties of Wood; Wood Quality. **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

Bowyer JL, Shmulsky R, and Haygreen JG (2003) *Forest Products and Wood Science: An Introduction*, 4th edn. Ames, IA: Iowa State University Press.

Butterfield BG, Meylan BA, and Peszlen IM (1997) *Three Dimensional Structure of Wood*. London: Chapman & Hall.

Core HA, Cote WA, and Day AC (1979) *Wood Structure and Identification*, 2nd edn. Syracuse, NY: Syracuse University Press.

Cote WA (ed.) (1965) *Cellular Ultrastructure of Woody Plants*. Syracuse, NY: Syracuse University Press.

Cote WA (1980) *Papermaking Fibers: A Photomicrographic Atlas*. Syracuse, NY: Syracuse University Press.

Harlow WM (1979) *Inside Wood*. Washington, DC: American Forestry Association.

Hoadley RB (1990) *Identifying Wood*. Newtown, CT: Taunton Press.

Lincoln W (1993) *The Encyclopedia of Wood*. London: Quarto Publishing.

Panshin AJ and de Zeeuw C (1980) *Textbook of Wood Technology*, 4th edn. New York: McGraw-Hill.

Wangaard FF (ed.) (1981) *Wood: Its Structure and Properties*. University Park, PA: Pennsylvania State University.

Mechanical Properties of Wood

B Kasal, North Carolina State University, Raleigh, NC, USA

Introduction

This article covers mechanical properties of wood and wood-based materials. Wood is a nonisotropic material with directionally dependent elastic and mechanical properties. Rules governing wood as an anisotropic, orthotropic, and transverse isotropic material are outlined. Wood materials are classified into groups based on their structure. The relationship between mechanical properties of wood and moisture, temperature, and time are also covered.

Elastic Properties

Wood is an anisotropic nonhomogeneous material. Anisotropic means that the physical properties (including mechanical) are directionally dependent. Its nonhomogeneous character is related to wood being a porous material that is not continuous but contains voids. The anisotropy is cylindrical anisotropy (**Figure 1**) but it is often, for purpose of modeling, replaced by the orthogonal anisotropy (orthotropy). This is done to achieve simplicity and to avoid coordinate transformation from a cylindrical to Cartesian system. A cylindrical coordinate system can be superimposed on the tree cross section such that the longitudinal axis is oriented along the tree axis and the radius, R, is oriented in a radial direction. Angle φ will rotate counterclockwise and mechanical properties will be a function of R and φ. Strictly speaking, wood will only loosely follow anisotropy and transformation rules due to its natural variability. If we remove a block of finite dimensions (such as cutting a board from a log) and

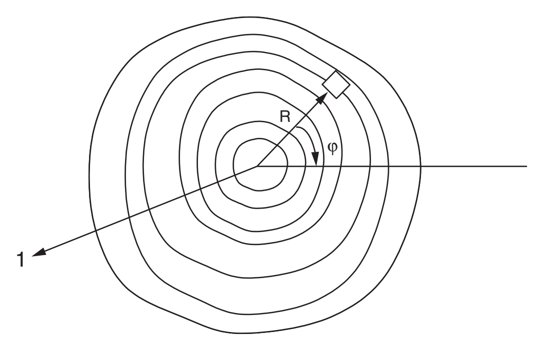


Figure 1 Cylindrical coordinate system superimposed on the tree cross-section.

let the radius, R, be relatively large with respect to the board cross-sectional dimensions (**Figure 2**) such that $R \rightarrow \infty$, we can then neglect the radius and superimpose a Cartesian coordinate system, where mechanical properties in any coordinate system rotated with respect to the original one will be a function of properties in directions 1, 2, and 3. From **Figure 2** it follows that the simplification requirements are never met and therefore discrepancies between different experimentally obtained elastic constants will occur. Orthotropic representation of wood also requires that the properties follow orthotropic symmetry rules. This means that one can superimpose three mutually perpendicular planes of symmetry and all properties (not only mechanical but also, e.g., electrical) will be symmetrical with respect to these planes. If the above assumptions are met then wood can be fully defined by 9 elastic constants (three moduli of elasticity E_1, E_2, E_3, three Poisson's ratios μ_{12}, μ_{23}, μ_{13} and three shear moduli G_{12}, G_{23}, G_{13}). The remaining constants (36 total) can be calculated using reciprocity theorem and material symmetry. Unlike isotropic materials, the shear modulus of wood is independent of other elastic parameters and must be determined experimentally. More details can be found in any standard text dealing with composite materials. The ratios of elastic moduli in longitudinal (L), radial (R), and tangential (T) directions are approximately 20:1.7:1 for softwoods and 13:1.7:1 for hardwoods. Stress, σ, can be calculated from the generalized Hooke's Law as $a_{ij}\varepsilon_j = \sigma_i$, where σ_i = stress tensor, a_{ij} = stiffness matrix, and ε_j = strain tensor, i, $j = 1, 2 \ldots 6$. Defining wood as an orthotropic material is not practical due to the large number of experimental variables that must be determined. In structural applications, it is impossible to distinguish between radial and tangential directions and wood is represented as transverse isotropic material. The transverse isotropic means that the material has isotropic properties in the transverse plane. Thus, only two moduli of elasticity (parallel and perpendicular to fibers), one shear modulus, and one Poisson's ratio are needed to define such material. One must pay attention to Poisson's ratios since values exceeding 0.5 have been reported in the literature. Such values are impossible to measure for elastic solids (value of 0.5 represents an incompressible fluid). Since wood is an inhomogeneous material with hollow cell structure, high values of expansion are possible resulting in apparent Poisson's ratio close to 0.5. Viewing wood material as rigid plastic foam can explain such high values. The values of Poisson's ratios for most common woods are listed in **Table 1**.

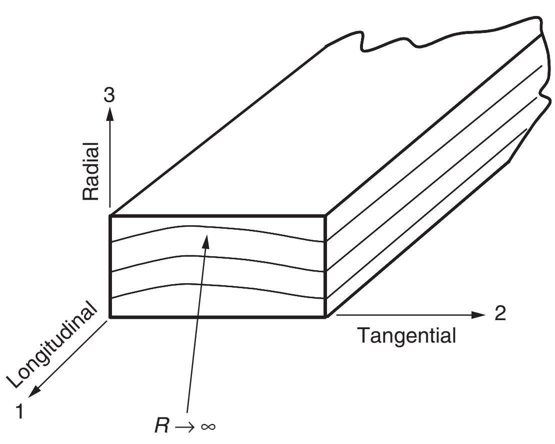


Figure 2 Orthotropic representation of solid wood cross-section.

Most wood composites are two-dimensional and can be considered as orthotropic or isotropic in two dimensions whereby the third dimension across the thickness is not considered (in two dimensional elasticity problems, the strain in the thickness is constant). **Table 2** lists various composite materials based on orientation of particles and their definitions. The elastic properties of wood composites are affected by their structure and the way the composites are manufactured. **Table 3** represents the range of elastic properties for some common wood composites.

Constitutive Equations

Wood and wood composites are generally regarded as brittle, elastic materials, with the exception of compression across fibers where large strains can be introduced without failing the material. Thus, Hooke's law can be used to describe a short-term stress–strain relationship and modulus of elasticity represents the slope of the stress–strain diagram. In compression perpendicular to fibers, the modulus of elasticity has meaning only at the pseudoelastic region of the stress–strain diagram. A typical stress–strain diagram for wood loaded in compression perpendicular to fibers direction is shown in **Figure 3**. The yield strain in compression across fibers is about 3%. The failure strains for tension and compression along fibers is in the range 2–3%. For tension across fibers, the failure strain can be less than 0.2%. Wood behavior in tension parallel, perpendicular and compression parallel to the grain is brittle and wood can be considered linearly elastic all the way up to the failure.

Strength

Strength is defined as the stress at failure. Therefore, the definition of failure plays an important role in defining strength. Because of the nonisotropic

Table 1 Poisson's ratios for various species and wood composites at approximately 12% moisture content

Species	μLR	μLT	μRT	μTR	μRL	μTL
Hardwoods						
Ash, white (*Fraxinus americana*)	0.371	0.440	0.684	0.360	0.059	0.051
Aspen, quaking (*Populus tremuloides*)	0.489	0.374	—	0.496	0.054	0.022
Balsa (*Ochroma pyramidale*)	0.229	0.488	0.665	0.231	0.018	0.009
Basswood (*Tilia americana*)	0.364	0.406	0.912	0.346	0.034	0.022
Birch, yellow (*Betula alleghaniensis*)	0.426	0.451	0.697	0.426	0.043	0.024
Cherry, black (*Prunus serotina*)	0.392	0.428	0.695	0.282	0.086	0.048
Cottonwood, eastern (*Populus deltoides*)	0.344	0.420	0.875	0.292	0.043	0.018
Mahogany, African (*Khaya grandifoliola*)	0.297	0.641	0.604	0.264	0.033	0.032
Mahogany, Honduras (*Swietenia macrophylla*)	0.314	0.533	0.600	0.326	0.033	0.034
Maple, sugar (*Acer saccharum*)	0.424	0.476	0.774	0.349	0.065	0.037
Maple, red (*Acer rubrum*)	0.434	0.509	0.762	0.354	0.063	0.044
Oak, red (*Quercus rubra*)	0.350	0.448	0.560	0.292	0.064	0.033
Oak, white (*Quercus alba*)	0.369	0.428	0.618	0.300	0.074	0.036
Sweetgum (*Liquidambar styraciflua*)	0.325	0.403	0.682	0.309	0.044	0.023
Walnut, black (*Juglans nigra*)	0.495	0.632	0.718	0.378	0.052	0.035
Yellow-poplar (*Liriodendron tulipifera*)	0.318	0.392	0.703	0.329	0.030	0.019
Softwoods						
Baldcypress (*Taxodium distichum*)	0.338	0.326	0.411	0.356	—	—
Cedar, northern white (*Thuja occidentalis*)	0.337	0.340	0.458	0.345	—	—
Cedar, western red (*Cedrela guianensis*)	0.378	0.296	0.484	0.403	—	—
Douglas-fir (*Pseudotsuga menziesii*)	0.292	0.449	0.390	0.374	0.036	0.029
Fir, subalpine (*Abies lasiocarpa*)	0.341	0.332	0.437	0.336	—	—
Hemlock, western (*Tsuga heterophylla*)	0.485	0.423	0.442	0.382	—	—
Larch, western (*Larix occidentalis*)	0.355	0.276	0.389	0.352	—	—
Pine						
Loblolly (*Pinus taeda*)	0.328	0.292	0.382	0.362	—	—
Lodgepole (*Pinus contorta*)	0.316	0.347	0.469	0.381	—	—
Longleaf (*Pinus palustris*)	0.332	0.365	0.384	0.342	—	—
Pond (*Pinus serotina*)	0.280	0.364	0.389	0.320	—	—
Ponderosa (*Pinus ponderosa*)	0.337	0.400	0.426	0.359	—	—
Red (*Pinus resinosa*)	0.347	0.315	0.408	0.308	—	—
Slash (*Pinus elliottii*)	0.392	0.444	0.447	0.387	—	—
Sugar (*Pinus lambertiana*)	0.356	0.349	0.428	0.358	—	—
Western white (*Pinus monticola*)	0.329	0.344	0.410	0.334	—	—
Redwood (*Sequoia sempervirens*)	0.360	0.346	0.373	0.400	—	—
Spruce, Sitka (*Picea sitchensis*)	0.372	0.467	0.435	0.245	0.040	0.025
Spruce, Engelmann (*Picea engelmannii*)	0.422	0.462	0.530	0.255	0.083	0.058
Plywood	0.44	0.10	0.08	0.30	0.05	0.23
Particleboard	0.02	0.27	0.02	0.25	0.30	0.23

Data from US Department of Agriculture (1999) *Wood Handbook: Wood as an Engineering Material*. Madison, WI: US Department of Agriculture Forest Service; Niemz P (1993) *Physik des Holzes und der Holzwerkstoffe*. Weinbrenner, Germany: DRW-Verlag.

Table 2 Types of wood composite materials and their representation

Material	*Representation*	*Number of elastic constants needed*[a]
Layered systems (plywood)	Orthotropic, two-dimensional	4 (E_1, E_2, G_{12}, μ_{12})
Particle-based systems with oriented particles (OSB)	Orthotropic, two-dimensional, or isotropic	4 (E_1, E_2, G_{12}, μ_{12}) 2 (E_1, μ_{12})
Particle-based with randomly oriented particles (particleboard)	Isotropic	2 (E_1, μ_{12})
Fiber-based (fiberboard)	Isotropic	2 (E_1, μ_{12})
Composite lumber products (LVL, laminated veneer lumber; LSL, laminated strand lumber)	Transverse Isotropic	4 (E_1, E_2, G_{12}, μ_{12})

[a] E_1, modulus of elasticity in the direction 1; E_2, modulus of elasticity in the direction 2; G_{12}, shear modulus; μ_{12}, Poisson's ratio.

character of wood and wood-based composites, several strength values are required to describe completely the strength of the material. These include tensile, compressive, and shear strengths. Since tensile and compressive strengths are not equal, bending strength is also used as an additional

Table 3 Elasticity properties of common wood-based composites

	E_1 *(MPa)*	E_2 *(MPa)*	μ_{12}	G_{12} *(MPa)*
Softwood plywood	6000–12000[a] 4100–10000[b]	2000–7000[a] 2500–7000[b]	0.1–0.44	
Hardwood plywood			0.1–0.44	
Oriented strandboard (OSB)				
Particleboard	1500–7000	1500–7000		
Medium density fiberboard (MDF)	1500–4500	1500–4500		
Hardboard	4000–7000	4000–7000		
Laminated veneer lumber (LVL)	13000–19000	3000–4000		
Laminated strand lumber (LSL)	13000–19000	3000–4000		

[a] Less than 5 layers.
[b] More than 7 layers.
Data from Bodig J and Jayne BA (1993) *Mechanics of Wood and Wood Composites*. Malabar, FL: Krieger; Wesche K (1988) *Baustoffe für Tragende Bauteile*, vol. 4, *Holz und Kunstoffe*, 2nd edn. Wiesbaden, Germany: Bauverlag GmbH.

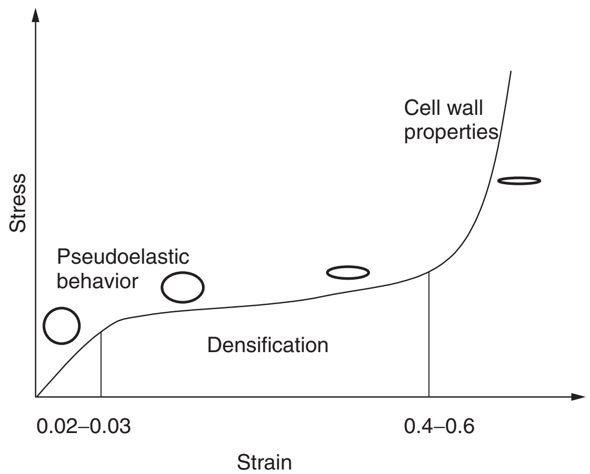


Figure 3 Typical stress–strain diagram of wood loaded in compression perpendicular to fibers.

parameter. Tensile and compressive strengths are defined in direction parallel and perpendicular to the fibers. Tensile strength in the direction perpendicular to the fibers is an unreliable quantity due to the likelihood of checks in wood. Failure can be relatively easily defined for all stresses, except for the compression perpendicular to fibers where the strength is defined as the stress at certain value of the strain. Thus, compressive strength in the direction perpendicular to fibers is a deformation-based quantity. Values of strengths for common woods are listed in **Tables 4** and **5**.

Shear strength depends on the orientation of the shear plane. Since the shear forces in an element always act in pairs, the shear stress will always act on two opposite planes in an elementary shear block. When a shear force acts in the direction perpendicular to fibers, rolling shear occurs. Shear through the thickness of wood composites (horizontal shear) is defined when shear force acts across the material thickness.

If wood or wood composites are under multiaxial stress (such as biaxial tension), a single value of strength is not sufficient to determine failure and a failure surface must be constructed. Various strength theories can be used to define the strength envelope with tensorial strength criterion being the most general. A generalized function describing the material strength can be written as $a_i\sigma_i + a_{ij}\sigma_i\sigma_j + a_{ijk}\sigma_i\sigma_j\sigma_k + \cdots = 1$. The coefficients a_i, a_{ij}, a_{ijk} represent the strength tensor components and σ_i, σ_j, σ_k are the stresses in directions 1, 2, 3 and planes 3, 4, 6. **Figure 4** shows a strength envelope for plywood loaded by in-plane forces. Note that for the most simple, two-dimensional stress state, the envelope will be in three dimensions and additional characteristic, a strength in biaxial tension, will be needed to define mutual interaction between stresses in two principal directions (along and across the face veneer fibers). Another way to determine failure is use of fracture mechanics. Fracture mechanics studies mechanisms of crack initiation, development, and growth. Several parameters are needed to describe the functions governing the various stages of crack development. The problem in applying fracture mechanics to wood and wood materials is that an infinite number of cracks of unknown dimensions is present in wood.

Variability of Mechanical Properties

Variability of mechanical properties must always be considered because variability is extremely high in wood and wood materials. For example, modulus of elasticity within a species may vary by 20–30% (variability is defined as a standard deviation divided by arithmetic average). One will always have an estimate of material characteristics (arithmetic average is one of the estimators to estimate mean, the value of which is never known). The high variability of mechanical properties requires that relatively large

Table 4 Mechanical properties[a] of common woods at 12% moisture content

Common and botanical names of species	Specific gravity[b]	Static bending		Compression parallel to grain (kPa)	Compression perpendicular to grain (kPa)	Shear parallel to grain (kPa)	Tension perpendicular to grain (kPa)
		Bending strength (kPa)	Modulus of elasticity[c] (MPa)				
Hardwoods							
Alder, red (*Alnus rubra*)	0.41	68 000	9 500	40 100	3 000	7 400	2 900
Ash							
black (*Fraxinus nigra*)	0.49	87 000	11 000	41 200	5 200	10 800	4 800
white (*Fraxinus americana*)	0.60	103 000	12 000	51 100	8 000	13 200	6 500
Aspen							
bigtooth (*Populus grandidentata*)	0.39	63 000	9 900	36 500	3 100	7 400	—
quaking (*Populus tremuloides*)	0.38	58 000	8 100	29 300	2 600	5 900	1 800
Basswood, American (*Tilia americana*)	0.37	60 000	10 100	410	32 600	2 600	6 800
Beech, American (*Fagus grandifolia*)	0.64	103 000	11 900	1 040	50 300	7 000	13 900
Birch							
paper (*Betula papyrifera*)	0.55	85 000	11 000	860	39 200	4 100	8 300
Sweet (*Betula lenta*)	0.65	117 000	15 000	1 190	58 900	7 400	15 400
Butternut (*Juglans cinerea*)	0.38	56 000	8 100	610	36 200	3 200	8 100
Cherry, black (*Prunus serotina*)	0.50	85 000	10 300	740	49 000	4 800	11 700
Chestnut, American (*Castanea dentata*)	0.43	59 000	8 500	480	36 700	4 300	7 400
Cottonwood							
balsam poplar (*Populus balsamifera*)	0.34	47 000	7 600	—	27 700	2 100	5 400
black (*Populus trichocarpa*)	0.35	59 000	8 800	560	31 000	2 100	7 200
Eastern (*Populus deltoides*)	0.40	59 000	9 400	510	33 900	2 600	6 400
Elm							
rock (*Ulmus alata*)	0.63	102 000	10 600	1 420	48 600	8 500	13 200
slippery (*Ulmus rubra*)	0.53	90 000	10 300	1 140	43 900	5 700	11 200
Hackberry (*Celtis occidentalis*)	0.53	76 000	8 200	1 090	37 500	6 100	11 000
Hickory, pecan							
bitternut (*Carya cordiformis*)	0.66	118 000	12 300	62 300	11 600	—	—
Hickory, true							
mockernut (*Carya tomentosa*)	0.72	132 000	15 300	61 600	11 900	12 000	—

continued

Table 4 Continued

Common and botanical names of species	*Specific gravity*[b]	*Static bending*		*Compression parallel to grain (kPa)*	*Compression perpendicular to grain (kPa)*	*Shear parallel to grain (kPa)*	*Tension perpendicular to grain (kPa)*
		Bending strength (kPa)	*Modulus of elasticity*[c] *(MPa)*				
Honeylocust (*Gleditsia triacanthos*)	—	101 000	11 200	51 700	12 700	15 500	6 200
Locust, black (*Robinia pseudoacacia*)	0.69	134 000	14 100	70 200	12 600	17 100	4 400
Magnolia							
cucumber tree (*Magnolia acuminata*)	0.48	85 000	12 500	43 500	3 900	9 200	4 600
Southern (*Magnolia acuminata*)	0.50	77 000	9 700	37 600	5 900	10 500	5 100
Maple							
bigleaf (*Acer macrophyllum*)	0.48	74 000	10 000	41 000	5 200	11 900	3 700
black (*Acer nigrum*)	0.57	92 000	11 200	46 100	7 000	12 500	4 600
red (*Acer rubrum*)	0.54	92 000	11 300	45 100	6 900	12 800	—
silver (*Acer saccharinum*)	0.47	61 000	7 900	36 000	5 100	10 200	3 400
sugar (*Acer saccharum*)	0.63	109 000	12 600	54 000	10 100	16 100	—
Oak, red							
black (*Quercus coccinea*)	0.61	96 000	11 300	45 000	6 400	13 200	—
Northern red (*Quercus rubra*)	0.63	99 000	12 500	46 600	7 000	12 300	5 500
Scarlet (*Quercus coccinea*)	0.67	120 000	13 200	57 400	7 700	13 000	6 000
Southern red (*Quercus rubra*)	0.59	75 000	10 300	42 000	6 000	9 600	3 500
Water (*Quercus palustris*)	0.63	106 000	13 900	46 700	7 000	13 900	6 300
Oak, white (*Quercus* spp.)							
white (*Quercus alba*)	0.68	105 000	12 300	51 300	7 400	13 800	5 500
Sweetgum (*Liquidambar styraciflua*)	0.52	86 000	11 300	43 600	4 300	11 000	5 200
Sycamore, American (*Platanus occidentalis*)	0.49	69 000	9 800	37 100	4 800	10 100	5 000
Walnut, black (*Juglans nigra*)	0.55	101 000	11 600	52 300	7 000	9 400	4 800
Willow, black (*Salix nigra*)	0.39	54 000	7 000	28 300	3 000	8 600	—
Yellow-poplar (*Liriodendron tulipifera*)	0.42	70 000	10 900	38 200	3 400	8 200	3 700
Softwoods							
Baldcypress (*Taxodium distichum*)	0.46	73 000	9 900	43 900	5 000	6 900	1 900
Cedar							

Atlantic white (*Chamaecyparis thyoides*)	0.32	47 000	6 400	32 400	2 800	5 500	1 500
Eastern redcedar (*Cedrela* spp.)	0.47	61 000	6 100	41 500	6 300	—	—
Incense (*Libocedrus decurrens*)	0.37	55 000	7 200	35 900	4 100	6 100	1 900
Northern white (*Thuja occidentalis*)	0.31	45 000	5 500	27 300	2 100	5 900	1 700
Port-Orford (*Chamaecyparis lawsoniana*)	0.43	88 000	11 700	43 100	5 000	9 400	2 800
Western redcedar (*Cedrela* spp.)	0.32	51 700	7 700	31 400	3 200	6 800	1 500
yellow (*Chamaecyparis nootkatensis*)	0.44	77 000	9 800	43 500	4 300	7 800	2 500
Douglas-fir[d]							
coast (*Pseudotsuga menziesii*)	0.48	85 000	13 400	49 900	5 500	7 800	2 300
interior West (*Pseudotsuga menziesii*)	0.50	87 000	12 600	51 200	5 200	8 900	2 400
Fir							
balsam (*Abies balsamea*)	0.35	63 000	10 000	36 400	2 800	6 500	1 200
grand (*Abies grandis*)	0.37	61 400	10 800	36 500	3 400	6 200	1 700
noble (*Abies procera*)	0.39	74 000	11 900	42 100	3 600	7 200	1 500
pacific silver (*Abies amabilis*)	0.43	75 800	12 100	44 200	3 100	8 400	—
subalpine (*Abies lasiocarpa*)	0.32	59 000	8 900	33 500	2 700	7 400	—
white (*Abies concolor*)	0.39	68 000	10 300	40 000	3 700	7 600	2 100
Hemlock							
Eastern (*Tsuga canadensis*)	0.40	61 000	8 300	37 300	4 500	7 300	—
Western (*Tsuga heterophylla*)	0.45	78 000	11 300	49 000	3 800	8 600	2 300
Larch, western (*Larix occidentalis*)	0.52	90 000	12 900	52 500	6 400	9 400	3 000
Pine							
Eastern white (*Pinus strobus*)	0.35	59 000	8 500	33 100	3 000	6 200	2 100
Jack (*Pinus banksiana*)	0.43	68 000	9 300	39 000	4 000	8 100	2 900
loblolly (*Pinus taeda*)	0.51	88 000	12 300	49 200	5 400	9 600	3 200
lodgepole (*Pinus contorta*)	0.41	65 000	9 200	37 000	4 200	6 100	2 000
longleaf (*Pinus palustris*)	0.59	100 000	13 700	58 400	6 600	10 400	3 200
Pitch (*Pinus ponderosa*)	0.52	74 000	9 900	41 000	5 600	9 400	—
pond (*Pinus serotina*)	0.56	80 000	12 100	52 000	6 300	9 500	—
ponderosa (*Pinus*	0.40	65 000	8 900	36 700	4 000	7 800	2 900

continued

Table 4 Continued

Common and botanical names of species	*Specific gravity*[b]	*Static bending*		*Compression parallel to grain (kPa)*	*Compression perpendicular to grain (kPa)*	*Shear parallel to grain (kPa)*	*Tension perpendicular to grain (kPa)*
		Bending strength	*Modulus of*				
ponderosa)							
red (*Pinus resinosa*)	0.46	76 000	11 200	41 900	4 100	8 400	3 200
shortleaf (*Pinus echinata*)	0.51	90 000	12 100	50 100	5 700	9 600	3 200
slash (*Pinus elliottii*)	0.59	112 000	13 700	56 100	7 000	11 600	—
spruce (*Pinus glabra*)	0.44	72 000	8 500	39 000	5 000	10 300	—
sugar (*Pinus lambertiana*)	0.36	57 000	8 200	30 800	3 400	7 800	2 400
Redwood (*Sequoia sempervirens*)							
old-growth	0.40	69 000	9 200	42 400	4 800	6 500	1 700
young-growth	0.35	54 000	7 600	36 000	3 600	7 600	1 700
Spruce							
black (*Picea mariana*)	0.46	74 000	11 100	41 100	3 800	8 500	—
Engelmann (*Picea engelmannii*)	0.35	64 000	8 900	30 900	2 800	8 300	2 400
red (*Picea rubens*)	0.40	74 000	11 100	38 200	3 800	8 900	2 400
Sitka (*Picea sitchensis*)	0.36	65 000	9 900	35 700	3 000	6 700	2 600
white (*Picea glauca*)	0.40	68 000	9 200	37 700	3 200	7 400	2 500
Tamarack (*Larix decidua*)	0.53	80 000	11 300	49 400	5 500	8 800	2 800

[a] Definition of properties: impact bending is height of drop that causes complete failure, using 0.71-kg hammer; compression parallel to grain is also called maximum crushing strength; compression perpendicular to grain is fiber stress at proportional limit; shear is maximum shearing strength; tension is maximum tensile strength; and side hardness is hardness measured when load is perpendicular to grain.

[b] Specific gravity is based on weight when ovendry and volume when green or at 12% moisture content.

[c] Modulus of elasticity measured from a simply supported, center-loaded beam, on a span depth ratio of 14/1.

[d] Coast Douglas-fir is defined as Douglas-fir growing in Oregon and Washington State west of the Cascade Mountains summit. Interior West includes California and all counties in Oregon and Washington east of, but adjacent to, the Cascade summit.

Data from US Department of Agriculture (1999) *Wood Handbook: Wood as an Engineering Material*. Madison, WI: US Department of Agriculture Forest Service; Niemz P (1993) *Physik des Holzes und der Holzwerkstoffe*. Weinbrenner, Germany: DRW-Verlag.

Table 5 Average parallel-to-grain tensile strength of some wood species

Common and botanical names of species	*Tensile strength*[a] *(kPa)*
Hardwoods	
Ash, European (*Fraxinus excelsior*)	130 000
Beech, American (*Fagus grandifolia*)	86 200
Beech, European (*Fagus silvatica*)	135 000
Birch, European (*Betula verrucosa*)	60 000
Hornbeam, European (*Carpinus betulus*)	135 000
Elm, cedar (*Ulmus crassifolia*)	120 700
Maple, European (*Acer pseudoplatanus*)	108 200
Maple, sugar (*Acer saccharum*)	108 200
Oak	
overcup (*Quercus* spp.)	77 900
pin (*Quercus palustris*)	112 400
European red oak (*Quercus robur*)	110 000
Poplar, balsam (*Populus balsamifera*)	51 000
Sweetgum (*Liquidambar styraciflua*)	93 800
Willow, black (*Salix nigra*)	73 100
Yellow-poplar (*Liriodendron tulipifera*)	109 600
Softwoods	
Baldcypress (*Taxodium distichum*)	58 600
Cedar	
Port-Orford (*Chamaecyparis lawsoniana*)	78 600
Western redcedar (*Cedrela* spp.)	45 500
Douglas-fir, interior North (*Pseudotsuga menziesii*)	107 600
Fir	
California red (*Abies magnifica*)	77 900
Pacific silver (*Abies amabilis*)	95 100
European (*Abies alba*)	80 000
Hemlock, western (*Tsuga heterophylla*)	89 600
Larch	
western (*Larix occidentalis*)	111 700
European (*Larix decidua*)	105 000
Pine	
Eastern white (*Pinus strobus*)	73 100
European (*Pinus sylvestris*)	100 000
loblolly (*Pinus taeda*)	80 000
ponderosa (*Pinus ponderosa*)	57 900
Virginia (*Pinus virginiana*)	94 500
Redwood	
virgin (*Sequoia sempervirens*)	64 800
young-growth (*Sequoia sempervirens*)	62 700
Spruce	
Engelmann (*Picea engelmannii*)	84 800
European (*Picea abies*)	80 000
Sitka (*Picea sitchensis*)	59 300

[a] Results of tests on small, clear, straight-grained specimens tested green. For hardwood species, strength of specimens tested at 12% moisture content averages about 32% higher; for softwoods, about 13% higher.

Data from US Department of Agriculture (1999) *Wood Handbook: Wood as an Engineering Material*. Madison, WI: US Department of Agriculture Forest Service; Niemz P (1993) *Physik des Holzes und der Holzwerkstoffe*. Weinbrenner, Germany: DRW-Verlag.

number of tests must be performed to obtain a reasonable estimate of parameters. Likewise, any calculation of dependent elasticity parameters based on experimental data must account for the stochastic nature of these parameters. Various sources of variability exist: for example, variability 'within' refers to the variability between specimens from within one board; variability 'between' is the variability resulting from differences between boards. **Table 6** lists the average variabilities of some mechanical properties of clear wood specimens.

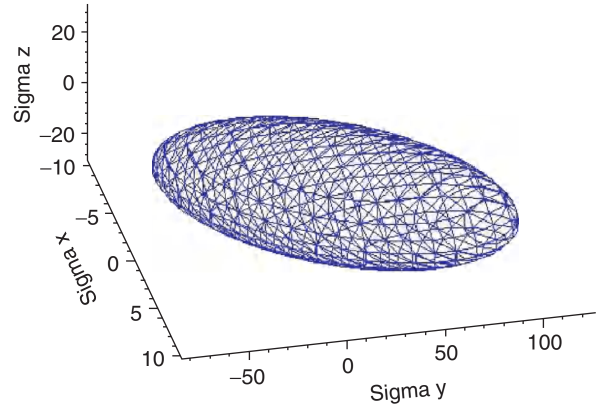


Figure 4 Typical strength surface for wood loaded by biaxial normal stress and shear.

Variability of mechanical properties of wood composites is significantly lower than that of solid wood but the same sources of variability exist.

Effect of Environmental Factors on Mechanical Properties

Environmental factors such as temperature, relative humidity of air (and associated equilibrium moisture content (EMC)), and their combination affect mechanical properties of wood and wood materials. Generally, the elasticity and strength parameters decrease with increased temperature and moisture content. Commonly, a linear function is used to approximate the change in mechanical properties with change in moisture content and temperature. It is assumed that moisture content change beyond fiber saturation point (FSP) will not significantly affect mechanical properties (**Figure 5**). One can calculate the mechanical property at any moisture content between 0% and FSP as

$$A_{MC} = A_{12}\left(\frac{A_{12}}{A_g}\right)^{\frac{12\text{-MC}}{M_P\text{-}12}}$$

where A_{MC} = property at desired moisture content, MC; A_{12} = property at 12% moisture content; A_g = property at MC above FSP; M_P = moisture content at which the properties of wood start to change when wood is dried from green (wet) condition (above FSP). This value can be taken as 25 for most species. The relationship between the

Table 6 Average coefficients of variation for some mechanical properties of solid wood and wood composites

Property	*Coefficient of variation (%)*			
	Solid wood	*Particleboard*	*Plywood*	*Medium density fiberboard (MDF)*
Bending strength	7–20[a]	8–10		
Modulus of elasticity in bending	9–23[a]			
Impact bending	25[b]			
Compression parallel to grain	8–20[a]		5–13[c]	
Compression perpendicular to grain	28[b]			
Shear parallel to grain, maximum shearing strength	14–22[a]		6–11[c]	
Tension parallel to grain	25[b]	12	18 6–16[c]	8
Side hardness	20[b]			
Toughness	34[b]			
Specific gravity	5–13[a]	2–6		

[a] Range of variabilities based on results of about 20 different species.
[b] Values based on results of tests of green wood from approximately 50 species. Same variation can be expected for wood at 12% moisture content.
[c] 6–27 specimens. Askhenazi EK and Ganov EV (1980) *Anizotropia Konstrukcionnych Materialov*. Leningrad, USSR: Machinostroenie.
Data from US Department of Agriculture (1999) *Wood Handbook: Wood as an Engineering Material*. Madison, WI: US Department of Agriculture Forest Service; Niemz P (1993) *Physik des Holzes und der Holzwerkstoffe*. Weinbrenner, Germany: DRW-Verlag.

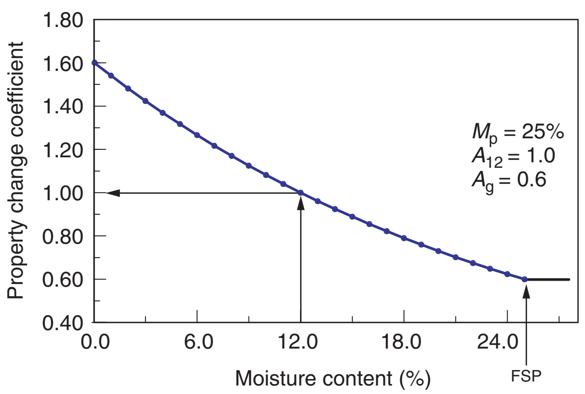


Figure 5 Effect of moisture content on mechanical properties of wood at constant temperature. For equations, see text. FSP, fiber saturation point.

MC and wood mechanical properties below FSP can also be approximated by a straight line. In general, values of mechanical properties of wood decrease with increased temperature. As with any polymeric material, the change in mechanical properties will depend on a glass transition temperature of individual wood components (*see* **Wood Formation and Properties**: Chemical Properties of Wood). The temperature effects can be either reversible (for temperatures below 100°C and relatively fast temperature changes, e.g. heating followed by immediate cooling) or irreversible (temperatures above 100°C or extended exposure to elevated temperature even below 100°C). Up to about 150°C, the decrease in elasticity and strength properties is approximately proportional to the increase in temperature and duration of heating.

Table 7 Effect of heating of Sitka spruce and Douglas-fir wood on bending strength of small clear wood (% at time = 0)

Time (hours)	*Temperature (°C)*			
	93	*120*	*150*	*175*
0	100	100	100	100
8	98	92	75	50
16	98	86	68	—
24	98	84	65	—
32	98	84	62	—

Data from US Department of Agriculture (1999) *Wood Handbook: Wood as an Engineering Material*. Madison, WI: US Department of Agriculture Forest Service.

The combined effect of moisture content and temperature is more complicated due to interaction between temperature and moisture content. **Table 7** shows the effect of temperature on bending strength of clear wood and **Figure 6** shows the effect of temperature and moisture content. Strength of wet wood decreases more rapidly with increased temperature than does strength of dry wood. **Figure 7** shows that temperature change affects various mechanical properties differently. From **Figures 6** and **7**, it follows that the time–temperature–moisture content interaction affects the rate at which mechanical properties of wood degrade. The relationships in the figures represent the trends and average properties. **Figure 8** shows the relative change in some strength and elasticity parameters of beech under elevated temperature and moisture.

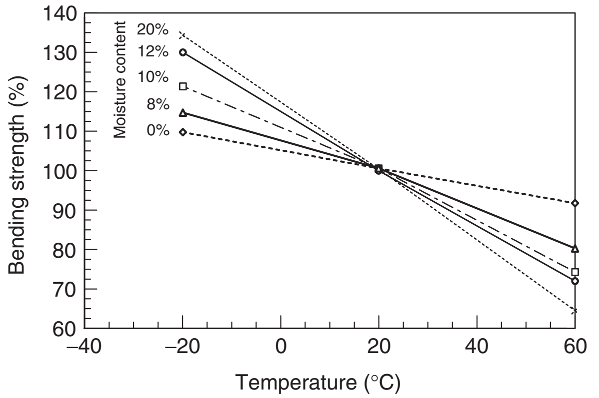


Figure 6 Combined effect of temperature and moisture on bending strength of wood. Data from Niemz P (1993) *Physik des Holzes und der Holzwerkstoffe*. Weinbrenner, Germany: DRW-Verlag and Dinwoodie JM (1981) *Timber, its Nature and Behavior*. New York: Van Nostrand Reinhold.

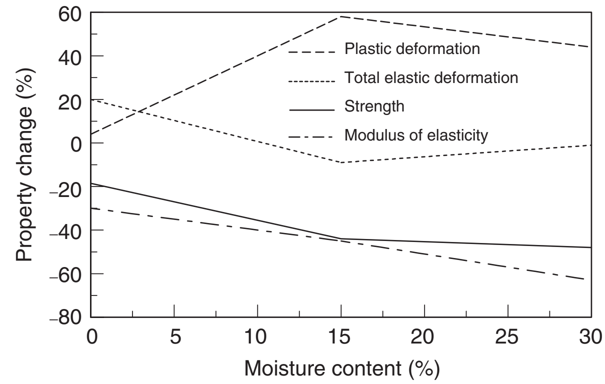


Figure 8 Relative change in mechanical properties of beech wood in bending under elevated temperature and moisture. Data from Kúdela J (1990) *Effects of Moisture Contents and Temperature on Mechanical Properties of Beech Wood*. PhD dissertation. Zvolen Slovakia: Technical University Zvolen.

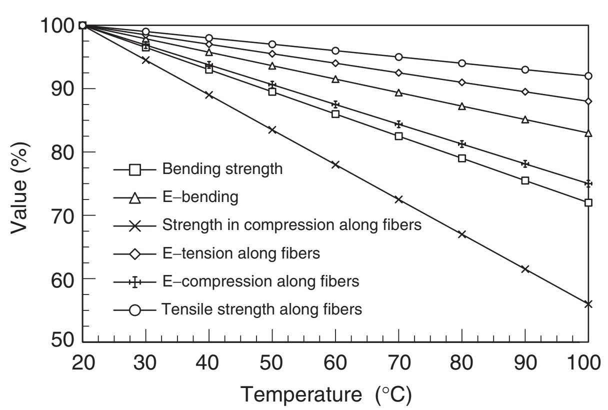


Figure 7 Effect of temperature on mechanical properties of wood. Data from Niemz P (1993) *Physik des Holzes und der Holzwerkstoffe*. Weinbrenner, Germany: DRW-Verlag.

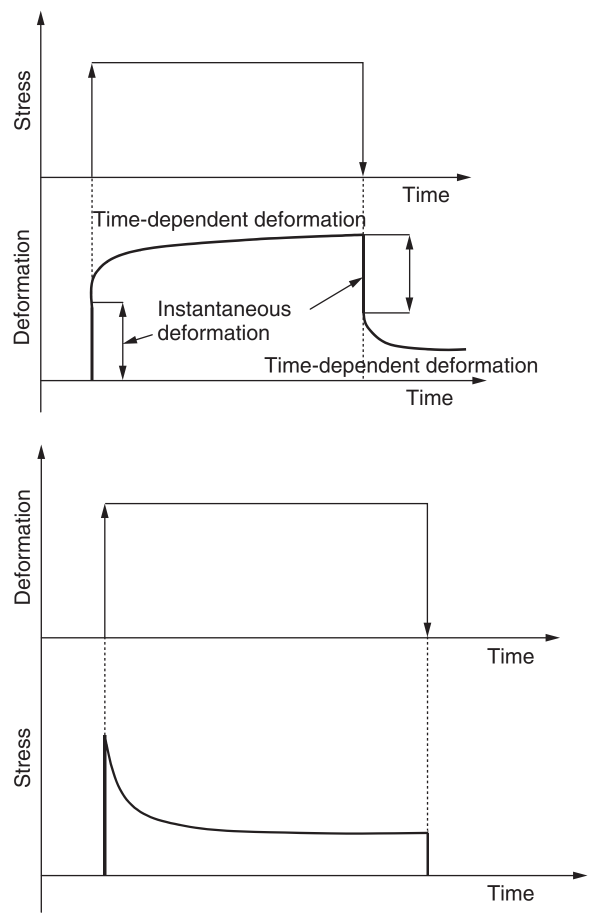


Figure 9 Creep and stress relaxation experiments.

Effect of Load History (Time) on Mechanical Properties of Wood and Wood Composites

Wood and wood materials can be considered viscoelastic materials. This means that the response of wood to the load will be affected by the load history. For example, deflection of a beam loaded by a constant load will increase with time (creep). If a fixed displacement is induced on a beam, then, over time, the load to maintain this displacement will decrease (stress relaxation). **Figure 9** shows the results of creep and stress relaxation experiments. The creep rate (or stress relaxation rate) increases with increased moisture contents (mechanosorptive creep) and temperature. Cyclic changes (temperature, moisture, or a combination of the two) further accelerate creep with increased creep rate during drying. However, wet wood will creep faster than dry wood if no changes in moisture content take place.

Increase in temperature will significantly increase the creep rate. Creep can be observed in wood composites where the total creep is a sum of the creep in wood material and wood–adhesive interface. Generally, creep rate of composites with nonwater resistant adhesives can be significantly higher than the creep rate for solid wood, especially under changing moisture conditions. Time delayed failure (creep failure) can occur as a result of creep or mechanosorptive creep. Various phenomenological models are used to model creep or stress relaxation of wood and wood composites (combination of dashpots, springs, and other elements such as ratchet element or frictional element) (**Figure 10**).

Dynamic Load and Fatigue

The apparent strength of wood and wood materials increases with increased rate of loading. The effect of load rate is shown in **Figure 11**. From **Figure 11** it follows that the apparent strength under impact load will be about 120% of the strength value obtained from the static test. Material (viscous) damping of wood and wood composites is very low, generally not exceeding 3%. Fatigue of the material is defined as number of cycles at given stress level (usually as a percentage of the ultimate stress) at which the material fails. The cycles can be zero or nonzero mean cycles. **Figure 12** shows the average fatigue life of wood loaded in bending by a cyclic load. The fatigue life is influenced by the environmental factors in the same way as the static parameters (monotonic load), except for the moisture content effect that is about twice larger for dynamically loaded wood.

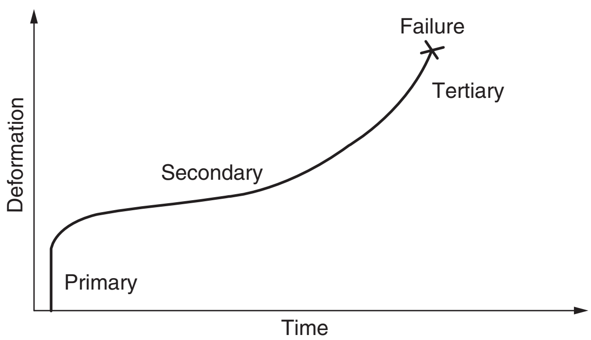


Figure 10 Primary, secondary, and tertiary stages of creep.

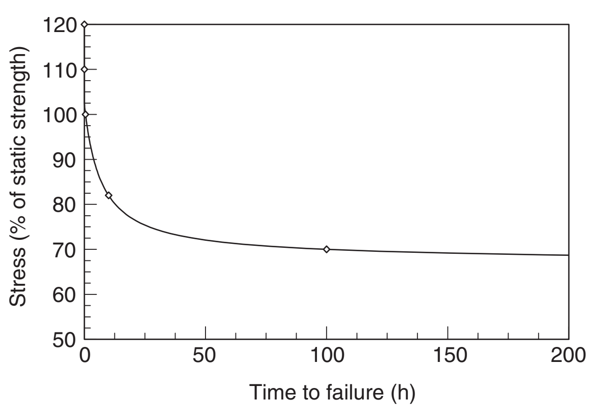


Figure 11 Time to the failure for small clear specimens of wood loaded in bending. Wood Handbook 1999.

Nonengineering Mechanical Properties

Other mechanical properties that can be defined are those associated with various end-use requirements and may include: abrasion properties, cleavage strength, nail or screw withholding capacities, dynamic impact resistance (toughness), hardness, etc. Since most of these parameters depend on testing procedures, the values have only comparative character.

Small Clear Specimens versus Full-Size Member Tests

Material properties of wood and wood composites are determined from standard tests of small clear specimens. Small clear specimens do not contain any defects such as knots or slope of grain and the values listed for small clear specimens, in most cases, will represent upper bounds for mechanical properties. In structural applications (*see* **Solid Wood Products**: Structural Use of Wood), members will contain natural defects and mechanical properties will be determined from full-size members containing the defects. The size, location, and number of the defects significantly affect the material strength and the variability of the properties.

Relationship between Mechanical Properties and Anatomical Structure of Wood

Wood anatomical structure significantly affects the mechanical properties of wood and wood

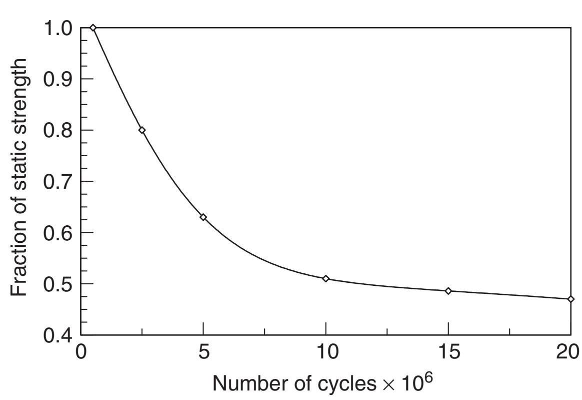


Figure 12 Fatigue life of wood. Data from Kollmann F (1952) *Technologie des Holzes und der Holzwerkstoffe*, 2nd edn. Berlin: Springer-Verlag.

composites. Parameters such as fiber length, wood density, orientation of microfibrils, and chemical composition of wood affect the properties of wood significantly. While a qualitative effect of anatomical features can be defined, the quantitative effect of these parameters is more difficult to establish. The mechanical properties are significantly affected by wood density, which is directly related to the cell wall thickness. Increasing the thickness of cell walls of latewood tracheids of pine by 36% and larch by 20% results in an increase in wood density by 18% and 20%, respectively. This increase in cell wall thickness will result in increase in compressive strength along fibers by 70–83%. **Figure 13** shows the influence of specific gravity on wood mechanical properties. The figures are based on average data and the relationships for individual species vary. The relationships are approximately linear. **Figure 14** shows the relationship between percentage of latewood and wood density and **Figure 15** demonstrates the effect of specific gravity on compressive strength. Other anatomical features, such as microfibril angle, ray size and proportion, and fiber length will significantly affect mechanical properties of solid wood. Slope of grain significantly affects mechanical properties and a simplified relationship between slope of grain and individual elastic or strength parameters known as Hankinson's formula is commonly used to estimate off-axis properties:

$$A_\alpha = \frac{A_0 A_{90}}{A_0 \sin^n(\alpha) + A_{90} \cos^n(\alpha)}$$

where A_α = property at angle α with respect to fibers, A_0 = property at zero angle with respect to fibers, A_{90} = property at 90° angle with respect to fibers, and α = angle.

Table 8 list values of exponent, n, based on the ratios of transverse and longitudinal properties $\frac{A_{90}}{A_0}$. The quantitative relationship between anatomical

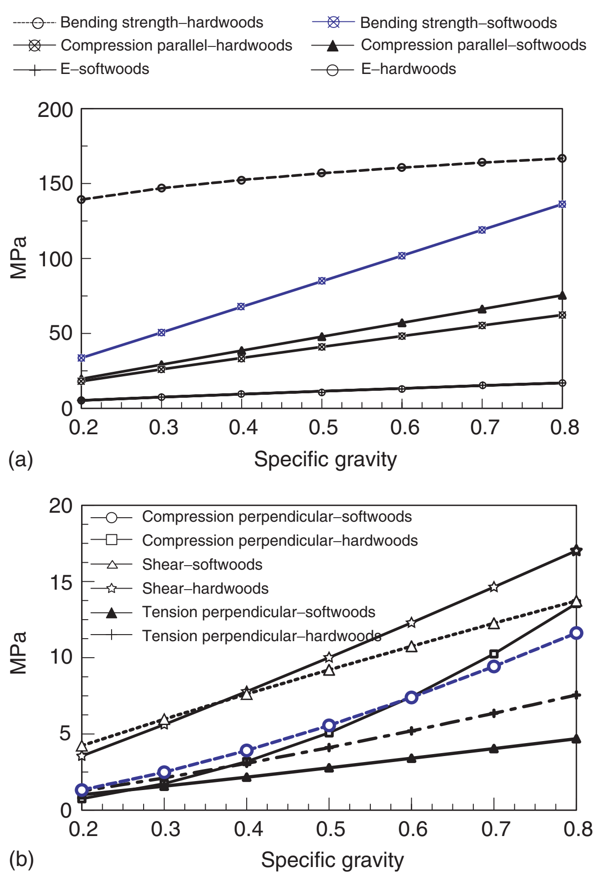


Figure 13 Effect of the specific gravity on mechanical properties of wood (oven dry weight and volume at 12% moisture content).

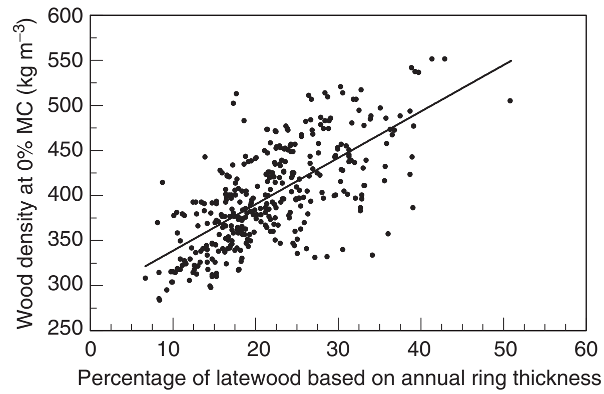


Figure 14 Effect of proportion of latewood on wood density for larch. Data from Dinwoodie JM (1981) *Timber, its Nature and Behavior*. New York: Van Nostrand Reinhold and Pozgaj A, Chovanec D, Kurjatko S and Babiak M (1993) *Structure and Properties of Wood*. Bratislava, Slovakia: Priroda Bratislava (in Slovak).

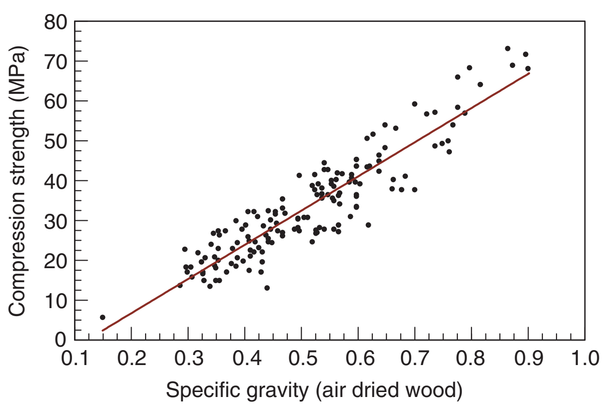


Figure 15 Effect of specific gravity on compression strength along fibers. Data from Dinwoodie JM (1981) *Timber, its Nature and Behavior*. New York: Van Nostrand Reinhold and Pozgaj A, Chovanec D, Kurjatko S and Babiak M (1993) *Structure and Properties of Wood*. Bratislava, Slovakia: Priroda Bratislava (in Slovak).

Table 8 Exponents in Hankinson's formula[a]

Property	*n*	A_{90}/A_0
Tensile strength	1.5–2	0.04–0.07
Compression strength	2–2.5	0.03–0.40
Bending strength	1.5–2	0.04–0.10
Modulus of elasticity	2	0.04–0.12
Toughness	1.5–2	0.06–0.10
Average exponent recommended for all properties	2.0	—

Wesche K (1988) *Baustoffe für tragende Bauteile*. Band 4. Holz und Kunstoffe. 2. Auflage (in German). Bauverlag GmbH. Wiesbaden und Berlin.

[a]Wood Handbook (1999) *Wood handbook: Wood as an Engineering Material*. US Forest Service, Forest Products Laboratory, Madison, WI. p. 482.

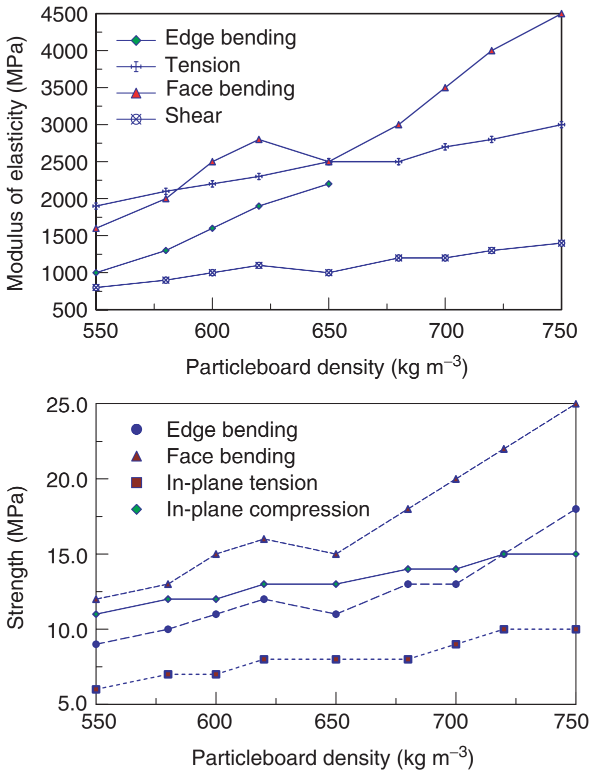


Figure 16 Effect of density on mechanical properties of particleboard. (Data from Niemz P (1993) *Physik des Holzes und der Holzwerkstoffe*. Weinbrenner, Germany: DRW-Verlag.)

features, chemical composition and wood mechanical properties is largely unknown.

Density significantly affects mechanical properties of wood composites and this is shown in **Figure 16.** All mechanical properties will increase with increased density with a linear trend.

See also: **Solid Wood Products**: Structural Use of Wood; Wood-based Composites and Panel Products. **Wood Formation and Properties**: Chemical Properties of Wood; Formation and Structure of Wood; Physical Properties of Wood. **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

American Society for Testing and Materials (2000) *Annual Book of ASTM Standards 2000*, Section 4, *Construction*, vol. 04.10, *Wood*. West Consthohocken, PA: American Society for Testing and Materials.

Bodig J and Goodman JR (1973) Prediction of elastic parameters for wood. *Wood Science* 5(4): 249–264.

Bodig J and Jayne BA (1993) *Mechanics of Wood and Wood Composites*. Malabar, FL: Krieger.

Calcote LR (1969) *The Analysis of Laminated Composite Structures*. New York: Van Nostrand Reinhold.

Dinwoodie JM (1981) *Timber, its Nature and Behavior*. New York: Van Nostrand Reinhold.

Hankinson RL (1921) *Investigation of Crushing Strength of Spruce at Varying Angles of Grain*. Air Service Information Circular no. 3(259), Material Section Paper no. 130. Washington, DC: Washington Government Printing Office.

Kollmann F (1952) *Technologie des Holzes und der Holzwerkstoffe*, 2nd edn. Berlin: Springer-Verlag.

Niemz P (1993) *Physik des Holzes und der Holzwerkstoffe*. Weinbrenner, Germany: DRW-Verlag.

Perelygin LM (1965) *Wood Science*, 2nd edn. Bratislava, Czechoslovakia: SNTL. (In Slovak.)

Timoshenko S and Young DH (1968) *Elements of Strength of Materials*, 5th edn. New York: Van Nostrand. NY. 377 p.

US Department of Agriculture (1999) *Wood Handbook: Wood as an Engineering Material*. Madison, WI: US Department of Agriculture Forest Service.

Physical Properties of Wood

S Avramidis, University of British Columbia, Vancouver, Canada

Introduction

This article addresses the fundamental physical properties of wood (sorptive, fluid transfer, thermal, electrical, and acoustical) that directly affect its processing and service characteristics such as sawing, drying, preservation, machining, gluing, insulation, and mechanosorptive behavior in service as a structural member or as simple panel or piece of furniture. Processing optimization and enhanced design of wood-based products is expected to result from a better understanding of how wood interacts with the environment.

Moisture Content

Wood is a porous, hygroscopic, anisotropic, nonhomogeneous biopolymer of cellular structure. Water is always naturally found in freshly cut green wood since it is a necessary component of the living tree. Therefore, when wood is cut from a tree in the form of lumber, veneer, particles, or fibers, it always contains water, the oven-dry basis percentage of which is defined as the green moisture content (M_g). Generally speaking, moisture content, M, is defined as the weight of water in wood (W_w) divided by the oven-dry wood weight (W_o) times 100%:

$$M = \frac{W_w}{W_o} \times 100\% \qquad (1)$$

where W_o is obtained by placing the wood specimen in an oven at 103 ± 2°C for 24 h or until constant weight. The nominator of eqn [1] is then obtained by subtracting the W_o from the initial wood weight (W_i). The level of green moisture content is a function of wood species, type of wood (sapwood vs. heartwood, the former always at much higher M_g), and season of tree harvest, and for the temperate zone species it can range between 31% and 250%.

Water in wood can be divided into two types. The first is the water of constitution, which is the water included in the chemical structure of wood, and it is inherent to the organic nature of its cell walls. This type of water cannot be removed without modifying the chemical composition of wood, and the wood therefore losing its natural appearance. The second type comes in three different phases according to the moisture content level. The bound phase comprises the water molecules dissolved or adsorbed by the sorption sites (hydroxyls) mostly in the amorphous areas of the cellulose chains and the hemicelluloses. The free water, which is liquid water, is found in the cell lumina, and the vapor water is also found in the lumina when they are not completely saturated with free water.

In the hygroscopic range ($0\% \leq M \leq 30\%$), all of the water in wood is considered as bound, located within the cell wall. At about 30%, all sorption sites are considered to be saturated with water molecules and the moisture content is then called fiber saturation point (FSP) or M_{fsp}. Any additional water molecules taken up by wood normally appear as free water in the lumina and pits. It is below M_{fsp} where most of the physical and mechanical properties of wood are affected by moisture content, e.g., strength decreases, wood shrinks, electrical resistance increases, and the biodeterioration hazard diminishes as moisture content tends toward 0%.

Owing to its hygroscopic nature, freshly cut wood exposed to ambient conditions will tend to assume a moisture content which is in balance with the water vapor conditions in the surrounding atmosphere. This is a quite slow process (called sorption) that is highly dependent on the ambient temperature (T) and relative humidity (H). When green wood finally reaches the equilibrium state, two things have happened to its original water content: (1) it has lost a considerable amount of water (all of the free plus some bound water) by a process called desorption and (2) its final moisture content, which is then called equilibrium moisture content (M_e), is somewhere within its hygroscopic range. The speed of desorption is proportional to T and inversely proportional to H.

Throughout the hygroscopic range, the relationship between the equilibrium moisture content and relative humidity (or relative vapor pressure in the ambient environment) at constant temperature is represented by a sigmoid curve commonly called the sorption isotherm (**Figure 1**). The M_e values of a green piece of wood exposed to successively decreasing relative humidities (desorption) will always be higher than those of the same specimen exposed to successively higher humidities (adsorption), both cases under the same temperatures (**Figure 1**). This phenomenon is called hysteresis; and the area enclosed between the hysteresis loop represents the difference in free energy between adsorption and desorption.

It must be emphasized here that given enough time, the M_e value after exposure of green wood to the ambient environment always range between 0% and 30%. There is no free water in wood when it has reached equilibrium with the normal ambient environment. This M_e range is maintained during service unless wood comes into contact with liquid water.

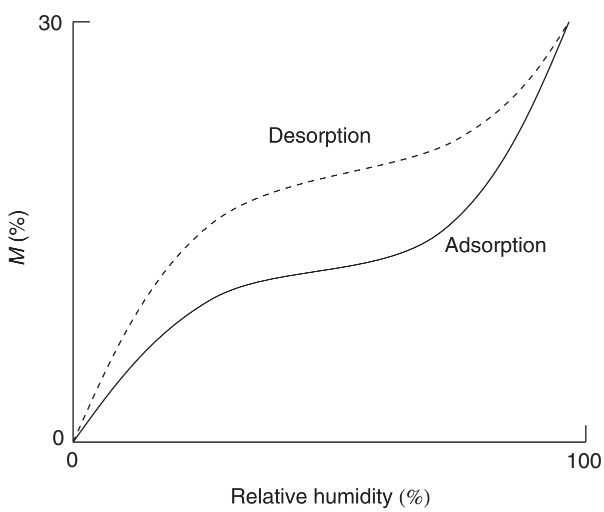


Figure 1 Typical moisture sorption isotherm for wood.

Density, Specific Gravity, and Porosity

Wood is made up of a mix of cells of a tubelike shape connected to each other in parallel and mostly oriented along the length of a tree. The cells are made of a thin wall and an empty area called the lumen. The existence of the cell wall material and the empty space in the lumen are the reasons why wood is classified as a porous material.

One important property that characterizes porous materials is density (ρ), defined as the amount of mass per unit volume and is expressed in kilograms per cubic meter. On the other hand, specific gravity (G) is the density of wood divided by the density of water and is dimensionless. Both ρ and G are used by the forest products industry interchangeably without considering the fact that both are highly dependent on moisture content and only in the case 0% moisture content (oven-dry or bone-dry) are numerically equal. This becomes evident from the equations that are used to calculate these two parameters:

$$\rho = \frac{W_M}{V_M}\,(\text{kg m}^{-3}) \tag{2}$$

$$G = \frac{W_o}{V_M \rho_w} \tag{3}$$

where W_M is the wood weight at moisture content M (kg), W_o is the oven-dry weight of wood (kg), V_M is the volume of wood at moisture content M (m^3), and ρ_w is the density of water (1000 kg m^{-3}). It is apparent, that eqns [2] and [3] are equal only in the case of oven-dry wood ($M = 0\%$) and above that, their difference increases as M increases (ρ always greater than G). A typical plot of both as a function of moisture content is shown in **Figure 2**. Once G is known, ρ can then be calculated from

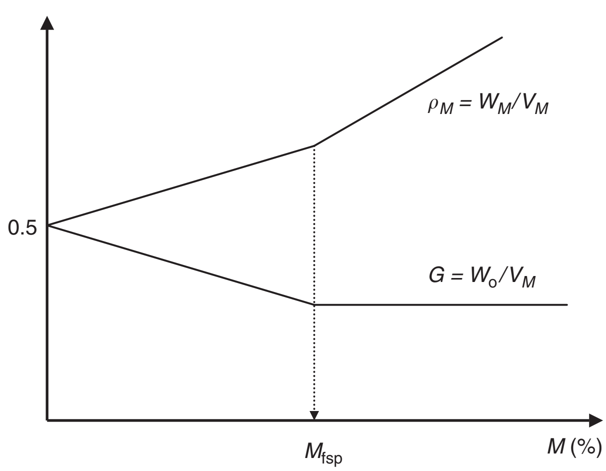


Figure 2 Change of wood density and specific gravity below and above the fiber saturation point.

$$\rho = G(1 + 0.01M)\rho_w \tag{4}$$

In industry, G is occasionally referred to as basic density. When knowing the specific gravity at one moisture content (M_1), we can calculate the specific gravity at another moisture content (M_2) by

$$G_2 = \frac{G_1}{1 + 0.01(M_2 - M_1)G_1} \tag{5}$$

valid only over the hygroscopic range.

The values for G of temperate zone hardwoods at 12% moisture content ranges between approximately 0.35 and 0.78, and for softwoods, between 0.34 and 0.62. The growth characteristics and age of trees within the same species and the location of wood also affect these values horizontally and vertically within the same tree. Density is a very important physical property since it directly affects dimensional changes, and mechanical, electrical, and acoustical properties, and furthermore the drying and machining characteristics of wood and wood-based products.

Porosity (V_a) is a number between 0 and 1 that indicates the fraction of void volume in wood. For example, a V_a that is equal to 0.6 indicates that 1 m^2 of wood is made up of 0.4 m^3 of solid cell-wall material and 0.6 m^3 of empty space (void volume) due to lumen and pit capillaries. Porosity is an important property because it helps with the estimation of the amount of liquids that can be introduced into the material for protection or for creating polymer-impregnated wood. It also provides an indirect indication of the ease of fluid flow through wood and of the thermal and acoustical insulation properties of wood.

Deriving from its definition, porosity is directly affected by density and moisture content their relationship given by

$$V_a = 1 - G(0.653 + 0.01M) \tag{6}$$

which is valid for all moisture contents above and below M_{fsp}. At full saturation of wood (all lumina are fully saturated with a liquid), porosity is equal to zero.

One of the highest porosity temperate-zone softwoods is northern white cedar with a V_a value of 0.77 and one of the lowest porosity softwoods is longleaf pine with a V_a value of 0.52. For hardwood, these values are 0.73 for black cottonwood and 0.40 for true hickory.

Dimensional Changes (Hygroexpansion)

Wood is a very unstable material when it gains or loses water molecules as a result of changes in ambient relative humidity and temperature. This is because the sorbed water molecules are mainly located in the amorphous areas of the microfibrils forming hydrogen bonds with the free hydroxyls (sorption sites). If water leaves wood because the air is quite dry, the cellulose chains tend to move closer to each other and this results in a reduction of the wood volume, i.e., shrinkage. The opposite phenomenon, adsorption, will therefore result in wood swelling.

Since the type of water that causes dimensional changes is bound water, this phenomenon is a characteristic of moisture content changes only in the hygroscopic range. Above M_{fsp}, free water accumulates in the wood pores and does not contribute to further separation of the amorphous chains and consequently, dimensional changes.

The amount of total volumetric swelling (V_{sw}) and shrinkage (V_{sh}) of wood over the hygroscopic range is a strong function of its specific gravity and moisture content and can be calculated from the following equations by assuming $M_{\text{fsp}} = 30\%$:

$$V_{\text{sw}} = 30G_{\text{o}} \tag{7}$$

$$V_{\text{sh}} = 30G_{\text{fsp}} \tag{8}$$

and between two moisture contents within the hygroscopic range:

$$V_{\text{sw}} = G_1(M_2 - M_1) \tag{9}$$

$$V_{\text{sh}} = G_2(M_2 - M_1) \tag{10}$$

The volumetric swelling (V_{sw}) and shrinkage (V_{sh}) between two moistures within the hygroscopic range can be calculated from the following equations:

$$V_{\text{sw}}^T = 2/3G_1(M_2 - M_1) \quad \text{and} \quad V_{\text{sw}}^R = 1/3G_1(M_2 - M_1) \tag{11}$$

$$V_{\text{sh}}^T = 2/3G_2(M_2 - M_1) \quad \text{and} \quad V_{\text{sh}}^R = 1/3G_2(M_2 - M_1) \tag{12}$$

where the superscript T denotes tangential direction and R denotes radial direction.

The anisotropic behavior of wood is evident when examining the total linear dimensional changes over the hygroscopic range. The total linear swelling from 0% to 30% moisture content is about 0.1% to 0.3% whereas the radial swelling ranges between 3% and 6% and the tangential between 6% and 12%. It is obvious that wood swells and shrinks very little in the longitudinal direction due to the same direction microfibrillar orientation, a trend that is not observed in the transverse direction (tangential and radial). Furthermore, there is a relationship of 2 to 2.5 between radial and tangential dimensional changes due to the presence of rays (one of the most accepted theories) that are restraining dimensional movement in the former direction. Abnormal and juvenile wood exhibit different levels of swelling and shrinkage, the latter exhibiting excessive longitudinal changes.

Dimensional instability is a major problem with wood that is exposed to wide variations of ambient relative humidity or it is in direct contact with liquid water. This can cause, in combination with anisotropicity, shape distortions and internal stresses that can manifest themselves as fissures through the structure of the wood. This problem can be avoided by dimensional stabilization, namely, the introduction of chemicals that introduce stability to wood at the microscopic level or by alteration and reduction of its hygroscopic nature and water affinity. Both methods have their advantages, disadvantages, and associated costs, and are mostly used for small-sized wood articles and specialty products. Examples of these stabilization processes are coating with film-forming finishes, heat treatment under vacuum or nitrogen, bulking with polyethylene glycol, acetylation, and formaldehyde crosslinking.

Fluid Flow through Wood

In drying and chemical treatment of wood (preservation, stabilization, veneer bolt steaming, pulping), we always have to deal with the flow of fluids (liquids and gases) to the surface of a timber or bolt from either its center or from the outside. In this case, the fluid is transferred mainly under a pressure differential through the interconnected void space of wood. It is important to emphasize here that although porosity is a measure of the scale of void volume in wood, high porosity does not suggest high flow rates. The voids must be connected to each other for this to happen; in other words, the pits should be 'open' to allow fluid flow from one lumen to the next. There are many examples where wood species with very high porosity value have a very low tolerance to fluid flow (refractory species).

Darcy's law governs the flow of liquids and gases through wood and the equations that describe this process under steady-state conditions are:

$$k_{\text{l}} = \frac{VL}{tA\Delta P}\left(\text{m}^3(\text{liquid})/\text{m Pa s}\right) \tag{13}$$

$$k_{\text{g}} = \frac{VL}{tA\Delta P}\left(\frac{P}{\bar{P}}\right)\left(\text{m}^3(\text{gas})/\text{m Pa s}\right) \tag{14}$$

where k_{l} and k_{g} are the superficial permeability coefficients to liquids and gases, respectively; V is the volume of flow (m^3); L is the length of wood (m); t is time (s); ΔP is the pressure drop across wood (Pa); and $\bar{P}$ is average pressure between the two ends of wood (Pa). The superficial permeability coefficient is a measure of how fast fluid will flow through various wood species, but as it can be seen in eqns [13] and [14], it is highly affected by the compressibility of the fluid (gases vs. liquids). A better way of expressing permeability levels is by excluding the effect of the fluid and converting this property to one that is only affected by the structure of wood, i.e., specific permeability (K), which is calculated by:

$$K = \mu_l k_l = \mu_g k_g \qquad (15)$$

measured in $m^3\,m^{-1}$, where μ is the viscosity of the measuring fluid (Pa s). It is obvious from eqn [15] that K is independent of the type of measuring fluid and once the superficial permeability is measured by, e.g., dry air the specific permeability can then be calculated.

Although Darcy's law is mainly used to measure the permeability coefficient of various species so that fluid flow under different pressures can be predicted, it must be emphasized here that the law applies to laminar flow which is not always the case in wood. Further to laminar or viscous flow, in wood with such small pore sizes, we may have turbulent flow, nonlinear flow due to kinetic energy losses at the entrance of short capillaries (i.e., pits), and slip flow or Knudsen diffusion due to mean free path of gases being larger than the size of a pore (i.e., margo membranes). Total levels of volumetric fluid transfer can then be a combination of two or more of the above types of flow.

Permeability is also a physical property that is greatly affected by the anisotropic nature of wood. Longitudinal permeability coefficients are 15 to 50 000 times larger than the transverse ones due to the orientation of the wood fibers. Not much difference exists between radial and tangential direction; however, the K values of the former are slightly higher due to the extra flow path provided by the rays. Sapwood is normally more permeable than heartwood and the species anatomy will also affect K. An example very commonly cited is the difference between red oak and white oak. Both have the same density and porosity, but red oak is more permeable by a factor of 10 000 due to the lack of tyloses which are very pronounced in white oak and greatly reduce fluid flow.

Aspiration and embolism are two phenomena that also reduce permeability. The former is the result of moving the torus/margo system of the bordered pits due to capillary forces during drying and permanently attaching them by hydrogen bonds to the cell wall thus closing any capability of communication between two adjacent lumina. The latter is the result of air bubbles plugging the pits thus not allowing further fluid flow through them. Both significantly reduce the value of K and hence reduce the uptake of liquid preservatives and pulping chemicals during wood processing.

Molecular Flow (Diffusion)

Molecular flow or diffusion is a mass transfer mechanism involved in processes such as drying below M_{fsp}, mechanosorptive behavior of wood in service, and flow of moisture through wall systems, amongst others. The flow of molecules is by activation and random and spontaneous 'jumps' from one sorption site to another under the influence of a concentration (or moisture) gradient. Bound diffusion through the cell walls is quite pronounced during drying and sorption, but also diffusion through the lumina (inter-gas) is also an important component of the total diffusive flux.

Fick's law describes the process of steady-state diffusion as follows:

$$D = \frac{wL}{tA\Delta C} \qquad (16)$$

where D is the diffusion coefficient ($m^2\,s^{-1}$), w is the weight of fluid transferred (kg), and ΔC is the driving force for diffusion, namely, the concentration difference ($kg\,m^{-3}$), and the other terms are the same as in eqn [14]. Since moisture diffusion is probably the most important for wood processing, ΔC can be substituted in eqn [16] by ΔM, which in turn will make more sense from the calculation point of view. After this, eqn [16] becomes

$$D = \frac{100wL}{tA\rho_w G_M \Delta M} \qquad (17)$$

The gross wood diffusion coefficient is a composite of bound water and inter-gas vapor diffusion and it is highly affected by moisture content, temperature, species and type of wood, and last but not least, direction. Specifically, D is directly proportional to moisture content and temperature since higher moisture levels will swell the cell walls thus creating new paths of flow and the higher temperature will provide the extra thermal energy required for faster molecular movement. The wood species and type (heartwood vs. sapwood) have an effect on D through density and chemical composition, which affect accessibility to sorption sites. Finally, longitudinal D values are higher that transverse ones at low moisture content values in the hygroscopic range, but the difference decreases by increasing moisture content toward the fiber saturation point.

It must be emphasized here that the process of diffusion is very slow when compared to bulk flow or heat transfer, and thus it is the controlling mechanism in drying where total processing time is concerned. Unfortunately, there are no reliable methods of improving the diffusion coefficient of wood at an industrial scale so that the drying speed of timbers can be increased. Attempts have been made with presteaming, hot water and surfactant solution dipping, ultrasonic field exposure, and freezing as possible methods with some success, more in improving permeability than diffusion.

Thermal Properties

Wood is always exposed to thermal loads either during processing, i.e., drying, heat stabilization, preservation, finishing, etc., or in service, i.e., as part of a wall system or a structural component, due to changing environmental temperatures. The amount of thermal energy absorbed and transferred through wood is affected by its thermal properties, namely, specific heat and thermal conductivity.

The specific heat of wood is defined as the amount of heat required to raise the temperature of 1 gram of wood by 1°C. The specific heat can be calculated from the following empirical formula:

$$c_p = \frac{1176 + 5859m}{1 + m} \qquad (18)$$

where c_p is the specific heat (kJ kg^{-1} K^{-1}); and m is the fractional moisture content between 0.05 and 0.30. Equation [18] is valid at $T = 30$°C. It is apparent that c_p is a strong function of moisture content, but it also is a function of temperature and wood species. Values of c_p will range between 1.3 and 1.9 (kJ kg^{-1} K^{-1}) at 30°C and between 0% and M_{fsp}.

Transfer of thermal energy through wood by conduction takes place by molecular interaction in the cell walls. Fourier's law describes steady-state flow of heat as follows:

$$K_\theta = \frac{HL}{tA\Delta T} \qquad (19)$$

where K_θ is the thermal conductivity coefficient (W m^{-1} K^{-1}); H is the quantity of heat transfer (J); and ΔT is the driving force, temperature difference, that drives heat flow (°C). K_θ will range between 0.08 and 0.17 W m^{-1} K^{-1} for oven-dry hardwoods and 0.08 and 0.14 W m^{-1} K^{-1} for oven-dry softwoods. For moisture content of 12%, the ranges are 0.10 to 0.21 W m^{-1} K^{-1} and 0.09 to 0.17 W m^{-1} K^{-1} for hardwoods and softwoods, respectively. For comparison, the K_θ of water is 0.59, and of dead air, 0.024 W m^{-1} K^{-1}.

Wood is a good thermal insulator; however, K_θ increases as wood density and moisture content increase. Furthermore, it is also affected by the anisotropic behavior of wood, that is, K_θ is greater in the fibers direction (longitudinal) than across (transverse) the timber.

Wood can also be a source of thermal when it burns (exothermic reaction) and this heat release per kg of wood is called heat of combustion (Q_c) measured in kJ kg^{-1}. During combustion, gases are released by thermal decomposition of wood that ignite and burn and ash is left as a solid byproduct. Spontaneous combustion can take place when wood is heated to 275°C in the presence of oxygen. This temperature is highly affected by the moisture content of wood, the species (anatomy), extractive types, and content, density, and wood dimensions. Fire resistance of wood can be increased by partially filling the lumina with special chemicals (fire retardants) that either increase its ignition point or delay its burning rate.

The Q_c value between species does not differ much and is about 19 600 kJ kg^{-1} when wood is oven-dry (no moisture present). When water is adsorbed in the wood cell walls, Q_c tends to decrease and when free water is present in the lumina ($M > 30\%$), Q_c normally drops to about 15 000 kJ kg^{-1}.

Continuous and long exposure of wood to elevated temperatures can also result in thermal degradation. This phenomenon is manifested by chemical breakdown of mostly hemicelluloses and cellulose with time and a loss of mass and strength. The rate of thermal degradation varies between wood species and increases with temperature and time of exposure. Controlled thermal exposure in the absence of oxygen can result in crosslinking reactions in the amorphous areas of cell walls, thus resulting in improved dimensional stability.

Electrical Properties

Wood, when dry, is an excellent electric insulator. However, this advantage diminishes when moisture content increases within the hygroscopic range and above the fiber saturation point (**Figure 3**). At a moisture content of 7%, the Douglas-fir's electrical resistance, a measure of the ease with which electric current flows through wood under the influence of a voltage differential, is 22 400 MΩ but it decreases to 0.60 MΩ at 24% moisture content. This dramatic

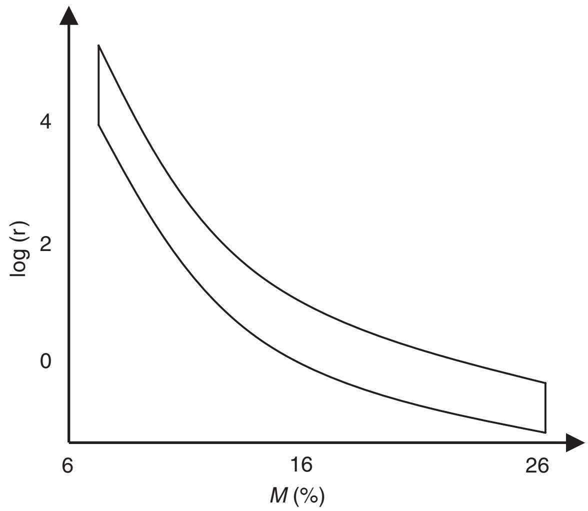


Figure 3 Curves of logarithm of electrical resistance against moisture content for most North American wood species.

drop as a function of moisture content is used by the industry to measure the amount of bound water present in wood with a specially designed piece of equipment call pin-type resistance moisture meter (or *M*-meter). The *M*-meter directly measures electrical resistance between the tips of two metal pins and through a conversion formula, calculates and displays the moisture content of the wood matter between the pins.

The electrical resistance is a strong function of species, temperature and fiber direction (anisotropicity). This is why when resistance *M*-meters are used, they need to be calibrated for species and temperature and also the pins should be placed parallel to the fiber direction. Density has no clear effect on electrical resistance.

When wood is placed within an alternating field, thermal energy is produced within the piece of wood due to the friction of the water molecules in the cell walls and lumina. The friction is the result of their dipolar nature and thus the rotation, vibration, and linear motion of ions when under an electric field of high frequency. This phenomenon is called dielectric heating. The amount of heat generated is predicted by the loss factor of wood that is one of the material's dielectric properties. The loss factor is strongly affected by moisture content (proportional relation), field frequency, species, and, to a lesser degree, wood temperature. This is a complicated dielectric property of wood that is quite difficult to measure directly. However, dielectric heating has served the wood processing industry in accelerated gluing and drying processes such as radio-frequency vacuum drying.

Wood also has piezoelectric properties, like quartz crystals, where electric polarization appears under compressive or tensile stress or mechanical strain develops under the application of electric field. The intensity of piezoelectricity in wood depends on its degree of crystallinity and the degree of orientation of crystallites. This phenomenon has been used in the development of nondestructive methods of evaluating local wood strain and the influence of knots, density, fiber angle, etc., on a dynamic system.

Acoustical Properties

The acoustical properties of wood relate to the production of sound with direct impact, and to the behavior of wood in relation to sound produced by other sources that is transmitted through air impacting wood in the form of sound waves.

Wood is seldom used as a direct source of sound. The pitch of sound produced is dependent on the frequency of the wood vibration. This frequency is a function of the wood dimensions, moisture content, density, and stiffness. When sound waves are produced by another source, they impact the surface of wood and a portion of their acoustic energy is absorbed by wood whereas the rest is reflected. Of the absorbed sound, some will be converted to thermal energy and some will be transmitted through the piece of wood. The density and thickness of the wood substrate and the frequency of the sound waves affect the amount of sound absorbed. The transmission of sound is quite fast, namely, 3500 to 5500 m s^{-1} in the longitudinal direction and 2300 to 3200 m s^{-1} in the transverse direction, as compared to 340 m s^{-1} through air and 1400 m s^{-1} in water. Sound velocity level is strongly affected by density, direction in relation to fiber, wood defects and abnormal growths, and moisture content.

Industry has used the strong relationship of sound transmission to various wood attributes in order to develop nondestructive evaluation techniques that estimate stiffness and strength of wood, internal decay in trees and timbers, fiber angle and the presence of juvenile and reaction wood, among other attributes, with variable level of success.

See also: **Tree Breeding, Practices**: Biological Improvement of Wood Properties. **Wood Formation and Properties**: Formation and Structure of Wood; Mechanical Properties of Wood; Wood Quality. **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

Haygreen JG and Bowyer JL (1996) *Forest Products and Wood Science: An Introduction*, 3rd edn. Ames, IA: Iowa State University Press.

Kollman FFP and Cote WA (1968) *Principles of Wood Science and Technology*, vol. 1, *Solid Wood*. New York: Springer-Verlag.
Siau JF (1995) *Wood: Influence of Moisture on Physical Properties*. Blacksburg, VA: Department of Wood Science and Forest Products, Virginia Polytechnic Institute and State University.
Skaar C (1988) *Wood–Water Relations*. New York: Springer-Verlag.
Stamm AJ (1964) *Wood and Cellulose Science*. New York: Ronald Press.
Tsoumis GT (1991) *Science and Technology of Wood*. New York: Chapman & Hall.
US Department of Agriculture Forest Products Laboratory (1999) *Wood Handbook: Wood as an Engineering Material*. Madison, WI: Forest Products Society.

Chemical Properties of Wood

I S Goldstein, North Carolina State University, Raleigh, NC, USA

Introduction

The chemical properties of wood are inextricably associated with and dependent upon its chemical composition. Fortunately, the major wood components are not numerous, and with only minor variations are found across all woody species. The chemical behavior results from the interaction of the structural features known as functional groups with either other chemical entities or physical factors such as heat and light. After a description of the chemical components of wood including their relevant functional groups, the most important chemical interactions will be discussed.

Composition of Wood

The chief components of woody plant cell walls are cellulose, hemicelluloses, and lignin. In bark these structural components may be exceeded by suberins and phenolic acids. The final category of wood components is known as extractives. These materials are much less abundant, variable in structure or quantity, usually soluble, and often species or genus specific.

Cellulose

Cellulose is the chief cell wall component, and comprises 40–45% of the wood. It is a long chain polymer of glucose units linked together by glycosidic bonds, a type of acetal ether linkage (O–C–O–C). The other, and most important, functional group in cellulose is the hydroxyl (–OH). Each glucose unit in the chain has three free hydroxyl groups that are capable of reacting with others in a neighboring chain or with water to form hydrogen bonds (H–O–H—H–O–C). Unlike starch which is also a glucose polymer, but with an α-configuration leading to an amorphous structure, the β-configuration in cellulose leads to stiff and straight chains that can form highly ordered crystalline regions. Cellulose contains disordered or amorphous regions as well.

Hemicelluloses

Associated with the cellulose in the cell wall are carbohydrate polymers known as hemicelluloses. They consist for the most part of sugars other than glucose, both pentoses and hexoses, and are usually branched and of much lower molecular weight than cellulose. In softwoods they comprise 25–30% of the wood in decreasing abundance as mannose, xylose, glucose, galactose, and arabinose. In hardwoods the hemicelluloses account for 20–35% as xylose, mannose, glucose, and galactose. The functional groups as in cellulose are glycosides and hydroxyls, with the addition of acetyl ester groups formed by the reaction of acetic acid with hydroxyls.

Lignin

Lignin is the third major wood cell wall component (20–30%). It serves as a cement between wood fibers, as a stiffening agent within the fibers, and as a barrier to the enzymatic degradation of the cell wall. Lignins are three-dimensional network polymers of phenylpropane units. More than two-thirds of the linkages are ether bonds, the rest are carbon–carbon bonds. Some free phenolic hydroxyls are found on the phenyl groups, but most have been etherified with methanol to methoxyl. Softwood and hardwood lignins differ in methoxyl content and in the degree of crosslinking. Hardwood lignins have more methoxyls, but these groups block potential reactive sites and reduce crosslinking. There is evidence that covalent linkages exist between lignin and the hemicelluloses.

Bark Components

Bark fibers contain cellulose, hemicelluloses, and lignin, but in much lower concentration. The cellulose content may be as low as 20–30%. Two other components unique to bark, suberins and phenolic acids, account for this. Suberins consist of long-chain esters. Their content varies from 2–8% in pine, fir, and oak to 20–40% in birch, and 35–40% in cork oak. Phenolic acids are high molecular weight phenols, but lower in weight than lignin. They have a high carboxylic acid content, and lower methoxyl content. They may comprise 50% of the weight of conifer bark.

Extractives

Extractives are the extraneous wood components that may be dissolved in water or organic solvents. They are often genus or species specific. Major categories include sugars, fatty acids and their esters, acids, aldehydes, alcohols, terpenes, tannins, quinones, and volatile oils.

Chemical Interactions of Wood and its Components

It is customary in considering the interactions of wood and chemicals to concentrate on the result of the chemical action. The chemical technology of wood is usually divided into such categories as fractionation of wood into its separate components, the conversion of the wood components into various low molecular weight or polymeric products, or the deterioration of wood by chemicals.

However, all these processes possess a common feature. They all begin with the interaction of a chemical reagent with the bonds and functional groups present in the wood. The structures of wood and its components have been defined above. Chemical properties of wood may thus be related to specific reactions of reagents and reactive sites in the wood. Physical factors such as heat, light, and ionizing radiation can also effect chemical changes in wood and its components.

Water

Wood–water relationships are usually considered from a physical or mechanical perspective, involving either drying or dimensional change. However, the underlying phenomenon is chemical in nature, involving the formation of hydrogen bonds between the hydroxyl groups in water and the many hydroxyl groups in the 75% of wood that is carbohydrate in nature.

All the hydroxyl groups are not available for hydrogen bonding and thus adsorption of water. In the crystalline regions of the cellulose, hydroxyls in adjacent linear chains hydrogen bond with each other. This prevents the dissolution of cellulose in water, in contrast to starch whose helical or branched chains cannot bond to each other by hydrogen bonds. In the noncrystalline or amorphous regions of the cellulose, and in the hemicelluloses, the hydroxyl groups are free to bond with water, and the bound water can bond to more water, leading to adsorptions of up to 30% of the wood weight at the fiber saturation point with commensurate changes in wood volume.

Hydrogen bonds are much weaker than covalent bonds, but in the aggregate they represent large amounts of energy, and require large inputs of heat for their disruption in the drying process in kilns. Even at low relative humidities the driving force of hydrogen bond formation ensures that wood contains appreciable quantities of bound water.

Hydrolysis

Hydrolytic reactions are the most important in their effect on the properties of wood. Both carbohydrates and lignin are susceptible. In carbohydrates the affected groups are the acetal and ester linkages. The acetals are more important because of their greater abundance and their structural role in chain formation. Both acids and alkalis can cause hydrolysis, but the chain scission by acids has the greatest impact on wood properties.

Ester hydrolysis by alkali liberates free hydroxyl groups on the hemicellulose with a reduction in alkalinity in the solution. In acid hydrolysis, however, the liberation of free acetic acid can increase the acidity leading not only to further ester hydrolysis, but also to cleavage of acetal linkages and lignin bonds in the autohydrolysis reaction. At its maximum extent acetic acid liberated by steam can completely hydrolyze the hemicellulose to its constituent monosaccharides and convert the lignin into soluble fragments.

Acid hydrolysis of the acetal linkages in wood polysaccharides proceeds by fission of the glycosyl oxygen bond between the rings. Because of steric factors the rate of hydrolysis of crystalline cellulose is several orders of magnitude less than that of simple glycosides or noncrystalline polysaccharides. However, in the amorphous regions of the cellulose and the hemicelluloses the acetals are subject to ready attack. Under alkaline conditions acetal hydrolysis is much slower and proceeds only at higher temperatures.

Hydrolysis of the lignin linkages under both acidic and alkaline conditions has been studied extensively because of its importance in the pulping of wood. The various ether linkages respond differently to different reagents. Some respond to mild hydrolysis with hot water or dilute acetic acid. Others are cleaved by acid sulfite pulping, while alkaline reagents at elevated temperatures as in Kraft pulping break ether linkages between the phenylpropane units with liberation of phenolic hydroxyl groups. Cleavage of C–C bonds can also occur during acid hydrolysis, as well as in trace amounts under alkaline conditions.

Oxidation

Both the carbohydrate and lignin components of wood are affected by oxidizing reagents. Mild oxidants such as chlorine, bromine, or iodine convert the aldehyde end groups in the wood polysaccharides to carboxylic acids. Nitrogen dioxide converts primary hydroxyl groups to carboxyl groups. Periodic acid is a specific oxidant for adjacent diols. Stronger oxidants such as nitric acid, potassium dichromate, and potassium permanganate cause extensive degradation of carbohydrates to a series of dicarboxylic acids.

Molecular oxygen in the presence of alkali generates hydroperoxides which can result in stepwise depolymerization of polysaccharides known as peeling. Carbonyl groups are introduced into polysaccharides by the action of chlorine, hypochlorite, and ozone. Hydrogen peroxide and chlorine dioxide react much more slowly and are less degrading, so they are favored in pulp bleaching.

Oxidations of lignin may be placed in three categories: degradation of lignin to aromatic carbonyl compounds and carboxylic acids, degradation of aromatic rings, and oxidation of specific functional groups.

The first category includes oxidations with nitrobenzene, molecular oxygen, or metal oxides under alkaline conditions. Aromatic ring degradation results from exposure to peracetic acid, nitric acid, chlorine, chlorine dioxide, ozone, and the anions of hypochlorous and chlorous acids. Neutral permanganate can oxidize both side chains and rings. Periodic acid and alkali peroxides oxidize specific functional groups. Lignin oxidation is also involved in the photodegradation of wood and the enzymatic degradation of lignin.

Strong oxidants such as permanganate and dichromate in acidic solution degrade lignin completely to carbon dioxide and dibasic acids. A group of oxidants between the strong ones and the side chain oxidants, attack primarily the aromatic nuclei of the lignin. Because they show a relative selectivity in attacking lignin more rapidly than carbohydrate, chlorine, nitric acid, chlorine dioxide, sodium hypochlorite, peracetic acid, hydrogen peroxide, and ozone have found utility in the bleaching of the residual lignin in pulp after removal of most of the lignin by pulping.

Decrystallization

The crystallinity of cellulose is an inherent property that governs its mechanical properties, affinity for water, and accessibility to chemical reagents. Since the crystallinity is the result of interchain hydrogen bonding, changes in crystallinity reflect decreases or increases in this bonding.

Although water alone cannot break the interchain hydrogen bonds, decrystallization can be brought about by many reagents. The extent of decrystallization may vary from partial swelling to increase chemical accessibility to complete dissolution that permits reprecipitation and the formation of regenerated cellulose fibers such as rayon.

These reagents include concentrated sodium hydroxide; amines; metalloorganic complexes of copper, cadmium, and iron; quaternary ammonium bases; concentrated mineral acids (sulfuric, hydrochloric, phosphoric); concentrated salt solutions (beryllium, calcium, lithium, zinc); and mixtures of organic solvents.

An increase in crystallinity is unusual, but it does occur after hydrolysis of amorphous cellulose. The broken chains have greater freedom to form more highly organized structures.

Discoloration

Staining or discoloration of wood may result from chemical processes that convert originally colorless or light-colored, naturally occurring extractives into intensely colored products.

Most of the so-called chemical stains result from oxidation of certain wood extractives by air during air seasoning or kiln drying. Colors observed include shades of brown, blue, green, yellow, and red. Affected species include both hardwoods (oak, birch, maple, alder, basswood, gum, etc.) and softwoods (pines, hemlock).

Wet wood can also discolor by contact with iron or copper when tannins are present to form black iron tannate or reddish copper tannate. These metals may also initiate oxidation of the wood by free radical mechanisms.

Other Functional Group Reactions

The functional groups in wood and its components can also enter into the normal reactions of the various groups. Thus hydroxyl groups may undergo esterification or etherification. Cellulose esters of both inorganic and organic acids are important industrial products, most notably cellulose nitrate and cellulose acetate. Cellulose ethers such as methylcellulose and carboxymethylcellulose are also important. These reactions have also been carried out on whole wood. Organic chemicals that have been used to react with the hydroxyl groups include acid anhydrides and chlorides, aldehydes, alkyl chlorides, carboxylic acids, epoxides, isocyanates, lactones, and nitriles.

The carboxylic acid and phenolic hydroxyl groups in wood contribute to its natural acidity. These acidic groups can act as ion exchange agents with sodium in alkaline solutions, or with copper and zinc in wood-preserving solutions.

Reducing end groups such as aldehydes in wood sugars are the agents which convert hexavalent chromium in some wood preserving formulations to insoluble forms.

Surface Chemistry of Wood

The utilization of wood and wood fibers involves in more cases than not the interaction of the woody material with natural and synthetic polymers in the form of adhesives and coatings. The chemistry of the wood surface may influence the conversion of liquid formulations to solid form, and certainly plays a critical role in the wetting and bonding of these substances to the wood surface. Aside from the bonding forces themselves, such factors as pH, moisture content, and extractives have a direct influence on bonding.

The bonding forces may be of three types. London, van der Waals, or dispersion forces act between all atoms and are mainly responsible for the cohesion of all materials. Dipole–dipole interactions between positive and negative charge centers are especially important in wood with its many hydroxyl groups. In the hydrogen bond the positive proton is shared between two electronegative atoms, most frequently nitrogen or oxygen. Finally, true chemical bonds, either covalent or ionic, may form between the functional groups in the wood and those in the coating or adhesive.

Most important resins used with wood are of the thermosetting type whose cohesive strength exceeds that of the wood. They include urea–formaldehyde, melamine–formaldehyde, phenol–formaldehyde, diisocyanates, polyisocyanates, and polyamides. Their polar groups can form strong hydrogen bonds with the hydroxyl groups in wood, and their functional groups can interact with the wood.

The polymeric adhesives and coatings are generally applied in liquid form, and then cured to solids. The acidity of some species of wood can interfere with these reactions, especially those that are base catalyzed. Both soluble and insoluble acids have been implicated. Wood extractives that compete with the resins for formaldehyde can also disrupt the curing process.

Modification of the wood surface to introduce more functional groups capable of covalent bond formation has been studied. Activation of the surface by heat, acids, or oxidants may be followed by three approaches. Direct covalent bonds may be formed between two wood surfaces. Bifunctional monomers may be used to join the surfaces. And finally, polymeric chains may be used to bridge the surfaces.

Chemical Effects of Physical Factors

The chemical properties of wood and the wood itself may be modified by physical factors. Heat is most important, but light and ionizing radiation also cause changes in the wood chemistry.

Heat

Chemical reactions involve the breaking of bonds in the reactants and the formation of new bonds in the reaction products. These processes are accelerated by thermal energy or heat since the bonds represent states of minimum energy. However, even in the absence of external reagents the chemical bonds holding molecules together are subject to scission and rearrangement when sufficient thermal energy is applied.

In the case of wood a description of the effect of heat is complicated by the variations in composition between species. Examination of the behavior of the individual components can provide insights that may be extended to whole wood.

As wood is heated above room temperature the water adsorbed by the hygroscopic wood components is first driven off. At higher temperatures the wood components start to decompose with the evolution of gases. Hemicelluloses show initial decomposition at about 120°C, lignin above 130°C, and cellulose above 160°C. The gases evolved during this slow, low-temperature pyrolysis are not flammable. Water vapor and carbon dioxide predominate, with lesser amounts of carbon monoxide and traces of organic acids being present. It is evident that dehydration and decarboxylation are taking place. Wood that has been heated above the boiling point of water for extended periods becomes less hygroscopic and more dimensionally stable with some sacrifice of strength.

Above 200°C the rate of decomposition increases until rapid exothermal weight losses occur at 260°C, 280°C, and 330°C, probably representing the different behavior of the separate wood components. With the onset of rapid pyrolysis, flammable gases are evolved such as carbon monoxide, methane, formaldehyde, formic and acetic acids, and methanol. Also evolved are highly flammable tars containing furfural and other furan derivatives from the decomposition of pentosans, levoglucosan from the decomposition of the cellulose, and aromatic fragments such as phenols, xylenols, guaiacols, cresols, and catechols from the decomposition of the lignin.

In the presence of air these flammable gases and tars evolved during rapid pyrolysis can further react with oxygen in the process we call burning, adding their heat of combustion to the degradation process, and intensifying it. The residue becomes charcoal, with carbonization becoming complete at 400–500°C and the crystalline structure of graphite developing.

In the presence of acidic or alkaline compounds the decomposition takes a different course. Instead of the liberation of flammable gases and tars the modified pyrolysis leads to increased amounts of charcoal by dehydration of the cellulose and hemicelluloses. The increased char formation occurs at the expense of flammable volatile tars. The cellulose is preferentially converted to carbon and water. When this dehydration occurs at temperatures below the normal decomposition temperature of wood, the wood has been effectively flameproofed.

Light

Exposure to light causes photodegradation and photooxidative degradation. Ultraviolet light interacts with lignin resulting in discoloration and deterioration. In a surface phenomenon, since light does not penetrate beyond 200 μm, the free radicals generated interact with oxygen to form hydroperoxides which in turn decompose. The results are large color changes and chemical degradation.

Wood is an excellent light absorber. Cellulose absorbs strongly below 200 nm. Hemicelluloses are structurally similar, so their ultraviolet absorption characteristics resemble those of cellulose. Lignin and polyphenols absorb light strongly below 200 nm and have a strong peak at 280 nm, with absorption continuing through the visible region. Extractives absorb between 300 and 400 nm.

The strong absorption of ultraviolet light by lignin results in preferential lignin degradation. The process is initiated by the formation of free radicals, and begins with the oxidation of phenolic hydroxyls. Methoxyl and lignin content decrease, while acidity and carboxyl content increase. The products of decomposition, in addition to gases and water, are mainly organic acids, vanillin, syringaldehyde, and higher molecular weight, but water soluble, compounds.

The color of wood exposed to light changes rapidly. Woods rich in extractives may become bleached before photooxidation of lignin results in a loss in brightness. The general change in color in all woods is toward a yellow to brown as degradation proceeds. The yellowing of newsprint after brief exposure to light is typical behavior. The final gray color seen in wood exposed to light for long periods of time represents residual cellulose after degradation and removal of most of the lignin.

Ionizing Radiation

High energy radiation can depolymerize the wood components by creating free radicals along the C–C backbone. If two free radicals are formed on separate chains in close proximity, crosslinking can take place. If the free radicals are created near a reactive or functional group other types of reactions can occur. When the free radical is on a tertiary carbon, disproportionation with chain scission can take place.

Surprisingly, lignin is more resistant to gamma-radiation than cellulose, even though it is more susceptible to the lower energy ultraviolet radiation. Irradiated cellulose is degraded by the cleavage of glycosidic bonds. But the radical sites created on the cellulose at lower levels of irradiation have been used for initiation of grafting on the cellulose and copolymerization in the presence of vinyl monomers.

High-energy radiation in the form of gamma-rays and X-rays can penetrate wood readily, whereas photoirradiation is only a surface phenomenon from ultraviolet penetration of up to 75 μm and visible light penetration of up to 200 μm. Thus extended high-energy radiation can be very destructive. White oak wood irradiated to 1900 Mrad with gamma-rays had an increase in extractives from 9% to 69% showing extensive solubilization. Holocellulose was reduced from 58% to 4%, while lignin showed only a slight loss from 33% to 27%.

See also: **Non-wood Products**: Chemicals from Wood. **Solid Wood Processing**: Chemical Modification. **Tree Breeding, Practices**: Biological Improvement of Wood Properties. **Wood Formation and Properties**: Formation and Structure of Wood; Wood Quality. **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

Browning BL (ed.) (1963) *The Chemistry of Wood*. New York: John Wiley.

Hon DNS and Shiraishi N (eds) (2001) *Wood and Cellulose Chemistry*. New York: Marcel Dekker.

Lewin M and Goldstein IS (eds) (1991) *Wood Structure and Composition*. New York: Marcel Dekker.

Rowell R (ed.) (1984) *The Chemistry of Solid Wood*. Washington, DC: American Chemical Society.

Sjostrom E (1981) *Wood Chemistry*. New York: Academic Press.

Wenzl HFJ (1970) *The Chemical Technology of Wood*. New York: Academic Press.

Wood Quality

J Barbour, US Department of Agriculture Forest Service, Portland, OR, USA

Published by Elsevier Ltd., 2004

Wood Product Streams

The classical definition of wood quality is the suitability of a given piece of wood for a specific end use, and, accordingly, individual wood characteristics are not usually seen as universally good or bad. The exact set of characteristics that constitute high or low quality varies depending on the specific use. Some characteristics are, however, almost always desirable and others are almost always undesirable. Some examples of desirable characteristics are soundness (lack of decay), straight grain, small scattered knots or the complete absence of knots, and dimensional stability (a tendency to dry without warping and to remain straight in use). Some examples of undesirable characteristics are decay, large or unsound knots, lack of dimensional stability, and poor mechanical properties. Some wood products are very forgiving of variation in wood characteristics. Others require raw material with a narrow range of wood characteristics. Consequently, it makes sense to begin a discussion of wood quality by thinking about the broad categories of wood products and the characteristics that are important for each group. A convenient way to do this is to divide all possible wood utilization options into a small number of 'end product streams' with similar raw material requirements, for example (1) heat and chemicals, (2) fibers and particles, and (3) solid products.

Heat and Chemicals

The energy production stream is the least demanding in terms of wood characteristics. Raw materials with lower moisture contents and higher specific gravities are more desirable but fuelwood can include a variety of low-quality raw materials. These could come from small stems, crooked stems, stems with large numbers of knots, or stems with high proportions of defects such as cross grain, rot, reaction wood (wood associated with leaning or deformed stems), etc.

Many chemicals used every day are derived from wood, bark, extractives, or foliage. Raw materials used for their production must be cleaner than for energy and, although some species work better than others because of their chemical composition, fiber characteristics or other wood properties are relatively unimportant.

Fiber and Particles

Composite wood products such as oriented strandboard (OSB), parallel-strand lumber (PSL), waferboard, particleboard, medium-density fiberboard (MDF), hardboard, wood–plastic composites, wood–cement composites, and pulp for paper and paperboard are included in the fiber and particle product stream. Manufacture of these products requires cleaner raw material than energy production, although perhaps not more so than chemical production. In most cases, bark is seen as detrimental, so ease of bark removal from roundwood is an important feature. Manufacture of fiber- and particle-based products is also less tolerant of decay, reaction wood, pitch pockets, or other irregularities. It is, however, technically feasible to make these products from small stems or stems with substantial grain deviation as long as it is not associated with reaction wood and does not interfere with debarking or primary processing such as waferizing.

Solid Products

This stream is divided into structural products and appearance products. Solid products include roundwood, such as posts and poles, sawn lumber, and veneer. In some ways, the structural product stream is the most demanding. Products in this stream must meet engineering standards, such as specified mechanical requirements and they are intolerant of grain deviations or decay. On the other hand, they can contain some knots and discoloration without adversely affecting their performance.

The raw material requirements for structural products have changed greatly during the twentieth century. Technological improvements now allow sawing of logs as small as 9 cm in diameter on the small end, although economic constraints often preclude processing logs quite so small. Techniques were also developed to use weaker or less stiff lumber in parts of engineered products where mechanical properties were less important and abundant fast-growing species such as aspen (*Populus* spp.) replaced slower-growing softwood species for structural panel products. Not long ago, the only way to make a large beam was to saw it from a large log, but now it is possible to manufacture glulam beams, wood I-beams, or parallel strand lumber (PSL) from small logs. This means that as forest managers plan new plantations they have to take potential changes in technology very seriously. Raw material requirements for structural products still favor trees with fewer and smaller knots, straight grain, and less taper but tree size is not nearly as important as it was less than a rotation ago in many timber-growing regions.

Appearance products are similar to structural products except that they contain characteristics that people consider beautiful. Some examples are dark- or light-colored heartwood, various grain patterns, and lack of knots. In some cases, appearance products perform a structural function, such as in furniture, architectural beams, or posts, but in many applications such as fascia and molding they have no structural role. This means that for many applications the mechanical properties of appearance products are relatively unimportant. A high level of dimensional stability is, however, always important for these products.

Appearance products are typically the highest-priced wood products, although certain specialty structural products such as very long power transmission poles or large structural beams can rival them in price per unit volume. Even with high prices, it is not normally economically feasible to grow trees suitable for appearance products to replace traditional hardwood and 'old-growth' softwood supplies. Pruning trees to grow clear lumber and veneer is an exception, but profitable pruning requires shortening rotations by combing pruning with intensive thinning. The wood from these fast-growing trees looks quite different from clear wood sawn from trees grown more slowly. An alternative is to extend the supply products that look like old-growth by covering wood or non-wood substrates with thin veneers sliced from slow-growing hardwoods or softwoods.

Growth Conditions Influence Tree and Wood Characteristics

Foresters began to formalize theories about how growing conditions influence tree form, branch size, and other factors that control wood characteristics as long ago as the late nineteenth century. They observed that the size and vigor of the crown was important in determining both the morphological, or externally visible, characteristics and the basic wood properties (chemical, anatomical, and physical properties) of softwood trees. Since then, wood scientists have built on these early observations by using a combination of structured experiments and retrospective studies to develop an understanding of how silvicultural manipulation of stand conditions can influence tree characteristics and, consequently, wood products manufactured from them. Field foresters now routinely use this knowledge, but their understanding of all aspects of how to manipulate wood properties is far from complete. Some general inferences that apply to most softwoods are, however, possible.

Most silvicultural treatments that influence wood quality modify the size and vigor of the crown. Treatments that increase crown length or vigor create trees more like open-grown trees with deeper crowns, larger branches, and more conically shaped stems (taper) (**Figure 1**). Treatments that reduce crown length or vigor produce trees with characteristics more like those observed in trees from dense stands with short crowns, small branches, and more cylindrical stems. Understanding these simple relations between growing space, crown length, branch size, and stem shape is important in understanding how growing conditions influence the suitability of the wood from a tree for a specific end use.

A fairly well-developed theory involving the production of growth hormones and nutrients has arisen to explain why this happens. Simply stated, trees with larger crowns produce more growth hormones and more nutrients. Growth hormones encourage cell division and radial expansion of longitudinal wood cells (tracheids) as they mature. Nutrients contribute to the growth and thickening of cell walls. Growth hormones are mainly produced in actively growing branch tips, and nutrients are mainly produced by vigorous foliage. Trees with deeper, more vigorous crowns have both more foliage and a greater number of buds, so they produce higher hormone concentrations and larger quantities of nutrients than trees with short, suppressed crowns. The change in concentration of hormones and nutrients from the apical meristem (topmost bud) to the base of the tree has been suggested as an explanation for the changes in various wood properties from the center of the tree (pith) to the bark. This inner zone of changing wood properties is generally used to differentiate juvenile, or crown-formed, wood from mature, or stem-formed, wood.

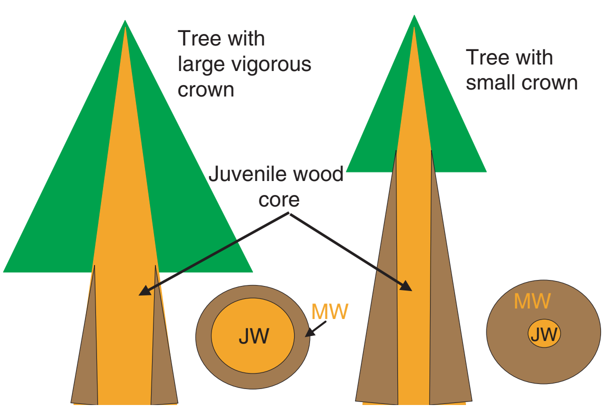


Figure 1 Relation of juvenile wood core size with crown size and vigor. With larger more vigorous crowns grow more quickly and therefore produce more juvenile wood (JW) and less mature wood (MW) than trees of the same diameter with smaller crowns.

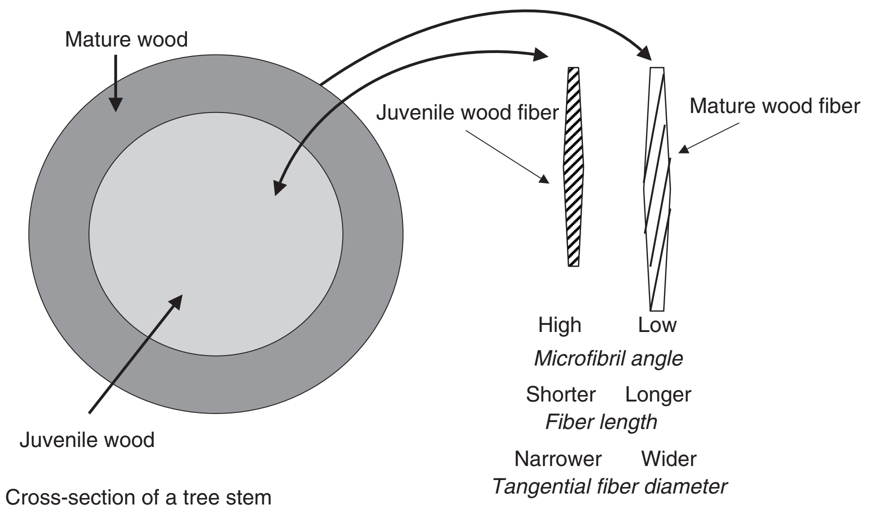


Figure 2 Variation in fiber characteristics in juvenile wood and mature wood. Juvenile wood tends to have shorter, narrower fibers with higher microfibril angles than mature wood.

For practical purposes, the transition from juvenile wood to mature wood is often thought to begin at the base of the live crown.

Another theory explains the changes in basic wood properties from the pith to the bark as the expression of aging by the cambial initials (actively dividing cells) in the vascular cambium. This theory holds that each time a cambial initial divides, it changes slightly (lengthens, grows wider, alters its cell wall structure, etc.) and as a result, wood properties change over time (**Figure 2**). This theory has been used to develop a plausible explanation of why some trees develop spiral grain as they age.

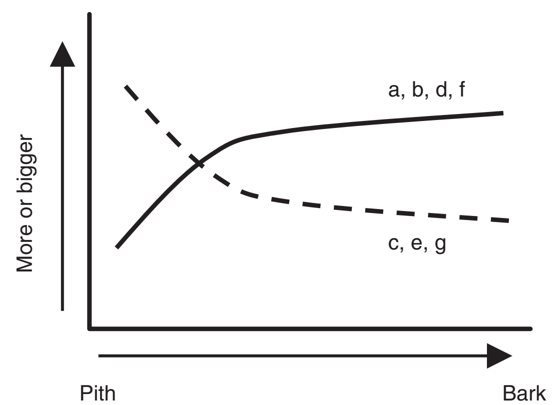


Figure 3 Pith to bark relation of various wood properties. The way some wood characteristics change from the pith to the bark is more or less universal among species. Example wood characteristics: (a) fiber length, (b) tangential cell diameter, (c) microfibril angle, (d) extractive content, (e) branch number, (f) branch size, (g) longitudinal shrinkage.

The Importance of Juvenile Wood

Juvenile wood often has different properties than mature wood. The duration of the period when juvenile wood is produced, the rate of transition from juvenile wood to mature wood, and the differences in properties between juvenile wood and mature wood are all important in determining the suitability of wood for specific end uses. There are always more knots in juvenile wood because it is formed when the crown is alive. Differences in chemical, physical, anatomical, and visual characteristics have all been reported for various species, and the importance of each depends on the wood product being manufactured (**Figures 3** and **4**). For example, differences in cell wall thickness and cell wall mechanical properties that are undesirable for lumber and veneer might actually result in fibers with excellent pulp and papermaking properties. Problems generally arise when solid products contain both juvenile wood and mature wood, but papermakers can use blends of juvenile and mature wood to obtain desired characteristics.

Variation within Growth Rings

Intraring variation of basic wood properties, or changes within individual annual rings, is another important factor in determining the suitability of wood for specific uses. The annual fluctuation in hormone and nutrient levels has been used to explain some of this variation. In the spring, when buds are most active, they produce high hormone concentrations. This promotes rapid radial expansion of new xylem cells, but the foliage has not yet fully matured so there are insufficient nutrients for substantial cell wall thickening. Large-diameter thin-walled

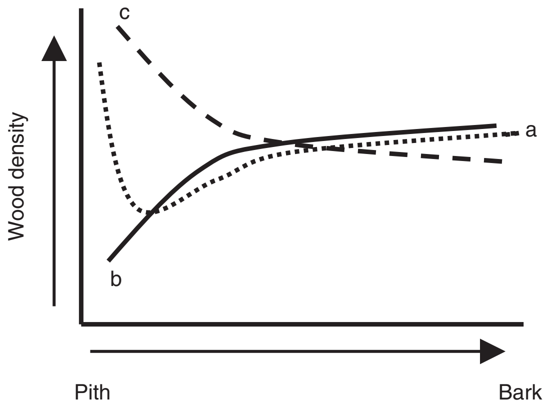


Figure 4 Different species tend to have different pith to bark wood density profiles. Pith to bark trends also tend to change with tree height so that the pattern is not always the same within a single tree. Typical patterns by species: (a) Douglas-fir and hemlock, (b) most pines, (c) most spruces.

earlywood tracheids are produced during this period. Later in the growing season, as expansion of growing tips is completed and the foliage is fully expanded, the situation is reversed; the concentration of hormones available for cell expansion is minimal, but there are plenty of nutrients to promote rapid thickening of the cell walls. As a result, thick-walled latewood cells are produced. A related theory suggests that the size of various cells is controlled by the need to move water through the stem to the foliage.

Factors such as soil nutrients, moisture availability, and temperature also are thought to influence the initiation of radial growth in the spring and cessation of radial growth in the fall. The time when growth begins or when it ends can influence the characteristics of individual growth rings. If growth starts late in the spring, perhaps owing to a late thaw, less earlywood is laid down before the transition occurs; if growth stops early in the autumn, perhaps because of a drought, less latewood is produced.

The Importance of Basic Wood Properties

Intraring characteristics are important because they play a role in determining the suitability of wood for specific uses. The proportion of earlywood and latewood and whether the transition between them is gradual or abrupt influences mechanical properties, machining, nailing and fastening, penetration of treating chemicals, and appearance of solid products. For some products, such as fine papers, an abundance of long, stiff, thick-walled fibers is seen as detrimental because they interfere with sheet formation in papermaking.

It is important to recognize that the influence of growth conditions on tree and wood characteristics is complicated by the interactions of many different factors. The interactions described here are complicated by other relations that control the orientation of cellulose microfibrils in the cell walls, cell length, and the proportions of cell wall components (cellulose, hemicelluloses, and lignin). Each of these basic wood properties varies within growth rings, from pith to bark, and from the base to the top of the stem according to a different relation with growth conditions, so it is often difficult to understand precisely why physical properties of larger pieces of wood change in the ways that they do.

The Importance of Morphological Characteristics

Morphological characteristics such as branching and grain orientation are equally or perhaps even more important in determining the suitability of a given piece of wood for a specific end use than are basic wood properties. More and larger knots are almost universally considered detrimental whether wood is used for lumber, veneer, composites, or fiber products. Notable exceptions are knotty-pine paneling and certain grades of lumber used in furniture manufacture, but these account for a tiny fraction of all wood products.

Knots are a primary factor used to determine lumber and veneer grade and value. In general, the more abundant and the larger knots are the lower the grade. Knots interfere with adhesives and reduce the mechanical properties of composite products like OSB, laminated-veneer lumber (LVL), and PSL, but they are generally not recognized in pricing raw materials for these products. This is probably because no reliable models exist to relate knot size, knot condition, and knot abundance to performance of these products or to waste during their manufacture. The effect of knots is better understood for fiber products like paper because they tend to interfere with the pulping, grinding, and refining processes used to turn raw wood into fibers. Knots are usually detrimental in composite products, but their high wood density produces more heat per unit volume when they are burnt for energy. They also contain high levels of extractives, which is desirable for manufacturing certain solvents.

Knot shape is also important. Shape comes partly from the morphology of branching and partly from manufacturing processes. Branches that join the stem at right angles to its long axis are known as low-angle branches. Low-angle branches produce the smallest knots for a given branch diameter. Branches that leave the stem at an angle result in larger oval knots and are, therefore, less desirable.

Trees with deeper, broader crowns produce larger, more persistent branches. They also tend to have more branches. One way this happens is when trees 'flush' or initiate height growth more than one time during a season (**Figure 5**). Trees with plenty of growing space located on good sites also tend to retain their branches longer and can produce more knots per whorl than those in denser stands or on poor sites. Depending on the species, more vigorous trees produce and retain more internodal branches (branches that grow between branch whorls). Taken together, these factors tend to cause the largest, fastest-growing trees to have more and larger knots.

The quality of knots also changes along the length of the stem. Live knots typically have the lowest impact on structural wood products and are even seen as desirable for some appearance products. Knots resulting from dead branches are generally more of a wood quality problem than those derived from live branches. When branches die, the vascular cambium loses its connection to the branch. This creates 'tight' or 'sound' knots which act like plugged holes in solidwood products. Dead branches begin to rot, and further below the live crown (down the stem) they become black or unsound knots. Unsound knots often fall out of products during the manufacturing process and leave holes. Unsound knots and holes are much less desirable than sound knots for most wood products. Finally, the branch is shed and eventually clear wood is produced but the process can take many decades in naturally grown stands.

A major challenge to forest managers is to design silvicultural prescriptions that maximize growth without producing trees with numerous large branches. One way to do this is to limit growing space early in the rotation then thin stands once there is sufficient height growth to allow crowns to recede above the top of the first log, typically about 10.5 to 12 m. The problem with this strategy is that it results in smaller trees but technological change is making this less important than it once was. Another option is to prune trees to shorten crown length, but this is an expensive process that is only appropriate in special cases where 'clear,' or knot-free, wood is desired. The high costs and uncertain markets for clear wood make foresters hesitant to prune unless they are confident that they can sell pruned logs for a much higher price than unpruned logs.

Branch initiation and branch growth are well enough understood that there are fairly reliable simulation models available for many of the important commercial conifer species. These models connect to individual tree growth and yield models used by forest managers to estimate the growth of stands under different conditions and evaluate whether branch size will exceed predetermined specifications related to wood product requirements. Financial analysis tools are available to help foresters evaluate the influence of branch size and pruning on the potential financial return from stands. These types of models help forest managers think about whether it makes sense to manage for small groups of end products or even specific products.

Designer Trees

If trees could be grown with particular sets of characteristics then they might be tailored for

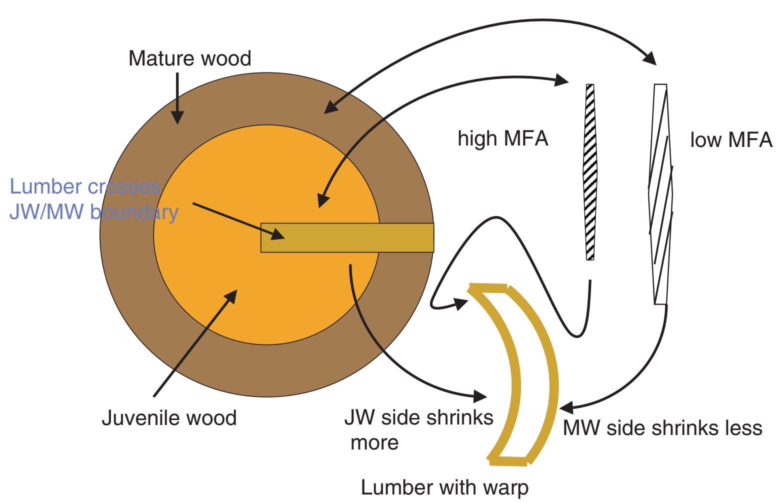


Figure 5 Effect of juvenile wood on warp. Higher longitudinal shrinkage of juvenile wood (JW) caused by high microfibril angles of cellulose fibrils can result in warp in lumber that contains both juvenile wood and mature wood (MW). MFA, Myofibril angle.

specific end products. Until recently, the length of time it took to grow a crop of trees always made this goal somewhat unrealistic and open to criticism. The uncertainty associated with predicting future demand for particular wood properties many decades in the future often seems too high. On the other hand, there have been a few situations where the economic value of large crops of trees was adversely affected by failure to consider the potential quality of the final crop. Two prominent examples are the extensive plantings of chir pine (*Pinus roxburghii*) established in South Africa early in the twentieth century for harvest in the 1930s and 1940s and the 'old-crop' radiata pine (*Pinus radiata*) that was planted during the 1930s and 1940s in New Zealand. The seed source of chir pine used in South Africa tended to produce severe spiral grain, which made the trees virtually unusable for anything other than pulp. This material was even unsuitable for roundwood applications such as posts and poles because they tended to twist as they dried and then to move with cyclic changes in moisture content. This movement loosened or broke power lines, fence wires, and fence boards attached to the posts and poles. The old-crop radiata pine was planted with 'wild' unimproved seed at relatively narrow spacings and left untended. Under such conditions radiata pine produces particularly poor stem form and variable branches. This made lumber sawn from these trees unsuitable for many uses. The size and frequency of the branches also made this wood less desirable for pulp chips. Given these experiences, foresters began to pay more attention to producing trees with good form and fewer, smaller, branches but it was still impractical to commit to specific plans for the use of trees scheduled for harvest three or four decades in the future. Today it is becoming more common for foresters in regions where trees can be grown in less than about 25 or 30 years to think seriously about the specific use or at least the product stream expected for a crop of trees.

There is also considerable interest in screening seed sources, genetic improvement, and clonal forestry to increase growth rates and improve wood quality. Combined with simulation models for planning silvicultural systems, these techniques reduce the likelihood of undesirable characteristics such as large or frequent branches or low wood density and increase the feasibility of growing trees quickly enough to fill specific market niches. For example, some of the hardwood species grown for pulp in tropical regions mature in as little as 5–10 years and rotations of conifers in temperate regions of 25 years or less are now common.

Economics and Wood Quality

Wood utilization is often more a question of what is economically feasible than what is technically possible so a discussion about wood quality is not particularly meaningful unless economics is considered. Every wood product requires some minimum set of wood characteristics in order to perform satisfactorily. There is also a maximum price above which consumers will look for a substitute material, will find another way to fill the need, or go without the product altogether. The interaction between performance and price is not particularly easy to quantify but it unquestionably influences whether individual trees or stands of trees are harvested for wood products. The idea of 'cull' trees and logs has been a part of forestry practices for many decades. Cull trees and logs do not have sufficient value to justify their harvest or processing. Often they contain too much defect (juvenile wood, rot, stain, spiral, grain, etc.) or they may be crooked or have too many or too large knots, or in some cases they are simply the wrong species. Size is often an important factor. In almost all wood-producing regions, precommercial thinning, or cutting small trees and leaving them in the forest, is a practice commonly used to accelerate growth of the trees remaining in the stand so they will reach merchantable size quickly enough to make forestry profitable. In remote areas, larger trees and logs are often treated as cull regardless of their quality. In some parts of the USA minimum merchantable log size is 23–25 cm on the small end, even though sawmilling and veneer peeling technology makes it feasible to use logs as small as 9 cm on the small end and most energy, chemical, fiber, and particle process can use even smaller logs. Even so, there are simply no markets for logs smaller than 23 cm in these places.

Topography and location frequently tip the balance between performance and price. Trees on flat ground are generally more easily harvested and therefore more profitable than those growing on steep slopes. In the past, when new areas were opened up for logging, the valley bottoms were almost always harvested first. Even today, there are vast tracts of old-growth timber with excellent wood characteristics that have not been harvested largely for economic reasons. The Russian Far East and much of Alaska are two examples where costs and accessibility kept these forests from being harvested over the past half-century. Social concerns about preservation of old-growth forests are now more important than costs in preventing harvest in Alaska, even though these forests contain some of the best-quality softwood timber remaining in the world today.

As the timber industry moves away from harvesting unmanaged stands to more intensive management systems of either naturally regenerated or planted stands, the interaction between price and performance will continue to determine whether individual trees or stands are harvested and the way they are grown. Managed stands that grow too slowly or are in places difficult to reach, far from transportation routes, or even in places where there are insufficient commercial forests, are less likely to be profitable. In some countries, agricultural land (which may originally have been forest) is being converted to plantations in preference to cheaper land located on steeper ground, because of the lower costs of land preparation, higher growth rates, and lower harvesting costs.

Most of the advances in manufacturing technology that eliminated the need for large trees were brought about by a desire to find ways to continue to use wood for structural products without having to grow trees for so long. The increased manufacturing costs required for these products is more than offset by the lower costs of holding investments in stands of trees for one-third to one-half as long as under unmanaged conditions. In fact, it is quite likely that without peeling (plywood and LVL), gluelam, engineered fasteners, and composites technology it would not be possible for wood to compete with alternative materials.

See also: **Solid Wood Products**: Lumber Production, Properties and Uses. **Tree Breeding, Practices**: Biological Improvement of Wood Properties; Genetics and Improvement of Wood Properties. **Wood Formation and Properties**: Formation and Structure of Wood; Mechanical Properties of Wood; Physical Properties of Wood.

Further Reading

Bowyer JL, Shmulsky R, and Haygreen JG (2002) *Forest Products and Wood Science: An Introduction*. Ames, IA: Iowa State University Press.

Brazier JD (1977) The effect of forest practices on quality of the harvested crop. *Forestry* 50(1): 49–66.

Cave ID and Walker JCF (1994) Stiffness of wood in fast-grown plantation softwoods: the influence of microfibril angle. *Forest Products Journal* 44(5): 43–48.

Clark A, Saucier JR, Baldwin VC, and Bower DR (1994) Effect of initial spacing and thinning on lumber grade, yield, and strength of loblolly pine. *Forest Products Journal* 44(11/12): 14–20.

Fight R, Snellgrove T, Curtis R, and Debell D (1986) Bringing timber quality considerations into forest management decisions: a conceptual approach. In: Oliver C, Hanley D, and Johnson J (eds) *Douglas-Fir: Stand Management for the Future*, pp. 20–25. Seattle, WA: University of Washington Press.

Hoadley RB (2000) *Understanding Wood: A Craftsman's Guide to Wood Technology*. Newtown, CT: Taunton Press.

Larson PR (1969) *Wood Formation and the Concept of Wood Quality*. Yale University School of Forestry Bulletin no. 74. New Haven, CT: Yale University.

Megraw RA (1985) *Wood Quality Factors in Loblolly Pine: The Influence of Tree Age, Position in Tree, and Cultural Practice on Wood Specific Gravity, Fiber Length, and Fibril Angle*. Atlanta, GA: TAPPI Press.

Nepveu G (ed.) (1996) *Connection between Silviculture and Wood Quality through Modelling Approaches and Simulation Software*, Proceedings of the 1st Workshop IUFRO WP S5.01.04, 13–17 June 1994, Hook, Sweden.

Nepveu G (ed.) (1997) *Connection between Silviculture and Wood Quality through Modelling Approaches and Simulation Software*, Proceedings of the 2nd Workshop IUFRO WP S5.01.04, 26–31 August 1996, Berg-en-Dal, Kruger National Park, South Africa.

Nepveu G (ed.) (1999) *Connection between Silviculture and Wood Quality through Modelling Approaches and Simulation Software*, Proceedings of the 3rd Workshop IUFRO WP S5.01.04, 5–12 September 1999, La Londe-Les-Maures, France.

Nepveu G (ed.) (2003) *Connection between Forest Resources and Wood Quality through Modelling Approaches and Simulation Software*, Proceedings of the 4th Workshop IUFRO WP S5.01.04, 8–15 September 2002, Harrison Hot Springs, BC, Canada.

Spurr SH and Hsiung WY (1954) Growth rate and specific gravity in conifers. *Journal of Forestry* 52(3): 191–200.

Thörnqvist T (1993) *Juvenile Wood in Coniferous Trees*. Stockholm, Sweden: Document D13: 1993. Swedish Council for Building Research.

Biological Deterioration of Wood

T L Highley, Henderson, NV, USA

Introduction

Wood does not degrade as a result of aging alone. Under proper conditions, wood will give centuries of service. The service life of forest products depends on their being protected from a variety of degrading agents. Given the appropriate conditions, degradation encountered will fall into one of three categories: (1) biological; (2) physical; or (3) chemical. This article concerns only biological degradation of wood, which is the most damaging of the causal agents.

Biological degradation of wood is caused primarily by fungi, bacteria, insects, and marine borers. Wood degradation by these organisms has been studied extensively, and many preventive measures are available. By taking ordinary precautions with the finished products, the user can contribute substantially to ensuring a long service life.

Fungus Damage

Fungus damage to wood is caused by decay, molds, and fungus stains. Fungi are microscopic, thread-like microorganisms that obtain their nutrients from wood or other organic materials. The growing stage of fungi consists of microscopic threads called hyphae which in mass form cottony or feltlike growths (mycelium). Hyphae penetrate and ramify within wood, causing decay or other damage. The growth of fungi depends on suitably mild temperatures, moisture, and oxygen.

Decay

Decay is the most serious kind of fungal damage because it causes structural failure, sometimes very rapidly. Because widespread damage to wood from decay is seldom spectacular, the tremendous economic and resource loss resulting from decay is often overlooked.

Conditions for decay Most decay can progress at temperatures that favor plant life in general. Decay is usually relatively slow at temperatures below 10°C and above 35°C. Decay essentially stops when the temperature drops as low as 2°C or rises as high as 38°C.

Serious decay occurs only when the moisture content of wood is above the fiber saturation point (average 30%). The fiber saturation point in previously dried wood will be reached only when contacted by water, such as provided by rain, condensation, or contact with wet ground. By itself, the water vapor in humid air will not wet wood sufficiently to support significant decay, but it will permit development of some mold fungi. Fully air-dried wood will usually have a moisture content less than 20% and should provide a reasonable margin of safety against fungus damage. Thus, wood will not decay if it is kept dry, and decay already present from prior infection will not progress.

Wood can be too wet for decay as well as too dry. If wood is water-soaked, the supply of air to the interior may not be adequate to support development of typical decay fungi. This is why fungal decay will not occur in foundation piles buried beneath the water table and in logs stored in a pond or under a suitable system of water sprays.

Decay usually results in abnormal coloration of the wood. Abnormal mottling of the wood color, with either unnatural brown or bleached areas, is often evidence of decay infection. As wood approaches advanced stages of decay, it loses luster and may exhibit pronounced changes in color depending on the organism and the substance it removes. Advanced decay is also easy to recognize from changes in the physical appearance of the wood, such as localized depressions or sunken areas over decay pockets, and cracking in cubical patterns.

Classification of decay The most important and potent wood-destroying fungi are white- and brown-rot fungi, which utilize various components of the wood cell wall. Most white-rot fungi utilize cellulose and hemicelluloses at approximately the same rate relative to the original amounts present, whereas lignin is usually utilized at a somewhat faster relative rate. A few white-rot fungi remove lignin and hemicelluloses preferentially, but ultimately they degrade all wood cell wall components. White-rot fungi cause the wood to lose color, eventually reducing it to a fibrous, whitish mass. It does not crack across the grain, and, until severely degraded, it retains its outward dimensions, does not shrink or collapse, and often feels spongy. Brown-rot fungi utilize cell wall hemicelluloses and cellulose, leaving the lignin essentially undigested. However, brown-rot fungi do modify lignin, as indicated by demethylation and accumulation of oxidized polymeric lignin degradation products. These fungi cause the wood to darken, shrink, and break into pieces that crumble easily into a brown powder. Brown-rot fungi commonly colonize softwoods, and white-rot fungi commonly occur on hardwoods, but both brown- and white-rot fungi occasionally colonize both types of wood.

Brown, crumbly rot, in the dry condition, is sometimes called dry rot, but the term is incorrect because wood must be damp to decay, although it may become dry later. A few fungi, however, have water-conducting strands; such fungi are capable of carrying water (usually from the soil) into buildings or lumber piles, where they moisten and rot wood that would otherwise be dry. They are sometimes referred to technically as dry-rot fungi or water-conducting fungi. The latter term describes the true situation better because these fungi, like the others, must have water.

A third and generally less important kind of decay is known as soft rot. Soft rot is caused by fungi related to the molds rather than those responsible for brown and white rot. Soft rot typically is relatively shallow; the affected wood is greatly degraded and often soft when wet, but immediately beneath the zone of rot, the wood may be firm. Because soft rot is usually rather shallow, it is most likely to damage relatively thin pieces of wood such as slats in cooling towers.

Soft rot similar to other types of microbial wood decay occurs in certain ecological niches where the fungi can be active mainly due to lack of competition from other microorganisms. This is why soft rot is favored by wet situations where the more aggressive white- and brown-rot fungi are less competitive. However, it is also prevalent on surfaces that have been alternately wet and dry over a substantial period. Heavily fissured surfaces, familiar to many as weathered wood, have generally been quite degraded by soft-rot fungi.

Mold and Fungus Stains

Molds and fungus stains are confined to a great extent to sapwood and are of various colors. The principal fungus stains are usually referred to as sapstain or blue stain. The distinction between molding and staining is made primarily on the basis of the depth of discoloration. With some molds and the lesser fungus stains, there is no clear-cut differentiation. Typical sapstain or blue stain penetrates into the sapwood and cannot be removed by surfacing. Also, the discoloration as seen on a cross-section of the wood often appears as pie-shaped wedges oriented radially, corresponding to the direction of the wood rays. The discoloration may completely cover the sapwood or may occur as specks, spots, streaks, or patches of various intensities of color. The so-called blue stains, which vary from bluish to bluish-black and gray to brown, are the most common, although various shades of yellow, orange, purple, and red are sometimes encountered. The exact color of the stain depends on the infecting organisms and the species and moisture condition of the wood.

Mold discolorations usually become noticeable as fuzzy or powdery surface growths, with colors ranging from light shades to black. Among the brighter colors, green and yellowish hues are common. On softwoods, although the fungi may penetrate deeply, the discoloring surface growth can often easily be brushed or surfaced off. However, on large-porous hardwoods (for example, oaks), the wood beneath the surface growth is commonly stained too deeply to be surfaced off. The staining tends to occur in spots of varying concentrations and size, depending on the kind and pattern of the superficial growth.

Under favorable moisture and temperature conditions staining and molding fungi may become established and develop rapidly in the sapwood of logs shortly after they are cut. In addition, lumber and such products as veneer, furniture stock, and millwork may become infected at any stage of manufacture or use if they become sufficiently moist. Fresh cut or unseasoned stock that is piled during warm humid weather may be noticeably discolored within 5 or 6 days.

Mold growth in the indoor environment is not new, but in recent years the issue of toxic molds has generated national media attention. However, the scientific and medical literature contains differing opinion regarding the potential health impacts of exposure to mold. There are few case reports that molds producing mycotoxins inside homes can cause unique health conditions such as pulmonary hemorrhage or memory loss. Certain individuals with allergies may be more sensitive to molds. Individuals with immune suppression or underlying lung disease are at increased risk for infection from molds.

Ordinarily, stain and mold fungi affect the strength of the wood only slightly; their greatest effect is usually confined to strength properties that determine shock resistance or toughness. They increase the absorbency of wood, and this can cause over-absorption of glue, paint, or wood preservative during subsequent processing. Increased porosity also makes wood more wettable, which can lead to colonization by typical wood-decay fungi.

Bacteria

Most wood that has been wet for a considerable length of time will probably contain bacteria. The sour smell of logs that have been held under water for several months, or of lumber cut from them, manifests bacterial action. It has been known for a long time that bacteria cause selective degradation of nonlignified wood cells (for example, parenchyma cells of wood rays and resin ducts) and pit membranes. The major effect of this type of bacterial attack on wood is an increase in the wood's capacity to absorb liquid. This can result in excessive pick-up of moisture, adhesive, paint, or preservative treatment in use. This effect has been a problem in the sapwood of millwork cut from pine logs that have been stored in ponds. There is also evidence that bacteria developing in pine veneer bolts held under water or sprayed with water may cause noticeable changes in the physical character of the veneer, including some strength loss.

In the last 25 years or so evidence has been obtained that bacteria can degrade lignified cell walls. Currently only two major forms of wood-degrading bacteria have been recognized – tunnelling and erosion bacterial decay. These two forms are recognized from the micromorphological decay patterns they cause during degradation of wood cells and do not represent any form of taxonomic classification. Wood-degrading bacteria apparently cannot compete with fungal decay and thus will degrade wood where fungal decay is suppressed. For example, bacterial degradation will occur under conditions of oxygen limitation for fungi that usually exist in piling supporting piers, buried shipwrecks, or lumber exposed to very wet conditions such as air-conditioner water slats or mine props. Furthermore, wood made more resistant to fungal attack by high loading of wood preservatives or extractive content provides a niche in which fungi are suppressed, allowing for successful bacterial decay. The ability of researchers to identify bacterial decay patterns better has generated greater interest in bacterial degradation wood in recent years, and it is being more frequently reported in the literature.

Insect Damage

Of the insects that damage wood, termites and beetles cause the most serious damage. Carpenter ants and bees cause occasional damage to wood but do not use it as food; they hollow it out for nesting. Termites are the most destructive insects that attack wood.

Termites superficially resemble ants in size, general appearance, and habit of living in colonies. From the standpoint of their methods of attack on wood, termites can be grouped into two main classes: (1) ground-inhabiting or subterranean termites; and (2) wood-inhabiting or nonsubterranean termites.

Subterranean Termites

Subterranean termites are responsible for most of the damage to wood structures in the USA. This damage can be prevented. Subterranean termites are more prevalent in the southern than in the northern states, where low temperatures do not favor their development. The hazard of infestation is greatest first, beneath buildings without basements that were erected on a concrete slab foundation or were built over a crawl space that is poorly drained and ventilated, and second, in any substructure wood component close to the ground or an earth fill (for example, an earth-filled porch).

The subterranean termites develop their colonies and maintain their headquarters in the ground. They build their tunnels through earth and around obstructions to reach the wood they need for food. They must also have a constant source of moisture, whether from the wood on which they are feeding or the soil where they nest. The worker members of the colony cause destruction of wood. At certain seasons of the year, usually spring, male and female winged forms swarm from the colony, fly a short time, lose their wings, mate and, if successful in locating a suitable home, start new colonies. The appearance of 'flying ants' or their shed wings is an indication that a termite colony may be near and causing serious damage. Not all 'flying ants' are termites; therefore, suspicious insects should be identified before investing in eradication.

Subterranean termites normally do not establish themselves in buildings by being carried there in lumber; they primarily enter from ground nests after the building has been constructed. An introduced species, the Formosan termite, is adept at initiating aboveground infestations and nests in structures where wood remains wet for a prolonged period, such as from roof leaks. Telltale signs of subterranean termite presence are the earthen tubes or runways built by these insects over the surfaces of the foundation or other exposed areas to reach the wood above. Another sign is the swarming of winged adults early in the spring or fall. In the wood itself, the termites make galleries that generally follow the grain, leaving a shell of sound wood to conceal their activities. Because the galleries seldom show on the wood surfaces, probing with a pick or knife is advisable if the presence of termites is suspected.

The best protection for wood in areas where subterranean termites are prevalent is to prevent the termites from gaining hidden access to a building. The foundations should be of concrete, pressure-treated wood, or other material through which the termite cannot penetrate. With brick, stone, or concrete block, cement mortar should be used because termites can work through some other kinds of mortar. Also, it is a good precaution to cap the foundation with 100 mm of reinforced concrete. Posts supporting floor girders should, if they bear directly on the ground, be of concrete. If there is a basement, it should be floored with concrete. Untreated posts in such a basement should rest on concrete piers extending several centimeters above the basement floor. However, pressure-treated posts can rest directly on the basement floor. With the crawl space type of foundation, wood floor joists should be kept at least 460 mm and girders 300 mm from the earth and good ventilation should be provided beneath the floor. A rule of thumb is to have a minimum of 1 unit area of ventilation for every 150 units of crawl space.

Moisture condensation on the floor joists and subflooring, which may cause conditions favorable to decay and contribute to infestation by termites, can be avoided by covering the soil below with a moisture barrier, maintaining adequate ventilation, and assuming proper drainage of rainwater away from all sides of a structure. All concrete forms, stakes, stumps, and wastewood should be removed from the building site because they are possible sources of infestation. Generally, the precautions effective against subterranean termites are also helpful against decay.

The principal method of protecting buildings in high termite areas is to treat the soil adjacent to the foundation walls and piers beneath the building thoroughly with a soil insecticide. When concrete slab floors are laid directly on the ground, all soil under the slab should be treated with an approved insecticide before the concrete is poured. Furthermore, insulation containing cellulose that is used as a filter in expansion joints should be impregnated with an approved chemical toxic to termites. Sealing the top 13 mm of the expansion joint with roofing-grade coal-tar pitch also provides effective protection from ground-nesting termites. New modifications in soil treatment and an insecticidal bait control method appear promising. Current references should be consulted to take advantage of the new developments in termite control.

To control termites already in a building, contact between the termite colony in the soil and the woodwork must be broken. This can be done by blocking the runways from soil to wood, treating the soil, repairing leaks that keep wood within the structure wet (for example, plumbing leaks), or some combination of these techniques. Possible reinfestations can be guarded against by frequent inspections for signs of termites.

Nonsubterranean Termites

In the USA, nonsubterranean termites have only been found in a narrow strip of territory extending from central California around the southern edge of the continental USA to Virginia and in the West Indies and Hawaii. Their principal damage is confined to an area in southern California, to parts of southern Florida, notably Key West, and to the islands of Hawaii. They are a localized problem in Arizona and New Mexico.

The nonsubterranean termites, especially the dry-wood type, do not multiply as rapidly as the subterranean termites and have somewhat different colony life and habits. The total amount of destruction they cause in the USA is much less than that caused by the subterranean termites. The ability of dry-wood termites to live in dry wood without outside moisture or contact with the ground, however, makes them a definite menace in the regions where they occur. Their depredations are not rapid, but they can thoroughly riddle timbers with their tunnellings if allowed to work undisturbed for many years. Nonsubterranean termites are moved from structure to structure in infested items such as furniture.

Marine Borer Damage

Damage by marine-boring organisms to wood structures in salt or brackish waters is practically a worldwide problem. Evidence of attack is sometimes found in rivers even above the region of brackishness. The rapidity of attack depends upon local conditions and the kinds of borers present. Along the Pacific, Gulf, and South Atlantic coasts of the USA, attack is rapid, and untreated pilings may be completely destroyed in a year or less. Along the coast of the New England states, the rate of attack is slower because of cold water temperatures but is still sufficiently rapid to require protection of wood where long life is desired. The principal marine borers from the standpoint of wood damage in the USA are described here.

Mollusks

Wood-degrading mollusks include species of the shipworms *Teredo* and *Bankia* and of the pholad *Martesia* and *Xylophaga*. Shipworms are the most destructive of the marine borers. They are mollusks of various species that superficially are worm-like in form. In the early stages of their life, they are minute, free-swimming organisms. Upon finding suitable lodgement on wood, they quickly develop into a new form and bury themselves in the wood. A pair of boring shells on the head grows rapidly in size as the boring progresses, while the tail part or siphon remains at the original entrance. Thus, the animal grows in length and diameter within the wood but remains a prisoner in its burrow, which it lines with a shell-like deposit. It lives on the wood borings and the organic matter extracted from the sea water that is continuously being pumped through its system. The entrance holes never grow large, and the interior of wood may be completely honeycombed and ruined while the surface shows only slight perforations. When present in great numbers, shipworms grow only a few centimeters before the wood is so completely occupied that growth is stopped. However, when not crowded, they can grow to lengths of 0.3–1.2 m depending on the species.

Another group of wood-boring mollusks is the pholads, which clearly resemble clams and therefore are not included with the shipworms. They are entirely encased in their double shells. The *Martesia* are the best-known species, but another well-known group is the *Xylophaga*. Like the shipworms, the *Martesia* enter the wood when they are very small, leaving a small entrance hole, and grow larger as they burrow into the wood. They generally do not exceed 64 mm and 25 mm in diameter but are capable of doing considerable damage. Their activities in the USA appear to be confined to the Gulf coast, San Diego, and Hawaii.

Crustaceans

Another distinct group of marine borers are crustaceans, which are related to lobsters and shrimp. The principal borers in this group are species of *Limnoria* and *Sphaeroma*. Their attack differs from that of the shipworms and the *Martesa* in that the bore hole is quite shallow; the result is that the wood is gradually thinned from the surface inward through erosion by the combined action of the borers and water erosion. Also, the *Limnoria* and *Sphaeroma* do not become imprisoned in the wood but may move freely from place to place.

Limnoria are small, 3–4 mm long, and bore small burrows in the surface of wood. Although they can change their location, they usually continue to bore in one place. When great numbers of *Limnoria* are present, their burrows are separated by very thin walls of wood that are easily eroded by the motion of the water or damaged by objects floating upon it. This erosion causes the *Limnoria* to burrow continually deeper; otherwise, the burrows would probably not become greater than 51 mm long or 13 mm deep. Because erosion is greatest between tide levels, piles heavily attacked by *Limnoria* characteristically wear within this zone to an hourglass shape. In heavily infested harbors, untreated piling can be destroyed by *Limnoria* within a year.

Sphaeroma are somewhat larger, sometimes reaching a length of 13 mm and a width of 6 mm. *Sphaeroma* are widely distributed but are not as plentiful as *Limnoria* and cause much less damage. Nevertheless, piles in some structures have been ruined by them. Occasionally, they have been found working in fresh water. In types of damage, *Sphaeroma* action resembles that of *Limnoria*. It has been reported that *Sphaeroma* attack salt-treated wood in Florida.

The average life of well-creosoted structures is many times the average life obtained from untreated structures. However, even thorough creosote treatment will not always stop *Martesia*, *Sphaeroma*, and especially *Limnoria*; shallow or erratic creosote penetration affords only slight protection. The spots with poor protection are attacked first, and from there the borers spread inward and destroy the untreated interior of the pile.

When wood is to be used in salt water, avoidance of cutting or injuring the surface after treatment is ever more important than when wood is to be used on land. Not cutting or injury of any kind for any purpose would be permitted in the underwater part of the pile. Where piles are cut to grade above the waterline, the exposed surfaces should be protected from decay. This may be accomplished by in-place application of a wood preservative followed by a suitable capping compound.

See also: **Pathology**: Heart Rot and Wood Decay; Insect Associated Tree Diseases. **Solid Wood Processing**: Drying; Protection of Wood against Biodeterioration. **Wood Formation and Properties**: Formation and Structure of Wood.

Further Reading

Beal RH (1967) Formosan invader. *Pest Control* 35(2): 13–17.

Coulson RJ and Lund AE (1973) The degradation of wood by insects. In: Nicholas DD (ed.) *Degradation and Protection of Wood*, pp. 277–305. Syracuse, New York: Syracuse University Press.

Daniel G and Nilsson T (1998) Developments in the study of soft rot and bacterial decay. In: Bruce A and Palfreyman JW (eds) *Forest Products Biotechnology*, pp. 37–62. London, UK: Taylor and Francis.

Findlay WPK (1967) *Timber Pests and Diseases*. London, UK: Pergamon Press.

Highley TL (1999) Biodeterioration of wood. In: *Wood Handbook – Wood as an Engineering Material*, pp. 13-1–13-16. Madison, WI: USDA Forest Service, Forest Products Laboratory.

Highley TL and Dashek WV (1998) Biotechnology in the study of brown-rot and white-rot decay. In: Bruce A and Palfreyman JW (eds) *Forest Products Biotechnology*, pp. 15–36. London, UK: Taylor and Francis.

Jones EBG and Eltringham SK (eds) (1971) Marine borers, fungi and fouling organisms of wood. In: *Proceedings of Organization for Economic Cooperation and Development*, 1968, March 27–April 3. Paris, France: OECD.

Krishna K and Weesner FM (eds) (1969) *Biology of Termites*, vol. I. New York: Academic Press.

Krishna K and Weesner FM (eds) (1970) *Biology of Termites*, vol. II. New York: Academic Press.

Zabel RA and Morrell JJ (1992) *Wood Microbiology: Decay and its Prevention*. San Diego, CA: Academic Press.

WOOD USE AND TRADE

Contents

History and Overview of Wood Use

R L Youngs, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA

Introduction

Wood is a natural product of the growth of trees. It is primarily composed of hollow, elongated, spindle-shaped cells that are arranged more or less parallel to each other in the direction of the tree trunk. This makes wood basically fibrous in nature. The characteristics of these fibrous cells and their arrangement in the tree strongly affect wood's physical and mechanical properties, as well as its grain patterns and workability. In its thousands of years of use, these properties have become familiar, but not well understood. They are becoming understood as a result of research during the past century.

Humans throughout history have used wood. The *International Book of Wood* records that "Man has no older or deeper debt than that owed to trees and their wood." The Bible notes that Noah built the ark from gopher wood, the first Ark of the Covenant was made from acacia wood, and the cedars of Lebanon formed Solomon's temple. Today wood is still a primary building material and fills many specialized needs in industrial and consumer use as well as in scientific and military applications.

Historical Overview

Wood has been one of humankind's most important raw materials for at least a hundred thousand years, for building and manufacture of tools, weapons, furniture, and other commodities of daily life. Wood was used early in human existence because it was available, had many useful properties, and no elaborate tools were needed to work it. However, in the early days the characteristics of the wood, rather than the tools available, were primarily responsible for the quality of products made from it. By 5000 BC copper tools began to be available and made possible improved craftsmanship, which is evident in some surviving relics of the time. By about 2600 BC wood was being used for coffers and chests for storage of precious possessions. The first coopering to make barrels was evident in records from about 2800 BC. Wood use and wood craftsmanship continued to develop over the years. Where wood was readily available, it was used widely for materials of industry, war, transportation, construction, and daily life.

Through the eighteenth century in Europe, wood was the principal material for construction of buildings and for tools, machines, vehicles, buckets, furniture, and barrels, plus many other articles of defense, transportation, and daily life. Wood was a basic material of the Industrial Revolution. The first printing press was made with wooden type in Germany in about 1450, although the Chinese are reported to have used woodblock printing about 700 years earlier than that. From its initiation in Germany, the printing press spread rapidly through Europe and continued to use wooden type for a hundred years. Most of the machines and inventions essential to establishing the machine age were developed in wood. Wood played a dominant role in industrial operations. About the sixteenth century in Europe, ready availability of wood began to diminish due to heavy demand for both fuel and materials and expansion of agriculture to feed the increasing population, which removed much of the land base for growing wood. In North America, wood use reached a plateau during the middle to late nineteenth century. Seemingly inexhaustible forests and other material resources were exploited to feed rapidly growing economic needs. Railroads, telegraph lines, steel mills, and other industries consumed wood at a rapidly increasing rate.

Wood in Construction

Wood has been, and still is, a particularly versatile and useful building material in its many forms and adaptations. Until the relatively recent development of metallic and plastic structural materials, it was the only material from which complete structural frameworks could be built. Wood structures built at various times and places have reflected the kind and quality of timber available and the culture and way of life of the people concerned. In earliest times, pole structures were built from small trees growing along the rivers. The techniques used by these early humans have been carried down over the ages and are very similar to those used by nomadic peoples today. However, the ability to erect permanent structures has been basic to most significant developments in the use of wood building materials. In zones that were well forested with plentiful timber, structures were built using solid walls of tree trunks or heavy planks. In other areas, wood has been used in more refined ways using careful design and engineering.

Europe

In Neolithic Europe walls of timber houses were frequently made of split trunks set vertically in or on the ground or on a bottom sill plate. Examples excavated from moor settlements in Germany demonstrated this type of construction. The mortise-and-tenon type of construction using heavy beams began early in history and continued through the Iron Age up to Norman times. A Viking fortress built in Denmark in about AD 1000 had this kind of construction, as did stave churches built during that century. Later construction used similar principles but employed vertical squared lumbers or sawed planks. Early French settlers along the Mississippi River brought this palisade type of house construction to North America. Construction in wood during the eleventh to the fourteenth centuries in Europe took advantage of Gothic construction, a concept in which the roof timbers formed an integral part of the frame and the principal framing members were typically large and heavy. This type of construction persisted until the seventeenth century in Europe but variations of it were used in America even into the nineteenth century.

North America

Wood construction has had an interesting evolution in North America because of the relatively abundant timber resource and the scattered development of much of the country. Native Indians in the forested areas of eastern and northwestern America built homes and community houses from indigenous woods. In the eastern United States these structures were commonly made of poles covered with bark and palisades of vertical logs were used for protection. The Indians along the northern Pacific Coast built houses from planks of split cedar or redwood and even had gabled roofs and decorative carving. In some of the sparsely forested areas of the Great Plains and western mountains, Indians built frames of timber and covered them with earth to make strong, permanent dwellings. The architectural designs used by early American colonists were based very much on those of their homelands adapted to the climatic and cultural differences of the colonies. The log cabin, which had been used for almost 3000 years in Europe, was introduced into North America by Scandinavian immigrants in the seventeenth century and was adopted in the eighteenth century by Scottish–Irish immigrants. In the far northwest, explorers and settlers from Russia moved south from Alaska and built houses, forts, and churches of log cabin type construction.

New England immigrants from England during the seventeenth and eighteenth centuries built their dwellings by following the pattern of the English timber-frame house with wattle daub or brick between the framing members. The classical ‘salt box’ type of house evolved from adaptations of that pattern to provide more protection against the severe weather. Exteriors of brick or stone were more likely to be used on houses in the middle Atlantic and southern states, but they had elaborately decorated interiors. The fact that in the colonial days timber was readily available for building led to the preference for detached or free-standing homes, as compared with the typical row house in much of Europe and other parts of the world.

Public buildings of North America followed similar trends in the eighteenth century. Churches were made, simply or ornately, of wood using many of these types of construction. Many of the public buildings in eastern America were made of both wood and brick in ways that took advantage of the good features of both materials. Wood is still the principal construction material for housing in North America and in Scandinavia and other parts of the world where timber supplies are plentiful and the tradition of wood construction remains strong. Until well into the nineteenth century, this was true also of building construction other than housing. Problems of fire and the need for high-rise buildings to conserve land space have contributed to the demise of wood frame construction in the centers of large cities.

A concept gaining increased attention is reuse of construction wood as buildings are removed or reconstructed. Under some social and economic conditions, this may provide an additional source of wood materials. Research is providing information on properties of such wood. That is being carried forward into grading systems that provide information on the suitability of reuse of deconstruction wood under specified conditions.

Wood for Weapons and Tools

Wood was a key material for building the weapons, equipment, and tools needed for military, industrial, and domestic use from ancient well through medieval times. Military devices, such as the battering ram, the scaling ladder, and the catapult were made of wood and much attention was given to their effective design. The reason for this widespread use of wood was its high strength to weight ratio, which made it valuable for many structural applications just as it is now. One of the oldest weapons recovered is the pointed end of a spear made of yew from the Lower Paleolithic era found waterlogged in an English bog. New techniques for working wood led to much more efficient use of wood in a variety of materials for tools and military supplies as well as for daily living. In the Neolithic era, about 2000 BC, improved tools were developed and have been found in the records of those times. The lathe was used from the Mediterranean area to northern Europe by about 1500 BC. By about 700 BC the plow made of wood was in common use. Early efforts to make weapons and tools from wood began the concept of selecting particular woods for specific uses depending on their properties and performance characteristics. Early selection was based on experience but observation of performance led to more effective use of wood for both weapons and tools of many kinds.

Wood for Transport

Wood has played an important role in the transportation of people and products for thousands of years. This has been both as a material for constructing vehicles and as a fuel for driving them.

Land Vehicles

In northern Europe as far back as 7000 BC sledges made of wood were used for transport. These were for heavy loads such as stones; archeologists believe that the massive stones of Stonehenge must have been moved on wood sledges placed on rollers. From the roller developed the concept of wheels. Pictures of wheels date from 3500 BC and wheeled vehicles have been found in tombs dating from 3000 to 2000 BC. The spoked wheel is a development of medieval times and in classical Greece both the spoked wooden wheel and a three-part solid wooden wheel were in common use. Solid wheels of plank were used on farm carts, and wheels with 10 to 14 spokes have been found in Roman forts of northern England of that period. Inserting rods of wood into grooves and placing them so that they would turn between the hub and the axle made the first roller bearings.

Railroads and Roads

Railroads well into the nineteenth century, the early twentieth century, and to some extent even today use wood for tracks, sleepers, bridges, trestles, tunnel linings, sheds, and stations. Through the nineteenth century wood was also heavily used for fuel. Nineteenth-century public transport in cities was mostly of wood vehicles including horse cars, electric trolleys, cable cars, carriages, and buggies. During the period from about 1820 to 1860 in America, roads made of planks laid across parallel rows of timbers imbedded in the earth were widely used. When they were in good condition, these were the best roads in the country and more than 3000 km of such roads were built in the middle years of the century. However, they were excessively expensive to maintain and they gradually disappeared from use.

Bridges

Before effective wood preservation systems were developed, wood bridges were built with advanced design concepts, and covered bridges were common in North America and parts of Europe. Walls and roofs were designed to protect the wood framework of the bridge from deterioration. Covered bridges were gradually replaced as new techniques of wood preservation provided more economical means of protection and as iron, steel, and concrete became more common materials for bridge construction. A resurgence of timber use in bridge construction occurred in late twentieth century and continues as the technology of bridge design and protection is developed and as the economy and environmental soundness of such structures is recognized.

Water Transport

One of the first uses for wood for water transport was probably a raft or hollowed-out log. The Egyptians had made boats of reeds by about 4000 BC and the earliest wooden ships copied the form of these reed boats. As cedar was imported from Lebanon, larger ships were built in Egypt. The barge built for Queen Hatshepsut in 1500 BC to transport granite obelisks from Aswan to Thebes had a displacement of some 6800 tons and needed 30 oar-powered tugs to tow it. Theophrastus, a pupil of Aristotle, was one of the earliest students of wood and published information on wood structure and properties. He also was involved with shipbuilding woods in ancient Greece. He noted that they were silver fir, fir, and cedar – silver fir for light strong construction and fir for decay resistance and cedar in Syria and Phoenicia because of lack of fir.

The Phoenicians had large galleys with two banks of oars, called biremes. With these they dominated trade in the Mediterranean for a thousand years before the time of Christ. The Vikings had wooden ships that were at least 25 m long. Design of wooden ships evolved over the years up to the nineteenth century, by which time paddlewheel steamboats were cruising the major rivers of the United States and consuming large quantities of wood fuel in the process. American clipper ships built of wood were the fastest seagoing ships of the late nineteenth century. The sleek shape and large expanse of sail enabled them to reach speeds of over 30 km per hour. However, by the 1880s iron steamships dominated the fleets of most naval powers and the economics of the use of wooden ships became unfavorable.

Shipping Containers and Pallets

Wood has provided containers for the world's goods for hundreds of years, its economy, availability and natural strength facilitating its use for chests, boxes, and crates. The engineering design of boxes and crates was greatly accelerated by wartime needs to ship material securely. This was particularly accelerated during the two world wars of the twentieth century, in which long-distance shipping of material became essential. During World War II design of wooden containers was further advanced, but research led also to substantial improvement in the design and use of corrugated fiberboard containers. Such containers were made weather resistant and highly resistant to the rigors of shipping. The economy and convenience of such containers contributed strongly to the decline of wooden containers, a decline that still continues.

The middle of the twentieth century saw the emergence of wooden shipping pallets for transporting goods of all kinds. As the need arose for efficient bulk shipment of corrugated containers, and as forklifts became available, shippers turned to pallets as a means of consolidating containers to expedite such shipments. Many manufacturers who had been making wooden boxes turned to making pallets, and many new pallet companies emerged as the pallet industry began to grow in the latter half of the twentieth century. This growth began in the United States and by the end of the century had grown to the point where pallets were the primary use for much hardwood lumber, especially the lower grades. Pallet production in American has grown from 25 million units per year in the 1950s to over 500 million in the late 1990s. Production of new pallets is supplemented by their repair and reuse. It is estimated also that about 71% of these are made from recycled lumber or other recycled material. As the forklift truck became available around the world, use of wooden pallets has followed and international trade in pallet lumber and pallets expanded using both hardwoods and softwoods.

Aircraft

Use of wood in aircraft is a relatively modern concept, though wood has been used in aircraft construction since the beginning of aviation. This reached a peak during the early and mid twentieth century in World Wars I and II. Although many woods have been used, Sitka spruce has been favored because of its high strength to weight ratio and ready availability in large sizes as clear, straight-grained material. Aluminum alloys, steel, composites, and new materials have taken over the structural role in commercial and major military aircraft, but wood is still used extensively for light aircraft.

Wood for Furniture

Wooden furniture appears to have been developed first in Europe about 3000 BC. Its development related very closely to the development of tools for working the wood. Reeds and rushes had earlier been used for furniture and early wood furniture designs copied the style of that material. Well-refined woodworking was employed when copper tools became available. These made possible much more precise careful operation of material for furniture and much more refined furniture. Shortages of furniture wood, which was a commodity of some rarity in many parts of the world, led to the early improvements in economical wood use. Planks cut from the same log were laid side by side and carefully fitted together. Defects were cut out and replaced. Furniture and cabinet-making reached a high level of sophistication in several areas of Europe by the sixteenth century. New designs and styles were developed and executed by outstanding designers and furniture makers. New styles of furniture were developed in Italy, England, and France as the Renaissance led to the improvements available in the Middle Ages. The furniture and interior furnishings used in colonial America were first quite simple and usually homemade. However, the new world contained a rich array of woods suitable for and available for furniture and other similar uses. The highly skilled craftsmen who had served their apprenticeship came to America took advantages of the wood, and from their skills developed in Europe became designers and manufacturers of high-quality furniture in styles that were both excellent copies of the European styles and original designs conceived in America.

Wood Use Today

Wood production throughout the world has continued to increase over the years. In the latter half of the twentieth century, increasing from something over 2 billion m^3 to nearly 3.5 billion m^3 (**Figure 1**). There is a marked difference, however, in the nature of wood production in the developed world and that in the developing world (**Figures 2** and **3**). Forty-seven percent of the world's wood production is for industrial roundwood, the wood used for a wide variety of wood and paper products (**Figure 2**). Fifty-three percent is for wood fuel, primarily in the developing world (**Figure 3**).

Increasing amounts of the world's wood supply are from plantations, even though plantations occupy a very small proportion of the forest area. Forest plantations provide a critical substitute for wood supply from natural forests, for both industrial wood and fuelwood. Industrial wood plantations account for only about 3% of the world's forest area, but are estimated to supply about 35% of the world's roundwood. Furthermore, this proportion is increasing steadily, supplying increasing quantities of wood that poses new challenges by having different working characteristics and physical and mechanical properties than wood from the natural forest.

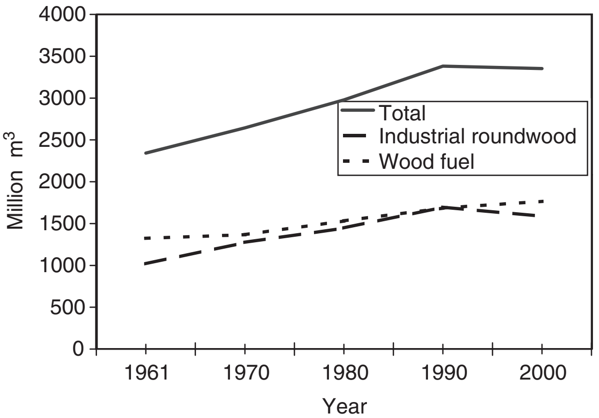


Figure 1 World wood production. Data from FAOSTAT Database 2002.

Research and its prudent application in the industry are also making possible conservation of the timber supply in the natural forest by effective and economical use of a wide range of timber previously considered unsuitable or uneconomic for use. Wood plastic composites are a new development in wood product production. They represent a new blending of the wood industry and the plastics industry. A wide variety of wood plastic composites are entering the market, especially for products like decking. This product may be encouraged by environmental pressure on, and increasing cost of, wood preservation.

Wood industries are continually adapting to changes in raw materials, particularly those due to the increased supply of plantation wood and to the introduction of additional species into the supply chain. These adaptations are leading to increased emphasis on engineered wood products and new composites, some of which are taking markets formerly served by plywood and lumber. Improved technology and the reduced availability of some traditional forest-based raw materials have encouraged innovative ways of expanding the wood supply and effective use of residues and waste.

Assumptions of continued economic growth and its effect on wood use indicate that consumption of industrial wood products will continue to increase in the future. Economic studies forecast continuing expansion of gross domestic product and increased demand for wood products at national, regional, and global levels. Increased demand for wood fuel is not related in the same way to economic growth, but may be expected by the rapid increase in population of regions of the world where it is most common.

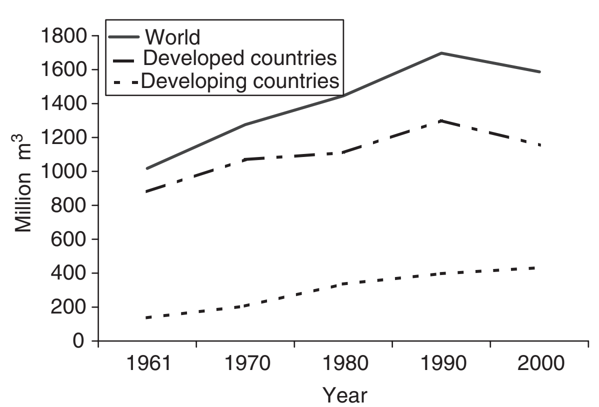


Figure 2 World industrial roundwood production. Data from FAOSTAT Database 2002.

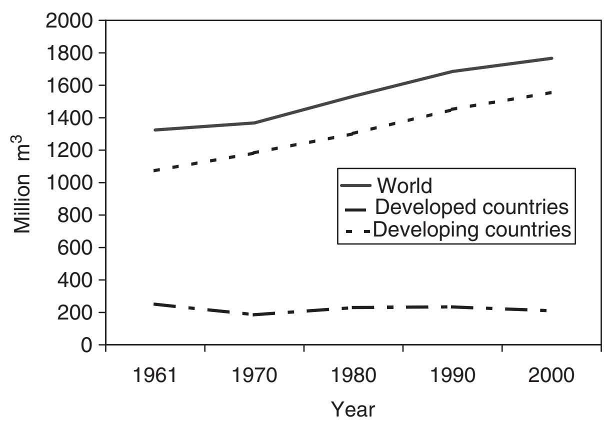


Figure 3 World wood fuel production. Data from FAOSTAT Database 2002.

Articles that follow in this section describe the current situation in wood use over a wide range of applications and employing much modern science and technology. New technologies have been developed to use the wood resource prudently to meet an increasing variety of consumer needs and provide dependable long-term service.

See also: **Solid Wood Products**: Construction; Logs, Poles, Piles, Sleepers (Crossties); Glued Structural Members; Lumber Production, Properties and Uses; Structural Use of Wood; Wood-based Composites and Panel Products. **Wood Formation and Properties**: Chemical Properties of Wood; Mechanical Properties of Wood; Physical Properties of Wood. **Wood Use and Trade**: Environmental Benefits of Wood as a Building Material.

Further Reading

Bramwell M (ed.) (1976) *The International Book of Wood*. New York: Simon & Schuster.

Davey N (1963) *A History of Building Materials*. London: Phoenix House.

Derry TK and Williams TI (1960) *A Short History of Technology*. Oxford, UK: Oxford University Press.

FAO (2002) *State of the World's Forests 2001*. Rome: Food and Agriculture Organization of the United Nations.

FAO (2002) FAOSTAT Database. http://apps.fao.org/default.htm

Hindle B (ed.) *America's Wooden Age: Aspects of Its Early Technology*. Tarrytown, NY: Sleepy Hollow Restorations.

Mumford L (1963) *Technics and Civilization*. New York: Brace & World.

Perlin J (1989) *A Forest Journey: The Role of Wood in the Development of Civilization*. New York: W W Norton.

Singer C, Holmyard EJ, Hall AR, and Williams TI (eds) (1954–59) *History of Technology*. Vols. 1–5. Oxford, UK: Clarendon Press.

Youngs RL (2001) Wood: history of use. In: Buschow JKH, Cahn RW, Flemings MC, *et al*. *Encyclopedia of Materials: Science and Technology*. pp. 9641–9646. Amsterdam: Elsevier Science.

International Trade in Wood Products

R A Sedjo, Resources for the Future, Washington, DC, USA

Global Forest Resources

The *Forest Resources Assessment* (2000 Summary Report) of the Food and Agricultural Organization (FAO) of the United Nations indicates that the world's forests total 3.867 billion ha in 2000, or 29% of the world's land area. Of this, 47% are tropical forests, 9% subtropical, 11% temperate, and 33% boreal. Over the past half century the area of temperate and boreal forest has remained relatively stable, even modestly expanding in recent decades, while net deforestation occurred at a rate of 9 million ha annually during the 1990s, almost entirely in the tropical and subtropical forests.

Production and Consumption

The world requires approximately 1.5 billion m^3 of harvested wood annually to produce the manufactured wood and paper products it consumes. The developed countries account for over 70% of industrial roundwood (log) production and nearly 75% of the wood and paper production consumed. The global value of primary forest products (wood, pulp, and paper) in 1999 are estimated by the FAO at approximately US$750 billion, with about US$350 billion for pulp, paper, and paperboard products and $400 billion for solid wood products. Developed countries of the Organization for Economic Co-operation and Development (OECD) account for over 80% of this production. Tropical solid wood products, coming primarily from the developing world, are estimated at about US$28 billion. Total international trade in forest products was estimated at about US$135 billion in 1996 or roughly 18% of the total value of production.

The United States and Canada account for approximately 35% of global demand for wood and paper products and the European countries of the OECD account for about 25%. All developed countries account for about 75% of world consumption, while 25% is consumed by developing countries.

Table 1 presents the volume of timber harvest by major regions in a recent year while **Table 2** provides information on the value of exports, imports, and net forest product trade in a similar year. The high-harvest countries are almost all major forest-product exporters, although some, most notably the United States, are net importers due to very high demand levels. Thus, while we focus on the value of net forest products exports, this figure is also a good proxy for harvest levels.

Why Trade?

In general, forest products trade flows from countries with abundant forest resources to countries with more modest forest resources. However, raw forest resources are often transported to an intervening regional location for initial or subsequent processing.

Trade occurs because some raw materials or products are less expensive in one region than in another, even when considering transport costs. This may be because the raw material is cheaper or because the processing is less expensive. It may also reflect differences in regional demand due to population and income differences. If the costs are sufficiently higher in one region so that the wood and transport costs can be covered, well functioning wood markets would be expected to promote wood trade from low-cost to high-cost regions, if trade barriers do not offset the inherent cost advantages.

Table 1 World industrial roundwood production (volume), 1997

Country	*Volume (m^3)*	*Percent total*
USA	416 092	27.32
Canada	185 859	12.21
Europe, excluding Nordic	218 526	14.35
Nordic	111 844	7.34
Brazil	84 661	5.56
Russian Federation	63 190	4.15
Japan	21 545	1.42
Indonesia and Malaysia	83 077	5.46
China and India	133 748	8.78
Other	204 216	13.41
World	1 522 758	100.00

Source: FAO (1997) *Forest Products Yearbook*. Rome: Food and Agriculture Organization of the United Nations.

Trade occurs at various stages of the production process. Roundwood is usually the raw material in the production process. Processed wood, e.g., sawnwood, wood panels and pulp, is typically an intermediate input in production that is used in the production of other products such as furniture, construction, and paper products. The basis of trade is found in differences in the location of the raw material (roundwood) from the locations of processing and the locations of final product markets. Often, but not always, the first stage of processing is done near the location of the raw wood, while subsequent processing is commonly done in another location, often near the final market. However, there are major trade flows of raw logs, which may involve processing in locations far from the origins of the raw wood.

Wood-producing countries may trade raw logs, process the logs to wood products and paper, or both. This is seen in the flows of sawlogs from North America to Asia for processing to lumber for Asian markets and pulpwood imported from South America into the United States for processing to pulp and paper. Trade constitutes about 7% of world consumption of logs (roundwood), 30% of wood products, and 29% of paper products. Major forest products exporters include Canada, the United States, Russia, Finland, Sweden, New Zealand, Chile, Indonesia, Malaysia, and Brazil.

Table 2 Major global exporters and importers of forest products (value), 1996

Country	*Exports (US$ × 10^3)*	*Imports (US$ × 10^3)*	*Net (US$ × 10^3)*
Canada	25 333 157	2 622 203	22 710 954
Sweden	10 996 199	1 323 936	9 672 263
Finland	10 301 017	699 632	9 601 385
Indonesia	5 206 522	865 424	4 341 098
Malaysia	4 161 279	881 539	3 279 740
Austria	4 149 678	1 988 878	2 160 800
Brazil	3 233 476	1 154 971	2 078 505
Russian Federation	2 995 568	115 030	2 880 538
Norway	2 059 960	1 402 551	657 409
Switzerland	1 797 767	2 501 957	− 704 190
France	4 193 914	5 356 351	− 1 162 437
Belgium and Luxembourg	2 180 694	3 544 574	− 1 363 880
Hong Kong	1 872 717	3 488 083	− 1 615 366
Spain	1 523 810	3 552 249	− 2 028 439
Netherlands	2 406 430	4 489 773	− 2 083 343
China (and Taiwan)	1 490 413	3 858 254	− 2 367 841
Germany	9 438 751	11 926 822	− 2 488 071
Korea	1 258 793	4 425 527	− 3 166 734
Italy	2 486 782	6 148 593	− 3 661 811
USA	16 939 897	22 558 536	− 5 618 639
United Kingdom	1 957 907	8 476 689	− 6 518 782
Japan	1 781 177	18 890 397	− 17 109 220
World	134 656 439	138 652 187	− 3 995 748

Source: FAO (1996) *Forest Products Yearbook*. Rome: Food and Agriculture Organization of the United Nations.

Traded Products

Forest products trade runs the spectrum from raw wood materials, such as logs and wood chips, to highly processed products such as furniture and fine papers. Within the wood products sector some countries specialize in the production of the raw wood, others specialize in various facets of the processing, while still others produce both raw wood and processed value added. Thus, the value of wood products appears to be only a crude proxy of the amount of raw wood harvested, both domestic and imported. Nevertheless, since there are often advantages in processing located near the source of the raw material, most of the countries with large dollar values of production and exports also have large volumes of forest resources.

Sawnwood, wood milled in a sawmill and commonly referred to as lumber, is the most prevalent produce produced in the solidwood side of the forest industry and the most intensively traded globally. Sawnwood is typically used for structural purposes in construction, as well as in furniture, flooring, and woodwork. Wood panels, such as plywood, are the second most traded wood product. Plywood is manufactured from wood veneer sheets that are glued and pressed. The United States is the largest producer of conifer plywood while Indonesia is the world's largest producer of nonconifer plywood, using tropical hardwoods in its construction. Europe is a major producer and consumer of plywood, most of it being produced from hardwoods. In addition, panels, such as particleboard and oriented strandboard, made from wood fibers that are compacted and glued, are increasing in use for a variety of purposes.

Global and Regional Production and Trade Flows

As noted, international trade in forest products was estimated at about US$135 billion in 1996. Traditionally, most of the trade occurs in the northern hemisphere between industrial countries. About 75% of industrial wood comes from temperate forests. Tropical timbers are produced and consumed largely in the tropical world, with modest international exports to the temperate developed countries from Africa and South America. The Asia–Pacific region is the only really large regional exporter of tropical wood, with large volumes of wood exports flowing from Malaysia and Indonesia, largely to the Asian countries, including Japan and China, and also to the United States and Europe. Smaller tropical wood flows originate in South America and Africa.

Industrial wood is produced throughout the northern hemisphere. In the Soviet era Russia was a major producer of industrial wood, primarily for its own consumption. Today Russia continues to be an exporter of industrial wood to parts of Europe, e.g., pulpwood to Finland, and to Asia, e.g., logs to Japan. Also, wood flows from Russia to the former centrally planned economies of Europe have decreased as these countries have been using more of their domestic wood resources directly and also exporting some of their raw wood to other European countries.

North America continues to be the world's major producer and exporter of industrial wood, producing over one-third of the world's production. This overall situation has not changed substantially from that of the 1970s. The United States continues to be the world's major wood producer and also its number one consumer market for industrial wood and wood products. Within the United States wood is produced in the South, which is the dominant producing region, as well as the West, the Lake States and the Northeast. In general, North American markets draw upon regional wood resources with supplies provided from these various wood-producing regions within the United States supplemented by huge exports from Canada. Canada, with it vast wood resources and its relatively small population, is the world leader in wood products exports with the major portion of these filling the gap between production and consumption in the United States. While log exports from Canada are generally restricted, for many years over 30% of the United States consumption of softwood lumber has been imported from Canada, as well as large amounts of other wood products. The volumes of wood products imported from outside North America are relatively small, but have been growing in recent years.

Europe is a huge wood market. Most of the total wood consumed in Europe is produced within Europe, including the Nordic countries. The Nordic countries of Europe also have historically provided large volumes of wood products to continental countries. Sweden and Finland are large producers and exporters of forest products, with most of the exports going to other countries within Europe, in the form of pulp and paper and some wood products. In recent years the Nordic raw wood supply is being supplemented by imports of raw wood from Russia and Estonia. As elsewhere, in recent years the amount of processing in the Nordic countries has increased and more processed products, including large volumes of paper, are exported. In addition to imports from Nordic countries, there is a great deal of forest-products trading within the broad European setting, with France, Germany, Austria, and Poland being the primary wood-producing continental countries. Western and central Europe also import large volumes of wood products from eastern Europe and Russia and North and South America, with more modest volumes from Africa and Asia. Overall, however, Europe is a wood-deficit region with the wood deficits provided from a variety of suppliers throughout the world including, importantly, North America and Russia.

Asia is the most rapidly growing of the major global wood markets and Japan has been the dominant consuming country in Asia and indeed, Japan is the world's largest net importer of forest products and has the world's largest wood deficit (**Table 2**). Japan draws the vast majority of its wood resources and products from a host of producing countries in the Pacific Basin. In the post-World War II period the Pacific Basin has been a vast arena of wood products trade with Japan as the hub of a huge trade inflow. Traditionally, Japan has imported large volumes of logs, which were subsequently processed to meet Japanese unique sizes and standards. Log flows into Japan have come from many sources, both tropical and temperate and include log exports from Malaysia, Indonesia, Russia, and the United States. In recent years the log flows have declined and have been replaced by wood product imports. For example, logs from Indonesia have declined, being replaced by processed wood like plywood and lumber, and log flows from North American have also declined in recent years, having been replaced by North American lumber and by increased logs flows from New Zealand and Australia.

In recent decades other Asian countries have been or are becoming major wood importers, including Korea and Taiwan. China particularly has become an important importer for forest products, with its imports largely being unprocessed wood. Other countries in Asia, such as India, consume substantial volumes of wood products. However, South Asian wood consumption is mostly produced domestically.

Finally, Africa and Asia tend to supply largely tropical wood, while South America supplies growing volumes of wood pulp, primarily to Europe but increasingly to other regions too, produced by plantations, and also some tropical woods.

Traditionally, most of the raw wood used by the world global forest industry has been obtained by harvesting natural forests. Thus, the wood is obtained through an essentially foraging operation with the location of the forest resource determined by natural processes. Forest raw material trade thus began in the natural forest and made its way to the final market with various processing activities along the way. In this situation the productive advantage goes to forests with large volumes of healthy desired species. In recent years, however, the source of raw wood production has been undergoing substantial changes. Wood fiber from natural forests is being replaced by wood fiber from planted forests. In some cases these forests simply replaced earlier natural forests on the same sites, as in much of Europe. Increasingly, however, planted forests are being established on sites not recently in forest, as in planted forests established on lands on which agriculture has been abandoned, e.g., in the South of the United States. However, in other areas forest plantations are being established on lands that may never have been forested, as in grasslands of parts of Latin America or regions of Australia not previously forested.

Sources of Changing Trade Patterns

The advent of planted forests has resulted in important new supplies of industrial wood that are reflected in new patterns of wood products trading. Countries such as New Zealand, Chile, and Australia have, in recent decades, become important exporters of wood products, particularly to the growing markets of Asia. Brazil, too, has become an important producer of forest products and the nature of its product mix has changed. In the case of Brazil, its tropical hardwood exports, drawn from its vast Amazonian forests, are now dwarfed by the export of wood pulp, which uses plantation forests as its raw material.

Another factor influencing the pattern of forest products trade is growing environmental concerns. The establishment of protected forests, free from commercial timber harvests, together with the institution of new forest practices requirements, is influencing harvest levels and harvesting costs and thereby influencing wood trade flows. The dramatic reduction in timber harvests from US National Forests undoubtedly has resulted in increased lumber imports from Canada as well as increased production from the US South. Higher costs of harvesting in the coastal forest of British Columbia, due to a more stringent forest practices code enacted in the 1990s, likely is an important contributor to reduced wood trade flows from coastal British Columbia to Japan.

Trade Barriers

Trade barriers are often inserted to reduce or preclude trade. Trade barriers can consist of prohibitions of exports or imports of certain products, e.g., log export prohibitions; import taxes (tariffs), which place a tax on the imported product; export taxes, which place a tax on the product when it is exported; and quantitative restrictions, which place limits on the amount of a product that can be imported (or exported). Trade barriers have the effect of reducing the volume of imports (or exports) and thus influencing supply or prices within a country.

Quantitative restrictions in trade are common with forest products. **Table 3** provides an estimate of wood products' import tariff averages in selected countries. Note that this average does not include consideration of trade prohibitions and quotas. Trade barriers are usually introduced to achieve certain policy or political objectives and typically are designed to protect a product, industry, or other group. A restriction of lumber imports, for example, increases the price of lumber in the importing country thereby benefiting domestic producers of lumber (both firms and perhaps lumber workers). The common rationale for an export restriction, as on logs, is that the raw material be processed within the country where the log is found, thereby generating increased employment and value added. An export restriction, for example logs, has the effect of making log prices lower in the exporting country and encouraging domestic wood processing. Canada has used this rationale for decades to support a policy decision to insure that logs would be available for domestic processors at low prices. The United States restricted the export of logs from national forests in the West to insure an adequate log supply to western mills. Some countries place restrictions on processed imports for a similar reason. Japan placed an import tariff on certain types of processed wood in order to protect the domestic processing industry.

Table 3 Average of forest products tariffs in selected countries

Country	*Tariff % (Most Favored Nation average)*
Australia	2.88
Canada	3.88
Chile	11
China	20.86
Taiwan	3.22
Hong Kong and China	0
Indonesia	9.7
Japan	1.14
Korea	4.98
Malaysia	12.26
Mexico	11.32
New Zealand	6.06
Singapore	0
Thailand	20.04
USA	1.4
European Union	5.26

Source: FAOSTAT website (1998).

In general, forest product tariffs tend to be low. An analysis carried out in 1999 estimated that the effects of the Uruguay Round of the General Agreement on Tariffs and Trade (GATT) reduced tariffs of 33% on most forest products and increased total forest products world trade by US$460–593 million. This is an increase of only a very small fraction of global trade in forest products. Modest levels of change in trade suggest only modest levels of change in production. In the specific markets analyzed in this study, which included products with relatively modest amounts of processing valued added (logs, sawnwood, veneer, particleboard, fiberboard, plywood, wood pulp, and newsprint), trade increases constituted an increase of 1.6–2.0%. The largest trade increase was 5% for plywood, a product where tariffs have tended to be relatively high, in the 10–15% range. The lowest trade effect was a 1% export increase for wood pulp, a product which in most countries has little or no tariff. This study also found that the trade effects of tariff reductions would generally increase the exports of developed countries while reducing exports of developing countries.

Trade Liberalization

Trade liberalization has generally been regarded as a socially desirable activity in that production efficiency is increased thereby lowering costs and providing benefits to consumers. The last several decades have seen a series of trade negotiations to rationalize the global trading system with the general objective of liberalizing trade, e.g., reducing tariffs and other restrictions. An extension and further reduction of the scheduled tariff reductions associated with the Uruguay Round was proposed to the World Trade Organization (WTO), the international organization charged with overseeing the international trade process. The 1999 proposal would have accelerated scheduled tariff reductions on both solid wood products and on pulp and paper. Concerns have been raised, however, that trade liberalization could have an adverse influence on the environment.

In forestry, for example, the conflict between freer trade and concerns regarding the implications of freer trade on forest sustainability were raised in response to the proposal to accelerate the Uruguay Round agreement to decrease tariffs on forest products. This proposal, which was raised at the G7 meeting of finance ministers in Seattle in late 1999, was met with street protests that derailed the effort. The concerns raised suggested that tariff reduction would increase timber harvests thereby accelerating pressures on forests to increase the rates of harvesting. This was viewed as undermining forest sustainability and promoting deforestation. One can view this concern as a variant of the 'race to the bottom,' often cited by environmentalists, whereby countries with lax environmental standards have a cost advantage in production and trade. Here, freer trade is viewed as imparting an additional competitive advantage to countries with lax logging standards thereby leading to excessive rates of logging and the associated forest damage and destruction.

Another 1999 study estimated the trade effects on global harvests and deforestation and found them to be very modest. It was estimated that the effects generate an increase in harvest of 6–10 million $m^3 year^{-1}$ or about a 0.4–0.7% increase in the global industrial wood harvest. Further, it was suggested that the effects would be confined largely to the northern hemisphere countries which are likely to be able to facilitate additional harvests with minimal effects on the forest environment. This is due to the modest nature of the impact, new laws on forest practices, new forest set-asides, and movement toward improved practices designed to achieve multifaceted sustainable forestry. Nevertheless, the negotiations held by WTO countries in Seattle in 1999 did not result in an acceleration of wood products tariff reductions.

Trade and Forest Environmental Issues

The years since the 1992 United Nations Conference on the Environment and Development (UNCED) Earth Summit in Rio have seen significant changes in our perceptions of forest issues. Although Rio was not primarily about forests, a number of important international forest initiatives, many involving trade, emerged from Rio. In the dialogue leading up to UNCED in 1992, concerns had been expressed about forest sustainability, the loss of biodiversity, and the overall rate of deforestation, especially in the tropics.

A total of 178 governments were represented at UNCED, and a contentious debate revolved around forest issues. UNCED ultimately produced four documents related in whole or in part to forests:

- *Agenda 21*, a global environmental action plan
- a framework convention on global climate change
- a convention on biological diversity
- a *Statement of Principles on Forests*.

The *Statement of Principles on Forests* reflects a global consensus on a set of nonbinding principles of management, conservation, and sustainable development of all types of forests. One of the major outcomes of the Earth Summit was the industrial world's nonbinding agreement that sustainable forestry should be practiced by all countries, both tropical and temperate. The discussion and documents coming out of the Earth Summit also broached some specific management issues, such as the issue of forest certification and ecolabeling. For example, *Agenda 21* encourages

> expansion of environmental labeling and other environmentally related product information programs designed to assist consumers to make informed choices.

In response to international and domestic concerns, many major wood-producing countries have made changes to their domestic laws and policies concerning forests. These include changes to improve water quality, protect biological diversity, and implement less intensive silvicultural treatments. Some of these policies are regulatory in nature while others rely on taxation or other incentives. In many temperate forested countries significant revisions have been made in the legal and institutional framework dealing with forest matters.

Additionally, perhaps the most impressive changes have been the activities leading to the certification of forest practices and the movement to use certified wood in ecolabeled products. Over the past decade a number of forest certifying organizations have emerged. There are currently a number of alternative approaches to auditing and certification of forestry management under consideration and there are a host of different organizations that can act to set standards, oversee monitoring, undertake auditing and award certification of forest management. These approaches were led by the World Wildlife Fund (WWF) Forest Stewardship Council (FSC), which has initiated an aggressive forest certification campaign over the past decade.

In addition to the FSC, there have been a number of other similar efforts. In some countries and regions the forest industry has taken the initiative to create organizations similar to but strongly competitive with the FSC, sometimes in cooperation with governments. These include country and regional organizations such as the Sustainable Forestry Initiative (SFI) of the American Forest and Paper Association, a forest industry associated in the United States; the Canadian Standards Association in Canada, and, more recently, the Pan European Forest Council (PEFC) in much of Europe. Additionally, there are local and regional certification systems such as the Nordic Forest Certification System and the Finnish Forest Certification System (FFCS).

Changes in domestic forest practices regulation and the introduction of the certification to forest management are designed to address concerns of poor logging practices and excessive harvest rates, while promoting forest sustainability. However, changes in domestic forest policies and movement toward certification can have differential impacts on the underlying production cost structure of various countries thereby influencing the comparative production and trading capacities and costs. Thus, trading patterns would be expected to respond to these changes and countries are seen to strive to modify rules and practices so as to advantage their forestry production sector in relation to its competitors.

See also: **Mensuration**: Yield Tables, Forecasting, Modeling and Simulation. **Papermaking**: World Paper Industry Overview. **Resource Assessment**: Regional and Global Forest Resource Assessments. **Tree Breeding, Principles**: Economic Returns from Tree Breeding.

Further Reading

Barbier ER (1999) The effects of the Uruguay round tariff reduction on forest products trade: a partial equilibrium analysis. *The World Economy* 22(1): 87–115.

Bourke IJ and Leitch J (1998) *Trade Restrictions and Their Impact on International Trade in Forest Products*. Rome: Food and Agriculture Organization of the United Nations.

Brooks DJ, Ferrante JA, Haverkamp K, *et al*. (2001) *Economic and Environmental Effects of Accelerated Tariff Liberalization in the Forest Products Sector*, General Technical Report no. PNW-GTR-517. Madison, WI: US Department of Agriculture, Forest Service.

Brown C (1997) *The Implications of the GATT Uruguay Round and Other Trade Arrangements for the Asia–Pacific Forest Products Trade*, Forestry Planning and Statistics Branch Working Paper no. APFSOS/WP/03. Rome: Food and Agriculture Organization of the United Nations.

Federal Register (1999) Office of the United States Trade Representative, Council on Environmental Quality, 64(122) June 25, pp. 34304–34306.

FAO (2000) *The Forest Resources Assessment 2000 Summary Report*. Rome: Food and Agricultural Organization of the United Nations.

ITTO (1999) *Annual Review and Assessment of the Timber Situation 1999*. Yokohama: International Tropical Timber Organization.

Sedjo RA and Radcliff SJ (1981) *Postwar Trends in US International Forest Products Trade: A Global, National, and Regional View*. Baltimore, MD: Johns Hopkins Press for Resources for the Future.

Sedjo RA and Simpson RD (1999) Tariff liberalization, wood trade flows, and global forests. *Resources for the Future*, Discussion Paper 00-05, December. Washington, DC: Resources for the Future.

Sedjo RA, Goetzl A, and Moffat SO (1998) *Sustainability in Temperate Forests*. Washington, DC: Resources for the Future.

Environmental Benefits of Wood as a Building Material

J L Bowyer, University of Minnesota, St Paul, MN, USA

Introduction

The management of forests to obtain wood for use in the production of houses and a host of manufactured products is often criticized based on environmental concerns. Such concerns have led some to conclude that periodic harvesting of forests and the use of wood should be minimized, or even halted altogether. However, careful consideration of global environmental concerns in the context of the realities of today's world leads to a much different conclusion: to protect the environment, forests and the wood they produce should be utilized to the maximum extent possible within sustainable limits.

It is essential that forests be managed in a manner that sustains a myriad of forest values over the long term. At the same time, it is vitally important that forests be managed in such a way as to minimize impacts on the global ecosystem, of which forests are one part. Thus, there are a number of things to consider when contemplating the proper role of forests. One of these is the fact that growing populations worldwide consume vast quantities of raw materials, including wood. Another is that wood is the only widely available industrial raw material that is renewable. Yet another, and very important consideration, is that the environmental impacts associated with the manufacture and use of wood products are less, and in many cases substantially less, than those associated with the manufacture and use of products made of non-wood materials.

Assessing Environmental Impacts of Industrial Activity

An effective means of assessing the relative environmental impacts of a product is to examine them over the life cycle of the product from raw materials extraction, through processing and conversion, and ultimate use. Examination of energy use is particularly revealing, since a number of serious environmental problems are related to consumption of energy including acid deposition, oil spills, air pollution (SO_2, NO_x), and increasing concentrations of atmospheric carbon dioxide.

Research involving systematic examination of the environmental impacts of a product over its life is commonly referred to as life cycle assessment or simply LCA. An LCA typically begins with a careful accounting of all the measurable raw material inputs (including energy), product and coproduct outputs, and emissions to air, water, and land; this part of an LCA is called a life cycle inventory, or LCI. The LCI can be set up to deal with raw material extraction and product manufacture only, or the boundaries of an inventory may be defined more broadly to include product use, maintenance, and disposal. A full LCA seeks to assign values to factors that are currently not precisely measurable, such as impacts of an industrial activity on the landscape, flora, fauna, air, or water. Most life cycle assessment studies to date have focused primarily on the life cycle inventory.

Environmental Impacts of Wood Products Manufacturing

Energy Consumed in Manufacturing

One of the first comprehensive life cycle assessments of wood products was completed in the United States in the mid-1970s. Commissioned by the National Academy of Sciences, the study examined the energy required to build wall systems for residential homes. Energy use associated with raw material gathering (harvesting or mining), transport, manufacturing, and building construction was considered. Wood-frame construction was found to require the use of only one-half to one-seventh the energy needed for construction using steel, aluminum, concrete block, or brick (**Table 1**).

Although technologies in all industries, as well as protocols governing the conduct of LCA/LCI studies, have changed significantly since the mid-1970s, a growing number of studies have confirmed the energy advantages of wood. Dramatic differences have been shown in the quantities of energy needed to manufacture primary materials used in construction or in the manufacture of secondary products. Researchers at the University of Tokyo in the early 1990s determined, for example, that the energy needed to manufacture 1 cubic meter of steel, aluminum, and concrete was 191 times, 791 times, and 3.5 times greater, respectively, than that needed to manufacture 1 cubic meter of kiln dried lumber (**Table 2**). Energy calculations were based on production of virgin materials in all cases. When comparisons were made on a mass basis, the manufacturing energy ratios in comparison to wood became 12.5, 155, and 0.7, again for steel, aluminum, and concrete. Although these figures suggest the very large impact that materials choice can have on energy consumption, such numbers are difficult to compare, since equal volumes or masses of materials are almost never used for a given application.

The most meaningful comparisons of materials are made when comparing products that have the same function. For instance, a comparison of energy requirements for producing wood and steel siding products for structures can be very informative as long as care is taken to ensure that the same boundaries are used in defining the scope of analysis. The same is true of analysis of entire buildings. Though more complicated than examination of single products, analysis of complete structures is often favored by LCA researchers since a large segment of industrial wood globally is used in building construction.

Substantial differences in the quantity of energy needed for building construction have been shown for a wide range of building types. For example, a 1992 Canadian assessment of alternative materials for use in constructing a large research laboratory building showed all-wood construction on a concrete foundation to require only 35% as much energy as steel construction on a concrete foundation (**Table 3**). A New Zealand study in the same year found wood-frame construction of residential buildings with wood-framed windows and wood fiberboard cladding to require only 42% as much energy as

Table 1 Relative quantity of energy (oil equivalent) needed to manufacture various wall systems using construction practices common to the United States

	GJ of energy needed to manufacture 100 m^2 of wall (#2 = 1.000)
1. Plywood siding, no sheathing, 2 × 4 wood frame	0.782
2. MDF siding, plywood sheathing, 2 × 4 wood frame	1.000
3. Concrete building block, no insulation	6.725
4. Aluminum siding, plywood, insulation board, 2 × 4 wood frame	1.949
5. MDF siding, plywood sheathing, steel studs	2.009
6. Brick veneer over sheathing	7.039

MDF, medium density fiberboard.

Source: National Research Council (1976) *Renewable Resources for Industrial Materials*. Washington, DC: National Academy of Sciences.

Table 2 Energy consumption and carbon dioxide emissions in the production of various materials

Material	*MJ kg^{-1}*	*MJ m^{-3}*	*Carbon emission during production (kg m^{-3})*	*CO_2 storage*	*Net CO_2 emissions*
Lumber (air dry, SG 0.55)	1.5	750	15 (16)[a]	250	– 235 (– 234)[b]
Lumber (kiln dry, SG 0.55)	2.8	1 390	28 (100)[a]	250	– 222 (– 150)[b]
Plywood (SG 0.55)	12	6 000	120 (156)[a]	248	– 128 (– 92)[b]
Particleboard (SG 0.65)	20	10 000	200 (224)[a]	260	– 60 (– 36)[b]
Steel	35	266 000	5 320	0	5 320
Aluminum	435	1 100 000	22 000	0	22 000
Concrete	2.0	4 800	120	0	120

[a] Values in parentheses indicate total carbon emissions during production assuming fossil fuels used to supply all manufacturing energy. Values outside of parentheses indicate typical carbon emissions from fossil fuels during manufacturing assuming that wood residues generated in manufacturing are used to produce process energy. Although burning of wood liberates carbon, the process is carbon neutral if it is assumed that trees are replanted following harvest.

[b] Negative values result from the fact that wood is 49% carbon by weight and that the quantity of carbon released in generating process energy is less than the carbon stored in the finished wood product. For explanation of values within and outside of parentheses see footnote above.

SG, specific gravity.

Source: Arima T (1991) Tokyo University Prof. Arima points to contribution of wood products to environmental preservation. *Rinkei Shimbun* July 17.

Table 3 Calculated energy consumption and carbon dioxide emissions for alternative wood and steel construction: Forintek Canada Western Laboratory

Location	*Energy consumption (GJ)*		*CO_2 emissions (tonnes)*	
	Wood assembly	*Steel assembly*	*Wood assembly*	*Steel assembly*
Office/Laboratory floor	2 837	9 458	157	581
Office/Laboratory roof	3 653	7 648	197	463
Pilot plant	1 646	5 818	94	352
Total	8 136	22 924	448	1 396

Source: Marcea R and Lau K (1992) Carbon dioxide implications of building materials. *Journal of Forest Engineering* 3(2): 37–43.

Table 4 Embodied energy carbon dioxide emissions analysis of a large office building

Construction	*Total energy use ($GJ \times 10^3$)*	*Above grade energy use ($GJ \times 10^3$)*	*CO_2 emissions ($kg \times 10^3$)*
Wood	3.80	2.15	73
Steel	7.35	5.20	105
Concrete	5.50	3.70	132

Source: Canadian Wood Council (1997) *Comparing the Environmental Effects of Building Systems*, Wood the Renewable Resource Series no. 4. City: Publisher.

brick-clad, steel-framed dwellings built on a concrete slab and fitted with aluminum-framed windows. When office and industrial buildings were considered, those constructed of timber were found to require only 55% as much energy as steel construction and approximately 66–72% as much energy as concrete construction. Another late-1990s Canadian study involving analysis of a large three-story building yielded almost identical results (**Table 4**). A 2002 study in Western Europe found significant differences in energy required to build wood and brick houses, although the differences were lower than in the studies just mentioned. In this case, the total energy needed to produce a wood timber-frame house was 83% of that needed to produce a concrete and brick house of the same design; both houses were built on concrete foundations and both had concrete shingles. Removing these and other common elements from the comparison, and focusing only on the parts of the structures built with different materials showed much larger differences in energy requirements, again favoring wood construction. In another mid-1990s comparison of wood- and steel-frame construction for light-frame commercial structures in Canada, which examined a wide range of factors in addition to energy, low environmental impacts of wood construction relative to steel were again demonstrated (**Table 5**).

Most LCA studies to date have assumed the use of virgin materials (i.e., no recycled content). One mid-1990s study that did consider incorporation of recovered material examined the use of recycled steel in wall studs. In this case, the manufacturing energy differences between wood and steel were found to narrow, but wood retained a significant advantage. As part of the wood vs. steel wall comparison, load-bearing wood and steel-framed walls, in which the steel contained 50% recycled steel content, were examined. In this case the steel-framed wall was found to be

> some four times as energy intensive, and correspondingly…at least that much more environmentally damaging, despite its recycled steel content.

Several interesting studies have examined differences in energy required to manufacture various kinds of building components. A team of Swiss researchers compared window units made of wood, aluminum, and PVC and found the manufacture of the wood-framed window to require only 75% of the energy needed for production of aluminum windows and 95% of that needed for production of PVC windows. It was noted that the wood waste generated in the process is often burned to produce energy, increasing the magnitude of difference in total energy consumption while also replacing fossil fuels in the process. In a 1995 Swedish study of linoleum, vinyl, and wood flooring, very large differences in net manufacturing energy were found for the three material types, with wood favored by a wide margin.

Table 5 Comparative energy consumed in manufacturing wood vs. steel-framed interior wall

	Energy consumption (GJ)	
	Wood-framed wall	*Steel-framed wall*
Extraction	0.7	1.2
Manufacturing	2.1	9.7
Construction	0.6	0.6
Total	3.4	11.5

Source: Meil J (1994) Environmental measures as substitution criteria for wood and nonwood building products. In *Proceedings, The Globalization of Wood: Supply, Processes, Products, and Markets*, pp. 53–60. Madison, WI: Forest Products Society.

An early 1990s study lent some perspective to the significance of the differences in processing energy associated with different kinds of building materials. While commenting on a proposal to reduce markedly timber harvesting activity in the Pacific Northwest region of the United States, Peter Koch noted that one possible outcome could be substitution of nonrenewable structural materials such as steel, aluminum, concrete, and plastics to replace the wood not harvested. He calculated that the impact on energy consumption and carbon dioxide releases, were this to occur, could be as high as 6 billion gallons of oil and 62 million tonnes of carbon dioxide annually – equivalent to operating a fleet of about 11 million automobiles.

Carbon Storage and Emissions

Recent concern about the possibility of global warming has focused attention on liberation of carbon dioxide in materials production and use. Wood is at the center of the global warming debate because of the ability of forests to store or sequester carbon. Dry wood is 49% by weight carbon, meaning that 0.5 kg of carbon is contained within each 1 kg of dry wood. Moreover, for each kilogram of wood produced, 3.7 kg of carbon dioxide is removed from the atmosphere. Thus, substantial carbon storage accompanies the growth of trees.

Findings of recent studies consistently indicate that wood has a large advantage over other materials with respect to carbon emissions resulting from manufacture and use for at least three reasons:

1. Relatively little energy is required to manufacture wood products as compared to non-wood materials. As a result, the quantity of greenhouse gases liberated through combustion of fuels is significantly lower when manufacturing wood products.
2. Wood is 49% carbon by weight, and thus wood used in structural and other long-lived products stores or sequesters carbon over extended time periods.
3. The majority of energy (65–70%) used in producing wood products is obtained from burning of wood residues such as sawdust, bark, and paper-mill waste liquors. Thus, quantities of fossil fuels used in wood products manufacture are typically vastly lower than those used in the manufacture of

Table 6 Net carbon emissions in producing 1 tonne of different materials

Material	*Net carbon emissions (kg t^{-1})*
Framing lumber	−460
Concrete	45
Concrete block	49
Brick	148
Glass	630
Steel	1 090
Aluminum	2 400
Plastic	2 810

Source: Honey BG and Buchanan AH (1992) *Environmental Impacts of the New Zealand Building Industry*, Research Report no. 92-2. Canterbury, New Zealand: Department of Civil Engineering, University of Canterbury–Christchurch.

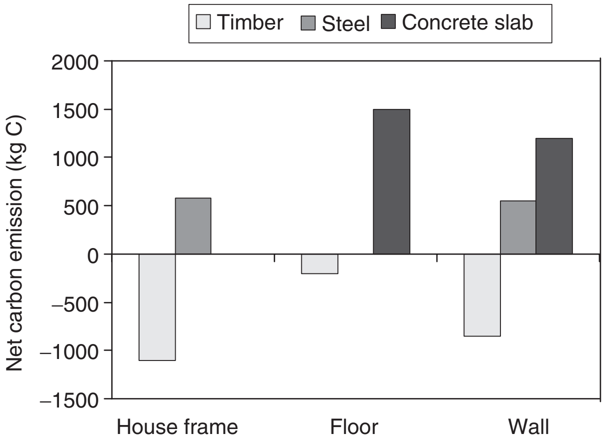


Figure 1 Carbon dioxide emissions of various components in a typical house. (Reproduced with permission from Honey BG and Buchanan AH (1992) *Environmental Impacts of the New Zealand Building Industry*, Research Report no. 92-2. Christchurch, New Zealand: Department of Civil Engineering, University of Canterbury.)

non-wood products; this translates to avoided carbon emissions from fossil fuels.

Many LCA/LCI studies have shown substantial differences in carbon liberation when comparing wood products manufacture and use with non-wood products. For example, the New Zealand study that examined manufacturing processes, including raw material extraction and transportation, not only revealed large differences in net carbon dioxide emissions from material to material, but a carbon emission figure for lumber that is actually negative (**Table 6**). Others (see **Table 2**) have reported similar findings. The negative values for wood are due to its carbon content.

When carbon dioxide emissions associated with constructing wood and other kinds of structures are examined, large differences favoring wood again become evident. Data presented in **Tables 3** and **4** and **Figure 1** are typical of findings from recent studies. One study, a portion of which is highlighted in **Figure 1**, involved analyses of alternative designs of structures ranging from single family homes, to an industrial building, to a large office structure. Included among the findings of the authors is the observation that

> The choice of building material has a huge effect on the carbon emissions to the atmosphere. Timber used for framing, floor, and wall components of a house compare much more favorably than other common materials.

Recognizing that the potential for global warming is related to compounds in addition to carbon dioxide, such as methane, LCA researchers have very recently begun expressing total greenhouse gas emissions in terms of a global warming potential (GWP) value. A life cycle assessment of houses built in Minneapolis and Atlanta in the United States (**Tables 7** and **8**) showed the GWP of steel-framed and concrete block structures to be 49% and 65% greater, respectively, than otherwise identical wood-framed structures. In both comparisons houses had common foundations (concrete) and roof systems (wood). Much larger differences, again favoring wood, resulted when common elements were removed from the comparisons.

The study of windows referred to earlier showed the GWP of aluminum and PVC-framed windows to be 10–20% greater than those framed in wood. Similarly, the potential for acid rain, eutrophication, and photochemical ozone was found to be 114–136%, 45–55%, and 42–65% greater when manufacturing aluminum and PVC windows than when manufacturing wood windows.

It should be noted that although it is often assumed that trees grown to offset carbon dioxide emissions need then to be preserved in order to keep the carbon dioxide from returning to the atmosphere, recent research shows that carbon storage can be significantly enhanced by periodic harvest of trees and their use in long-lived products. Several researchers recently determined the carbon storage implications of short- and long-term wood products use, low energy consumption and carbon liberation associated with wood products manufacture, and avoided fossil fuel use, and concluded that carbon accumulation in forests is more rapid when a portion of the wood is harvested and used in long-lived products (**Figure 2**). They noted that the greater the manufacturing efficiency and useful product life, the stronger the case for wood becomes.

In short, concerns regarding global warming potential point to greater use of wood as a part of the solution.

Table 7 Environmental performance indices for residential structure in Minneapolis, USA

	Wood			*Steel*			*Increase resulting from use of steel*
	Wall	*Floor*	*Total*	*Wall*	*Floor*	*Total*	
Energy	97	12	186	148	83	308	+66%
Global warming potential	20 790	1 970	39 810	28 930	13 332	59 290	+49%
Air emissions	1 497	242	2 778	2 246	1 414	4 711	+70%
Water emissions	31	10	185	492	544	1 179	+537%
Solid waste	7 600	1 130	12 110	6 320	1 323	11 020	−9%

Source: Consortium for Research on Renewable Industrial Materials (2002) *Life Cycle Environmental Performance of Renewable Building Materials in the Context of Residential Building Construction: Phase I Interim Research Report on the Research Plan to Develop Environmental-Performance Measures for Renewable Building Materials with Alternatives for Improved Performance*. Seattle, WA: CORRIM, Inc., University of Washington.

Table 8 Environmental performance indices for residential structure in Atlanta, USA

	Wood		*Concrete*		*Increase resulting from use of concrete*
	Wall	*Total*	*Wall*	*Total*	
Energy	22	115	69	162	+41%
Global warming potential	1 400	20 020	14 510	33 130	+65%
Air emissions	116	1 035	954	1 862	+80%
Water emissions	10	86	23	99	+15%
Solid waste	562	4 270	4 260	7 970	+86%

Source: Consortium for Research on Renewable Industrial Materials (2002) *Life Cycle Environmental Performance of Renewable Building Materials in the Context of Residential Building Construction: Phase I Interim Research Report on the Research Plan to Develop Environmental-Performance Measures for Renewable Building Materials with Alternatives for Improved Performance*. Seattle, WA: CORRIM, Inc., University of Washington.

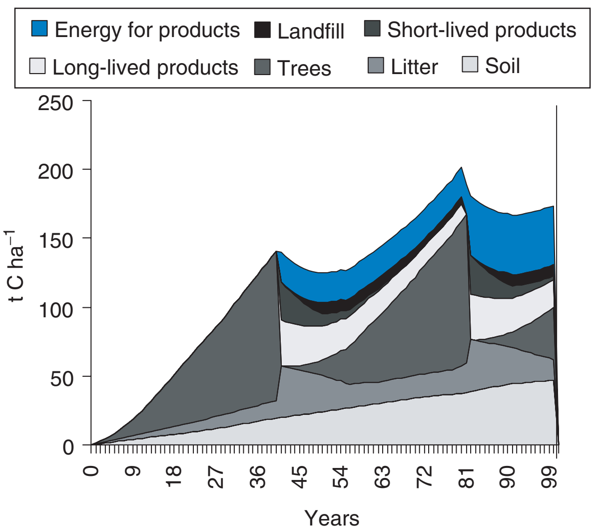


Figure 2 Cumulative changes in carbon stocks with afforestation and subsequent harvest after 40-year rotation. (Reproduced with permission from Marland G and Schlamandinger B (1999) The Kyoto Protocol could make a difference for the optimal forest-based CO_2 mitigation strategy: some results from GORCAM. *Environmental Science and Policy* 2: 111–124.)

Table 9 Comparative emissions in manufacturing wood- vs. steel-framed interior wall

Emission/effluent	*Wood wall*	*Steel wall*
CO_2 (kg)	305	965
CO (g)	2 450	11 800
SO_x (g)	400	3 700
NO_x (g)	1 150	1 800
Particulates (g)	100	335
Volatile organic compounds (g)	390	1 800
Methane (g)	4	45
Suspended solids (g)	12 180	495 640
Nonferrous metals (mg)	62	2 532
Cyanide (mg)	99	4 051
Phenols (mg)	17 715	725 994
Ammonia (mg)	1 310	53 665
Halogenated organics (mg)	507	20 758
Oil and grease (mg)	1 421	58 222
Sulfides (mg)	13	507

Source: Meil JK (1994) Environmental measures as substitution criteria for wood and nonwood building products. In *Proceedings*, *The Globalization of Wood: Supply*, *Processes*, *Products*, *and Markets*, pp. 53–60. Madison, WI: Forest Products Society.

Manufacturing Effluents

Life cycle analysis involving wood was elevated to a new level in a 1994 study that examined not only energy and related emissions associated with wood- and steel-framed construction, but manufacturing effluents as well (**Table 9**). Differences can only be described as spectacular, with emission levels for steel-framed construction ranging from 1.6 times to 41 times higher than for wood-framed construction. More recent studies support these findings.

Energy Efficiency of Wood vs. Non-Wood Structures

All of the studies of building construction cited herein were based on analysis of structures built according to local building codes and practices. Recent research in the United States showed that because of thermal bridging issues, the differences as shown in **Tables 1, 3–5**, and **7–9** become even greater when exterior walls are constructed so as to achieve equal thermal insulation or *R* values. Moreover, because of differences in thermal bridging performance of wood, steel, and concrete walls at corners and around doors and windows, even when basic insulation properties of wall sections are equal, both steel-framed and concrete walls require more heating energy over the life of a structure than do wood-framed walls. Thus, energy implications of materials selection in building construction extend well beyond the construction process.

Summary

There is no question that periodic harvesting of forests to obtain wood raw materials results in environmental impacts. What is sometimes forgotten, however, is that the gathering and processing of all raw materials impacts the environment. When the harvesting and processing of wood is examined in this context, the inescapable conclusion is that the global environment would benefit from the maximum use of wood possible within sustainable limits.

See also: **Solid Wood Processing**: Recycling. **Wood Formation and Properties**: Formation and Structure of Wood. **Wood Use and Trade**: History and Overview of Wood Use.

Further Reading

Arima T (1993) Carbon dioxide emission and carbon storage for building materials and construction in Japan. *Wood Design Focus* 4(2): 9–12.

Baird G and Aun CS (1983) *Energy Costs of Houses and Light Construction Buildings*, Report no. 76. Auckland: New Zealand Energy Research and Development Committee.

Bowyer J, Briggs D, Johnson L, *et al.* (2002) CORRIM: A report of progress and a glimpse of the future. *Forest Products Journal* 51(10): 10–22.

Cole R, Roussau D, and Taylor S (1992) Environmental audits of alternate structural systems for warehouse buildings. *Canadian Journal of Civil Engineering* 19: 886–895.

Honey BG and Buchanan AH (1992*) Environmental Impacts of the New Zealand Building Industry*, Research Report no. 92-2. Christchurch, New Zealand: Department of Civil Engineering, University of Canterbury.

Jönsson Ä, Tillman A-M, and Sevensson T (1995) *Life Cycle Assessment of Flooring Materials: A Case Study*. Gothenberg, Sweden: Chalmers University of Technology.

Koch P (1992) Wood versus nonwood materials in US residential construction: some energy-related global implications. *Proceedings*, *Wood Product Demand and the Environment*, pp. 252–265. Madison, WI: Forest Products Society.

Koehler N (1987) Energy consumption and pollution of building construction. *Proceedings of the 3rd International Congress on Energy Management*, Lausanne, Switzerland, vol. 2, pp. 233–240.

Marland G and Schlamadinger B (1999) The Kyoto Protocol could make a difference for the optimal forest-based CO_2 mitigation strategy: some results from GORCAM. *Environmental Science and Policy* 2: 111–124.

Meil JK (1994) Environmental measures as substitution criteria for wood and nonwood building products. In *Proceedings*, *The Globalization of Wood*: *Supply*, *Processes*, *Products*, *and Markets*, pp. 53–60. Madison, WI: Forest Products Society.

Pierquet P, Bowyer J, and Huelman P (1998) Thermal performance and embodied energy of cold climate wall systems. *Forest Products Journal* 48(6): 53–60.

Richter K and Sell J (1992) *Environmental Life Cycle Assessment of Wood-Based Building Materials and Building Products*, Report no. 115/24. Dubendorf: EMPA (Swiss Federal Laboratory for Materials Testing and Research, Wood Division).

Richter K, Kònninger T, and Brunner K (1996) *An Ecological Comparison of Windows Manufactured Using Various Materials*, May. Dubendorf: EMPA (Swiss Federal Laboratory for Materials Testing and Research, Wood Division).

Sakai K and Urushizaki N (1992) Analysis of resources consumption and estimation of environmental load by construction activities. *Journal of the Center for Environmental Information Science* 21(2): 130–135.

Scharai-Rad M and Welling J (2002) *Environmental and Energy Balances of Wood Products and Substitutes*. Rome: Food and Agricultural Organization of the United Nations.

Y

YIELD TABLES *see* MENSURATION: Forest Measurements; Growth and Yield; Timber and Tree Measurements; Yield Tables, Forecasting, Modeling and Simulation.

GLOSSARY

2*n*: The diploid number of chromosomes found in dividing root tips, and other cells, undergoing mitosis.

3D computer models: Digital (mathematical) models representing three-dimensional forms, surfaces and spaces which can be viewed in perspective (see also Geometric modeling).

A horizon: Dark colored horizon in surface mineral soil high in organic matter.

Abiotic: Aspects of the environment that are nonliving.

Aboveground biomass: All living biomass above the soil, including stems, stumps, branches, bark, seeds, and foliage of trees.

Abundance surveys: Studies undertaken to determine the number of given species in an area.

Access: The ability to use land or another resource.

Accessibility: Refers to distance, need of transportation, safety, and tranquillity of route to a forest site (for recreation or harvesting).

Accuracy of measurement: Freedom from error or the closeness of a measurement or estimate to the true value. More broadly, it is the degree to which a statement or quantitative result approaches the truth. Note that

$$\text{Accuracy} = \sqrt{\text{Precision}^2 + \text{Bias}^2}$$

using these statistical definitions. Thus, if bias is eliminated, Accuracy = Precision.

Accuracy of visualization: The similarity in appearance between the simulated scene and the real scene as it would look in the circumstances being simulated. Accuracy can be expressed in terms of color matches between real and visualized scenes, difference in size and location of observed/represented objects, and presence or absence of key visible features.

Acervulus, acervular: A disc-like asexual fruiting structure characterized by a thin spore-bearing layer covered either by a thick layer of fungal tissue or host epidermis that peels back at maturity to allow spore release. Usually 2 mm or less in diameter and typically formed on foliage.

Acid rain: Rain contaminated with industrially derived pollutants such that pH has been reduced.

Acidic papermaking: Values of pH between 3.5 and 6 before paper is formed.

Actinomorphic: Radially symmetrical and capable of being divided in more than one plane into two equal parts that are mirror images of one another, e.g., the flowers of *Gustavia*.

Actinomycete: A group of minute organisms (order Actinomycetales), commonly considered to be filamentous bacteria.

Actinorrhiza: A symbiotic association between plant roots and strains of *Frankia* bacteria that form specialized root nodules within which nitrogen fixation occurs.

Acute pollution effects: Changes to forest health and structure that are the result of very high pollutant loads, often of relatively short duration.

Adaptability: The ability of populations to adapt to a selective force.

Adaptation: A general measure of the ability of an organism to change and cope with the physical and biotic elements of a particular environment enabling it to reach its potential for growth and reproduction. For seed orchards, adaptation refers to the degree to which seedlings derived from orchard seed will cope with the environment of the target plantation zone.

Adaptive genetic variation: Genetic variation that is related to the general fitness of the plant, particularly as it relates to growth and reproductive capabilities. These traits are typically affected by many genes, each of relatively small effect.

Adaptive trait: A trait under some degree of genetic control that affects fitness (survival and reproduction) in a given environment.

Adaptive variation: See Adaptive genetic variation.

Additive gene effects: Average effects of allele substitutions; in practice, effects whereby offspring tend to be intermediate between their parents.

Additive: Any material other than fibers and water that is added to paper.

Adhesion: The process of joining dissimilar materials with an adhesive to form a bond having structural integrity. Adhesion involves chemical and physical interactions between the adhesive and the joined substrates.

Adhesive: A substance capable of holding materials together by surface attachment. It is a general term and includes cement, glue, mucilage, and paste.

Adsorption: The process of forming intermolecular associations, or secondary bonds, as when a liquid contacts a solid surface. This is similar to wetting, but it also refers to the intermolecular forces between different materials as in the case of adhesion.

Advance reproduction: Seedlings and saplings existing under the canopy of mature trees.

Advanced regeneration: Immature individuals including seedlings, saplings, and pole-sized individuals of commercial species under a mature canopy.

Adventitious: Roots arising at the nodes of rhizomes and culms and not from the initial (primordial) root.

Aerobic organism: Any organism that requires oxygen gas for respiration.

Aesthetic quality: Aesthetics refers to the human response to landscapes which result from the perceptual characteristics of the environment and the observer's sensory experience. Aesthetic qualities are capable of inducing or influencing human emotions, mood, and levels of satisfaction with the environment, and can be pleasurable or otherwise.

Afforestation: The planting of trees on previously unforested land.

AFLPs: Amplified fragment length polymorphisms; codominant genetic markers for polymorphic base sequences similar to those involved in RFLPs, but studied using the polymerase chain reaction rather than radionuclides.

After-effects: The effect of parental environment on progeny performance.

Age: The age, t, of an individual tree is calculated from the time of germination, budding, or planting, or from the year in which the tree reached a certain reference height. Stand age, T, generally refers to some sample average and is relevant mainly for more-or-less even-aged forest types. The scale of resolution for age is often one year.

Agroforestry: The practice of combining agricultural crops or animal husbandry with the maintenance and cultivation of trees on the same patch of land.

Agrosilviculture: Agroforestry practice predominantly involving trees and crops; also known as silvoarable.

Agrosilvopastoral system: Land-use system in which woody perennials are used on the same land as agricultural crops and animals, in some form of spatial arrangement or temporal sequence. In fire management agrosilvopastoral systems are planned as fuelbreaks (particularly shaded fuelbreaks) to reduce fire risk by modifying understory vegetation and soil cover (cf. fuelbreak).

Air vesicles: Air sacs in the pollen grain of some species that improve its distribution by wind.

Alfisol: See Brown forest soil.

Alkaline papermaking: Values of pH above 7 before paper is formed.

Alkyd resin: Synthetic paints and varnish resins formed by the condensation of polyhydric alcohols with polybasic acids.

Allele: One of two or more possible variants of a gene at a locus (site on a specific chromosome).

Allele frequency: The frequency of an allele in a population. The combined frequency of all the alleles at a locus in a population equals 1.

Allochthonous: Material derived from external sources.

Allogamy: The mating system in which species are outcrossing, i.e., as a rule only pollen from another individual of the same species can fertilize the ovules and produce viable seed.

Allohexaploid: An allopolyploid with six sets of chromosomes.

Allopatric: Occurring in disjunct geographic areas.

Allopatry: The situation in which species are closely related members of the same genus but growing in geographically separate regions, e.g., Europe and North America.

Allopolyploidy: A polyploid where chromosome sets are derived from more than one species.

Allozyme: One of several forms of an enzyme coded by different alleles at a locus.

Alpine: The altitudinal belt between the subalpine belt (above the montane belt) and the nival belt, which in the tropics is generally situated between 3500 and 4500 m elevation.

Alternate hosts: Two different plant species that are the host for different stages of the life cycle of rust fungi.

Amchi: This is the Tibetan system of medicine which has a rich heritage and is mostly practised in the Himalayan region of Bhutan, China, India, and Nepal. In this system the practitioners use a variety of natural products like plants, animals and minerals for healing purposes.

Amenity: The quality of being pleasant or attractive, associated with value of the environment.

Amictic: Involving no mixing.

Anaerobic organism: Any organism that grows only in the absence of oxygen.

Anamorph, asexual states, conidia: Many ascomycetes and basidiomycetes can reproduce by production of asexual spores called conidia. Structures associated with the production of conidia are termed the asexual state or anamorph, and these states are usually given a separate Latin name, even if they are known to be connected to a certain sexual state (teleomorph). Thus the same fungus species can actually have several different names for the sexual state and different asexual states. Often the sexual state is absent or rare, and the organism is more commonly known by the name of its asexual state.

Androecium: The collective term for the staminate structures of the flower; the stamens as a unit.

Andromonoecy: Having male and hermaphrodite flowers on the same plant.

Anemophilous: Plant pollinated by wind.

Aneuploid: A cell or organism that does not have an exact multiple of the haploid number of chromosomes.

Angiosperms: Flowering plants, distinguished from the gymnosperms by producing seeds that are enclosed by material tissue as a fruit or nut.

Anoxic: A low-oxygen environment caused by long-term inundation by water.

ANPP: Aboveground net primary productivity: the amount of biomass added to the shoots of a plant in a year.

Anther gland: Glands associated with the anthers and commonly found in mimosoid legumes.

Anthesis: The period or stage of full expansion of the flower structures, or (in the case of conifers) strobili. Bud burst is the anthesis of the seed cone (female strobili), and pollen shedding is the anthesis of the pollen cone (male strobili).

Anthophilous: Living among, or feeding upon flowers, usually pollen and/or nectar.

Anthracnose: A foliage disease characterized by sunken, brown necrotic spots and patches. Usually caused by ascomycete pathogens having acervular asexual states, for example *Colletotrichum gloeosporioides*.

Anthropogenic: Landscapes and ecosystems created by human activity.

Antibiosis: Resistance to an insect herbivore in which compounds produced by the plant affect the biology of the insect adversely.

Antioxidant: A chemical compound that prevents or retards oxidation. It acts by scavenging free radicals generated in oxidation processes.

Antixenosis: The ability of a plant to repel an insect and thus reduce or prevent oviposition and/or feeding.

Anuran: Of or pertaining to frogs and toads.

***Aphelenchoides xylophilus*:** A nomenclatural synonym to *Bursaphelenchus xylophilus*.

Apical placentation: Form of placentation found in ovaries with only one ovule, where the placenta forms at the top of the ovary.

Apomictic: Term describing seed originating from any kind of asexual modifications of sexual reproduction. Apomictic seed is genetically identical to its seed parent.

Apomixis: Asexual reproduction by seed without benefit of fertilization or meiosis, deriving from somatic cells of the nucellus or integument.

Apophysis: The subterminal structure of the cone scale.

Apoplast: The cell walls collectively of a tissue or a complete plant.

Application rate: This can refer to any substance but in the case of wastewater, the amount of wastewater applied per unit time of an operational cycle; usually expressed as inches or millimetres per hour.

Arboriculture: The art, science, and technology of planting and care of individual trees and other woody vegetation.

Archegonial polyembryony: A feature of gymnosperms whereby several embryo genotypes can be produced from different pollen grains within the seed structure where only one embryo can normally survive.

Areolate: Divided into small, distinct spaces by intersecting lines.

Aril: An often fleshy and brightly colored appendage growing at or near the hilum, often forming a covering around the seed as in the Myristicaceae.

Arillate: Possessing an aril.

Aromatic rings: Hydrocarbons characterized by the presence of one of more ring structures and having strong odor.

Arsenicals: Class of waterborne preservatives which contain arsenic and other metallic biocides. The principal arsenical is CCA (copper-chrome arsenate).

Ascoma (pl. ascomata): The sexual fruiting structure of an ascomycete. This structure can be a disc or saucer shape, with the fertile layer bearing the asci and ascopores exposed (cup fungi, discomycetes), or with the asci and ascopores surrounded by a wall of sterile fungal tissue in a small flask-shaped structure (a perithecium). Ascomata are usually minute but sometimes aggregated and embedded in sterile tissue, called a stroma, which can be more than 1 cm in diameter, typically black and crust like.

Ascomycete: Fungi in the phylum Ascomycota. Characterized by sexual spores (ascospores) produced in a characteristic sac like cell called an ascus. Some ascomycetes can also reproduce asexually (see anamorph, asexual states, ascoma, conidia).

Ascomycotina: See Ascomycete.

Asexual (vegetative) multiplication (bulking): When seeds of desired families or populations are in short supply, embryos or seedlings are clonally reproduced by rooting cuttings, tissue culture, grafting, or somatic embryogenesis.

Assimilation: Incorporation of elements and compounds, building up substances vitally necessary for plant structure and function.

Asteraceous: Belonging to the daisy family (Asteraceae).

ATLAS: Aggregate Timber Land Assessment System.

Autochthonous: Term to describe a species that is native to the locality and naturally adapted to its circumstances. An autochthonous population, in the strict sense, is expected to arise from natural regeneration *in situ*, in contrast to cultivated *ex situ* material. (syn indigenous).

Autocorrelation: This is a term referring to the degree of relationship that exists between two or more spatial variables, such that when one changes, the other(s) also change. This change can either be in the same direction, which is a positive autocorrelation, or in the opposite direction, which is a negative autocorrelation. For example, soil type and vegetation may be highly correlated, either positively or negatively depending upon the type of soil and vegetation under examination.

Autogamy: The mating system in which plants are self-fertile and pollen grains of the same individual produce viable seed.

Autotrophic respiration: The term given to respiration by plant tissues.

Autotrophs: All photosynthesizing green organisms (green plants, trees, algae).

Ayurveda: The term Ayurveda has a Sanskrit root, ‘Ayu’ meaning life, and ‘Veda’ meaning pure knowledge. Ayurveda can thus be translated as the knowledge of the span of life, which deals elaborately with measures for healthful living including Ayurvedic medicine.

Backcrossing: Crossing a hybrid to one of its parental types.

Backfire: A fire spreading, or set to spread, into or against the wind: (1) As used in **fire suppression:** A fire set along the inner edge of a control line to consume the fuel in the path of a forest fire and/or change the direction force of the fire’s convection column (Note: doing this on a small scale and with closer control, in order to consume patches of unburned fuel and aid control-line construction (as in mopping-up) is distinguished as ‘burning out, firing out, clean burning’); (2) As used in **prescribed burning:** designation of fire movement in relation to wind.

Backhaul: Coordination of two (or more) transports in order to minimize empty travel.

Bamboo brakes: Distinct pure stands of bamboos.

Banyan-like habit: Form of large spreading tree with multiple stems grown from aerial roots.

Bark: The outer covering of the branches, roots and stems of woody plants. Measurement of bark thickness or bark volume may be needed to quantify bark for harvesting or to convert from over bark to under bark dimensions. Mensurationally, the bark comprises all tissues outside of the xylem, including the cambium. Bark thickness is generally defined as the difference in radius of two concentric circles, one defined by the bark surface, the other by the interior wood surface. Bark volume may be derived from thickness or measured directly.

Barriers: Features in the landscape which stop organisms dispersing such as water, treeline, or road.

Basal area: Basal area, g, is the stem cross sectional area at breast height. Stand basal area, G, i.e. total basal area per unit area of land, is a specific characteristic of stand density. Usually expressed in $m^2 ha^{-1}$ ($ft^2 ac^{-1}$ in the USA).

Basidiomycete: Fungi in the phylum Basidiomycota. Characterized by sexual spores (basidiospores) produced on a characteristic cell called a basidium. Some basidiomycetes can also reproduce asexually (see anamorph, asexual states, conidia).

Basidiomycotina: Fungi characterized by basidia formed in a fruit body from an external fertile layer called a hymenium. Hyphae sometimes with clamp connections at septations. See Basidiomycete.

Battering ram: A heavy timber used to batter down walls, gates, doors, etc.

Beam: A structural member supporting a load applied transversely to it.

Belowground biomass: All living biomass of live roots.

Beltian body: Protein-rich structure produced by *Acacia* species that have mutualistic associations with ants and used as a food source.

Bending stiffness: Essentially the force required to bend a given length of paper.

Benthos: Organisms associated with the bed of a water body.

Beta distribution: A probability distribution with density function $f(x) = (x)^{\alpha}(1-x)^{\beta}/B(\alpha, \beta)$ where α and β are parameters and B denotes beta function.

Beverages: Artificial drinks usually prepared from decoctions of plant parts.

Bias: A systematic error introduced into sampling, measurement or estimation by selecting or favoring, possibly unintentionally, one outcome or answer over others.

Bifurcate: To separate into two parts or branches; fork.

Biocide: The active ingredient(s) in a wood preservative system which will control one or more of the many different organisms which can degrade wood.

Bioclimatic zone: Vegetation characteristic of a particular set of climatic conditions.

Biodegradation: Destruction of organic contaminants through microbial activity.

Biodiversity: The variability among living organisms from all sources, including land-based and aquatic ecosystems. These include diversity within species, between species, and of ecosystems. Diversity is the key to ensuring the continuance of life on Earth. It is also a fundamental requirement for adaptation and survival and continued evolution of species.

Bioindicator: Species or species groups that can be sampled to provide accurate information about the health of an environment or ecosystem.

Biological diversity: (See Biodiversity)

Biological resources: This includes genetic resources, organisms, or parts thereof, populations, or any other biotic component of ecosystems with actual or potential use or value for humanity.

Biomass: (1) The amount of living matter in a given habitat, expressed either as the weight of organisms per unit area or as the volume of organisms per unit volume of habitat. (2) Organic matter that can be converted to fuel and is therefore regarded as a potential energy source. Note: Organisms include plant biomass (phytomass) and animal biomass (zoomass). (3) In fire science the term biomass is often used synonymously with the term 'fuel' and includes both living and dead phytomass (necromass); the zoomass is usually excluded.

Biome: A major regional or global biotic community, such as a grassland or desert, characterized chiefly by the dominant forms of plant life and the prevailing climate.

Biometrics: The application of statistical methods to the measurement of biological objects.

Biotemperature: A measure of the heat effective for plant growth. Mean annual biotemperature averages daily temperature for one year with all values less than 0°C as 0 and all values greater than 30°C as 30.

Bipinnate: Arrangement in which both the primary and secondary rachises of a leaf have leaflets set along them.

Bleachable pulp: Pulp which has the capability of being purified or whitened by chemical treatment to remove or change coloring matter so that it will achieve a higher brightness characteristic.

Bleed flow: The oncoming flow which filters through the shelterbelt.

Bluestain (sapstain): A blue, brown or black stain of the sapwood that is caused by deeply penetrating fungi that do not cause decay. The appearance of the wood may greatly reduce its value.

BLUP: Best linear unbiased prediction.

Board: Solid-sawn lumber less than 38 mm (2 in.) in nominal thickness.

Bond paper: Originally a cotton-content writing or printing paper designed for the printing of bonds and legal documents, and distinguished by superior strength, performance, and durability. The term is now also applied to paper for less demanding applications such as letterheads, business forms, and social correspondence papers.

Boreal: Northern.

Bound water: Water adsorbed onto the cell wall substance.

Box beam: A built-up beam with solid wood flanges and plywood or wood-based panel product webs.

Brash: Portions of trees (stems or branches) with diameter below the minimum set for utilization (ca. 70 mm).

Breast height: Breast height is the most widely used reference level for measurements of diameter and basal area. In countries that use the SI system breast height is generally located at 1.30 meter above ground level. Other points are 1.4 m and 4′6″.

Breed: A set of genotypes distinguished by having been selected for a common breeding goal.

Breeding: The science or art of changing the genetic constitution of a population of plants or animals through sexual reproduction. Used in a narrow sense it means crossing of parents through controlled pollination to create offspring. Used in a broad sense it means all the activities of a tree improvement program.

Brightness: The reflectivity of a sheet of pulp, paper, or paperboard for specified light (usually 457 nm) measured under standardized conditions on a particular instrument designed and calibrated specifically for the purpose.

Broadleaf (or broadleaved): Tree belonging to the botanical group Angiospermae. Synonym hardwood.

Brown forest soil: A neutral to moderately acid soil of temperate forest regions, with a mull humus, without free $CaCO_3$ at the surface and with no horizon in which sesquioxides accumulate.

Bucking: Cross-cutting a tree stem into logs of predetermined length.

Buffering: The process of resisting changes in the pH. Wood sometimes buffers an adhesive which requires a low or high pH for optimal curing; this may interfere with curing and bonding.

Bulb: Fleshy stem, formed by layers of tissue, which can be planted and which will produce flowers and seed.

Bundle of rights: The several rights that constitute a tenure; all the rights belonging to various persons or groups in a piece of property.

Bushmeat: Meat of wild animals hunted and gathered from African Savannahs.

C_3 photosynthesis: Mode of photosynthesis used in trees where CO_2 is fixed into 3-carbon sugars. Of the three types of photosynthesis (C_3, C_4, and CAM), C_3 is the least efficient at using carbon and conserving water.

C_4 photosynthesis: Mode of photosynthesis in which CO_2 is fixed into 4-carbon sugars.

Caatinga: A Portuguese term referring to a dry, thorn-scrub, deciduous vegetation of northeastern Brazil.

Calcining or calcination: Incineration of a mineral, driving off CO_2 or H_2O.

Calendering: The process of passing a web through a pressurized nip (or multiplicity of nips) for the purpose of leveling the normal profile variations in the web while compacting and smoothing the substrate in paper making.

Caliper (forestry): The forestry caliper is used to measure the diameter of stems, branches, stumps and roots. The most widely used calipers are for direct measurement. Calipers for indirect measurement rely on the geometry of instrument and stem or wood segment, often based on caliper arms forming tangents to the stem periphery. Based on sighting lines, similar principles are used for remote, optical measurement of diameter.

Caliper (paper use): The thickness of a sheet of paper measured under specified conditions.

CAM: Crassulacean acid metabolism. A form of photosynthesis in which CO_2 is taken up at night and fixed into malic acid which is then released to the Calvin cycle during the day when stomata are closed.

Canopy: The combined leafy crowns of (generally) the dominant plants.

Canopy architecture: The sizes, shapes, angles, distribution and development of tree crown elements, such as leaves, twigs and branches.

Canopy closure: Stage at which leaves on trees come to cover the entire site.

Canopy conductance: Average stomatal conductance for all leaves in the canopy.

Carbon allocation: The amount and distribution of organic carbon that is assimilated and translocated into different plant structures, such as foliage, reproductive structures, stems and roots.

Carbon pool: The reservoir containing carbon.

Carbon stock: The quantity of carbon in a pool.

Carrier: The solvent in which the biocide(s) and other inactive ingredients in a wood preservative are dissolved or suspended and which is used to 'carry' the preservative system into the wood.

Typical carriers are water (i.e., waterborne), light and heavy oils (oilborne), and oil-in-water emulsions.

Casehardening: A condition in which the wood is in tension on the inside and the surface is in compression.

Catapult: A military device for throwing stones, spears, etc.

Catena: Connected series.

Catkin: A unisexual inflorescence, consisting of rows of flowers ranged in circles along a slender stalk.

Cauliflorous: Flowers arising directly from the stem.

Cauliflory: Production of flowers on the main trunk or old woody branches.

Causation: If y and x are two events such that y would not have occurred without x, then x is the cause of y. If x, y, z are a finite series of events such that y depends causally on x, and z on y, then this is a causal chain. One event is the cause of another if – and only if – there exists a causal chain leading from the first to the second.

Cavitation: Development of air bubbles in xylem resulting in failure of xylem to transport water.

Cavity Zone: A region of recirculating very low velocity air behind a shelterbelt. Exists when the porosity is low and is absent when the porosity is above 40%.

Cellulose: A linear polysaccharide made up of glucose residues joined by β, 1,4 linkages.

CentiMorgan: A unit of length in a chromosome corresponding to a 1% marginal probability of recombination.

Centromere: The primary constriction, which divides a chromosome into two arms, often long and short. It contains the kinetochore, which attaches to the spindle during nuclear division.

Cerrado: A Portuguese term referring to a savanna-like vegetation best developed in central Brazil but also found in patches in the Brazilian Amazon.

CFS: CFS refers to coated wood-free papers.

CGTM: CINTRAFOR GTM.

Charcoal: Carbon-rich combustible solids that result from pyrolysis of wood in the early stages of combustion and that can be converted to combustible gases under certain conditions, or burned directly on grates.

Chemical woodpulp: Pulp obtained by using both chemical and heat energy to dissolve the lignin bond between fibers in wood. The primary chemical processes are the sulfate (kraft), sulfite, and soda.

Chemoautotroph: Any organism deriving energy from the oxidation of inorganic compounds and using CO_2 as the principal carbon source.

Chemoheterotroph: Any organism utilizing organic compounds as both energy and carbon sources.

Chemotaxonomy: The use of chemical characteristics as a basis for, or an aid to, classifying species or populations.

Chiasma: The point of crossing-over between homologous chromosomes.

Chlorosis: Breakdown of chlorophyll resulting in a white to yellow discoloration of the affected tissues.

Chromated copper arsenate (CCA): An arsenical preservative which also contains copper and chromium compounds and, until recently, was a major wood preservative.

Chromosomes: Stainable microscopic bodies in the nucleus that contain most of the genes. A chromosome is a linear arrangement with its genes linked together in consistent sequence. The size, morphology, and number of chromosomes (karyotype) is characteristic of each species. Extranuclear chromosomes (B chromosomes) also exist, but they are small, few in number, and of obscure function.

Chronic pollution effects: Changes to forest health and structure that are the result of many years of exposure to pollutant loads at relatively low intensities.

CINTRAFOR: Center for International Trade in Forest Products.

Circumpolar: Arctic; north.

CITES: Convention on International Trade in Endangered Species, an international treaty that controls trading and the import and export of endangered species of plants and animals. (International trade in Appendix II species is prohibited without an export permit, which can only be granted if supplies are obtained legally and without detriment to surviving populations.)

Cladoptosis: Vegetative regeneration arising from abscised twigs and branches that root and form new ramets under natural conditions.

Cleaning: In silviculture/management, a release treatment made in an age class not past the sapling stage to free favoured trees from less desirable individuals of the same age.

Clear felling: In silviculture/management, the removal of all the mature trees on an area at one time. Young regeneration trees have to be established without the protection of the older trees. Note that at very small scales (<0.25 ha), the distinction between clearfelling and continuous cover forestry can be difficult.

Cleistogamy: The extreme type of **autogamy**. Self-pollination takes place inside the flower bud.

Climate change: Changes in atmospheric gases "greenhouse gases" are thought to be causing global warming, more severe weather events, and droughts.

Climax/late successional stadium: Hypothetic final stadium of succession according to site conditions and competitive characteristics of the tree species that are able to settle there. Late successional stadia can be reached only on sites where several species have the chance to grow.

Climber: Plant that grows with the help of natural (e.g., tree) or mechanical support (e.g., string).

Cline: The phenomenon of a population mean shows a smooth geographic trend for one or more traits, typically tracking an environmental gradient.

Clonal forestry: Operational deployment of a few (5–50) proven superior clones for reforestation.

Clone: A group of plants derived from a single individual (ortet) by asexual reproduction such as rooting, grafting or tissue culture. All members (ramets) of a clone have the same genotype and consequently tend to be uniform.

Cloud stripping: Direct forest canopy interception of cloud water, i.e., the stripping of wind-blown fog.

Clumping bamboo: Sympodial bamboo. The culms are clustered together into a grove.

Cluster sampling: Monitoring of a plant species through a systematic group of subplots in a fixed pattern within a large defined area.

cM: centiMorgan, unit of genetic distance between two markers that do not segregate independently.

CMP: Chemical mechanical pulping.

Coagulant: Multivalent positive ion or a highly cationic polymer of moderate mass.

Coating formulation: In paper making, the aqueous mix of one or more pigments combined with one or more binders with a number of other components in much smaller percentages.

Codominant (crown class): See crown class.

Co-firing wood: Utilization of wood energy feedstocks as a supplementary energy source with another fuel such as coal or natural gas in combustors.

Cognition: The mental process of knowing, including aspects such as awareness, perception, reasoning, and judgment.

Cohort: A group of trees that establish following a disturbance. Analogous to age class.

Collaboration: Involvement of representatives of the public in an active process to develop solutions and influence decisions, working together with others which may include government staff, industry representatives, and technical experts.

Collaborative forest management: A forest management strategy in which professional forestry organizations and local community organizations cooperate in the planning and implementation of multifunctional management systems aimed at fulfilling the amalgamated forest related needs of all partners.

Colporate: A compound aperture in the pollen comprising a groove and one or more holes.

Combined heat and power (CHP): The simultaneous production of heat and mechanical work or electricity from a single fuel.

Combustion: Consumption of fuels by oxidation, evolving heat and generally flame (neither necessarily sensible) and/or incandescence. Combustion can be divided into four phases: preignition (or preheating), flaming, smouldering, and glowing.

Comminution: The process of breaking into smaller pieces.

Common property: A commons from which a community/designated group of users can exclude nonmembers and over which the community/designated group of users controls use.

Common property management: Use of a resource by a group of users, with powers to define membership of the group, to exclude those who are not members, and to set rules governing use of the resource.

Common-pool resource: Resource available to more than one person and subject to degradation as a result of overuse.

Commons: Land or another natural resource used simultaneously or serially by the members of a community.

Community: Naturally occurring group of different organisms inhabiting a common environment and interacting with each other.

Community forestry: The art, science, and technology of planning and managing forests and tree resources for the benefit of and together with local communities as part of their rural livelihood strategies.

Compartment: A portion of a forest under one ownership, usually contiguous and composed of one or more forest stand types, defined for purposes of locational reference and as a basis for forest management.

Complete cultivation: General term for ploughing (tillage) of all soil on a site. Sometimes used to describe a method of soil (or soil-forming material) loosening using the bucket of an excavator to dig out and drop material in a manner which emulates loose tipping.

Composite products: Fabricated materials consisting of wood used in combination with non-wood components such as various types of gypsum, Portland cement, plastics and resins.

Compost: A mixture that consists largely of decayed organic matter that is used for fertilizing and conditioning soils.

Compression resistance: The resistance of wood, paper and paperboard to compressive stresses.

Computer animation: Computer animation is the creation and compilation of a series of still images to represent movement, either between viewpoints, or in image elements (e.g. animation of different weather conditions, or simulation of tree growth over time). Individual images are created (rendered) by the computer visualization software and then strung together to create the animation.

Conductivity: Within the context of pollen viability testing, this is a technique that relates viability with the conductivity of an aqueous solution of pollen leachate.

Cone induction: Bringing about seed cone development by manipulating the environment, cultural practices or specific plant hormones (i.e., gibberellins).

Conidiophore: A specialized fertile hypha which bears a conidiogenous cell, that produces asexual spores (conidia).

Conifer/coniferous: Needle-leaved or scale-leaved trees; usually cone-bearing, and usually evergreen. (e.g., pines, cypresses, podocarps).

Conservation: The wise management of human use of natural resources and the environment including their preservation and protection.

Consistence: The attributes of soil material as expressed in degree of cohesion and adhesion or in resistance to deformation or rupture.

Construction log: A profiled log or timber used for the walls of log buildings.

Consultation: Where information is provided to the public and public opinions are sought for consideration in expert or managerial decision-making.

Contact angle: In the case of a liquid resting upon a solid surface, this is the angle drawn from the tangent of the liquid/solid/air intersection and measured from this tangent to the liquid/solid interface. The contact angle represents the balance of liquid and solid surface energies; it reveals the quality of wetting, be it favorable ($<90°$) or unfavorable ($>90°$).

Containerboard: Any type of single- and multi-ply, solid and corrugated boards used to make up boxes and other containers for shipping materials, and the type of paperboard used to make them up.

Contamination: In tree improvement, the incorporation of pollen external to orchard sources and generally considered to be deleterious to genetic worth either as poor growth performance and/or introducing poorly adapted genes into a production population.

Contingent evaluation: Placing a value on conditions or occurrences not yet established.

Continuous cover forestry: An approach to forest management characterized by the avoidance of clear felling. Young trees are established under the cover of and in the protection of the mature trees (hence 'continuous cover').

Continuous variable: A variable expressed in a numerical scale of measurement, where any interval of the scale can be subdivided into an infinite number of values.

Controlled pollination (CP): The transfer of pollen from a known source to known seed-cone parents while excluding all other pollen sources.

Coordinated inventories: Data collection efforts by different entities but designed to do so effectively. Collecting information needed by a number of resource functions coordinated either spatially or temporally, or both.

Copal: A hard translucent resin obtained from various tropical trees; may be semifossilized.

Coppice: 1. The production of new stems from the stump or roots. 2. To cut the main stem (particularly of broadleaved species) at the base to stimulate the production of new shoots for regeneration. 3. A plant derived by coppicing. 4. Any shoot arising from an adventitious or dormant bud near the base of a woody plant that has been cut back.

Coppice forest: Forest originating from coppice shoots, root suckers or both, i.e. by vegetative means.

Coppice-with-standards: A coppice system in which selected stems are retained as standards at each felling to form an uneven-aged overstory which is removed selectively on a rotation constituting some multiple of the coppice rotation; a crop partly of vegetative and partly of seedling origin.

Cordillera: Mountain chain (Spanish term).

Core area: Habitat area with relatively stable conditions, e.g., forest interior.

Coriaceous: Leathery.

Corm: Bottom part of the stem of a plant which, like a bulb, can be preserved and from which the plant sprouts again in spring.

Correlogram: A measure of the continuity of spatial phenomena expressed as an average correlation between measured quantities at different locations.

Corridors: Relatively narrow strips of habitat linking different forest fragments; natural or man-devised conduits in a landscape, intended to be used by dispersing organisms.

Corrugated board: (1) A pasted, single- or double-faced, multi-layered type of board in which the bottom or middle layer is fluted. (2) The fluted paperboard after it has gone through the corrugating operation and before it is pasted to the flat facing board sheets. It is used as a protecting, separating, or support medium in packaging fragile items.

Corrugated fiberboard: A type of paperboard made with strong paper faces separated by a corrugated paper core.

Corrugating medium: Paperboard that is made from chemical and semichemical pulps sometimes mixed with straw or recycled paper stock that is to be converted to a corrugated board by passing it through a corrugating machine.

Cotyledon: The primary leaf in the embryo of higher plants; the seed-leaf. The number varies between species of conifers and is typically two in the Dicotyledons.

Covalent bonding, primary forces: Strong and relatively permanent attraction between atoms, holding atoms together in the form of molecules.

Covariance: A variance or measure of association between paired measurements of two variables.

Covariate: A quantitative explanatory variable in a model such as a regression model. Covariates are often important in improving estimation.

Creosote: A thick, black oil from the fractional distillation of coal tar, mainly composed of polyaromatic hydrocarbons and used as a wood preservative for over 150 years.

Crepe angle: In paper making the angle the crepe blade makes with the Yankee dryer at the point of contact with the dryer.

Creping: A paper-manufacturing process in which the paper product is foreshortened scraping it from the Yankee dryer and then winding it at a slower velocity than that at which it is made.

Criteria and indicators: A monitoring system for the assessment of the economic, social, or ecological data about land management practices as an aid to improving sustainability.

Criterion: An aspect that is considered important and by which success or failure will be judged. The role of criteria is to characterize or define the essential elements or sets of conditions or processes by which sustainable forest management may be assessed.

Critically endangered species: Species whose populations are very small (usually smaller than 50). Such species are said to have an inviable population size.

Crop: In silviculture/management, the standing crop; the vegetation growing on a forest area, more particularly the major woody growth.

Crossdating: Matching different tree-ring series to identify their overlap.

Crossing-over: A process during meiosis that causes structural recombination of maternal and paternal segments of homologous chromosomes.

Crosstie: See Rail road tie.

Crown class: A category of tree based on its crown position relative to those of adjacent trees. Types of crown class are: **dominant** upper canopy trees with largely free-growing crowns exposed in entire vertical plan but usually in contact with others laterally; **codominant** upper canopy trees, similar to and often difficult to distinguish from dominants but crowns somewhat less free and more in contact with others; **subdominant** middle or lower canopy trees, partly exposed and partly shaded vertically by crowns but leading shoots free. Also known as intermediate or dominated trees; **suppressed** lower canopy trees entirely shaded vertically by other crowns. Also known as subordinate or overtopped trees.

Crown closure: Canopy closure.

Crown cover: A measure of stand density.

Crown management: Controlling the size and shape of a tree's crown while maintaining or increasing seed cone and pollen cone development.

Crown thinning: See thinning.

Cryogenic storage: Use of ultralow temperatures (e.g., of liquid nitrogen) for long-term storage of genetic material.

CTI: Central tire inflation

CTMP: Chemithermomechanical pulp.

Culm: Segmented aerial axis that emerges from the rhizome and forms the aboveground stem.

Cultivar: A clone or set of genotypes, representing a common breed and level of improvement, that is a unit for genetic deployment.

Cultural: Denoting deriving from, or distinctive of, the ways of living built up by a group of people.

Current annual increment (CAI): The growth observed in a tree or stand in a specific one-year period.

Cytogenetics: The science that deals with the material basis of heredity and genetic control at the cell level. It was initiated with microscopic studies on the morphology and behavior of chromosomes. It has later developed to include detailed analyses at the molecular level, such as gene mapping and transmission of genetic information.

Data element: A basic unit of information built on standard structures having a unique meaning and distinct units or values.

Data visualization/scientific visualization: Data visualization refers to the graphical representation of numerical information. Data visualization can take many forms, from simplistic representations such as tables and graphs, to more complex representations such as multi-dimensional computer simulations. Scientific visualization usually refers to data visualization of information that has a spatial component (geographic mapping can be thought of as a form of scientific visualization). Information visualization is the term used for data visualization of information that does not have any inherent spatial organization (e.g. a family tree can be thought of as a form of information visualization).

Dbh: See Diameter at breast height.

Decay: Wood degradation caused by wood-decaying (white rot, brown rot, or soft rot) fungi. Incipient decay describes the early stages of colonization and degradation with some loss in wood strength properties but little or no visual changes, followed by advanced decay where the wood has little or no strength and is obviously decayed.

Deciduous: Of perennial plants that are normally more or less leafless for some time during the year (e.g., temperature hardwood species).

Decking: Lumber used as the upper surface of an extended horizontal structure attached to a building.

Decomposition: 1. Integrated process of physical reduction in particle size combined with biochemical degradation of organic matter. 2. The breakdown of complex organic compounds into simpler compounds that may ultimately result in the return of CO_2 to the atmosphere and the release of energy stored during photosynthesis.

Defoliation: A term often misused to identify trees with thin, transparent crown. More correctly, it means the actual loss of foliage on a tree.

Deforestation: The complete or almost complete removal of tree cover and conversion of forested land to other uses as a result of human activities.

Degraded forest: A forest that has lost structure, productivity, and species richness. A degraded forest might still contain trees (i.e., a degraded site is not necessarily deforested) but it will have lost ecological integrity and its capacity to maintain the original ecological functions and processes.

Degree days: A measure of temperature implying heat energy available for plantgrowth. Degree days accumulated = [(maximum + minimum daily temperature)/2] − base temperature (usually 5°C).

Dehiscent fruit: A type of fruit that opens at maturity.

Delimbing: Removing the branches from the stem of a felled tree.

Deliquescent: Having a shape that branches out into numerous subdivisions that lack a main axis, such as the stem of an elm.

Demographic stochasticity: Temporal variation in population growth driven by chance variation in the fates of individuals; its magnitude is strongly dependent on population size.

Dendrochronology: The science of using tree rings and their characteristics to understand tree ages and past climate or management conditions.

Denitrification: The microbial reduction of nitrate to nitrous oxide and di-nitrogen gas.

Density (stand): An ecological measurement that provides an indication of how many individuals of a species are found in a forest, usually measured as the number of individuals per hectare.

Density (wood): Weight per unit volume. In USCS units it is expressed as pounds per cubic foot, and in ISO units it is expressed as kilograms per cubic meter.

Density-dependence: Population processes that are a function of the number of individuals (density) within a population. Extrinsic forces that act on populations irrespective of its size are density-independent.

Depithing: The process of removal of pith.

Deployment: The planting of improved genotypes for reforestation and all of the decisions of which genotypes to plant and how to propagate them. Clonal forestry and using seedlings from seed orchards are two examples of deployment schemes.

Deposit: Undesired material building up on process equipment at any point.

Desertification: The development of desert conditions as a result of human activity, frequently by overuse of trees and overgrazing, or climate change.

Destination: Aims to minimize the loaded transport distance between all forest supply nodes (active landings) and demand nodes (mills).

Detackifier: Talc or one or various organic polymers that reduce tackiness.

Detritus: Organically derived material of small particle size.

Deuteromycetes: A diverse assortment of fungi whose common feature is the lack of a sexual stage.

Development pathway: The sequence of structures through which a forest stand moves over time.

Devolution in forest management: The transfer of (part of) the decision-making authority over forest resources from state bureaucracies to local communities.

Diagnosis: Determination of the nature of an abnormal condition (e.g., a disease) from observation of symptoms.

Diagnostic horizons: Combinations of specific soil characteristics that are indicative of certain classes of soils. Those which occur at the soil surface are called epipedons, those below the surface, are diagnostic subsurface horizons.

Diallel: A scheme to artificially cross genotypes by assigning them to a small group and have the genotypes act as either male or females contributors to the diallel table. This design was commonly used with lines in maize but has been widely adopted to tree breeding.

Diameter: Diameter, girth or cross-sectional area of the stem or other woody parts of the tree is frequently used as an indicator of size, to calculate wood volume or as a predictor of other tree and stand properties. For standing trees, the most widely used tree and stand characteristic is stem diameter, d, measured outside of the bark at breast height, often referred to as diameter at breast height (dbh). In countries that use the SI system breast height is generally located at 1.30 meter above ground level. Commonly used stand variables includes arithmetic mean diameter, D, and quadratic mean diameter, D_g. In forestry terms, the quadratic mean is often considered more meaningful because of its direct relation to stand basal area and, in turn, stand volume.

Diameter at breast height (dbh): The diameter of the stem as measured at a common reference height. The reference height, usually known as breast height is set at a constant value, usually around 1 to 1.5 m. Different countries may adopt different reference heights from within this range as a national standard. A common example is 1.3 m (4.5 ft in the USA). The diameter is usually measured directly with callipers, or from tree girth by calibrated tape, assuming a circular cross section. Dbh is used to estimate basal area.

Dichogamy: Different timing of functionality of female and male flower parts.

Dicotyledons: One of the two great divisions of flowering plants in which the embryo usually has two cotyledons or seed leaves and the nervation is generally reticulate (cf. Monocotyledons).

Dieback: A term often used to mean 'death.' More correctly, it means a progressive death of a tree or a branch from its extremities towards the roots. In certain situations, dieback in individual trees should be seen as an adaptation to changed environmental condition (e.g. lower water table). Dieback can be reversible.

Digester: A pressure vessel used for pulping.

Dimension lumber: Solid-sawn lumber 38 mm (2 in.) to, but not including, 127 mm (5 in.) in nominal thickness.

Dimensional stability: A property of a sheet of paper that reflects the constancy of its dimensions that may occur with changes in moisture content, with applications of compressive or tensile stresses, or with time under stable ambient conditions.

Dioecious: Plant species in which male and female reproductive organs occur separately on different, unisexual, individuals.

Dioecy: The system in which plants of a species have separate sexes, each individual carrying either only female flowers or only male flowers. Dioecy guarantees cross-pollination.

Diploid: Term to describe cells or plants that have a double set of chromosomes (commonly shown as $2n$), one set coming from the seed parent and the other set from the pollen parent.

Diploxyon pines: Members of the subgenus *Pinus* of pines, characterized by having two fibrovascular bundles in each needle.

Dipterocarp: Member of the plant family Dipterocarpaceae.

Directive participation: Where information is exchanged but primarily in one direction, e.g. from government to the public.

Discrete variables: Qualitative variables or those represented by integral values or ratios of integral values.

Disease: A harmful and persistent deviation from normal physiological processes, caused by enviornmental or biotic factors.

Displacement Zone: The area ahead of and above the shelterbelt in which the flow is displaced upwards.

Distributions from the exponential family: binomial, Poisson, or gamma: Probability distributions with particular features. For example, the Poisson distribution relates to a variable where only integer outcomes are possible, and the mean is exactly equal to the variance.

Disturbance: A relatively discrete event that disrupts stand structure and/or changes resource availability, or the physical environment, or the function of an ecosystem.

Diversity: Variation at ecosystem, species and genetic levels measured by various indices; number of species in an ecological unit.

DNA content (1C): The amount of DNA in the haploid set of chromosomes.

DNA polymorphism: Genetic differences that can be detected with laboratory tests.

DNA primer: A short single-stranded DNA fragment used to initiate synthesis of new DNA.

Dominance: 1. An ecological measurement that provides an indication of how much basal area is occupied by a given species in a forest, usually measured as the number of square meters per hectare. 2. Inter-allele interaction at one locus on a chromosome.

Dominant (crown class): See crown class.

Dominant dbh: The average diameter of the dominant trees in the stand, sometimes used in the assessment of top height.

Dominant use silviculture: Silvicultural practices which seek to maximize the yield of a single output (e.g. timber, habitat for game birds) from a stand.

Dormancy: Absence of germination despite optimal conditions; may be due to several causes.

Double fertilization: Fusion of the egg with one sperm and the fusion of the polar nuclei with the second sperm; a process unique to flowering plants.

Down wood: Dead woody material on the ground, such as logs or branches. Also called ‘coarse woody debris’.

Draw: The tension applied to the paper between sections of a paper machine, such as the press section or drier section.

Drupe: Fleshy indehiscent fruit where the seed or seeds are surrounded by a hardened endocarp.

Dry deposition: The transfer of atmospheric pollutants from the air to terrestrial ecosystems by gravitational, physical, and chemical processes.

Dry strength: Ability of dry paper to resist tensile failure, tear, or delamination.

Dry strength agents: An ingredient added to paper stock that will improve the strength of dry paper. Starch is commonly used.

Drying oil: An oil that chemically reacts with oxygen from the air changing to a relatively hard, tough, insoluble, elastic substance after application to a surface as a thin layer.

DTRAN: An extension of the DUALPLAN (Dual formulation of the Linear Programming formulation for forest management scheduling) with transport considerations.

Duff mull: Forest humus type transitional between mor and mull.

Durability: A general term for permanence or resistance to deterioration. Frequently used to refer to the degree of resistance of wood or finished wood to weathering. Also to the degree of attack by wood-destroying fungi under conditions that favor such attack. In this connection the term ‘decay resistance’ is more specific.

E horizon: Light-colored mineral horizon resulting from removal of humus and sesquioxides by leaching with organic acids.

Early burning: Prescribed burning early in the dry season, before the leaves and undergrowth are completely dry or before the leaves are shed; carried out as a precaution against more severe fire damage later in the fire season.

Earthscraper: Engineering plant designed to strip soil materials at the beginning of mineral extraction, and often used to replace soils during site reclamation. Soil compaction is often induced using this machinery.

Ecological balance: A state of dynamic equilibrium within a community of organisms in which genetic, species and ecosystem diversity remain relatively stable.

Ecological carrying capacity: A measure of how much recreational use an area can stand without a permanent disturbance to the processes of its ecosystem.

Ecological services: Benefits provided by forests such the protection of biologicaldiversity, the protection of hill slope stability, the maintenance of soil fertility, or the maintenance and protection of hydrological functioning.

Ecophysiology: The study of cellular and biochemical processes within organisms that affect how and where organisms live in their environment.

Ecosystem: The complex of a unique community of organisms and its environment functioning as an ecological unit.

Ecotone: Transition zone between plant communities.

Eco-tourism: Ecologically sustainable tourism focused on human experience in natural areas.

Edaphic: Pertaining to the soil and its capacity as a media for plant and animal growth.

Edaphic climax: A later successional stage of vegetation which persists for long periods as a result of soil based limiting factors.

Eddy covariance: Covariance in vertical air movements and exchange rates of CO_2, water vapor and other gases to the atmosphere.

Edge effects: Biotic and abiotic changes along edges of forest fragments and the junction of different habitat patches.

Edge systems: Modifications of the shelterwood or clear cutting systems in which regeneration is encouraged along the edge of a crop or stand, and therefore growing under conditions of light and exposure different from those prevailing within the crop or stand, or in the open.

Edible: Any product that can be consumed safely.

Effect: The conscious subjective aspect of feeling or emotion.

Effective population breeding number: The average number of individuals contributing gametes to the next generation.

Efficient design: Selection of a particular experimental design that results in the highest power for a given level of cost, or, conversely results in the lowest cost for a given level of power.

EFISCEN: European Forest Information Scenario Model.

Egg gallery: A tunnel, often linear, created by a female bark beetle within the host tissue along which eggs are laid.

Eigenvalue: Value λ_r corresponding to eigenvector $\mathbf{x}_r$.

Eigenvector: Vectors $\mathbf{x}_r$ satisfying the equation $(\mathbf{A} - \lambda_r\mathbf{I})\mathbf{x}_r$ where $\mathbf{A}$ is the matrix considered, $\mathbf{I}$ is identity matrix and λ_r is the corresponding eigenvalue.

Elaiosome: Plant tissue attached to a seed that is offered as a reward to ants that in turn disperse the seed.

Elasticity: The property of a material which enables it to undergo deformation and to recover its original dimensions after removal of the deforming stress.

Eluviation: Removal of soil material in suspension or solution from one layer in the soil to another. Akin to leaching by solution.

Embryogenesis: 1. The natural process of creating embryos. 2. A laboratory technique utilizing specific cultures to produce many embryos from a single seed. These are developed into seedlings that are genetically identical to the original parent seed. Seedlings derived by this process are called emblings.

Embryonic lethals: Recessive genes that cause the abortion of homozygotic embryo (after self-fertilization). In many conifers embryonic lethals effectively restrict inbreeding.

Endangered: In danger of extinction or genetic erosion.

Endemic: A species confined to a particular area, and believed to have originated there.

Endocarp: The inner layer of the fruit wall.

Endosperm: The energy-rich food supply surrounding the embryo of a seed.

Engineered wood product: Any one of numerous building materials made from small pieces of wood joined with adhesives or fasteners and strategically arranged to create a structural member of designated stiffness and strength.

Enrichment planting: Planting commercially or ecologically important species in heavily logged or degraded forest to enrich the composition of that forest.

Environmental accountability: Assessment of the environmental impacts and values of a project or activity and defining responsibility of the project to the public.

Environmental stochasticity: Temporal variation in vital rates driven by changes in the environment that are inherently unpredictable.

Eocene: Geological epoch (54.8–37.7 million years ago) of Tertiary period.

Eophyll: The first leaf produced by a germinating seed.

EPA: Environmental Protection Agency.

Epidemic: Rapid spread of a disease in a population in a large geographic area over a short time.

Epilimnion: Upper (warmer) layer of thermally stratified lakes.

Epilithic: A species growing on top of a rock.

Epiphyte: A plant that lives on another plant for physical support but does not draw water or nutrition from the host.

Epiphytism: A way of growing (rooting) on the surface of trunks, branches, twigs, and leaves, commonly found among herbs (e.g., orchids, bromeliads, aroids) and certain shrubs (e.g., ericads) in tropical cloudy environments; epiphytes use other plants for support and generally do not parasitize on them, although sometimes this may be the case (e.g., in Loranthaceae and Viscaceae).

Epistasis: Interaction between alleles located on different loci on chromosomes of an individual.

Equilibrium moisture content (EMC): The moisture content wood attains when surrounded by air at a specified temperature and relative humidity.

Equity: Distribution or sharing of benefits in a manner so as to protect the interests of disadvantaged sections of the society.

Ericoid: Plants of the Health Family or Family Ericaceae. Also can be used as resembling or like a true heath (Family Ericaceae). In referring to an ecosystem may contain true heaths as well as species of similar form.

Error variance: The variance associated with the experimental error and residual unexplained variation.

Estimate: The numerical value calculated from an estimator for a sample.

Estimator: A function of the values in a sample or a formula used for estimating a parameter based on a sample.

Estuarine: Living in river mouths, joining the sea.

Ethnoagriculture: Tribal agriculture/traditional methods of raising crops.

Ethnobotany: The study of plants and their uses by humans.

Ethnoecology: The proper utilization of natural resources and maintenance of ecological balances as practised by primitive societies.

Ethnogynaecology: Medicines used by tribal peoples during childbirth and prenatal and postnatal medicine, and techniques adopted by them for family planning.

Ethnomedicobotany: Traditional knowledge and practices about herbal remedies.

Ethnomycology: The study of molds eaten by tribal peoples and their fermenting liquors since ancient times.

Ethnopharmacognosy: Traditional concepts or methods for distinguishing between various plant products, or the quality of such products from different seasons, particularly those used medically.

Ethnopharmacology: Study of the methods adopted by tribal peoples for selecting, experimenting, and administering herbal recipes in human or animal diseases.

Ethnophytotaxonomy: Traditional concepts or practices for classification, identification, and naming of plants.

Ethnotaxonomy: See Ethnophytotaxonomus.

Ethnotoxicology: The study of the plants used by tribal peoples as poisons to kill animals during hunting.

ETTS: European Timber Trend Studies.

Euchromatin: An expanded region of genetically active chromatin in the eukaryotic nuclei which stains lightly with basic dyes.

Eukaryote: An organism whose cells have a distinct nucleus (i.e., in all protists, fungi, plants, and animals) with nuclear envelopes, chromosomes, and nuclear divisions in forms of mitiosis and meiosis, in contrast to prokaryotic organisms (i.e., bacteria and blue-green algae).

Eutrophication: High levels of organic production.

Eutropic (soils): Soils rich in nutrients.

Evapotranspiration: The combination of evaporation from the soil and plant surfaces and transpiration from plant leaves.

Evergreen: Plants that do not shed all leaves at one time and hence appear green throughout the year.

Excurrent: Having a single, undivided trunk with lateral branches, as in spruce trees.

Exine: The outer layer of the pollen grain wall which is highly resistant to strong acids and bases and which is composed primarily of sporopollenin.

Exotics (Exotic species): Species or populations that are introduced from elsewhere and are not native to the site.

Expected mean-squares: The expected relationships between the mean-squares, calculated using the sample data, and the population variances.

Experimental design: A plan for establishing, measuring, and evaluating the results of an experiment.

Expressed sequence tag (EST): Sequence, usually brief, of DNA copied from messenger RNA (mRNA) that can serve for gene recognition.

***Ex-situ* conservation:** To conserve species or populations in areas other than their natural habitat.

***Ex situ* remedial technology:** Remediation that involves excavation or extraction of materials to be treated above ground or offsite, e.g., land disposal, incineration, soil washing, pump-and-treat.

Extinction: Complete loss of a population or a species.

Extirpate: Remove a species from a specified locality.

Extractant: Chemical solution used to remove nutrients from a soil sample for analysis or chemicals from wood and leaves for use (e.g., pine resin, pharmaceuticals).

Extractive reserves: A patch of forest where extraction of certain resources are allowed by a certain group of people (indigenous groups) while the rest of the resources are protected.

Extractivism: The practice of commercial harvesting of NTFPs from forests; particularly used in Latin America.

Extraporate: A pollen grain where the furrow and pores are not closely associated.

F_1: First filial generation; progeny resulting from crosses between two species or individuals (usually selected in breeding programs); in the case of interspecific hybridization it is the hybrid resulting directly from crossing two pure species.

F_1: First generation of hybrids between two populations.

F_{st} and G_{st}: Two genetic statistics used to measure differentiation between populations for molecular markers.

Factorial: A mating scheme which assigns one group of trees as only male and the other as female.

Facultative organism: Any organism that can adapt to the presence or absence of oxygen.

Fagaceous: Belonging to the beech and oak tree family.

Family: Seedling offspring from a particular tree. Half-siblings have one parent in common among family members and full-siblings have both parents in common.

Family forestry: Small-scale forestry carried out by ordinary families with the aim of enabling successive generations to enjoy the bounty of forests – both in an economic sense and as places that provide recreational value.

FAO: Food and Agriculture Organization, a Specialized Agency of the United Nations.

Farm forestry: Forestry practised by farmers and integrated into the farm business, generating revenue and environmental services to complement other enterprises on the farm.

Fascicle: The morphological unit in which pine needles are produced in clusters of 1 to 5 or more needles; this is generally, a species-specific characteristic.

FASOM: Forest and Agriculture Sector Optimization Model.

Fatty acid: Long chain carboxylic acids present in rosin or tall oil.

Fauna: Animals or a document on animals in an area.

Feller–buncher: Off-road forestry vehicle designed for felling trees and accumulating them in bunches.

Fertility potential: The potential for a particular pollen lot to fertilize an egg cell.

Fertilization: The union of the male gamete (sperm) with the female gamete (egg) to form a zygote from which a new plant will form.

Fiber: A slender, threadlike cell with tapered ends in wood, composed chiefly of cellulose. Note that fibers differ from tracheids in being more slender, having simple pits and thicker walls in relation to diameter, and often retaining protoplasm. They are separated from each other during the pulping operation in a pulp mill and reassembled into the form of a sheet during the papermaking process in the paper mill. Found in angiosperms; responsible for support and strength; includes fiber tracheids and libriform fibers.

Fillers: Materials such as china clay with particles often in the size range 0.5–4 μm added to paper to impart properties at less cost than using 100% fiber. Newsprint (the paper on which newspapers are published) is up to 33% filler.

Filmy ferns: Small, tiny ferns with thin, transparent, finely-lobed, film-like leaves, belonging to the family of Hymenophyllaceae.

Fines: 1. Small particles of wood residue that vary in size in the range common to different forms of sawdust. 2. Very short pulp fibers or fiber fragments and ray cells.

Finish: Coatings of paint, varnish, lacquer, wax, etc., applied to wood surfaces to protect and enhance their durability or appearance.

Fire behavior: The manner in which fuel ignites, flame develops, and fire spreads and exhibits other related phenomena as determined by the interaction of fuels, weather, and topography. Some common terms used to describe fire behavior include the following: ***smouldering*** A fire burning without flame and barely spreading. ***creeping*** A fire spreading slowly over the ground, generally with a low flame. ***running*** A fire rapidly spreading and with a well-defined head. ***torching*** Ignition and flare-up of foliage of a single tree or a small clump of trees, usually from bottom to top (syn. *candling*). ***spotting*** A fire producing firebrands carried by the surface wind, a fire whirl, and/or convection column that fall beyond the main fire perimeter and result in spot fires. ***crowning*** A fire ascending into the crowns of trees and spreading from crown to crown. (See: Three classes of Crown Fire under **Forest Fire**).

Fire belt: A strip, cleared or planted with trees, maintained as a firebreak or fuelbreak.

Fire break: Any natural or constructed discontinuity in a fuelbed utilized to segregate, stop, and control the spread of fire or to provide a control line from which to suppress a fire; characterized by complete lack of combustibles down to mineral soil (as distinguished from fuelbreak).

Fire control: All activities concerned with protection of vegetation from fire.

Fire cycle: The number of years required to burn over an area equal to the entire area of interest.

Fire danger: A general term used to express an assessment of both fixed and variable factors of the fire environment that determine the ease of ignition, rate of spread, difficulty of control, and fire impact; often expressed as an index.

Fire danger rating: A component of a fire management system that integrates the effects of selected fire danger factors into one or more qualitative or numerical indices of current protection needs.

Fire ecology: The study of the relationships and interactions between fire, living organisms, and the environment.

Fire exclusion: Planned (systematic) protection of an ecosystem from any wildfire, including any prescribed fire, by all means of fire prevention and suppression in order to obtain management objectives (cf. fire control).

Fire frequency: The average number of fires or regularly occurring fire events per unit time in a designated area.

Fire hazard: (1) A fuel complex, defined by volume, type, condition, arrangement, and location, that determines the degree both of ease of ignition and of fire suppression difficulty; (2) a measure of that part of the fire danger contributed by the fuels available for burning. It is worked out from their relative amount, type, and condition, particularly their moisture contents.

Fire history: The reconstruction and interpretation of the chronological record, causes and impacts of fire occurrence in an ecosystem in relation to changes of past environmental, cultural and socio-economic conditions. Fire history evidence is based on analysis of charcoal deposits in soils, sediments, and ice, dendrochronology (fire scar analysis), historical documents, and fire reports.

Fire information system: An information system designed to support fire management decisions. Advanced fire information systems integrate different sources of information required (e.g., vegetation conditions including fire history, topography, fire weather, fire behavior models, real- or near-real-time fire detection and monitoring data, fire management resources, infrastructures and pre-suppression information) on the base of a Geographic Information System (GIS) and allows real-time distribution or access via telecommunication.

Fire interval or fire-return interval: The number of years between two successive fires documented in a designated area; the size of the area must be clearly specified.

Fire management: All activities required for the protection of burnable forest and other vegetation values from fire and the use of fire to meet land management goals and objectives. It involves the strategic integration of such factors as a knowledge of fire regimes, probable fire effects, values-at-risk, level of forest protection required, cost of fire-related activities, and prescribed fire technology into multiple-use planning, decision making, and day-to-day activities to accomplish stated resource management objectives. Successful fire management depends on effective fire prevention, detection, and pre-suppression, having an adequate fire suppression capability, and consideration of fire ecology relationships.

Fire management plan: (1) A statement, for a specific area, of fire policy and prescribed action; (2) The systematic, technological, and administrative management process of determining the organization, facilities, resources, and procedures required to protect people, property, and forest areas from fire and to use fire to accomplish forest management and other land use objectives (cf. fire prevention plan or fire Campaign, pre-suppression planning, pre-attack plan, fire suppression plan, end-of-season appraisal).

Fire pre-suppression: Activities undertaken in advance of fire occurrence to help ensure more effective fire suppression; includes overall planning, recruitment and training of fire personnel, procurement and maintenance of fire fighting equipment and supplies, fuel treatment, and creating, maintaining, and improving a system of fuelbreaks, roads, water sources, and control lines.

Fire prevention: All measures in fire management, fuel management, forest management, forest utilization and concerning the land users and the general public, including law enforcement, that may result in the prevention of outbreak of fires or the reduction of fire severity and spread.

Fire protection: All actions taken to limit the adverse environmental, social, political, cultural and economical effects of wildland fire.

Fire regime: The patterns of fire occurrence, size, and severity – and sometimes, vegetation and fire effects as well – in a given area or ecosystem. It integrates various fire characteristics. A natural fire regime is the total pattern of fires over time that is characteristic of a natural region or ecosystem. The classification of fire regimes includes variations in ignition, fire intensity and behavior, typical fire size, fire return intervals, and ecological effects.

Fire risk: The chance a fire will start (be ignited) by a cause such as arson, accident, lightening or spreading from adjoining land.

Fire season: (1) Period(s) of the year during which wildland fires are likely to occur and affect resources sufficiently to warrant organized fire management activities; (2) a legally enacted time during which burning activities are regulated by State or local authority.

Fire suppression: All activities concerned with controlling and extinguishing a fire following its detection. (Syn. Fire Control, Fire Fighting). Methods of suppression are: ***direct attack*** A method whereby the fire is attacked immediately adjacent to the burning fuel. ***parallel attack*** A method whereby a fireguard is constructed as close to the fire as heat and flame permit, and burning out the fuel between the fire and the fireguard. ***indirect attack*** A method whereby the control line is strategically located to take advantage of favourable terrain and natural breaks in advance of the fire perimeter and the intervening strip is usually burned out or backfired. ***hot spotting*** A method to check the spread and intensity of a fire at those points that exhibit the most rapid spread or that otherwise pose some special threat to control of the situation. This is in contrast to systematically working all parts of the fire at the same time, or progressively, in a step-by-step manner. ***cold trailing*** A method of determining whether or not a fire is still burning, involving careful inspection and feeling with the hand, or by use of a hand-held infrared scanner, to detect any heat source. ***mop-up*** The act of extinguishing a fire after it has been brought under control.

Fire weather: Weather conditions which influence fire ignition, behavior, and suppression. Weather parameters are dry-bulb temperature, relative humidity, wind speed and direction, precipitation, atmospheric stability, winds aloft.

Fire-dependent species: Plant and animal species which require regular fire influence which triggers or facilitates regeneration mechanisms, or regulates competition. Without the influence of fire these species would become extinct.

Flammability: Relative ease of igniting and burning of a given fuel under controlled conditions, with or without a pilot flame. Flammability of a fuel is characterized quantitatively by the ignition delay of a sample of fuel exposed to a normalized radiation source.

Flat crush resistance: The maximum compressive resistance which corrugated combined board offers prior to collapse of the flute, to a force applied perpendicular to the plane of the board.

Flexographic printing: A rotary letterpress printing process in which the ink used consists of a dye or a pigment or both and generally a binder in a rapidly evaporating solvent vehicle. The printing press is much simpler than conventional machines, because only two rolls may be required, one running partially submerged in the fountain, the other transferring the ink to the plate. The rolls and plates are ordinarily made of rubber.

Floating chronology: In dendrochronology a ring-width series of unknown age that has not been associated with a particular calendar date.

Flocculant: Very-high-mass water-soluble polymer, usually having ionic groups.

Flocculation: Clumping of individual clay particles into larger aggregates.

Flora: Plants or a document on plants in an area.

Flower: The structure concerned with sexual reproduction in the angiosperms. (cf. **Strobilus** in gymnosperms)

Fluctuating asymmetry: Deviations from bilateral symmetry, often caused by genetic problems or environmental contamination.

Flute: The geometric configuration formed by one of the undulations of the corrugated medium in corrugated board. The exact dimensions of the flute will vary slightly depending on corrugating roll contour, material characteristics, converting equipment, and technique.

Flux: The movement of a substance from one compartment to another. Within the global change literature, a positive flux of carbon indicates a movement from a compartment into the atmosphere, and a negative flux indicates a movement from the atmosphere into another compartment.

Focus groups: Small groups of people, intended to represent a narrow or broad range of public interests, convened for the purpose of interactive and spontaneous discussions of a particular topic or plan.

Fodder banks: Fast-growing trees planted in blocks to provide a cut-and-carry fodder resource for livestock.

Fodder pollen: A type of pollen that cannot germinate and serves as a pollinator reward, e.g., the hood pollen of *Lecythis pisonis*.

Foliar analysis: Chemical analysis of leaves or needles of a tree to determine mineral content to provide information about nutritional state.

Foliar uptake: The ability of a pollutant to enter the interior of a leaf either through stomatal exchange or by transcuticular absorption.

Folivore: An organism that feeds primarily on the leaves of trees. Commonly used to describe foliage-feeding insects with chewing mouthparts.

Folk medicine: A culture- and ethnic community-specific, traditional healthcare system which is purely empirical in nature and exists in all rural communities throughout the world. Folk medicine practitioners generally use herbs and animal products found in the vicinity of their habitations for treating ailments.

FOLPI: Forestry-Oriented Linear Programming Interpreter.

Forb: A broadleaved herb other than grasses, sedges a especially one growing in a field, prairie, or meadow.

FORCABSIM: Forestry Development and Carbon Budget Simulation Model.

Forest: Traditionally considered an ecosystem dominated by trees and observed in multisized, multishaped landscape patches, of which at least two-thirds (66.7%) of its surface area is covered by trees. The FAO Forest Resource Assessment 2000 aims towards global standardization of the terminology: ***Forest*** Land with tree crown cover of more than 10 percent and area of more than 0.5 hectares. The trees should be able to reach a minimum height of 5 meters at maturity. ***Other wooded land*** Land either with a crown cover of 5–10 percent of trees able to reach a height of 5 meters at maturity; or a crown cover of more than 10 percent of trees not able to reach a height of 5 meters at maturity; or with shrub or bush cover of more than 10 percent. ***Other land*** Land with less crown cover, tree height, or shrub cover as defined under 'Other wooded land.'

Forest botanicals: Term used by US Congress; naturally occurring mushrooms, fungi, flowers, seeds, roots, barks, leaves, and other vegetation (or portions thereof) that grow on National Forest System lands.

Forest decline: The reduction in vigour of many trees growing together at the same site. In general, forest decline is due to a combination of biotic and abiotic factors and progresses slowly over time.

Forest degradation: Damage to forest ecosystems through human activities that does not result in the total elimination of forest cover.

Forest design plan: A type of forest planning used in the UK to plan the felling and restocking of a plantation forest and to use the process to improve the landscape quality, ecological value and recreational potential, and to diversify tree species and ages.

Forest fire: Any wildfire or prescribed fire that is burning in a forest, variously defined for legal purposes (see Forest). ***Other land fire*** Indication is desired if recurring wildfires affect 'Other land' by inhibiting regeneration to the 'Forest' and 'Other wooded land' categories. ***Ground fire*** A fire that burns **in:** the ground fuel layer (syn. Subsurface fire, *below* surface fire). ***Surface fire*** A fire that burns in the surface fuel layer, excluding the crowns of the trees, as either a head fire, flank fire, or backfire. ***Crown fire*** A fire that advances through the crown fuel layer, usually in conjunction with the surface fire. Crown fires can be classified according to the degree of dependence on the surface fire phase: ***Intermittent crown fire*** A fire in which trees discontinuously torch, but rate of spread is controlled by the surface fire phase (syn. Passive Crown Fire). ***Active crown fire*** A fire that advances with a well-defined wall of flame extending from the ground surface to above the crown fuel layer. Probably most crown fires are of this class. Development of an active crown fire requires a substantial surface fire, and thereafter the surface and crown phases spread as a linked unit (syn. Dependent Crown Fire). ***Independent crown fire*** A fire that advances in the crown fuel layer only (syn. Running Crown Fire).

Forest floor: All organic matter including litter and decomposing organic layers resting on the mineral soil surface.

Forest gardens: Often a form of multistrata agroforest, usually located close to settlements, where many useful species are grown in intimate association for a wide array of household subsistence items and some produce for sale.

Forest inventory: A system for measuring the extent, quantity, and condition of a forest cover, usually by sampling. An assessment of forest resources, including digitized maps and a database which describes the location and nature of forest cover (including tree size, age, volume, and species composition) as well as a description of other forest values such as soils, vegetation, and wildlife features.

Forest inventory non-disclosure: Procedures for safeguarding the locations of inventory plots and proprietary information obtained from them.

Forest landscape design: A branch of landscape architecture where the layout of a new forest or the felling/harvesting of an existing forest is designed to fit into the landscape while meeting a range of management objectives and taking account of practical, legal and economic constraints.

Forest landscape restoration: A planned process that aims to regain ecological integrity and enhance human well-being in degraded or deforested forest landscapes. In practice this means that any landscape will contain a mosaic of land covers including patches of original forest, areas with monoculture plantations, enriched forests and ecologically restored forests.

Forest mensuration: The art and science of locating, measuring, and calculating the length of lines, areas of planes, and volumes of solids; and the appropriate application of these calculations to trees and forest stands.

Forest protection: That section of forestry concerned with the management of biotic and non-biotic damage to forests, arising from the action of humans (particularly unauthorized use of fire, human-caused wildfires, grazing and browsing, felling), natural wildfires, pests, pathogens, and extreme climatic events (wind, frost, precipitation).

Forest recreation: Recreational activities and experiences conducted in forest and associated wildland environments that are dependent on the natural resources of these areas.

Forest sector model: Models that project market equilibria and/or forest resource conditions related to the forest-products industry.

Forest stand dynamics: The study of changes in forest stand structure over time, including responses of trees and stands to disturbances.

Forest stand: The smallest unit of forest management; a unit of land that is relatively homogeneous with respect to site conditions and tree characteristics (e.g., species composition, density, age).

Forest sustainability: Forest sustainability is a process with the objective of assuring that forest resources are and will be sufficient to satisfy present and future environmental, economic, and social needs.

Forest sustainability criteria: See criteria and indication.

Forklift: A device with projecting steel prongs mounted on a truck for lifting and moving heavy loads.

Form factor: The form factor, f, reflects the taper of a tree stem and is a reduction factor, by which the so-called reference cylinder volume ($g \cdot h$) is multiplied to obtain the volume of wood, v. Thus, $v = g \cdot h \cdot f$.

Formulation: The combination of the biocide(s), other inert ingredients, and carrier into a commercially viable system to treat wood.

FORPLAN: FORest PLANning.

FORSKA: A simulation model for the transient effects of climate change on forested landscapes.

Fortified rosin: Rosin stabilized by reaction with fumeric or maleic anhydride.

Forwarder: Off-road forestry vehicle designed for carrying logs.

Fourdrinier: A papermaking machine characterized by a horizontal forming section having a single forming fabric.

Fragmentation: The process of transforming large continuous vegetation or landscape patterns and habitats into smaller patches by disturbance. Natural agents of fragmentation are fire, landslides, windthrow, insects, erosion. Human-induced fragmentations include land use (e.g., agriculture, grazing, forestry), construction of residential areas, roads and other infrastructures. Fragmentation involves change of fire regimes due to alteration and discontinuity of fuels. It may influence forest ecology, diversity and regeneration.

Free sheet: A term denoting paper made from stock having rapid drainage on a paper machine or paper free of mechanical woodpulp.

Free water: Water in the cell lumens or capillaries not bound to cell walls.

Freehold: Full private ownership, that is, free of any obligations to the state other than payment of taxes and observance of land use controls, imposed in the public interest.

Frequency: An ecological measurement that provides an indication of how widely dispersed a species is found in a forest, usually measured as the number of times a species occurs in the sampling units.

Frost heaving: An upthrust of ground due to ice forming in the underlying soil.

FSC: Forest Stewardship Council.

F-test: A statistical test that compares variances, and is often used to test the null hypothesis of no difference among treatment means.

Fuel: All combustible organic material in forests and other vegetation types, including agricultural bio-mass such as grass, branches and wood, or infrastructure in urban interface areas, which create heat during the combustion process.

Fuel accumulation: Process or result of build-up of those elements of a vegetation complex which are not subject to biological decay, reduction by fire, animal grazing and browsing, or harvest by humans; it is used in characterizing fuel dynamics between two fires and has implications on fire behavior.

Fuel arrangement: The horizontal and vertical distribution of all combustible materials within a particular fuel type.

Fuel consumption: The amount of a specified fuel type or stratum that is removed through the fire process, often expressed as a percentage of the pre-burn fuel weight (or fuel load). It includes available fuel plus fuel consumed after the fire front passes.

Fuel management: Act or practice of controlling flammability and reducing resistance to control of wildland fuels through mechanical, chemical, biological, or manual means, or by fire, in support of land management objectives.

Fuel reduction: Manipulation, including combustion, or removal of fuels to reduce the likelihood of ignition and the potential fire intensity, and/or to lessen potential damage and resistance to control.

Fuelbreak: Generally wide (20–300 meters) strips of land on which either less flammable native vegetation is maintained and integrated into fire management planning, or vegetation has been permanently modified so that fires burning into them can be more readily controlled (as distinguished from firebreak). In some countries fuelbreaks are integrated elements of agro-silvopastoral systems in which the vegetative cover is intensively treated by crop cultivation or grazing. Some fuelbreaks contain narrow firebreaks which may be roads or narrower hand-constructed lines. During fires, these firebreaks can quickly be widened either with hand tools or by firing out. Fuelbreaks have the advantages of preventing erosion, offering a safe place for firefighters to work, low maintenance, and a pleasing appearance (cf. control line, agrosilvopastoral system, buffer strip/zone).

Fulvic acid: The portion of soil organic matter that is soluble under both alkaline and acid conditions.

Function: Processes that occur in the forest ecosystem (e.g., growth, nutrient cycling, etc.).

Functional additive: Chemical that mainly affects paper properties when used.

Fungal viruses: Viruses, commonly double stranded RNA (dsRNA), found in fungi that can result in reduced virulence – hypovirulence.

Fungi: Eukaryotic microbes having a branched, filamentous (hyphae, mycelia), or single celled (yeast) growth form. Fungi produce enzymes that degrade complex molecules, and absorb nutrients through their hyphal cell walls. The Eumycota, or true fungi, includes the phyla Ascomycota and Basidiomycota, as well as the Zygomycota and Chytridiomycota, which do not contain any pathogens of significance in forests.

Fungi imperfecti.: Ascomycetes or basidiomycetes that reproduce by asexual means only.

Funicle: The stalk by which a seed or ovule is attached to the placenta.

Furnish: The mixture of various materials that are blended in the stock suspension from which paper or board is made. The chief constituents are the fibrous material (pulp), sizing materials, wet-strength or other additives, fillers, and dyes.

Fynbos: Heath vegetation in South Africa. Derivation possibly from Dutch referring to timber too slender or fine for harvesting. It has also been suggested that the name 'fijnbosch' referred to the dominance of small- or fine-leaved shrubs.

Gall: An abnormal growth or swelling in a plant induced by attack from certain mites, nematodes and insects, or by fungal or bacterial infection.

Gamete: A mature sex cell, either male (sperm) or female (egg). For conifers, there are two sperm cells (derived from the body cell) within each pollen grain.

Gametic selection: Natural selection occurring at the gametic level.

Gametogenesis: The formation of female (eggs) and male (pollen) gametes.

Gametophytic self-incompatibility: A self-incompatibility mechanism prerenting self-fertilization in which successful fertilization is determined by the genotype of the pollen.

Gamma distribution: A probability distribution with density function

$$f(x) = \frac{(rx)^{a-1}}{\Gamma(a)} re^{-rx},$$

where a and r are parameters and Γ denotes gamma function.

Gasification: Thermal degradation process which preferentially produces gaseous products such as carbon monoxide, carbon dioxide, hydrogen, or methane.

Gasifier: A pyrolysis unit that produces combustible gas from solid wood feedstock.

GAYA-JLP: A Norwegian long-range forest management planning model.

Gender: Cultural ideas that construct images and expectations of males and females.

Gene flow: The movement of genes, via seed, pollen, or vegetative propagules, from one population to another.

Gene pool: The genetic resource of a population or species.

Genecology: Study of patterns of intraspecific variation shaped by evolutionary adaptation to environmental conditions.

Gene-for-gene system: Genetic interactions in a pathosystem in which a gene for resistance in a host is matched by a specific and complementary gene for avirulence in the pathogen.

General combining ability: The superiority (or inferiority) of a parent as measured by the relative performance of its offspring compared to the offspring of other parents in genetic tests.

General linear model: A linear model showing the relationships between the variable of interest (e.g., response or dependent variable) and the other variables, such as treatment levels, covariates, etc.

Generic guidelines: Relating to all members of genera.

Genetic diversity: The degree of variability of the genetic material of an organism. Variation of alleles at a particular gene locus, or at a number of gene loci, such that it can be detected through molecular analysis, or statistical analysis of phenotypes from pedigreed populations.

Genetic drift: The evolutionary process by which allele frequencies change due to random sampling error from generation to generation, important in small populations.

Genetic gain: The average (heritable) change from one generation to the next that results from selection.

Genetic load: Genes of deleterious effects, typically recessive in action and masked under conditions of outbreeding. Elimination of such genes is referred to as purging.

Genetic map: A diagram of the relative positions of genetic loci arranged into groups that may correspond to chromosomes.

Genetic marker: An allele with an easily recognized phenotype that can be used to follow the inheritance of genes in genetic crosses.

Genetic resistance: Inherited ability of organisms to avoid ill effects caused by a pathogen.

Genetic resource: The entirety of genes within a species that is available for tree breeding and domestication programs.

Genetic systems: The manner in which hereditary variation is regulated during transmission from the parental generation to the offspring.

Genetic testing: The process of planting pedigreed genotypes in randomized, replicated experiments for a range of purposes.

Genetic value or worth: A statistical measure based on quantitative genetic theory that indicates a level of genetic superiority of one genotype over another. The average breeding value of all seed from contributing parents weighted for the proportion of their contribution.

Genome: The DNA complement of the organism or of an organelle, which can be characterized in terms of total DNA, its organization into chromosomes, the coding and noncoding DNA, and the patterns of recombination within chromosomes. In addition to the main, nuclear genome, there are the chloroplast and mitochondrial genomes.

Genotype: The genetic constitution of an organism as distinguished from its physical appearance (phenotype). Clonal and progeny tests are used to evaluate sets of clones and seedlings (different genotypes) and furnish information on different genotypes but do not necessarily provide information on their breeding behavior.

Genus: Classificatory group containing species possessing certain common structural characteristics distinct from those of any other group.

Geographic information system: A GIS is a computer-based system that provides for the storage and representation of geographic data. GIS data are most commonly stored in a relational database format, from which they can be analyzed, combined and displayed as maps or in other data formats. The primary difference between GIS data and computer-aided design data (CAD) is that GIS data are referenced to a particular geographic location.

Geographic race: A race restricted to a geographical area. Other races may be less well adapted than the local race.

Geometric modeling: Geometric modeling is the creation of mathematical descriptions of the dimensions of real world objects, enabling these real world objects to be represented by 3D computer modeling software.

Germination: Resumption of embryo development after water imbibition and enzyme activation in the seed. 1. Normally beginning with the growth of the radix and ending with the lignification of the seedling. 2. Within the context of pollen viability testing, this is a technique that relates viability with the growth of pollen grains under controlled conditions.

Gibberellins: A class of plant hormones, which number over 100, that occur in most plants including conifers. The mixture of gibberellins A_4 and A_7 (GA4/7) are the active components for inducing flowering in western hemlock as well as most other Pinaceae species.

Girth: See diameter.

GIS: (See Geographic Information System).

Glass transition temperature: The temperature associated with the softening of amorphous polymers, macromolecules which have no crystallinity. Liquid-like flow begins to occur at the glass transition in amorphous polymers.

Glassine paper: A supercalendered, smooth, dense, transparent or semitransparent paper manufactured primarily from chemical wood pulps, which have been beaten to secure a high degree of hydration of the stock.

Gleichläufigkeit: A measure of the year-to-year congruence between the trend changes of two chronologies in dendrochronology.

Global positioning system: A satellite-based radionavigation system comprised of constellation of 24 space satellites and their supporting ground stations, used to obtain precise positions of targets on, or near, the surface of the Earth.

Global warming potential (GWP): A value based on net emissions of carbon dioxide, methane, and other gases shown to have the potential to warm the climate of earth when liberated to the atmosphere.

Gloss: That property of the surface which causes it to reflect light specularly and which is responsible for its shiny or lustrous appearance.

Glue-laminated timber or glulam: A large structural member made from multiple pieces of dimension lumber glued end-to-end and face-to-face.

Good manufacturing practices (GMPs): Standards published in the code of Federal Regulations and used by the Food and Drug Administration (FDA) to ensure the quality of marketed products and that products are produce under sanitary conditions. Any FDA-regulated product can be designated adulterated if the manufacturing methods or facilities for processing do not confirm with GMPs, which are developed through a consultative process between the FDA and the affected industry.

Good practices: To adopt appropriate procedures in order to achieve desired results.

Government land: Land legally belonging to a government at any level.

GPP: Gross primary productivity, i.e., total net photosynthesis of an entire ecosystem.

GPS: See Global positioning system

Grammage: The mass of paper measured in grams per square meter of area. Related to basis weight, which is the weight in pounds of a prescribed area measured in square feet.

Graphical user interface (GUI): A computer interface that uses visual icons and cues as the basis for navigation. GUIs are often referred to as 'point-and-click' interfaces, as they require the user to interact with them by making visual selections of buttons, menus, or slider bar positions, using a mouse or keyboard as the primary input device. Microsoft Windows and Apple Macintosh operating systems are examples of graphical user interfaces.

Gravure printing: Printing from plates in which the image is sunken below the surface, as distinguished from printing by letterpress or offset lithography.

Greenbelt: A fuelbreak maintained by the cultivation of strips of less flammable plants within a zone of high fire hazard, e.g., an irrigated, landscaped, and regularly maintained fuelbreak put to some additional use (e.g., golf course, park, playground).

Greenhouse gases: Gases such as carbon dioxide, methane, chlorofluorocarbons, nitrous oxide and tropospheric ozone that are building up in the atmosphere and that trap radiative heat near the Earth's surface causing global warming.

Gregarious flowering: Simultaneous flowering of all plants even though separate especially if from a given generation; common in bamboos.

Ground vegetation: The herbaceous or shrub species growing beneath a tree canopy.

Groundwood (GWD) pulp: A mechanical pulp produced by pressing debarked logs sideways against a rotating pulpstone in the presence of water and reducing the wood to a mass of relatively short fibers and fines.

Group systems: Modifications of the selection, shelterwood or clear cutting (clear felling) silvicultural systems in which small groups, rather than whole or sub-compartments are treated at a time.

Growing space: The net presence of the factors (light, moisture, nutrients, and physical space) required for tree growth.

Growth and yield model: Model that projects future stand or tree characteristics from a given set of initial conditions.

Growth form: The morphology and structure of a plant (e.g., grass, herb, shrub, deciduous tree).

Growth rings: Seasonal growth of wood in a ring around the central axis of a tree as seen on the cross (transverse) section; composed of two growth regions-that formed early in a season – earlywood or low density wood; and that formed later – latewood or high density wood; if one growth ring is formed annually, it is called an annual ring. (See Dendrochronology)

Growth/productivity: Changes in total volumes of plants or parts of plants.

Gt: Giga-ton (giga $= 10^9$).

GTM: Global Trade Model.

GW: Groundwood.

Gymnosperms: A subdivision of the seed plants, distinguished from angiosperms in that the ovules are not enclosed by material tissues but supported naked on the cone scales. Includes all coniferous trees.

h^2: Heritability: genetic parameter used to estimate the proportion of the phenotypic variation of a trait that is due to gene effects.

Habitat: The place or type of site where an organism or population naturally occurs.

Habitat fragmentation: See Fragmentation.

Haploid: Refers to the state of having only a single set of chromosomes, as in the pollen grains and the megagametophyte that produces the egg cells with which pollen nuclei fuse to produce zygotes.

Haploxylon pines: Members of the subgenus *Strobus* of pines, characterized by having one fibrovascular bundle in each needle.

Hardiness: The ability of plants to endure freezing temperatures without being killed.

Hardwood: 1. Tree belonging to the botanical group Angiospermae. Synonym broadleaved. 2. Common and timber tradename for broad-leaved, commonly deciduous, woody angiospermous trees. 3. Pulpwood from broad-leaved dicotyledonous deciduous trees. 4. A term applied to wood obtained from trees of the angiosperm class. The hardwoods are obtained from dicotyledonous trees such as birch, gum, maple, oak, and poplar. The leaves are broad except in rare instances and are usually deciduous in the temperate zones. The seeds are enclosed in a fruit that is either fleshy or dry at maturity. Hardwoods are also designated as porous woods.

Harvester: Off-road forestry vehicle designed for felling, delimbing and bucking trees.

Hazard reduction: Treatment of living and dead forest fuels to reduce the likelihood of a fire starting, and to lessen its damage potential and resistance to control (cf. Fuel Treatment). Activity gaining special importance in residential/wildland interface areas.

Heartwood: Physiologically inactive (dead) inner core of a tree stem or log, usually darker in color than the outer portion of the stem (sapwood); sometimes possessing odor, taste, and higher durability. The high amount of extractives and a low moisture content are features of heartwood. The wood of tree species with true heartwood is often more resistant to wood-decaying fungi than that of many other species. These include pine, larch, oak, robinia, elm, walnut, and cherry.

Heat pump: A device which alternatively compresses and expands a refrigerant and uses heat exchangers to move energy from a colder region to a warmer region.

Heat treatment: Heating wood, typically above 180°C, in an inert atmosphere to cause sufficient chemical changes to render the wood partially resistant to attack by wood-decaying fungi.

Hedgerow intercropping: An agroforestry practice in which fast-growing shrubs, that are often nitrogen fixing, are grown between strips of crops and periodically cut back to provide a nutrient rich mulch to fertilize the crop; also referred to as alley cropping. Woody parts may be retrieved for kindling fires.

Hedonic pricing: Placing cash value on pleasure.

Height: Total tree height, *h*, is defined as the shortest distance either between base and top of the tree, or between ground level and top of the tree. The first definition may be preferred because it is often compatible with the length of felled trees and a consistent measure for volume calculations, whereas the second definition may be generally more practical. Other height definitions may refer, for example, to merchantable parts of the tree. Also, see stand height.

Heliophilus: Adapted to high intensity of light.

Hemiepiphyte: Epiphytic plant which starts its development growing on the surface of trunks and branches of other plants, but later sends its roots down to the soil in order to access soil nutrients; in some cases, it may behave as a strangling plant (e.g., in *Clusia* and *Ficus*) affecting the health of its host.

Herbivory: The consumption of plant tissue by animals.

Herbs: Non-woody plants that die down at the end of the growing season.

Heritability: Degree to which a trait is transmitted from one generation to another (i.e., from the parent tree to its seed). Highly heritable traits are those under strong genetic control. Traits that are also influenced by the environment are less heritable. The proportion of total or phenotypic variation that is governed by genotypic effects. Narrow-sense heritability relates to purely additive gene effects, broad-sense to total gene effects.

Heterochromatin: Compact chromosomal segments or whole chromosomes with a dense structure which accept dyes in telophase, interphase, and early prophase, as distinct from euchromatic segments.

Heteroecious: Having certain spore forms of the life cycle on one host species and others on an unrelated host species.

Heterosis: Superiority of the F_1 generation compared with the parental generation with respect to a metric trait.

Heterozygote: An organism in a diploid state where the alleles at a given locus are different. Heterozygosity is common in allogamous plants.

Holistic management: A management approach that takes into account all relevant factors when making a decision.

Homeopathy: Homeopathy is a form of medicine system that treats the body as a whole and helps it to heal itself. It is based on the principle that substances that are poisonous in large doses can be beneficial in small doses. In this practice extremely small doses of medicines, mostly derived from herbs, are used to cure the disease.

Homozygote: An organism in a diploid state where both alleles at one locus are the same. Homozygosity is predominant in autogamous plants.

HOPSY: Houtoogst Prognose Systeem (Wood Harvest Forecast System).

Horizontal precipitation: Horizontal water influx into an ecosystem due to the condensation of small water particles originating from mist and fog, on top of the surface of the vegetation.

Hot spot: A recently coined term to draw attention to areas of both high species diversity and that are also under severe threat of destruction.

Humic acid: The portion of soil organic matter that is soluble under alkaline conditions but is acid insoluble.

Humidity or absolute humidity: Mass of water vapor contained in a unit mass of dry air.

Humin: The insoluble portion of soil organic matter.

Humus: Organic component of soil derived from dead and decaying plant and animal remains.

Hybrid breakdown: The reduction in fitness of F_2 and/or backcross generations compared to the F_1 and parental generations. This decline may involve weakness of vegetative growth, sterility, or both of these; it is over and above any loss of vigor due to the lowered heterozygosity if inbreeding is involved. Hybrid breakdown is also known, perhaps more appropriately, as advanced generation breakdown or later generation breakdown.

Hybrid geometric/photo-imaging: A combination of geometrically modeled objects (3D) and photographic elements. The combination may take the form of a photograph draped over a geometric shape (e.g. an aerial photograph placed on a landscape model, or a photograph of a building facade placed on a geometric representation of the building) or they may involve the placement of photographic elements onto a 3D terrain surface (such as 2D 'billboard' trees that turn so they always face the viewer).

Hybrid swarm: A natural population of hybrid offspring of two or more related species encompassing several generations including the backcross generation.

Hydraulic conductivity (or permeability): Property of a saturated porous medium which determines the relationship, called Darcy's law, between the specific discharge and the hydraulic gradient causing it.

Hydraulic loading: The amount of wastewater applied in a complete operational cycle; usually expressed in inches per week.

Hydrocarbons: C-H compounds, such as methane (CH_4).

Hydrogen bonds: Bonds that occur between the hydrogen of one molecule and the electronegative atom of another molecule such as oxygen.

Hydrolysis: Method by which polysaccharides from wood are depolymerized by the action of chemicals or enzymes, in preparation for fermentation to other products.

Hydroperiod: Period of time that an area is inundated.

Hygrophilous: Plants restricted to moist conditions.

Hypersensitive reaction (HR): Local necrosis of cells in response to pathogen invasion.

Hyphae: Vegetative 'threads' of growth in fungi that make up the mycelium.

Hypogeal: Of seed germination in which the cotyledons remain underground.

Hypolimnion: Lower (cooler) layer of thermally stratified lakes.

Hyporheic exchange: Interchange of streamwater with water occurring within or below the streambed.

Hyporheic zone: Area where surface water and groundwater interact.

Hypsometer: Instrument for measuring the height of standing trees. Direct height measurement may be carried out using a graduated rule, stick, pole or tape measure. Indirect height measurement is based on geometric or trigonometric principles. The geometric principle relies on the use of similar triangles, whereas the trigonometric principle makes use of trigonometric functions. Modern instruments use optical and laser methods and may be digitized for recording.

Ideotype: A set of characteristics, representing specific levels of expression of certain traits, that embody a breeding goal.

IFS: Interactive Forest Simulator.

IIASA: International Institute for Applied Systems Analysis.

Immunoassay: Use of immune reactions in animal material, in this case to evaluate plant taxonomic affinities.

Importance index: An index calculated from relative density and relative dominance of a selected plant family or species.

Imputation methods: Methods for substituting data for missing observations.

INA: Information needs assessment or analysis.

Incident Command System: A standardized on-scene emergency management concept specifically designed to allow its user(s) to adopt an integrated organizational structure equal to the complexity and demands of single or multiple incidents, without being hindered by jurisdictional boundaries (element of the Incident Command System [ICS]).

Inclusion: One or more polypedons or parts of polypedons within a delineation of a map unit that is not one of the named component soils.

Incompatibility: The state in which functional female and male organs are unable to achieve fertilization. Self-incompatibility prevents self-fertilization after self-pollination, and interspecific incompatibility blocks species hybridization.

Incompatibility system (genetic incompatibility): Inability of plants having functional gametes to set seeds when either self-pollinated or crossed with some of their genetic relatives.

Increment: The change in a particular measure of tree growth (e.g. height, diameter, basal area or volume) over a particular time period.

Indehiscent fruit: A type of fruit that does not open at maturity.

Independent, normally distributed, with equal variances: A trio of assumptions about residuals that are required for least-squares estimates to have desirable properties.

Indexing: Detrending a tree-ring curve to differentiate between short-term and long-term oscillation by dividing the measurements by a standardizing smoothing function, resulting in a time series of ring-width indices.

Indicator: A quantitative, qualitative, or descriptive measure that, when periodically measured and monitored, shows the direction of change. Indicators are species or communities that enable an evaluation of environmental conditions and detect changes. Indicator species are normally surrogates of other species in the area of interest and are usually sensitive to environmental change. Environmental variables may also be used as indicators.

Indigenous: See Autochthonous.

Indigenous knowledge: The knowledge belonging to a specific ethnic group.

Industrial roundwood: Wood to be used for manufacture of wood or paper products.

Infection: The process by which a pathogen establishes a parasitic relationship with a host organism. Infection is usually considered the initial establishment of a parasite with its host, and colonization is the expansion of the parasite in its host.

Inflorescence: The arrangement of the flowers on the flowering branch.

Information dissemination: To share information, with a purpose of raising awareness, improving skills and practices and enhancing knowledge in a given community.

Information open house: A venue where information on a project or issue is displayed or presented for a specified time period, to which the public is invited.

Infraspecific: At a lower taxonomic level than a species.

Infructescence: An aggregate fruit, with the same relation to a simple fruit that an inflorescence has to a single flower.

Inoculation: Arrival or transfer of a pathogen on to a host plant.

Inoculum: The amount of fungal, bacterial, viral, etc., propagules available and potentially capable of infecting a host plant.

Inoculum potential: A term to describe a sufficient base of energy enabling a fungal pathogen to spread.

***In-situ* conservation:** To conserve species or populations inside their natural habitat.

***In situ* remedial technology:** Remediation accomplished onsite without excavation and removal of material, e.g., bioremediation, phytoremediation, natural attenuation.

Integrated Forest Fire Management (IFFM): Designation of fire management systems which include one or both of the following concepts of integration: (1) Integration of prescribed natural or human-caused wildfires and/or planned application of fire in forestry and other land-use systems in accordance with the objectives of prescribed burning; (2) Integration of the activities and the use of the capabilities of the rural populations (communities, individual land users), government agencies, NGOs, POs to meet the overall objectives of land management, vegetation (forest) protection, and smoke management including 'community-based fire management' or CBFiM. The term IFFM is common for fire management approaches in less developed regions including forest and non-forest ecosystems. Note: In case of absence of forests in the area concerned the term *Integrated Fire Management* (IFM) is used instead (cf. prescribed burning).

Integrated inventories: Combined or coordinated data collection efforts designed to share data and to improve information flows between functions, sister units, parent units, and/or over time.

Integration: The act of combining or coordinating separate elements so as to provide a harmonious, interrelated whole.

Interactions among factors: Effects of a particular factor vary depending on the level of another factor. If there is no interaction, the two factors can be interpreted separately.

Interblock information: Information about the treatment effects that may be extracted from differences between the effects of blocking levels in incomplete block designs.

Interior spruce: Naturally occurring hybrid between white (*Picea glauca*) and Engelmann (*P. engelmannii*) spruce.

Intermolecular forces, secondary forces: The association and attraction between complementary charges (positive and negative) which occur on the surfaces of all molecules. These are called secondary forces (or bonds) because they are relatively weak and temporary, in contrast to primary forces (and bonds).

Interpolation: The computation of points or values between ones that are known using the surrounding points or values.

Intrageneric: At a lower taxonomic level than the genus but above that of the species.

Intraspecific taxonomy: Genetic or phenotypic variation within a species, i.e. varieties or subspecies.

Introgression: The progressive incorporation of genes from one population into another by hybridization events and back-crossing.

***In vitro* culture:** Propagation of plants from small pieces of tissue in enclosed sterile conditions on nutrient medium.

Inventory: Originally a commercial term consisting of the preparation of a detailed descriptive list of articles with number, quantity, and value of each item. As forest inventory: a set of techniques for collecting reliable and satisfactory information on species, volumes and values of forests.

Inverse density dependence: The effect decreases as a percentage of the population as the population increases in density.

Involucel: A whorl of bracts surrounding one of the divisions in an inflorescence.

Irregular: Of a regeneration method, characterized by variation in age structure (usually uneven-aged) or in spatial arrangement of trees.

ISO: International Standards Organization. Among many other things, it sets standards for aspects of paper manufacture, e.g., brightness.

Isozyme: Enzymes that exist in alternative forms that can be differentiated in laboratory tests and used to provide information or genetic variation.

IUCN: The World Conservation Union.

JLP: A linear programming package for management planning by Juha Lappi.

Johnson's SB distribution: A probability distribution with density function:

$$f(x) = \frac{\delta\lambda}{(x-\xi)(\xi+\lambda-x)}\frac{1}{\sqrt{2\pi}}\exp\left(-0,5z(x)^2\right)$$

where

$$z(x) = \gamma + \delta \ln\left(\frac{x-\xi}{\lambda-\xi-x}\right)$$

and γ, δ, ζ and λ are parameters.

Joint forest management: Management of forest by the State forest department and the village forest councils.

Kairomone: Chemical emitted by an organism that is detected by other species (e.g., tree kairomones detected by bark beetles).

Kappa number: A measure of residual lignin present in pulp.

Karyotype: The configuration of the chromosome complement, in terms of the number of chromosomes, relative lengths, and positions of the centromeres of individual chromosomes, plus secondary features such as constrictions, zones of heterochromatin, and banding patterns.

Keystone species: A species that has a major influence on the structure of an ecosystem.

Krummholz: A stunted growth form of trees at the upper treeline or in the alpine zone due to wind and blowing snow.

Kwongan: Western Australian Aboriginal term for heathland.

Lagged or delayed-density dependent factors: Factors of which the effect is not apparent until subsequent generations of the populations.

Laminated strand lumber (LSL): A dimension lumber-sized structural member composed of thin strands of wood glued together such that the grain of each strand is parallel to the member's length. Also parallel strand lumber.

Laminated veneer lumber (LVL): A dimension lumber-sized structural member composed of multiple sheets of veneer glued together such that the grain of each ply is parallel to the member's length.

Land limiting constituent (LLC): The waste constituent that requires the largest land area for assimilation.

Land race: Usually an introduced species which has undergone some form of natural selection to the local environment and has become well adapted after one or a few generations.

Land tenure: The terms on which land is held: the rights and obligations of the holder of the land.

Land treatment: The practice of applying partially treated liquid and/or solid wastes produced by municipalities and industries to the land for further treatment, recycling beneficial nutrients, improving site productivity, and protecting surface and ground water supplies.

Landing: Place where round timber is stored, sorted, and assembled for secondary transport, commonly with a change of transport method.

Landscape: Within the context of forests, this term holds different meanings for different types of professional. In the context of visual analysis, it refers to the overall visual appearance of a place or area together with the underlying biophysical and cultural factors which affect perception and the quality of experience of the viewer.

Landscape character: The combination of a set of physical, ecological, and visual factors which combine to give a landscape a unique sense of identity.

Landscape diversity: The spatial heterogeneity of the various land uses and ecosystems within a larger area.

Landscape (visual) sensitivity: A measure of the likely concern expressed by the public over landscape change in a given area. Usually assessed from a combination of degree of visibility, numbers of viewers, the nature of the viewing experience, and the value or quality of the landscape.

Landscape visualization/visual simulation: One or more images showing an existing, future, past, or imaginary set of conditions in perspective view, usually in the context of an actual place. These may have various levels of realism.

Larderhoarding: The collection, movement, and storage in single or few locations of resources, usually fruit or seed, by animals.

Larva: Grub-like, immature form of bark beetles and other insects.

Late burning: Prescribed burning activities towards the end of the dry season.

Latent pathogens: Pathogens, often endophytic and not associated with symptoms, that remain latent in plants until the onset of stress.

Laterite: Hard, impenetrable soil.

Latex paint: A paint containing pigments and a stable water suspension of synthetic resins (produced by emulsion polymerization) that forms an opaque film through coalescence of the resin during water evaporation and subsequent curing.

Lathe: A machine for shaping a piece of wood by holding it at its ends and rotating it rapidly against a cutting tool.

Laticifers: Latex-producing glands.

LEA proteins: Late embryogenesis abundant proteins, encoded by the *lea* genes. They appear late in embryogenesis and accumulate to a relatively high concentration.

Leaf area index: The area of foliage per unit area of ground. Leaf area is usually calculated based on the upper surface of flat leaves. It can also be the area of complex leaves projected onto a flat surface.

Least-squares analysis or techniques: Statistical methods where the objective is to find a solution that minimizes the sum of squared differences between observations and predictions.

Lentic: Associated with still water.

Leptomorph: Slender and continuous rhizome of monopodial bamboos.

Lerp: Starch shell of sedentary nymphs of psyllids, important sapsucking insects found on eucalypts.

Liana: Woody climbing plant that grows from the soil into the tree canopy; tropical woody vines.

Life cycle assessment (LCA): An evaluation of the environmental impact of a process or product including measurable inputs and outputs (as determined in an LCI), as well as impacts that are not precisely measurable (i.e., impacts on human health, landscape impacts).

Life cycle inventory (LCI): A systematic accounting of all measurable inputs and outputs to a manufacturing process, including raw materials, products and co-products, and emissions to air, water, and ground.

Light demander: See shade bearer.

Lignin: A very variable cross-linked polymer of phenyl propane units such as coniferyl alcohol (guaiacyl), sinapyl alcohol (syringyl) or hydrocinnamyl alcohol, and which stiffens the cell wall. The noncarbohydrate portion of wood that is removed to various degrees during chemical pulping.

Line-plot transects: Plots located along lines at various intervals across a central transect.

Linguistic: Of or relating to language.

Linkage disequilibrium: A nonrandom association between specific alleles at different loci, normally reflecting location on the same chromosome.

Linkage group: A group of coupled genes within a chromosomal segment.

Lipid: Any of a group of organic compounds, including the fats, oils, waxes, sterols, and triglycerides, that are insoluble in water but soluble in nonpolar organic solvents, are oily to the touch, and together with carbohydrates and proteins constitute the principal structural material of living cells.

Liquefaction: Thermal degradation process in which wood is liquefied under conditions of elevated temperature, in the presence of catalysts.

Litter: The surface layer of the forest floor that is not in an advanced stage of decomposition, usually consisting of freshly fallen, recognizable, leaves, needles, twigs, stems, bark, and fruits. It includes all nonliving biomass in various states of decomposition above the mineral or organic soil.

Litter raking: The practice of regularly gathering forest litter (leaves/needles, twigs, and branches) from beneath a forest stand for fuel, bedding for livestock and other domestic uses.

Llanos: A Spanish term referring to large expanses of plains found mostly in Colombia and Venezuela.

Loam: Soil with sand, silt, and clay in almost equal proportions.

Locus: A site on a chromosome occupied by a specific gene.

Lodging: Wind damage to crops either by uprooting or by stem/stalk breakage. Enhanced by high turbulence levels.

Log-normal distribution: A probability distribution with density function

$$f(x) = \frac{1}{x\sigma\sqrt{2\pi}} \exp\left(-\frac{1}{2}\frac{(\ln(x)-\mu)^2}{\sigma^2}\right),$$

where μ and σ are parameters.

Long-horn beetles: Wood-boring insects belonging to the family Cerambycidae that tend to have long antennae.

Long-term productivity: Yields of forest crops over long intervals of time, especially from successive rotations.

Loose tipping: This method of ground preparation involves the use of dump trucks to transport soil or soil-forming materials to the deposition area on the reclamation site. There, it is tipped in heaps on the surface of the overburden which are spread and levelled using an excavator working from the overburden surface.

Lotic: Associated with flowing water.

Low thinning: See thinning.

Lowland: The altitudinal belt between sea-level and the montane belt, with its upper limit in the tropics generally at about 1000 m elevation.

LP: Linear programming.

Lumber: The product of the saw and planing mill for which manufacturing is limited to sawing, resawing, passing lengthwise through a standard planing machine, crosscutting to length, and matching. Lumber may be made from either softwood or hardwood.

LWC: Light-weight coated papers.

Machine glazed finish: The finish produced on a Yankee machine, where the paper is pressed against a large steam-heated, highly polished revolving cylinder, which dries the sheet and imparts a highly glazed surface on the side next to the cylinder, leaving the other side rough.

Macromolecules: This is another term for polymer. Polymers are so unusually large that they are called macromolecules, as opposed to very small molecules like water.

Macrophyte: Any aquatic plant visible to the naked eye (includes algae and higher plants).

Macropores: Soil pores through which water can move rapidly and which are mostly formed by plant roots, soil structure, and burrowing animals (e.g., earthworms). Water flow in macropores is often turbulent and driven by gravity.

Major gene resistance (MGR): Resistance conditioned by single, dominant genes (R genes).

Mallee: Low-growing, multi-stemmed eucalypts generally 2–10 m tall and with woody lignotuber.

Mangal: Vegetation in swampy or tidal areas, often called mangroves.

Map unit: A group of delineations identified by the same name in a soil survey that represent similar landscape areas comprised of the same component soils plus inclusions.

Map-based estimation: A system that combines techniques for constructing maps of forest attributes and techniques for calculating estimates from those maps that are unbiased and sufficiently precise at the required spatial scales.

Maquis: Heath vegetation in New Caledonia. (Closest to Corsican use of the term rather than French.)

Marcotting: Propagation on the intact plant by air-layering (area where bark has been removed is enclosed in propagation medium).

Marginal thinning intensity: The maximum volume of growing stock that can be removed in thinning without decreasing future cumulative production. This volume is known to be close to 70 per cent of the maximum mean annual increment over the 'normal thinning period.'

Massart model: A tree growth and architecture model, which involves a straight trunk, horizontal branches, and rhythmic growth and branching.

Massenerhebung: A mass elevation or telescope effect causing a compression of altitudinal vegetation belts on smaller tropical and temperate mountains (German term).

Mast seeding: The synchronous and massive production of fruit by trees. Irregular variation between years in seed output with high output at variable intervals. Masting shows highest seed crop variability at mid latitudes and in the southern hemisphere, which are similar to the patterns in variability of rainfall. Masting may be an adaptive reproductive trait (e.g., to allow effective pollination or to overwhelm predators) overlaid on the direct influence of weather.

Mata Atlantica: The Atlantic Coastal forest of Brazil, a hot spot that is full of endemic species and is under severe threat with only 7% of its original area remaining.

***Matsukuimushi*:** A general term which formerly covered more than 70 species of pine bark beetles and pine wood borers. At present, an administrative term which indicates Japanese pine sawyer.

Matrix habitat: Habitat surrounding forest fragments; it is often highly disturbed or distinct.

Maximum likelihood techniques: Methods where the objective is to find a solution that maximizes the probability of observing the sample data.

Maximum size-density relation: Trees growing in single-species even-aged stands do not grow beyond a specific size for a given density. When expressed as the logarithm of size versus the logarithm of density the maximum size-density relation has the slope of $-3/2$. The relation is independent of site quality and age and the intercept depends on the species.

MDS: Mobile Data System; vehicle computer linked on-line to a central company server.

Mean: The average value of a variable for all units in a population or sample.

Mean annual increment (MAI): the total increment of a tree or a stand (standing crop plus thinnings) up to a given age divided by that age.

Mean (quadratic) dbh: The dbh corresponding to the average basal area of a group or stand of trees. This is the root mean square dbh and not the same as the arithmetic mean (average) dbh.

Mechanical woodpulp: A high-yield pulp produced from wood by a variety of mechanical pulping processes. It is characterized as a woodpulp with high lignin content. It is primarily suitable for printing grade papers, but can be used in other paper grades, like tissue, board, and fluffed pulps.

Median: The value of a variable so that half of the values are larger and half are smaller than this value in a population or sample.

Megagametophyte: Female gametophyte in heterosporous plants; embryo sac within the ovule in angiosperms.

Meiosis: Nuclear divisions leading to the formation of gametes (either egg or sperm cells). The first division results in reducing the number of chromosomes in half (haploid) and the second division results in the formation of four haploid daughter nuclei.

MELA: MetsäLAskelma, a Finnish forestry model.

Melting temperature: The temperature associated with melting of crystals, and in this context, the crystals present in semicrystalline polymers. Liquid-like flow begins to occur at the melting temperature of semicrystalline polymers, as in the case of hotmelt adhesives.

Mensuration: Generally the study of the measurement of geometric magnitude. In forestry the measurement of the number, volume, dimensions and shape of trees and stands.

Meristem: An undifferentiated plant tissue, often with rapidly dividing cells, from which new tissues or organs arise. In woody plants the primary epical meristems of shoots and roots provide principally for extension growth while secondary cambil meristems initiate the production of wood and diameter growth.

Mesic habitat: Moist habitat.

Mesocarp: The middle layer of the fruit wall.

Mesophyllous: Having leaves of medium size.

Mesophytic: Sites or habitats that are neither too wet not too dry.

Mesopredators: Predators of medium size.

Metacentric: Refers to the state of a chromosome having the centromere (the attachment point for the chromosome being pulled clear towards the end of cell division) located near the middle.

Metapopulation: A group of smaller populations whose persistence is dependent on the dispersal of individuals between them.

Methanogenesis: The biological production of methane.

Microfibril: Microscopic strands in a wood cell wall composed of a core of bundled, parallel cellulose chains encased in other polysaccharide, nonglucose sugars; the cellulose chains have crystalline and amorphous regions. The angle of the microfibril to the long axis of a wood fibre influences strength and flexibility.

Microgametophyte: Male gametophyte of a heterosporous plant; pollen grain in a seed plant.

Microphyllous: Having small leaves.

Micropores: Soil pores through which water moves very slowly and can retain water against gravity. The capillary concept is valid in micropores.

Micropyle: A wide, funnel-shaped structure arising from the integument and surrounding the nucellus through which the germinating pollen tube must pass to penetrate the nucellus to reach the egg cell.

Microsatellites: A class of highly variable, codominant (both alleles at a diploid locus may be visualized) DNA marker.

Microsclerotia: Very small thick-walled survival structures in fungi.

Microspore: The male pollen grain which is mature at shedding and consists of five cells; two prothallial cells, a stalk cell, a body cell, and a tube cell

Microtubules: Tubular structures composed of subunits of the protein tubulin. They occur in large numbers in all eukaryotic cells freely in the cytoplasm or as a structural component of organelles. In addition, they form part of the structure of the mitotic spindle.

Migratory users: Resource users who are not settled where the resource is located and use it at intervals often as part of a pattern of moving from one resource location to another. (e.g., branshumance, nomadic pastoralism)

Mineral soil: Soil comprised of less than 18% (weight) organic carbon.

Mineralization: Conversion of an element from an organic form to an inorganic state as a result of microbial decomposition. Release of inorganic forms of nutrients from complex-carbon bonded forms during decomposition of organic matter.

Ministerial Conference for the Protection of Forests in Europe: The periodic Conference and its inter-sessional activities promote and reinforce cooperation among European States in the field of forest protection and sustainable development.

Miocene: Geological epoch (23.8–5.3 million years ago) of Tertiary period.

Miombo: Open, African woodland dominated by ***Brachystegia*** and related legume genera.

Mode: The value of a variable that occurs most frequently in a population or sample.

Model: Abstract representation of a system, often mathematical.

Model forest: A partnership of individuals and groups representing diverse forest stakeholders working together to develop and demonstrate approaches to SFM that are locally acceptable and nationally relevant; people with an interest in the forest participate in decisions its sustainable management and demonstrate this in operational terms. A model forest is of a size that includes the full range of forest uses and needs that are considered in the surrounding geographic region and which is representative of a broad ecosystem.

Model resolution: Level of detail, or smallest item represented.

Model scope: Breadth or area of interest.

Moisture content: Mass of water contained in a unit mass of wood, usually expressed as a percentage of its dry mass.

Moment: The k^{th} moment of x is the expected value of x to k^{th} power $E(x^k)$.

Monad: A dispersal unit comprising one pollen grain.

Monitoring: The process of taking repeated observations of the same variables in the same area over time to note changes and to predict trends. Continuous forest inventories or repeated inventories across the same area over time are a form of monitoring.

Monocotyledons: One of two great division of flowering plants in which the embryo characteristically has one cotyledon and the nervation is generally parallel. (cf. Dicotyledons).

Monoecious: Plants in which male and female reproductive organs occur separately on the same individual.

Monoecy: The system in which plants have separate female and male flowers but borne on the same individual.

Monophyletic: A group that includes all the evolutionary descendants of a taxon's common evolutionary ancestor and only those descendants.

Monopodial bamboo: Bamboo with a single and continuous rhizome, with lateral buds that grow into culms.

Monopodial: Stem developing by repeated growth of the principal buds.

Monotypic genus: A genus that contains only a single species.

Montane: 1. Living in mountains. 2. The altitudinal belt between the lowland belt and the (sub)alpine belts, which in the tropics is generally situated between 1000 and 3000 m elevation.

Monte Carlo simulation: Random values for uncertain variables are generated many times to simulate the behavior of a stochastic system.

Montreal Process: An initiative of the Government of Canada to develop forest sustainability criteria and indicators for non-tropical boreal forests. Montreal Process member countries include: Argentina, Australia, Canada, Chile, China, Japan, Republic of Korea, Mexico, New Zealand, Russian Federation, United States of America, and Uruguay.

Moran effect: The synchronization of fluctuations in population density over a wide geographic area that are driven by environmental factors such as weather.

Mor: Forest humus type characterized by accumulation of organic matter on the mineral soil surface and an abrupt boundary between the organic horizon and the underlying mineral soil.

Mortality: Number of (tree) deaths caused by, e.g., a disease.

Mortise-and-tenon: A method of joining two pieces of wood in which a projecting part of one is fitted into a hole or recess in the other.

Motivations: The underlying reasons and forces that often serve as the antecedents to a person's observed actions and behavior.

Mottle: Mottle is a patchy appearance of paper due to a nonuniform coating distribution causing density, gloss, and brightness variations.

MRI: Multiple Resource Inventory.

Mulch: Ground cover put in place to reduce evaporation, maintain even soil temperature, prevent erosion, control weeds, or enrich the soil.

Mull: Forest humus type characterized by incorporation of organic matter in the mineral A horizon without the buildup of Oa and Oe horizons.

Multilayered paperboard: A paperboard made up of two or more plies that are hydrogen bonded to each other.

Multilocus genotype: Definition of an individual's genetic structure which incorporates information from multiple loci.

Multiple comparison and contrasts, and pairwise tests: Tests comparing particular treatments, once an overall difference among factor levels is detected.

Multiple population breeding: Method of integrating gene conservation and tree improvement goals based on subdivision and management of breeding populations to increase their genetic divergence over time.

Multiple resource inventories: Data collection efforts designed to meet all or part of the needs of two or more sectors (i.e., timber and wildlife, wildlife and range management).

Multiple use silviculture: Silvicultural practices which aim to provide a wide range of outputs from a stand.

Multiseriate: Formed of many rows of cells. (e.g. some rays in wood).

Multistrata agroforests: Involves mixtures of plants that grow to different heights. They often involve plantation tree crops such as cocoa, coffee, and rubber combined with shade trees and herb crops.

Municipal solid waste (MSW): Material in the regular periodic collection stream of discards from an urban community.

Mutualism: A symbiosis in which two associated organisms contribute mutually to the well-being of each other, especially where the relationship is not necessary for the survival or reproduction of the organisms involved.

Mycelium: A matted mass of fungal hyphae that form the vegetative body of a fungus.

Mycophagy: Fungus consumption, an important part of eucalypt forest ecosystems.

Mycorrhiza: Intimate symbiotic association of tree roots and fungal mycelia that greatly increases the absorptive area of the root system.

Nanic: Dwarfed state due to arrested development.

Nanophyllous: Having very small leaves (dwarfish).

NAPAP: North American Pulp and Paper.

National parks and sanctuaries: An area of land dedicated to the protection of a focal taxon or groups of taxa (e.g., tiger reserves, wildlife sanctuaries).

Natural attenuation: Destruction and/or immobilization of organic or inorganic contaminants through microbial, chemical, and physical processes.

Natural durability: Resistance of wood to degradation by wood decay fungi and/or insects, particularly by the heartwood of many tree species, mainly due to extractive compounds accumulated in the heartwood as the tree ages.

Natural forest: An area of land which supports a minimum of 20% tree cover that has arisen as a result of natural processes of establishment and succession.

Natural selection: The differential fitness (survival and reproduction) of individuals with different genotypes producing different phenotypes for adaptive traits.

Nearest neighbor methods: Methods is that produce estimates of attributes for selected units by combining observations of the attributes obtained from units that are similar in a covariate space to the unit for which the estimate is required. Nearest neighbor methods include *k*-nearest neighbors, most similar neighbor, and gradient nearest neighbor.

Nearest neighbor tree: The tree (with a DBH higher than the minimum DBH) with the minimum distance to the tree of subject.

Necromass: Dead biomass (litter, dead plant materials).

Necrosis: Process of cell death in plants, resulting in a brown discoloration of affected tissues.

NEE: Net ecosystem exchange of CO_2; the dynamic balance between photosynthesis and respiration.

Needle blight: A foliage disease of conifers in which the foliage is killed rapidly after infection, turns brown, and typically remains attached to the branch. Foliage blights often have asexual states that can produce numerous conidia (asexual spores) under favorable conditions, leading to increased disease severity. Needle blights of conifers include *Sphaeropsis sapinea* and *Mycosphaerella pini*.

Needle cast: Premature abscission of conifer needles caused by a needle cast pathogen. The pathogens typically have a prolonged development time (at least 9 months) and symptoms are slow to develop after infection. Needle cast pathogens include fungi in the Rhytismatacaeae (e.g., *Cyclaneusma)*, Hemiphacidiaceae (e.g., *Rhabdocline, Meria)*, and Mycosphaerellaceae (e.g., *Phaeocryptopus)*.

Negative draw: A tissue-manufacturing process in which the forming section of the paper machine is operated at a higher speed than the Yankee or TAD dryer.

Nematode: A microscopic unsegmented round worm with well-developed digestive and reproductive systems.

Neo-formed leaves: Leaves initiated throughout the growing season as opposed to preformed leaves that arise from primordia that over winter in buds.

Neotropics: The tropics of the New World, tropical America.

Networking: Developing a broad list of contexts for a common goal and interacting with a large number of like-minded people through different means.

Neutral variation: Genetic variation which has no selective advantage.

Newsprint: A generic term used to describe a grade of paper of the type generally used in the publication of newspapers. The furnish is largely mechanical woodpulp, with some chemical woodpulp.

NFI: National forest inventory.

Niche: Functional position of an organism in an ecosystem; the portion of the environment, defined in terms of conditions that a species needs to survive.

NIRA: Near-infrared reflectance analysis. The technique is widely used in agriculture and is now being used to assess expensive to measure wood properties such as pulp yield and cellulose content. The wood sample is ground to produce a pulp meal, which is then measured in a spectrophotometer. A calibration is developed that relates the spectra of large number of samples to their known chemical constitution, which is then used to predict the chemical constitution of further samples from their NIR spectrum.

Nitrification: The oxidation of ammonium compounds in dead organic matter to nitrite and nitrate by soil bacteria.

Nitrogen fixation: Biological conversion of elemental nitrogen (N_2) to organic combinations or to forms readily utilized in biological processes. It is commonly achieved by Actinomycetes (**Frankia**) and bacteria (**Rhizobium**) in special structures in plants, e.g., root nodules.

Nival: The snow belt on mountaintops.

Nodulating: Capable of forming root nodules with nitrogen-fixing bacteria.

Nonendospermous: Lacking endosperm, the nutritive material enclosed with the embryo, in seeds.

Non-industrial private forestry: Forestry practiced by farmers, other individuals and corporations that do not operate wood-processing plants.

Nonnodulating: Incapable of forming root nodules with nitrogen-fixing bacteria.

Nonparametric: Tests and models that are not based on assumptions of certain distributions or model forms, such as normality and linearity.

Nonpoint source: Non-localized, diffuse source of contamination, e.g., atmospheric deposition, agricultural runoff.

Nonpolar: The state of polarity for molecules which tend to have temporary and low-magnitude surface charge, as in the case of vegetable oils. Nonpolar molecules tend to have a low surface energy. Oil and water do not mix because of the relative differences in polarity.

Non-timber forest products (NTFPs): Plants, parts of plants, extractires, fungi, and other flora that are collected or cultivated from within and on the edges of natural, manipulated, or distributed forests. Some agencies exclude animals from the concept but the FAO definition includes food and game, fibers, resins, gums, and plant and animal products used for medicinal, cosmetic, or cultural purposes.

Non-timber forest resources (NTFRs): Relates to the biological organisms that provide NTFPs while they are still in the forest, prior to being harvested; includes fungi, moss, lichens, herbs, vines, shrubs, or trees.

Normal distribution: A probability distribution with density function

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{1}{2}\frac{(x-\mu)^2}{\sigma^2}\right)$$

where μ and σ are parameters.

NPP: Net primary productivity, i.e., gross primary productivity minus total autotrophic respiration.

Nucellus: At the base of the micropylar canal, the nucellus is the first tissue mass that a pollen tube must penetrate to reach the egg cells.

Nucleolar organization region (NOR): The chromosome region which is active in nucleolus formation, where the 45S ribosomal RNA gene is tandemly clustered. Such regions are identified as secondary constrictions, often seen as a gap, located towards the end of the chromosome. Nucleoli in the interphase nucleus are associated with NORs.

NUE: Nitrogen use efficiency.

Null hypothesis: Hypothesis stated as a neutral condition. For example, a null hypothesis might be that all treatment means are equal.

Nuptial chamber: Small chamber constructed by bark beetles immediately upon entry into the host tissue where mating occurs.

Nutrient use efficiency: The ability of a plant to minimize nutrient losses, computed as mass of litter divided by mass of nutrient in litter.

Nuts: Dry one-seeded fruits surrounded by hard shells generally rich in protein, fats and fibers.

Oa: Highly decomposed amorphous organic horizon with rubbed fiber content less than 17%.

Ocular estimation: Estimation of tree or stand properties without any measurement.

Oe: Partially decomposed organic horizon with rubbed fiber content between 17% and 75%.

Offset printing: An adaptation of the principles of stone (or direct) lithography, in which the design is drawn or photographically reproduced upon a thin, flexible metal plate which is curved to fit a revolving cylinder. The design from this plate is transferred to or offset onto a rubber blanket carried upon another cylinder, which in turn transfers the design to paper, cloth, or metal.

Oi: Relatively undecomposed organic horizon with rubbed fiber content exceeding 75%.

Oil paint: A paint containing a suspension of pigments in an organic solvent and a drying oil, modified drying oil, or synthetic polymer that forms an opaque film through a combination of solvent evaporation and curing of the oil or polymer.

Old growth: The phase of forest development during which younger cohorts that established beneath an initiating cohort replace the initiating cohort in the absence of a major disturbance.

Oleoresin: A solution of resin in an essential oil that occurs in or exudes from many plants, especially softwoods. The oleoresin from pine is a solution of pine resin (rosin) in turpentine that has many uses.

Oligocene: Geological epoch (33.2–23.8 million years ago) of Tertiary period.

Oligotrophic: Having low levels of organic production.

Oligotrophic peats: Soils poor in nutrients.

Ombrotrophic: Derived from rainfall.

Omnivory: Feeding on material from a variety of sources.

Onionskin paper: A lightweight writing paper used primarily for making carbon copies of typewritten matter.

Ontogenetic: Relating to the development of an individual from conception to maturity.

Ontogenetic resistance (OGR): Resistance that changes with host development and age.

Oomycetes: Filamentous, fungus-like organisms classified in the phylum Oomycota, of the kingdom Stramenopila (or Chromista). Formerly classified together with fungi because of their similar growth form and their parasitism of plants, oomycetes are more closely related to the golden brown algae than the true fungi. Dissemination is by asexual, motile zoospores that can swim short distances in water films in soil and on plant surfaces.

Oomycotina: Fungi with infrequent septation of the hyphae and cell walls that are primarily of cellulose rather than chitin.

Opacity: The property of a sheet that obstructs the passage of light and prevents one from seeing through the sheet any objects on or in contact with the opposite side.

Open access: Unregulated use of resources when they are available to all and consequently not owned or managed by anyone.

Open access resource: A resource to which access is open to all users and uncontrolled.

Optimization models: Models that use exact mathematical solution methods to achieve specific goals.

Organic soil: Soil comprised of 18% or more organic carbon.

Oriented strand board (OSB): A structural panel composed of multiple, cross-laminated layers of long, thin strands of wood.

Orthodox seed: Seed that can be stored for long periods without loss of germination capacity.

Outbreak: An increase in an insect population generally occurring over relatively short time frames and usually spanning several orders of magnitude. Outbreak populations usually consume a substantial proportion of the foliage resource in affected forests.

Outbreeder: A species for which outcrossing or cross-pollination is the norm.

Outcrossing: Production of zygotes by cross-pollination (cf. self-pollination).

Overdominant gene action: Gene action in which heterozygous loci lead to superior performance relative to homozygous loci.

Overland flow: Water flow at the surface due to infiltration excess or saturation excess of rainfall which results in a rapid runoff generation.

Overstory: Story of trees dominating other trees.

Overwood: That portion of trees, in a forest of more than one story, forming the upper or uppermost canopy layer, e.g., in a two-storied forest, seed bearers over regeneration, or standards over coppice.

Oviposition: The depositing of eggs.

Ovule: A structure in seed plants enclosing the female gametophyte and composed of the nucellus, one or two integuments, and funiculus; differentiates into the seed.

Oxisols: Soil that is highly weathered, low cation-exchange capacity.

Ozone: A secondary air pollutant that is the product of atmospheric reactions of nitrogen oxides and volatile organic carbon catalyzed by sunlight.

Pachymorph: Short and thick rhizome of sympodial bamboos.

Pachyphyllous: Having thick leaves.

Packaging papers: All grades of paper made especially for use in wrapping and making up packages for bundling and shipping purposes.

Paclobutrazol: A plant growth regulator that inhibits the natural production of a group of plant hormones called gibberellins (GAs). In eucalypts it can reduce vegetative growth, stimulate precocious flowering in seedlings and increase the abundance of flower buds on mature trees.

Paint: Any pigmented liquid, liquefiable or mastic composition, designed for application to a substrate in a thin layer that converts by drying to an opaque solid film after application.

Pallet: A platform on which material can be stacked to facilitate handling, moving, and storage.

Pandemic: Universal spread of a disease in a relatively short period of time.

Paniculate inflorescence: A compound raceme. An indeterminate inflorescence with flowers borne on branches of the main axis or on additional orders of branching.

Paper: A homogeneous sheet of felted cellulose fibers, bound together by interweaving and by the use of bonding agents, and made in a variety of types. Paper may be bleached or unbleached, coated or uncoated, filled or not filled, and composed of virgin or recycled fibers. It is used for a multitude of purposes such as writing, printing, wrapping, clothing, industrial, domestic, and sanitary.

Paperboard: A thick, heavy-weight, rigid, single- or multi-ply type of paper which was traditionally made on multi-cylinder paper machines, but is now also made on fourdrinier-type machines, with and without dual formers. Thickness and material vary, depending on its end use. It is used for wrappings, packaging, boxes, cartons, containers, advertising, merchandising displays, and building construction. Also known simply as *board*.

Parallel strand lumber (PSL): A timber-sized structural member composed of long, narrow strips of veneer glued together such that the grain of each strip is parallel to the member's length. Also laminated strand lumber.

Parameter: A characteristic or function of the values of the units in a population, i.e., the population characteristic of interest, such as average volume per hectare or total volume of trees in a forest.

Paraphyletic: A group which contains some, but not all, of the descendants of a common ancestor.

Parenchyma: Thin-walled, brick-shaped wood cells that function primarily to store and conduct nutrients and may be vertically or horizontally arranged in characteristic patterns that are used taxonomically.

Partial resistance (PR): Mechanisms that stop, retard, or confine disease spread.

Participation rate: In recreation the number in a population who participate in one or more outdoor recreation activities during a certain time period.

Participatory democracy: Direct involvement of individuals from a broad cross-section of society in decision making.

Particulate emissions: Minute solid airborne particles that result from biomass combustion.

Particulate wood fuels: Solids of small size that are combusted or gasified to produce energy. Examples are sawdust and chips.

Partnership (for sustainable forest management): A group composed of key land users and other stakeholders of the region who volunteer to work together towards the common goal of SFM. Generally there is a core group of partners that typically include the tenure holders (forest industries), government, environmental specialists, aboriginal and other local communities, non-governmental organizations and academia.

Pathogen: An organism, virus or viroid capable of inciting disease.

Pathosystem: One or more hosts that are attacked by a single pathogen, or pathogen complex.

Peat bog forests: Inundated forests growing in peat-rich soil.

PEC cycles(production, execution and control) The basic components of the logistic system to regulate the wood flow from forest to mill.

Pedogenesis: The factors and environmental conditions influencing soil formation.

Pedon: A three-dimensional body of soil with lateral dimensions large enough to permit the study of horizon shapes and relations. Its area ranges from 1 to 10 m^2.

PELPS: Price Endogenous Linear Programming System.

Pentachlorophenol (penta, PCP): A biocide developed in the 1930s and used in many applications. Many countries have reduced or banned penta due to environmental concerns.

Percentile: A value indicating the percentage of a distribution that is equal or below it; for example, the 95th percentile is the smallest value of x that is greater than 95% of the values in the distribution of x.

Percept: The object of perception.

Perception: The process of becoming aware of sensory stimuli through any of the senses to facilitate recognition and/or interpretation.

Perhumid: Under the Holdridge life-zone classification, humidity conditions corresponding to tropical wet forest ($>$4000 mm annual precipitation).

Perhumid climate: A climate with no dry season.

Periodic Mean Annual Increment (pmai): The annualized change in a growth variable over a particular period, typically 5 to 10 years.

Periodic cyclical dynamics: Regular oscillations in the abundance of an organism around an equilibrium position.

Periphyton: Plant material associated with submerged surfaces.

Perithecium: Fruiting body produced by ascomycetous fungi, producing sexual spores (ascospores).

Peri-urban forestry: Dealing with trees and forest resources around urban community ecosystems. (cf. Urban forests).

Permeability: The ease with which a fluid can move through a porous material.

PET: Potential evapotranspiration.

Petiolar glands: Secretory structures present on the leaf stalk.

Petiolate: Having a petiolule, a leaflet stalk.

PGW: Pressurized groundwood in pulping.

Phase change: The change from juvenile vegetative growth stage to sexually mature growth stage.

Phenology: Periodicity in function or behavior of organisms in relation to local climate or environment, often seasonal.

Phenotype: The observable characteristics of an organism produced by the interaction of its genotype with the environment.

Pheromone: Chemical emitted by animals that is detected by others of the same species (e.g., aggregation/pheromones in bark beetles).

Photosimulation/photo-imaging: Photosimulation refers to a number of techniques using manipulation of physical photographs to create realistic visualizations, using for example photoretouching by hand with paint, or physical photo-montage. Photo-imaging refers to the modern digital equivalent of photosimulation, using manipulation of scanned images with appropriate software to modify pixel colors or 'paste-in' other images.

Photosynthesis: The manufacture of organic compounds, particularly carbohydrates, in the chlorophyll cells of plants from carbondioxide, water, and enzymes in the presence of light as the energy source.

Photosynthetically active radiation: Light of wavelengths between 400–700 nanometers that corresponds to the waveband absorbed by photosynthetic pigments.

Phyllode: A modified leaf stalk that has the form and function of a leaf.

Physiognomy: External features; the form or appearance of a forest.

Phytochrome: A pigment with two interconvertible forms, Pr that absorbs mainly red photons (maximum at 665 nm) and Pfr that absorbs mainly far-red photons (maximum at 730 nm). Absorbance by one form converts it to the other. Many plant processes are sensitive to the ratio of Pfr to total phytochrome.

Phytogeography: Geographic distribution of plants.

Phytophthora: A soilborne oomycete that causes root rot and consequent dieback in many host plant species including trees.

Phytotechnology: Use of plants to remediate or contain contaminants in soil, groundwater, surface water, and sediments; sometimes referred to as phytoremediation.

Phytotelmata: (singular **phytotelm**) Water-container habitat formed from plant material.

Phytotoxicity: Toxicity induced in vegetation by elevated elemental concentrations (usually heavy metals) in certain mineral spoils, and mineral waste materials contaminated by industrial processes.

Pick strength: The ability of the surface of the paper to resist the lifting of coating from the surface of the paper during printing.

Picturesque: Distinctive in forming a good or pleasing picture.

Pile: A straight, bark-free, tree-length log partially or fully driven into the ground to support the foundation of a building or bridge.

Pilodyn: An instrument used to shoot a metal pin into the tree stem with known force. A small bark window is initially removed and the depth of penetration of the pin is inversely related to the stem's wood density.

Pinnate: Arrangement in which the primary rachis of a leaf has leaflets set along it.

Pinyon pines: A distinctive group of North American pines adapted to dry conditions which comprise the subsection *Cembroides* of the section *Parrya* within the subgenus *Strobus*.

Piscivory: Feeding on fish.

Pistillate: Pertaining to a flower or inflorescence of flowers that produces pistils and seed only. Synonymous with the female gender.

Pith: Nonfibrous cells found in plant organs.

Pixel: The ground area or "picture element" corresponding to a single element of a digital image data set.

Plagiotropic: Growing horizontally.

Plagiotropic habit: A nonvertical form as typified by a branch, which is nonreversible and persists in vegetatively propagated stock.

Plant nutrient: Chemical element essential for plant growth.

Plantation: An area of land that supports planted forest, usually for commercial exploitation.

Plantation forests: Forests composed of stands of perhaps 1–2 fast-growing species, often not native to that country. These stands are generally managed primarily to produce wood. The planting of abandoned agricultural land often created such forests, hence 'plantation'.

Pleistocene: Geological epoch (1.8–0.011 million years ago) of the Quaternary period.

Pleurogram: A distinct horseshoe-shaped line occurring on either side of some legume seeds.

Pliocene: Geological epoch (5.3–1.8 million years ago) of the Tertiary period.

Plotless sampling: Sampling without the use of a measured or defined perimeter. Examples include the point-centered quarter methods and 'random forest walks'.

Plywood: An all-veneer structural panel in which the grain of each layer is perpendicular to that of adjacent layers.

Pneumatophores: A porous, woody, specialized branch growing upright into the air from the buried roots of certain swamp trees, such as the mangrove, and providing access to the atmosphere.

Podsolization: Formation of soils with a leached horizon.

Podzols (podzolized sands): Soil with high silica (sand) content, low in clay and bases and in minerals that might weather into these products.

Point source: Localized source of contamination, e.g., outfall pipe, smokestack.

Point-centered quarter method: Random numbers are used to identify points along a central transect line. The area around the point is divided into four quadrants, and the plant closest to the point in each quadrant is measured. The distance from the plant to the point is measured to calculate average spatial arrangements.

Pointer year: Rings in dendrochronology that are considerably smaller or larger than neighboring rings, formed as a reaction to exceptional unfavorable or favorable growth conditions.

Poisson-forest: A forest where the trees are randomly distributed following a Poisson distribution.

Polarity: The state of electrical charges which exist on the surfaces of all molecules. Different states of polarity arise from the variety of elements and their configuration in different molecules.

Pole: A straight, bark-free, tree-length log with one end embedded in the ground that supports power and communications wires, highway sound barriers, and similar structures.

Pollarding: Cutting back, in a more or less systematic fashion, the crown of a tree, with the object of producing a close head of shoots (a pollard) beyond the reach of browsing animals.

Pollen: The mass of microspores containing the male genetic material, produced by the anthers in flowering plants or male cones of gymnosperms.

Pollen management: The use of various pollen handling techniques to store and test pollen and to aid or control pollination. See also Controlled Pollination and Supplemental (mass) Pollination.

Pollen mix: The application of mixed sources of pollen parents either under controlled crossing or open pollinated conditions.

Pollen tube: The tube formed by germinating pollen grains down which male nuclei is transferred to the ovules.

Pollination: The transfer of pollen grains from the anther to the stigma of a flowering plant thereby facilitating contact between male and female gametes leading to fertilisation.

Polyad: A dispersal unit comprising more than four pollen grains.

Polyembryony: The formation or presence of more than one embryo in a seed.

Polygon: A map feature class used to represent areas. A polygon is defined by the arcs that make up its boundary and a point inside its boundary for identification. Polygons have attributes that describe the geographic feature they represent.

Polymerase chain reaction (PCR): A method used to create millions of copies of a particular segment of DNA by repeated amplification in order to produce enough material for detection, analysis and interpretation.

Polymers: Very large molecules which contain long sequences of repeating chemical units; they resemble chains. Polymer chains may form linear, branched, or network structures. Cellulose is a typical polymer and most adhesives contain polymers because polymers form structurally sound solids.

Polymerization: The process for the preparation of polymer.

Polymictic: Frequently mixed.

Polymorphism: The presence of two or more differing versions (or alleles) of a gene, or of a non-coding DNA-base sequence, at a specific site (locus) on a specific chromosome.

Polyploid: Having more than two entire chromosome sets.

Polysaccharide: Any carbohydrate formed from long chains of simple sugars such as cellulose.

Polyvinyl chloride (PVC): A plastic in common use for a variety of purposes.

Population: A group of interbreeding individuals, usually defined geographically. An aggregate of items each with a common characteristic or common set of characteristics. In the statistical sense, a population is an assembly of individual units formed in order to describe the population quantitatively. For example, it might be all the trees in a particular forest stand or all the users of a recreation area.

Population genetic differentiation: The proportion of the total genetic diversity that is distributed between populations.

Population genetic diversity: An estimate of the genetic variation that exists within a single population.

Porate: A pollen grain with a simple aperture.

Porosity: The property of having connected pores or minute interstices through which fluids (liquids and gases) may pass. It is dependent on the number or pores and their distribution in size, shape and orientation. The porosity of paper is commonly evaluated by measuring its air permeability.

Porosity (shelterbelt): A measure of the ease with which air may move through a shelterbelt. Optical porosity is a rough guide to the aerodynamic porosity and is the ratio of sky visible through the shelterbelt to the area occupied by the shelterbelt. An optical porosity of 0% represents a very impermeable shelterbelt which cannot be seen through, a porosity of 90% would represent an extremely open shelterbelt.

ppmv: Parts per million of volume (e.g., 350 ppmv = 350 volume parts of CO_2 per million parts of air).

pps sampling: A sampling design where sample units are selected with a probability proportional to a measure of size, usually a covariate such as dbh or basal area in the case of tree volume.

Precautionary principle: In situations where knowledge is imperfect setting harvesting or pollution levels low in order to avoid possible detrimental impacts.

Precision: Relative freedom from random variation. In sampling it is expressed as the standard error of the estimate and relates to the degree of clustering of sample values about their own average or the reproducibility of an estimate in repeated sampling. It is also used to indicate the resolving power of a measuring device. See Accuracy.

Preferential flow: The rapid and nonuniform transport of water and solutes through macropores and subsurface channels.

Prescribed burning: Controlled application of fire to vegetation in either their natural or modified state, under specified environmental conditions which allow the fire to be confined to a predetermined area and at the same time to produce the intensity of heat and rate of spread required to attain planned resource management objectives (cf. Prescribed Fire). Note: This term has replaced the earlier term 'Controlled Burning.'

Prescribed fire: A management-ignited wildland fire or a wildfire that burns within prescription, i.e. the fire is confined to a predetermined area and produces the fire behavior and fire characteristics required to attain planned fire treatment and/or resource management objectives. The act or procedure of setting a prescribed fire is called prescribed burning (cf. Prescribed Burning). A wildfire burning within prescription may result from a human-caused fire or a natural fire (cf. prescribed natural fire, integrated forest fire management, wildfire).

Prescribed natural fire: Naturally ignited fires, such as those started by lightning, which are further used to burn under specific management prescriptions without initial fire suppression and which are managed to achieve resource benefits under close supervision (cf. prescribed fire, wildfire).

Preservative: Any substance that, for a reasonable length of time, is effective in preventing the development and action of wood-rotting fungi, borers of various kinds, and harmful insects that deteriorate wood.

Pressure process: Any process of treating wood in a closed container whereby a preservative is forced into the wood under pressures greater than one atmosphere. Pressure is generally preceded or followed by vacuum.

Pressurized groundwood (PGW) pulp: A mechanical pulp produced by pressing debarked logs against a rotating pulpstone under elevated temperatures and pressures. The resultant pulp has more long fibers than in groundwood produced at atmospheric conditions.

Prickle: A rigid sharp-pointed process developed from the bark or any part of the epidermis. Botanically, a prickle differs from a spine in that it may be peeled off with the epidermis.

Primary production: A term use to denote the turnover, expressed as dry weight, in a plant community – the annual production of wood, bark, leaves, flowers, fruits, and roots, whether harvested or not. It may be expressed as: 1. Gross primary production representing total assimilation including the portion subsequently used for respiration in the dark. 2. Net primary production is the amount of assimilated organic matter remaining after the requirements of respiration and other natural losses (e.g., predation and decay) have been met.

Primary species: In bark beetles, species that are the primary cause of tree death (kill healthy trees).

Printing paper: All types of paper that have characteristics suitable for printing purposes.

Private property: Property held by private persons including property held by legal persons such as corporations or partnerships.

Probabilistic sampling: Procedures in which samples are selected such that all units and each pair of units in the population have a positive probability of selection.

Process additive: Chemical that improves process efficiency.

Progeny: The offspring of sexual reproduction.

Progeny test: Evaluation of a parent (or parents) from the performance of its (their) offspring. The progeny test is essential in determining the genetic character and value of a specific tree.

Prokaryote: A cell or organism lacking a membrane-bound, structurally discrete nucleus and other subcellular compartments.

Propagule: A plant derived from vegetative propogation including tissue culture and rooted cutting, capable of developing into an adult.

Property: Social relations between people regarding the possession and use of things; a claim to some use or benefit of something that will be enforced by society or the government.

Protandry: The release of pollen prior to the stigmas becoming receptive.

Protected area: A geographically defined area that is designated or regulated and managed to achieve specific conservation objectives.

Protogyny: Female organs of the flower mature before the male organs.

Provenance: If the source is the native origin, it is termed origin or original provenance; if the source is an exotic tree or strand, it is termed derived provenance. See also Geographic race, Seed source.

***P*-value:** The probability of observing a higher value (or higher absolute value) than that obtained for the statistical test if the null hypothesis is true and the experiment is repeated. A very low value indicates that the null hypothesis is unlikely, based on the sample data.

PVC: Polyvinyl chloride.

Pruning: Removal of branches naturally following senescence and death or artificially by stick, blade or saw to reduce knots and improve the quality of timber.

Pteridophytic: Belonging to the ferns and allies plants.

PTMP: Pressure thermomechanical pulp.

Public Advisory Group (PAG) or Citizen Advisory Committee: A group or panel of individuals representing various interests in society, which advises forest managers on issues and initiatives in an ongoing forum for public discussion.

PUE: Phosphorus use efficiency.

Pulp: A fibrous material produced by mechanically or chemically reducing woody plants into their component parts from which pulp, paper, and paperboard sheets are formed after proper slushing and treatment, or used for dissolving purposes (dissolving pulp or chemical cellulose) to make rayon, plastics, and other synthetic products. Sometimes called *wood pulp*. Pulp may include cotton or rags used to manufacture paper and other natural fiber-containing products.

Pulping: Conversion of raw material into fibers by chemical/mechanical measures.

Pulpwood: Small logs suited for the production of pulp (cellulose), measuring approximately 2–3 m in length.

Pyrolysis: Oxidation at less than stoichiometric conditions, involving the physical and chemical decomposition of solid organic matter by the action of heat in the absence of oxygen into liquids, gases, and a carbon char residue in varying proportions depending on process conditions.

Pyrolyze: To decompose with heat in an environment that lacks sufficient oxygen for complete combustion.

Q_{st}: An analog to F_{st}, used to measure differentiation between populations for a quantitative trait.

Quadrat: A usually rectangular plot used for ecological or population studies.

Quantitative trait locus (QTL): A site or narrowly defined region in the genome where a polymorphism governs a detectable portion of the phenotypic variation.

Quaternary: Most recent geological period (1.8 million years ago to present day).

Radar data: Remotely sensed data from the microwave portion of the electromagnetic spectrum, collected by aircraft or satellite.

Radiation transfer: The radiative exchange of energy with another body or the atmosphere. During the day radiation transfer from the sun heats up the ground, plant canopies and animals. During the night radiation transfer to the sky cools the ground, canopies and animals. The cooling is most rapid when the sky is clear.

Railroad tie: One of the transverse supports to which railroad rails are fastened to keep them in line. Also called cross tie and sleeper.

Rainshadow: Area on the lee side of a mountain that receives less rain because orographic uplift of air masses has caused rain to fall on the windward side.

Ramiflory: Production of flowers on branches.

Random allocation: Assigning treatments at random to the experimental unit.

Random amplified polymorphic DNA (RAPD): A PCR technique which uses short and anomalous primers. Polymorphisms arise from mutations in the priming site that cause the amplification product to be present or absent. RAPDs are cheap genetic markers, but their informativeness is limited as they are dominant rather than codominant.

Randomization: A deliberately haphazard arrangement of observations to simulate selection by chance.

RAPDs: Random amplified polymorphic DNAs.

Rare, endangered and threatened species: A species that exists only in one or a few restricted geographic areas or habitats or occurs in low numbers over a relatively broad area is a rare species. An endangered species is one that is in danger of extinction throughout all or a significant portion of its range. A threatened species, is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.

Raster, grid, lattice: A method for the storage, processing and display of spatial data. Each given area is divided into rows and columns, which form a regular grid structure. Each cell must be rectangular in shape, although not necessarily square. Each cell within this matrix contains an attribute value as well as location co-ordinates. Groups of cells with the same value represent features.

Rate of spread: The speed at which a fire extends its horizontal dimensions, expressed in terms of distance per unit of time (m/min or km/h) (syn. fire spread, cf. rate of area growth, rate of perimeter growth).

Ray: A collection of wood cells that store and conduct nutrients radially across the grain in a tree stem; composed of parenchyma and some specialized cells in the angiosperms and parenchyma and sometimes tracheids in the gymnosperms.

Reaction wood: wood with distinctive anatomical and physical characteristics, formed typically in parts of leaning or crooked stems and in branches. It tends to restore the branch or stem to its original position. Reaction wood is known as tension wood in broadleaved trees and compression wood in conifers.

Realism: The degree to which a landscape visualization is lifelike, i.e., replicates the appearance and perceptual characteristics of a real-world setting or viewing experience. This is often interpreted as the degree of image accuracy or photorealism, though there are various dimensions of realism beyond pictorial accuracy, such as angle of view and speed of motion through a landscape. Realism can also be defined in terms of the perceptual responses the observer obtains (see Response equivalence). Apparent realism refers to the degree to which a visualization appears to be realistic, in the absence of knowledge about what the actual landscape represented would really look like, and is more a function of the medium than the image content.

Real-time interactivity: This indicates that a system reacts to user input with a very small lag time such that the user interprets their input as causing an immediate or near-immediate reaction in the system. For computer visualization systems, real-time interactivity is often reported in 'frames per second', which is the number of times per second that the image being presented to the user is changed to reflect changes in view position or image elements. In general, the more frames presented to the user per second, the more fluid and responsive the interaction will appear to them (up to a limit, at which time further increases in presentation speed are imperceptible to the human eye).

Ream: A number of sheets of paper, either 480 or 500 according to the grade.

Receptivity: The stage of phenological development of the seed cone that permits the entry and capture of pollen on exposed bracts, scales, and micropyle.

Reciprocal recurrent breeding: A method used to refine the breeding quality of two separate populations or species. Interpopulation or interspecific progeny information is used to direct the selection and mating within each population/species.

Recombination system: The way in which the release of genetic variability is controlled during sexual reproduction.

Recreation experience impact: A change in the social conditions of the recreation experience as a result of recreation use.

Recreation opportunity spectrum (ROS): A recreation planning tool for inventorying and classifying the diverse physical, social, and managerial condition of a recreation area into a spectrum of six opportunity classes.

Recreation quality: Perceived and/or objective condition of the recreation resource, recreation experience, and recreation management associated with an area.

Recreation resource impact: A change in the natural conditions of the recreation resource as a result of recreation use.

Recurrent breeding: A method of breeding in which selected parents are mated to form an improved population that in turn becomes the basis for a new cycle of selection and mating, continuing the improvement of the population.

Recurrent selection: The process of repeated cycles of selection of superior genotypes and breeding them together to induce recombination. Each cycle of selection achieves genetic gain in the few traits being selected, because the offspring selected have higher frequencies of favorable alleles.

Recycled fiber: Cellulose fiber reclaimed from recovered material and reused.

Red Data Book: The term for books that list the threatened and endangered species of a region or country and classify the degree of threat in accordance with the categories of the IUCN (The World Conservation Union).

Reel: A revolvable spool for winding and storing long lengths of flexible rope, cable, wire, or other material which may be wound.

Reforestation: the act or process of changing previously deforested lands back to forest by planting trees or other means of regeneration.

Regeneration: The act of renewing tree cover by establishing young trees naturally (natural seeding, coppice, or root suckers) or artificially (direct seeding or planting).

Regeneration rate: The amount of time needed for a population of plants to recover from harvest.

Rehabilitation: Re-establishment of the productivity and some, though not necessarily all, of the original biodiversity formerly present at a site. Rehabilitation may be done using monocultures or mixed species plantations. It includes the activities necessary to repair damage or disturbance caused by wildfire or the wildfire suppression activity (cf. restoration).

Relascope: (or angle gauge) An optical instrument used for measuring stand basal area by point sampling, rather than collecting data from sample plots. The instrument uses relative geometry to determine the number of trees included in a count; this number is then multiplied by a calibrated factor to determine stand basal area.

Relative humidity (RH): Partial pressure of the water vapor divided by the vapor pressure times 100.

Remote sensing: The science, technology and art of obtaining information about objects or phenomena from a distance, without being in physical contact with them. The practice of using data from satellites and aerial photography to infer or measure land cover.

Representation: The degree to which all interests concerned by the issue at hand or affected by the decision-making are included in or legitimately represented by other individuals or groups in the decision-making process.

Representative democracy: Decision-making which involves various interest groups that represent the balance of individual interests in society.

Representativeness: The degree to which a visualization or set of visualizations represents important and typical views of a scene and viewing conditions.

Residential/wildland interface: The transition zone between residential areas and wildlands or vegetated fuels (cf. Urban, Urban/Wildland Interface, Wildland, Wildland Fire, Rural Urban Interface).

Resilience: Ability to return to original conditions following a disturbance.

Resin acid: Diterpenoid extractives from wood, a component of rosin or tall oil.

***Resin canal*:** Typically, resin canals arise as schizogenous intercellular spaces by separation of parenchyma cells from each other in certain gymnosperms.

Resource inventory: The planning and collection of data for description and analysis of the status, condition, production, or quantity of resources for planning and implementing protection and management activities.

Resource management: Management of a valued reserve or supply of an element that can be drawn upon when needed.

Resources: The elements of supply inherent to an area, including lands, water, minerals, soils, flora, fauna, and cultural values.

Respiration: Within the context of pollen viability testing, this is a technique that relates viability with oxygen uptake in an aqueous solution.

Response equivalence: Response equivalence means that a person's reaction to one stimulus is the same as their reaction to another stimulus. In the landscape visualization context, response equivalence means that a person's response to the landscape visualization they are viewing is the same as their response would be to the same landscape in the real world.

Response function: Multiple regression technique to estimate, e.g., the climatic influence on tree growth.

Restoration: Re-establishment of the presumed structure, productivity, and species diversity originally present at a site. The ecological processes and functions of the restored forest will closely match those of the original forest. Restoration includes rehabilitation measures after fire, or prescribed burning where certain fire effects are desired (cf. rehabilitation, reclamation burning).

Restriction fragment length polymorphisms (RFLP): Variations in the length of DNA fragments caused by digesting DNA with a restriction endonuclease. Restriction endonucleases are enzymes derived from bacteria which cleave DNA molecules at specific recognition sites. Mutations at these recognition sites allow or prevent cleavage and hence cause variation in the length of DNA fragments. RFLPs reflect particular DNA base sequences that are not universally present in the subject population, which provide codominant genetic markers.

Retranslocation: Movement of nutrients from one site of use to another, i.e., usually from old leaves to young leaves.

Rheology: Rheology is the science dealing with the flow and deformation of matter.

Rhizobium: A genus of rod-shaped nitrogen-fixing bacteria that form symbiotic associations with some leguminous plants, usually in root nodules.

Rhizomorphs: Specialized root-like and often melanized structures produced by some fungi, enabling them to spread through the soil.

Ring fire: A fire started by igniting the full perimeter of the intended burn area so that the ensuing fire fronts converge toward the center of the burn.

Ripewood: In ripewood trees the heartwood exhibits a lower moisture content than the sapwood, but not a significant amount of extractives, e.g., spruce, fir, beech, lime, and pear.

Ripping: Decompaction of soil (or soil-forming material) using tines pulled by a crawler tractor. The tines are often winged to increase soil uplift and consequent fissuring.

Riverine: Along river banks.

RMP: Refiner mechanical pulp.

Roguing: Systematic removal of undesired individuals from a population to prevent their reproduction, particularly in progeny tested seed orchards.

Root cortex cells: Parenchyma cells forming the primary tissue of roots between the epidermis and vascular tissue.

Root grafts: Root grafts occur when two individuals of the same tree species grow close together; when the roots of the individuals come into contact, they can fuse.

ROS: Reactive oxygen species, i.e., free oxygen radicals (O^-).

Rotogravure printing: An intaglio printing process for rotary web presses, which is used by newspapers and magazines, for printing catalogs, and also for much specialty printing and paper converting.

Roundwood: See Timbers, round.

Routing: Pertaining to the planning or prescription of routes for off-road extraction and road transportation of timber and by-products, to minimize site and road damage, and for safe and cost-effective delivery of wood and by-products of forest harvesting.

RPA: Resource Planning Act.

Rubisco: Ribulose-bisphosphate carboxylase-oxygenase. The key enzyme for the carboxylation of CO_2 in most green plants.

Ruminate endosperm: A type of endosperm in which the seed coat is folded into it.

Running bamboo: Monopodial bamboo; the culms are spaced out since they arise along the running rhizome such that the plant looks like a patch of individual plants.

Rural development: Strategies and activities to improve the living conditions of rural people by either stimulating rural production processes, ensuring better distribution of resources and products, and/or stimulating emancipation and self-reliance.

Rural fire protection: Fire protection and firefighting problems that are outside of areas covered by municipal Fire and Rescue Services and its Fire Ordinance; these areas are usually remote from public water supplies and require all-terrain vehicles to reach.

Rural livelihood: The combination of capabilities, material and social assets and activities which characterize a person's means of living.

Rust diseases: Diseases caused by obligate basidiomycete pathogens belonging to the Uredinales and often having complex life cycles.

Sacred grove: A patch of forest protected in recognition of a certain deity, god, or goddess.

Salt glands: Glands on the surface of plant tissues that are used for the excretion of salt.

Samaroid: Resembling a samara (a winged fruit).

Sample: A subset of a population used to obtain estimates of one or more of its parameters. In this book we focus on probabilistic samples. For example, a sample can be the diameters (dbh) of all trees on a sample of plots or the amount of time spent picnicking by users of a recreation area on given days.

Sample plot: an area of a stand of trees selected and measured to represent the characteristics of the stand as a whole.

Sample surveys: The design and execution of surveys to provide estimates of characteristics (parameters) of well-defined finite populations.

Sample unit: A unit from a population, i.e., a tree or all trees located within a plot (i.e., fixed-area, strip or point sample).

Sampling design: A formalized method of selecting a sample from the population, for example simple random sampling.

Sampling frame: A list of all sample units used to represent a population.

Sampling strategy: Comprises both the sampling design and the estimator(s) used, for example simple random sampling with the estimator of the population mean, say the sample mean.

Saprophyte: Organism that uses dead or organic material as a food source.

Sapwood: Physiologically active outer rim of wood in a tree stem or log; usually lighter in color than the heartwood; contains living cells that serve to conduct water upward in a tree stem.

Savanna: Tropical or subtropical grassland.

Sawlogs: Larger logs, suited for the production of sawn wood (planks, beams), measuring approximately 3–4 m in length.

Scaling ladder: A ladder used to scale fortified walls.

Scatterhoarding: The collection, movement, and storage in dispersed location of resources, usually fruit and seed, by animals.

Schutzwald: A forest (often also referred as 'protective forest') expected to protect continuously settlements, infrastructure, or traffic lines against natural hazards (snow avalanches, landslides, erosion, debris flows, or rock fall).

Scion: A piece of a plant used for grafting.

Sclerophyllous: Having hard, thick and stiff leaves.

Scorch: A foliage disease with symptoms resembling the action of a flame. Scorch symptoms include extensive necrosis, browning and curling of leaves.

Screening: Process of removal of undesired materials and plastics from pulp.

Scrub: Bushwood or waste areas covered by bushes.

Secondary forest: An area of previously forested land that was subsequently degraded or deforested through human or natural action, but which now supports regenerating or mature natural forest.

Secondary species: In bark beetles, species that attack trees weakened or killed by another cause.

Security of tenure: Tenure held without risk.

Sediment delivery ratio: Ratio of sediment yield at a point (weight/area/time) to total erosion within the watershed above that point (weight/area/time).

Seed: Site of a partial development of the sporophyte (embryo) and the linkage between successive generations. The propagule that is distributed naturally or sown artifically to produce seedlings.

Seed orchard: A plantation consisting of clones or seedlings from selected trees, isolated to reduce pollination from outside sources, and cultured for early and abundant production of seed for reforestation. The individual trees in the orchard are allowed to freely intermate through open pollination to produce genetically improved seed for operational reforestation. Forest seed orchards are often established while genetic evaluation of the material is under way. When results of these tests are known, the undesirable individuals are rogued.

Seed set: The culmination of all steps of sexual reproduction from pollination to seed maturation. For purposes of evaluating field pollination trials, the number of filled seed per cone is used as the sampling unit for seed set.

Seed source: Usually, the locality where a seed lot was collected. If the stand from which collections were made was from non-native ancestors, the original seed source may be used to designate the original place of collection. See also geographic race, provenance.

Seemingly unrelated regression (SUR): Two or more equations are estimated simultaneously accounting for the correlation between the error terms of the models.

Selection methods: In silviculture these regenerate and maintain a multi-aged structure by removing some trees in all size classes either singly (true selection), in small groups, or in strips.

Selective logging: Extraction of commercial timber restricted to trees of specific characteristics, e.g., of certain species, size or quality, and which usually implies the removal of a relatively small proportion of the total number of stems in a given area.

Selective thinning: See thinning.

Selfing/self-pollination: Pollination of female strobili of a tree with that tree's own pollen.

Self-pruning: The ability of trees to shed their lower branches as tree crowns recede up the stem as a response to lower light conditions brought on by increased stand density.

Semichemical pulp: A pulp produced by a mild chemical treatment of the raw material followed by a mechanical fiberizing operation.

Semievergreen: Partly shedding leaves.

Semiochemical: Chemical emitted by organisms that causes a response in receiving organisms. Includes pheromones and kairomones.

Semitransparent stain: A suspension of pigments in either a drying oil – organic solvent mixture or a water – polymer emulsion, designed to color and protect wood surfaces by penetration without forming a surface film and without hiding wood grain.

Series: A grouping below the level of the genus.

Serotiny: Storage of seeds in closed seed containers in the canopy of shrubs and trees. For instance, serotinous cones of Lodgepole Pine do not open until subjected to temperatures of 45 to 50°C, causing the melting of the resin bond that seals the cone scales.

Shade bearer: Normally trees that have the ability to compete for survival and to grow in the shade, and in competition with other trees; if intolerant of shade, they are termed light demanders.

Shade tolerant: See shade bearer.

Shear: Any change of wind velocity with a change of position. Strong vertical shear exists over a shelterbelt and strong horizontal shear exists at the end of shelterbelts. Shear results in the production of turbulence.

Shelf life: The length of time before an item becomes obsolete or devoid of required quality specifications in the case of live materials.

Shelterwood cutting: Any regeneration cutting in a more or less regular and mature crop, designed to establish a new crop under the protection of the old, as typically in the shelterwood system.

Shelterwood system: An even-aged silvicultural system in which, in order to provide a source of seed and/or protection for regeneration, the old crop (the shelterwood) is removed in two or more successive shelterwood cuttings, the first of which is ordinarily the seeding felling and the last is the final felling, any intervening cuttings being termed secondary or intermediate fellings. This may be carried out over the whole of a (sub-) compartment, or in strips (shelterwood-strip system), groups or wedges.

Shelterwood-strip system: A shelterwood system in which regeneration cuttings are carried out on fairly wide strips, generally against the prevailing wind, and progress rapidly.

Shifting cultivation: Any temporally or spatially cyclical agricultural system that involves the clearing of land followed by cultivation and fallow periods.

Shoot Unit: The shoot is composed of shoot units, the stem node with its lateral appendage, usually a leaf, and structure in the axil of the lateral appendage plus the proximal internode.

Short shoot: Dwarfed foliage shoots or brachyblasts that do not elongate repeatedly.

Shredding: The repeated removal of side branches on a short cycle, leaving just a tuft at the top of the tree.

Shrubs: Woody plants generally less than 7 meters in height.

Siddha: Siddha is an ancient Indian health care system which is largely therapeutic in nature. According to this system the human body is the replica of the universe and so are the food and drugs, irrespective of their origin. The practitioners of this system, popularly known as Siddhars, use minerals and plants often in conjunction with divine powers for treatment of diseases.

Silvicultural operations: One or several silvicultural activities that alter a stand's development pathway.

Silvicultural pathway: The sequence of structures that a stand moves through over time following a series of silvicultural operations (such as thinning, weed control, harvesting, or planting).

Silvicultural system: A process following accepted silvicultural principles, whereby the crops constituting a forest are tended, harvested and replaced, resulting in the production of crops of a distinctive form. The extremes are the clear-cutting and the single tree selection system with many other ones in between.

Silviculture: The art and science of forest tending; the growing and tending of stands to meet management objectives. It may be considered the ultimate *application* of stand dynamics knowledge and its ultimate *test*.

Silvopastoral practice: A form of agroforestry which combines trees and grazed pasture.

Simulation models: Models that show change through time. In contrast to optimization models, usually not goal-driven.

Simultaneous estimation: Two or more equations which are estimated simultaneously.

Single tree (true) selection: Individual trees of all size classes are removed more or less uniformly throughout the stand, to promote growth of the remaining trees and to provide space for regeneration.

Single-level sampling: A sampling design where units are selected directly from the sampling frame of the population.

Sink: A process, activity, or mechanism that removes a greenhouse gas from the atmosphere.

Site class: A relative measure of the yield level or yield class, which are defined by the mean annual volume increment in the certain age.

Site index: A measure of the potential growth or productivity of a given tree species grown on a particular site, as estimated from a measurement taken on a tree or stand. For example, the dominant height achieved by a stand at a certain age (10, 25 or 50 years) might be taken as a site index. Site index is often derived by comparing growth assessments with standard curves or charts representing average patterns of growth for the species on different sites.

Sizing: Starches added either internally or on the surface of printing papers to provide certain ink holdout properties.

Skeleton plot: Evaluation of tree-ring time series based on visual examination, highlighting very narrow or very wide rings and plotting these as a skeleton of the time series.

Skidder: Off-road forestry vehicle designed for dragging trees or logs.

Slab avalanche: Most common form of damage-causing avalanche where the snowpack fractures on a fragile layer in the form of a slab. Typical dimensions are between 10–500 m wide and 50–1000 m, with the initial slab wider than it is long.

Slash: Debris (fuels) resulting from natural events (wind/fire) or human activities like forest harvesting.

Slash logs: Composite residue produced by a harvester that has been compacted and balled in round bundles, hence the term log, typically 3 m long and 60–80 cm in diameter.

Sledge: A sled for carrying loads along the ground.

Sleeper: A transverse support to which railroad rails are secured; see Crosstie and Railroad tie.

Small and medium enterprise: An enterprise with a turn over of less than $1 million to less than $50 million.

Small-scale forestry: Small-scale management of forests, a term to separate the type of forestry from industrial or public large-scale forestry. There is no consistent definition of what constitutes small-scale forestry but the definitions, e.g., the maximum size of a woodlot, vary between countries.

Smog: The mix of tropospheric ozone and other photochemical oxidants such as nitrogen oxides and peroxyacetyl nitrate that occurs on warm days downwind of major metropolitan areas.

Smoke haze: An aggregation (suspension) in the atmosphere of very fine, widely dispersed, solid or liquid particles generated by vegetation fires giving the air an opalescent appearance.

Smoothness: The property of a surface determined by the degree to which it is free of irregularities.

Snow gliding: Slow movement ($0.1–1\ \mathrm{m\ day}^{-1}$) of the entire snowpack at the soil–snow interface exerting strong forces on obstacles and plants, occurring especially on wet or sunny slopes.

Snow metamorphism: Change in shape and size of the snow crystals caused by temperature gradients in the snowpack or by melting and refreezing.

Social carrying capacity: The number and kind of recreationists that an area can stand without the volume and type of use causing a negative impact on the experiences of visitors.

Social class: A social distinction and division resulting from the unequal distribution of rewards and resources such as wealth, power, and prestige.

Social forestry: A development strategy to stimulate community involvement in the management of forest resources in order to improve local livelihoods and/or stimulate forest conservation.

Softness: A perceived tissue quality that is related to the bulk of the tissue, its surface smoothness, and mechanical strength.

Softwood: 1. Tree belonging to the botanical group Gymnospermae, and within it, predominantly to the order Coniferales; 2. evergreen, cone-bearing species of trees, such as the pines, spruces, and hemlocks, in which leaves are needlelike, linear, awl-shaped, or scalelike, and the seed are borne either in cones in the axil of a scale, or naked. Wood that is harvested from softwood coniferous species such as pine, spruce, and hemlocks. The wood typically lacks vessels and in many species it has resin ducts.

Soil aeration: Replenishment of O_2 and removal of CO_2.

Soil horizon: A layer of soil approximately parallel to the land surface and differing from adjacent genetically related layers in physical, chemical, and biological properties or characteristics such as color, structure, texture, consistency, kinds and number of organisms present, degree of acidity or alkalinity.

Soil infiltration capacity: Soil characteristic describing maximum rate at which water can enter the soil under specified conditions.

Soil moisture characteristic curve: Describes the relationship between soil moisture (soil water content) and soil water tension (matric suction). Also called soil moisture release curve or retention curve.

Soil preparation 'Wounding'(cultivating, scarifying, rotovating, tilling) the suboil in order to improve the germination chances (seed-bed) or to ease the planting process.

Soil survey: The systematic examination, description, classification, and mapping of soils in an area.

Soil-forming materials: Materials usually of geological origin (e.g., from selected geological strata or overburden types) selectively stored and then used to establish vegetation in the reclamation of the mine site. Often amended with organic materials (e.g., organic wastes such as sewage sludge and composts) to increase fertility and improve physical nature.

Solar radiation: Variation in solar energy input that plants require for photosynthesis.

Solid-color stain (opaque stains): A suspension of pigments in either a drying oil – organic solvent mixture or a water – polymer emulsion designed to color and protect a wood surface by forming a film. Solid-color stains are similar to paints in application techniques and in performance.

Somatic embryogenesis: The production of new embryos from individual cells of immature seed embryos.

Source: A process, activity, or mechanism that releases a greenhouse gas into the atmosphere.

Spatial correlation: Relationships among observations over space.

Spatial resolution: A measure of the smallest angular or linear separation between two objects usually expressed in meters. Often understood as the ground resolution, which is a measure of the resolving power of a sensor when expressed as cycles per unit length on the ground from a given altitude. For instance, the spatial resolution of the Landsat sensor is 30 by 30 meters.

Spatial scale: Large spatial scales generally indicate large tracts of land, whereas small spatial scales indicate smaller land areas.

Special forest products: Term used by the USDA Forest Service; excludes sawtimber, pulpwood, cull logs, small roundwood, house logs, utility poles, minerals, animal parts, rocks, water, and soil.

Species: Group of closely related, morphologically similar, and interbreeding individuals.

Species diversity: The number, types, and distribution of organisms found in a given area.

Specific leaf area: The surface area of an individual leaf divided by the mass of that leaf.

Spectral resolution: The ability of a sensing system to resolve or differentiate electromagnetic radiations of different frequencies, typically reported as the electromagnetic wavelengths captured with a given sensor.

SPECTRUM: An analytical tool for building natural resource management models.

Spices and condiments: Plant components or parts that are used for imparting flavor, aroma, piquancy, and for seasoning of foods.

Spinescent: Developing into, or terminating in, a spine or thorn.

Spore: A general term for the microscopic propagules of fungi. Spores can be one to several cells and are agents of dispersal and infection in pathogenic fungi. Spores are analogous to seeds and are capable of developing into a mature individual under appropriate growing conditions. See ascomycete, basidiomycete, anamorph.

Sporocarp: A fungal structure in which spores are produced; a fungal fruit body. The sporocarp of basidiomycetes is typically a mushroom or woody conk.

Spot fire: (1) Fire ignited outside the perimeter of the main fire by a firebrand (by flying sparks or embers transported by air currents, gravity, or fire whirls). (2) A very small fire which that requires little time and resources to extinguish that jumped over the fireline, by air currents, gravity, and/or fire whirls (cf. Long-Range Spotting).

SSRs: Simple sequence repeats, typically in non-coding parts of the genome, which can be used to provide 'genetic fingerprints.'

Stain: A discoloration in wood that may be caused by such diverse agencies as microorganisms, metal, or chemicals. The term also applies to materials used to impart color to wood.

Stakeholder analysis: A comprehensive documentation and analysis of the public and specific stakeholders interested in or affected by an issue or plan, with classification according to various criteria relevant to their involvement in decision-making.

Stakeholders: All individuals or groups interested in an issue or opportunity driving the participatory process. They are affected by a development outcome or have an interest in a development outcome. Stakeholders include customers (including internal, intermediate, and ultimate customers) but can include more broadly all those who might be affected adversely, or indirectly, by a specific activity who might be identified as a 'customer' or a stakeholder.

Staminal hood: In the Lecythidaceae, the apex of the male part of the flower that projects from one side of the staminal ring and curves over the top of the ovary and usually bears sterile stamens.

Staminal ring: In the Lecythidaceae, the base of the male part of the flower, in the form of a ring, that bears the fertile stamens.

Staminate: Pertaining to a flower or inflorescence of flowers that produces stamens and pollen only. Synonymous with the male gender.

Stand: A contiguous group of trees sufficiently uniform in age class distribution, composition, and structure, and growing on a site of sufficiently uniform quality, to be a distinguishable unit.

Stand boundary: Stand edge.

Stand development: Changes in stand structure over time.

Stand dynamics: The development of forest stands over time. This is typically considered in terms of decades or even centuries.

Stand height: Different indicators of stand height may be derived from a model of individual tree height versus diameter at breast height or directly from sample values. Commonly used indicators include arithmetic mean height, H, height corresponding to mean basal area, H_g, mean height weighted by basal area, H_L, top height or average height of 100 thickest trees per ha, H_{100}, and dominant height or average height of sociologically dominant trees, H_{dom}. While H, H_g and H_L are mostly useful for volume calculations, H_{100} and H_{dom} are better suited for classification of site and stand productivity.

Stand initiation: The first phase of forest development occurring after a disturbance kills some or all of the existing stand, growing space is released, and seedlings establish.

Stand structure: The physical and temporal distribution of trees (living and dead) and other plants in a stand: species, spatial patterns (both vertical and horizontal), size (including crown volume, leaf area, stem volume or cross section), and age or age class distributions. Some possible discriptions of structure include open, dense, understory, savanna, and complex.

Standard deviation: The square root of the variance.

Statistical survey: The design and execution of surveys to provide estimates of characteristics of well-defined finite populations.

Stellate: Star-shaped, referring to shape of individual hairs that make up the pubescence.

Stem density: Relation between the number of tree stems and the area they occupy, generally measured as the number of individuals per hectare.

Stem number: In a forestry context, stem number frequently replaces the number of live trees. Generally, stem number is expressed in count per unit area. Sometimes, stem number refers only to trees above a certain size.

Stem taper: Assuming circular cross sections the cubic volume of the stem or any segment of the tree can be calculated based on the general taper equation $y = k\sqrt{x^r}$, where y is the radius at any point along the length axis x, and k and r defines the rate of taper and the shape of the solid, respectively.

Stem volume: The volume, usually expressed in m^3, of the stem; this may be calculated either from direct measurement of diameters and lengths on the stem, or measurements may be taken on standing trees using an optical instrument.

Steppe: A vast plain dominated by grasses.

Sterm exclusion: The phase of forest development characterized by density-dependent mortality as trees compete with each other for limited site resources.

Stigma: The receptive surface on the female reproductive organs on which pollen is deposited.

Stipules: Paired structures that are found at the point where the leaf stalk joins the stem.

Stock: Wet pulp of any type at any stage in the manufacturing process.

Stockplant: The plant from which cuttings are harvested.

Stomata: Specialized cells located on the leaf epidermis that open and close to regulate carbon dioxide diffusion into, and water loss out of, the leaf.

Stomatal conductance: A measure of the degree of opening of the stomata. It is linearly related to stomatal pore size.

Stool: A living stump (capable of) producing coppice shoots.

Storey: Layer or stratum of forest.

Strain: A group of similar isolates.

Stratum: Horizontal vegetation layer, part of the vertical forest structure (e.g., understory, subcanopy, canopy).

Stream drainage density: Total length of streams per unit area in a watershed.

Stress concentration: The focus of mechanical stress on a very small location or point within a material, as in the case of crack tip in a solid. Stress concentration often leads to catastrophic mechanical failure.

Strip systems: See shelterwood system.

Strobilus: The reproductive structure in gymnosperms, consisting of a number of sporophylls, grouped on a central axis, e.g., a cone.

Stroma (pl stromata): See ascoma.

Structural lumber: Lumber that is intended for use where allowable properties are required. The grading of structural lumber is based on the strength or stiffness of the piece as related to anticipated uses.

Structure: 1. Physical features of the forest ecosystem (e.g., height, diversity, percentage cover, etc.). 2. The combination or arrangement of primary soil particles into secondary units or peds.

Stud: One of a series of slender wood structural members used as supporting elements in walls and partitions.

Subalpine: The altitudinal belt just below the upper forest line, separating the montane from the above-situated alpine belt, and which in the tropics is generally situated between 3000 and 3500 m elevation.

Subcanopy: Below the top canopy.

Sub-compartment: A portion of a compartment, usually contiguous and composed of a single forest stand type, defined for purposes of management.

Subdominant (crown class): See crown class.

Subfamily: Classificatory group below the level of the family but above that of the genus.

Subgenera: Classificatory group below the level of the genus but above that of the tribe.

Substrate: In papermaking the media to be coated or printed, i.e., paper, board, film.

Subsurface flow (also subsurface stormflow, interflow, or throughflow): Lateral water flow in soil or bedrock which results in a delayed runoff generation that is very common in forest soils.

Succession: Natural dynamics in plant societies beginning with the colonization of bare land by stress-tolerant, light-demanding species and shifting towards communities with more shade-tolerant, more competive but less stress-tolerant species.

Succulence: The tendency of a plant organ to store water.

Sucker: A shoot arising from below ground level either from a rhizome (e.g., bamboos) or from a root (e.g., *Populus* sp.).

Suffructex: A plant that is woody at the base but with herbaceous branches.

Supercalendered paper: Paper that has received a gloss finish by being passed between the rolls of a supercalender under pressure; supercalenders are usually composed of alternate chilled cast-iron and cotton rolls.

Supplemental pollination (SP): (sometimes called supplemental mass pollination–SMP) The broadcast spraying of large amounts of pollen (liters) used to both increase orchard yields and/or genetic efficiency.

Suppressed (crown class): See Crown class.

Surface deactivation: A reduction in solid surface energy which can lead to poor (unfavorable) wetting and poor adhesion. In the case of wood, extreme heat and extended exposure to sun light will promote wood surface deactivation, and poor adhesion.

Surface energy: The state of electrical charges which exist on the surfaces of all molecules, and in this case particularly the molecules located on the extreme surfaces of liquids and solids. Surface energy critically impacts adhesion through the interaction of complementary charges when a liquid adhesive contacts a solid substrate.

Surface hoar frost: Condensation of atmospheric vapor on the snow surface in the form of fragile crystals, between 5–30 mm deep and later buried by new snow, creating a preferred layer for slab avalanche formation.

Surfactants: Surface active molecules used as emulsifier or wetting agent, often with pesticides or as detergents and/or defoamers.

Sustainability: The state of providing resources and other benefits in perpetuity without threatening future supplies.

Sustainable forest management: 1. Management that maintains and enhances the long-term health of forest ecosystems for the benefit of all living things while providing environmental economic, social and cultural opportunities for present and future generations. 2. The application of the concept of sustainable development in forestry. Incorporating the concept of sustainable development is achieved through the integration and balanced optimization of social, economic and environmental goals of development over time. 3. Interventionist: any individual or group the undertakes to facilitate change to an ongoing management system. To be successful in introducing collaborative forest management, the interventionist must establish credibility as the honest broker among the stakeholders of the management system.

Sustainable use: The use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the needs and aspirations of present and future generations.

Sustained supply: Regular supply generally referred to industrial raw materials to maintain the operation of the assembly lines.

Swamp forests: Inundated forests growing in peat-poor soil.

Syconium: The enclosed inflorescence of a fig.

Symbiosis: Association of two different organisms each of which contributes to the nutrition of the other.

Sympathetic nervous system: The part of the autonomic nervous system that inhibits or opposes the physiological effects of the parasympathetic nervous system, as in tending to reduce digestive secretions, speeding up the heart, and contracting blood vessels.

Sympatry: The situation in which species grow within the same territory or region, often specialized to different environments.

Sympodial bamboo: Bamboo with rhizomes whose tips grow into culms; rhizomes form from bases of older rhizomes.

***Symptom*:** A visible abnormality arising from a disease or a disorder.

Symptom: A visible or otherwise detectable abnormality that is the result of disease.

Syncarp: An aggregate fruit with multiple carpels united.

Systematic thinning: See Thinning.

TAD(through air drying): A process for drying a sheet of paper by blowing warm air through the sheet to remove most or all of the moisture.

Taiga: A Russian term meaning northern, boreal, or coniferous forest.

TAMM: Timber Assessment Market Model.

Taper: The rate of diameter decrease in stems with increasing height.

Taungya: An agroforestry system under which food crops and forest trees are cultivated together during the plantation establishment phase. See also shifting cultivation.

Taxon: Any taxonomic group or rank (e.g., family, genus, species); the ranking being described is determined from context.

Taxonomic surveys: Studies undertaken to locate and document occurrences of particular species.

Taylor series expansion: The linearization of function f near point x_0 based on derivatives

$$f(x) = \sum_{m=0}^{\infty} \frac{f^{(m)}x_0}{m!}(x - x_0)^m.$$

Tear resistance: The force required to tear a specimen of paper of specified dimensions under standardized conditions.

Telemetrics: On-board electronic systems that are used for machine and harvesting process control, including optimization of stem cutting, communication equipment (voice and data), visual display screens, audio and visual warning systems, fault diagnostic systems, weighing scales for determination of payloads, and navigation and route optimization functions.

Telocentric: A chromosome with a terminal centromere.

Temperate: Relating to regions in which the average temperature is about 10°C for 2–4 months of the year.

Temporal correlation: Relationships among observations over time.

Temporal scale: Large temporal scales are long time periods, whereas small spatial scales are small time periods.

Tending: Any treatment or tending designed to enhance growth, quality, vigor and composition of the stand after establishment or regeneration and prior to final harvest.

Tensile strength: Resistance to forces that tend to pull the wood or paper apart. Measured as the force parallel with the plane of the wood or paper required to produce failure in a specimen of specified dimensions under specified conditions of loading.

Termites: Primitive social insects of the order Isoptera which can cause extensive degradation to wood. Termites are classified as either subterranean, which must be in ground contact and construct shelter tubes to reach aboveground wood, or drywood termites which do not need to be in ground contact.

Terpene: Volatile, isoprene-based extractive from wood, a component of turpentine.

Terra firme: Upland terraces with forests that are not flooded.

Tetrad: A dispersal unit comprising four pollen grains.

Tetraploid: A polyploid with four sets of chromosomes.

Texture: The relative proportions of sand, silt, and clay in a soil as described by the classes of soil texture in the textural triangle.

Theory of island Biogeography: Derived by R MacArthur and E Wilson, this theory postulated that the number of species on an island was a dynamic equilibrium reached via a balance between colonization and extinction.

Thermocline: Zone of rapid temperature change.

Thermomechanical (TMP) pulp: A mechanical pulp produced from wood chips, where the wood particles are softened by preheating in a pressurized vessel at temperatures not exceeding the glass transition point of the lignin, before a pressurized primary refining stage.

Thinning: A cultural treatment made to reduce stand density of trees primarily to improve growth, enhance forest health, or recover potential mortality. Types of thinning include the following: **crown thinning:** the removal of trees from the dominant and codominant crown classes in order to favour the best trees of those same crown classes; **low thinning:** the removal of trees from the lower crown classes to favour those in the upper crown classes; **selective**

thinning: the thinning of trees in even- or uneven-aged stands, involving the subjective selection by the forester of the trees to be removed, usually involving low or crown thinning; **systematic thinning:** (or mechanical thinning) the thinning of trees in even- or uneven-aged stands, involving removal of trees in rows, strips, or by using fixed spacing intervals. The felled trees are known as thinnings, and may or may not have economic value. Sometimes thinning operations are carried out exclusively to achieve economic out-turn of produce.

Thinning from below: Alternative name for low thinning or, for example, where the death of suppressed and unhealthy trees follows defoliation during insect outbreaks.

Threatened: Facing the threat of extinction. See Rare, endangered and threatened species.

Three-stage least squares (3SLS): Combination of the two-stage least squares and seemingly unrelated regression.

Timber: Solid-sawn lumber 127 mm (5 in.) or more in nominal thickness.

Timbers, round: Timbers used in the original round form, such as poles, piling, posts, and mine timbers.

Tissue filler: An anhydrous form of either natural or calcined calcium sulfate ($CaSO_4$), derived from ground gypsums, and used as a filler for tissue-type papers.

Tissue paper: Thin, low-weight (10–50 $gm\,m^{-1}$), gauze-like types of paper made from virgin and/or reclaimed pulp, used to manufacture such items as sanitary products, wrapping material, protective packing paper, and stock for waxing and twisting. The product is usually creped or treated in another manner to increase the apparent density.

TLF: Tropical lowland forest.

TLMF: Tropical lower montane forest.

TMCF: Tropical montane cloud forests.

TMF: Tropical montane forests.

TMP: Thermomechanical pulp.

TNAA: TAMM/NAPAP/ATLAS/AREACHANGE. Timber and forest models.

Tomentum: Another word for the collective pubescence or hair, in this case used for plant hairs.

Top or dominant height: The average, total height of the dominant trees in a stand. Top or dominant height is often used in determination of site index.

Topography: Land details like elevation, contour, etc.

Total genetic diversity: An estimate of the genetic variation that exists within species.

Total seed per cone: The total number of fully developed seed coats (from fully developed ovules) and rudimentary seed (from immature ovules).

TPMF: Tropical premontane forest.

Tracheid: An elongate, spindle-shaped wood cell that loses protoplasm at maturity when becoming conductive. Tracheids account for 90–95% of softwood volume, much less in hardwoods.

***Tracheid*:** Tracheids are xylem cells and the principal strengthening and water-conducting cells in gymnosperms.

Trait: A specified characteristic (i.e., growth) which is the criterion used to compare performance of clones or offspring of selected parents.

Transect: A sample area (as of vegetation), usually in the form of a long continuous strip.

Transect intercept: A point or perpendicular line that crosses a central transect.

Transgenic: Of an individual plant that contains a foreign gene introduced by genetic modification as opposed to traditional breeding techniques.

Transgressive segregant: An individual offspring of the F_2 generation whose value for a metric trait lies outside the range defined by the F_1 parent.

Transpiration: The evaporation of water from plants. It occurs mainly through the stomata on leaf surfaces. The rate of plant transpiration depends on the stomatal conductance and the dryness of the air relative to the leaf pore space, as expressed by the difference between the vapor pressure inside and outside the leaf.

Tree: Woody plant, not branching at ground level, with an average adult height of exceeding 5 m when healthy; perennial with branches forming a distinct elevated crown.

Tree improvement: Cumulative genetic improvement of a tree species for a few key traits through the activities of selection, breeding, genetic testing and deployment. Most tree improvement programs employ recurrent selection for general combining ability.

Tree tenure: The terms on which a tree or its products are held; the rights and obligations of the holder of the tree.

Tribe: Classificatory group below the level of the subgenus but above that of the species.

Trifoliate: Having a leaf comprising three leaflets.

Triploid: A polyploid with three sets of chromosomes.

TRMP: Thermorefiner mechanical pulp.

Trophic level: The functional position of an organism within an ecosystem according to its feeding relationships. Folivore populations may be influenced by natural enemies in the trophic level above them (top–down) and/or by the trophic level beneath them, the plants on which they feed (bottom–up). Tri-trophic interactions incorporate the herbivore, its natural enemies, and its host plants.

Tropophilous: Plants adopted to seasonal changes in water availability.

TSF: Tropical subalpine forest.

TSM: Timber Supply Model.

Tuber: Fat part of an underground stem or root which holds nutrients and which has buds from which shoots develop.

TUMF: Tropical upper montane forest.

Turbidity: Property of water that causes light to be scattered or absorbed.

Turbulence: Random motions in the air. Turbulence encourages exchange of gases between the atmosphere and plants. High turbulence can lead to lodging and abrasion.

Two-stage least squares (2SLS): Two or more equations are estimated simultaneously taking into account that an independent variable of any one equation may be the dependent variable of another (endogenous variables). The model is estimated in two stages so that, first, the parameter values are estimated with OLS and, second, the endogenous variables are surrogated with their estimated values and the estimation is done again.

Tyloses: Balloon-like outgrowths from adjacent parenchyma that block the vascular tissues of trees infected by wilt pathogens.

Type species: That corresponding to the individual specimen plant from which a given genus was first described.

Ultisols: Weathered, leached soils of low fertility, and containing few weatherable minerals, and a B-horizon with a marked accumulation of clay. Found in warmer regions where rainfall is considerably in excess of evapotranspiration, characteristically under forests in the humid tropics.

Ultrabasic rocks: Rocks rich in bases such as iron and magnesium and low silica content.

Ultramafic rock: Rock formed directly from magma from the earth's mantle (which is low in silica compared to crustal rocks). The rock has low silica and a very large amount of magnesium and iron. The "ma" and "f" in "mafic" are derived from magnesium and Fe for iron.

Umbel: The term often used to describe the inflorescence of many of the eucalypts where flowers are in clusters extending from a single peduncle. Such inflorescences are effectively a reduced dichasial cyme. There may be a single cluster of buds or they may occur in compound, branched inflorescences.

Umbo: The terminal structure of the cone scale.

Unani: Unani system of medicine (Unanipathy) originated in Greece. This system believes in the humoral theory which presupposes the presence of four humours–Dam (blood), Balgham (phlegm), Safra(Yellow bile) and Sauda (black bile) in the body. According to this system, if these four main humours are in a state of mutual equilibrium, one is considered healthy.

Uncinate hairs: Hooked hairs.

Underburning: Prescribed burning with a low intensity fire in activity-created or natural fuels under a timber canopy.

Understory re-initiation: The phase of forest development characterized by the periodic death of large trees and the establishment of a new cohort beneath the existing overstory. Analogous to gap phase dynamics.

Understory: Plants growing under the canopy of other trees and dominated by them.

Underwood: All forest vegetation growing under an overstory.

Unequal probability sampling: Sampling designs where units are selected with different probabilities. These probabilities need to be known for unbiased estimation.

Unifoliate: Having a leaf comprising one leaflet.

Unilocular, inferior ovary: Ovary with one chamber occurring below the other floral parts.

Uniseriate: Formed of a single row of cells.

Unit: The basic sample unit used, e.g., that used in the last stage of multistage sampling for say trees insects on trees.

Unstocked: Forests on which tree crown cover has been reduced below the minimum threshold defined for forest.

Upper tree line: Altitudinal limit of temperature-dependent tree growth, which separates forest on mountains from shrub and herb-dominated formations or ecosystems.

Urban forest: All trees and forest resources in and near urban areas; includes trees and tree stands in parks, private gardens, streets, cemeteries, on squares, on industrial, commercial and agricultural land, around hospitals and schools, on wasteland, and in existing woodlands.

Urban forestry: The art, science, and technology of managing trees and forest resources in and around urban community ecosystems for the physiological, sociological, economic, and aesthetic benefits trees provide society.

Urban greenspace: Vegetated open space in an urban area.

Urban woodland: A forested ecosystem in and near an urban area; although trees are the dominant element, it can contain other elements such as water and open space.

Urban/wildland interface: The transition zone (1) between cities and wildland (cf. urban, wildland, wildland fire), (2) where structures and other human development meets undeveloped wildland or vegetative fuels (syn. residential/wildland interface, wildland/urban interface, rural urban interface).

USDA: United States Department of Agriculture.

User need: A psychological and/or physiological requirement for the well-being of an individual.

User preference: Desired conditions and favored situations that recreationists expect will facilitate or satisfy unmet needs.

Usufructuary right: The right to use something.

Utricaceous stamens: Anther filaments held inflexed in the bud; at anthesis, they snap outward, propelling pollen into the air.

Validation: Accuracy test of model using data set independent from that used in model development.

Value addition: Process by way of which the economic and/or use value of the product is increased without affecting its intrinsic quality.

Values-at-risk: Natural resources, developments, or other values that may be jeopardized if a fire occurs.

Variable: A characteristic that varies from unit to unit, for example the age of a tree.

Variance: The average of the squares of the deviations between the values of the variables and the overall mean in the case of a population or between the values of the variables and the sample mean in the case of a sample; in the first case it is a population parameter, in the second a sample statistic.

Varnish: A liquid composition of a resin or drying oil dissolved in a suitable solvent which is converted to a transparent solid film by a chemical reaction after application to a surface as a thin layer.

Vascular cambium: Dividing, reproductive cells found in a ring situated between the inner bark (phloem) and wood (xylem) of a tree; responsible for formation of xylem and phloem and diameter expansion, remains active throughout the life of a tree. See also Meristem.

Vector: One method of data type, used to store spatial data. Vector data are comprised of lines or arcs, defined by beginning and end points, which meet at nodes. The locations of these nodes and the topological structure are usually stored explicitly. Features are defined by their boundaries only and curved lines are represented as a series of connecting arcs.

Vegetable tannin: Astringent vegetable extract which has the ability to combine with animal hide and convert it into leather.

Vegetation period: In regions with seasonal climate, the period in which plants grow, flower, and seed.

Vegetative reproduction: Nonsexual reproduction. See Propagule.

Vegetative: Nonsexual.

Vehicle routing functions: Aims to maximize capacity utilization of the transport fleet within the constraints imposed by destination.

Verifiable indications: The factors asserting any logic.

Verification: Check of internal logic of model.

Vessel: The principal vascular or water-conducting component in hardwoods. Composed of vessel elements which are conductive cells with perforated ends; found in the wood of angiosperms but rarely gymnosperms and are of indeterminate length; form axial columns centimetrs to meteres long in the tree and function to conduct water and nutrients throughout the tree stem and branches.

Viability: The ability of a pollen grain or pollen lot to set seed as determined by its assay performance in laboratory tests (viability assays). Various assays are used including staining, respiration, conductivity and germination. Correlation analyses are used to determine the strength of the relationship between laboratory assay response and field fertility (seed set).

Viability selection: Natural selection occurring at the whole organism level.

Viewer sensitivity: The degree of concern that viewers have for visual qualities; used interchangeably with 'visual sensitivity.'

Viewshed: A specific term describing the mappable visible area as seen by an observer from a given location or locations.

Virgin pulp: Pulp that has not previously been used in the papermaking process.

Virtual reality: Virtual reality involves the immersion of a user in a virtual world. This usually involves two main aspects: first, the user is generally presented with an immersive display, either through the use of a head-mounted display or through the use of display screens arranged to surround the user; second, the user has interactive control, such that they can explore the virtual environment, and effect change upon that environment.

Virulence: Degree of pathogenicity of an organism, its ability to cause disease. A more virulent strain of a pathogen causes more damage to its host than does a less virulent strain.

Visitor counting: Method to measure the volume of recreational use of an area in terms of number of visits; observations are often made with the help of electronic equipment.

Visitor survey: Method used to collect visitor information in recreation areas. Data collection is made by questionnaire or interview techniques.

Visual absorption capability: The relative capacity of the landscape to absorb visual alterations and still maintain its visual integrity or landscape character.

Visual impact assessment: An assessment of the type, magnitude, and importance of predicted or existing visual effects of an activity on the landscape.

Visual quality: The part of aesthetic quality that is due to visual characteristics of the landscape; it is often used interchangeably with the term scenic quality, referring to the degree of attractiveness or scenic value in the landscape.

Visual quality objective: A description of the acceptable degree of change to a landscape expressed in terms of the amount and nature of any alteration created through logging practices or other forestry activity. An integral part of VRM systems.

Visual resource management (VRM): A system of classifying, assessing sensitivity and applying visual quality objectives to areas of forest landscape.

Visual resource management: A planning and management system for visual values and resources.

Visual symptoms: Color changes or growth defects resulting from an inadequate supply of a particular nutrient.

Visualization: A visual depiction of landscape conditions, which displays terrain and other recognizable geographic features in perspective view, with varying degrees of realism.

Vivipary: Premature germination of seeds on the maternal plant before they are released.

Volume: Volume is the most widely used measure of wood quantity. The wood volume of a tree includes stem, branches, stump and roots. For standing trees, above-ground volume production is generally calculated as stem wood volume for conifers, but may include branch volume for broad-leaved tree species. Measurements or predictions of wood cubic volume may refer to, for example, total stem volume, v, total tree volume (stem and branches), v_b, or volume above a certain merchantable limit ($d>a$), v_a. Volume estimates may exclude or include bark and, for above-ground estimates, exclude or include stump. Wood cubic volume may be determined by direct or indirect measurement. Direct methods are based on the principle of water displacement or pycnometry (see xylometer), while indirect methods are based on geometry. Indirect methods prevail because these are often more practical. Indirect volume measurement relies on geometrical models of stem, branches, stump and roots and may be carried out for felled as well as for standing trees. In practice, the cubic volume of each segment of a sample tree is calculated from the product of its cross sectional area and length.

Vulnerable: Facing high risk of extinction. See Rare, Endangered and Threatened species.

Wake Zone: The main area of shelter behind a shelterbelt. This is the region in which faster moving air displaced above the trees begins to mix back towards the ground.

Wall-to-wall coverage: Complete spatial mapping of a land area by satellite data.

Washing: Process of removal of dissolved organic and inorganic substances with the use of water.

Watermarks: A localized modification of the formation and opacity of sheet of paper while it is still quite wet, so that a pattern, design, or work groups can be seen in the dried sheet when held up to the light.

Water potential: A measure of the energy that causes water to enter plant cells. There is a net movement of water from a region of high water potential to one of low water potential.

Water repellent: A liquid that penetrates wood which, after drying, materially retards changes in moisture content and in dimensions without adversely altering the desirable properties of wood.

Water-repellent preservative: A water repellent that contains a preservative which, after application to wood and drying, accomplishes the dual purpose of imparting resistance to attack by fungi or insects and also retards changes in moisture content.

Wattle daub: Woven work of sticks intertwined with twigs or branches or bark and covered with plaster, used as sealing between wood members.

Weathering: The mechanical or chemical disintegration and discoloration of the surface of wood caused by exposure to sunlight (ultraviolet light), the action of dust and sand carried by winds, and the alternate shrinking and swelling of the surface fibers with the continual variation in moisture content brought by changes in the weather. Weathering does not include decay.

Wedge system: A modification of the shelterwood-strip system in which cuttings begin as narrow, interior, wedge-shaped strips with the apex into the prevailing wind, and are then successively enlarged and advanced. See Shelterwood system.

Weibull distribution: A probability distribution with density function

$$f(x) = \frac{c}{b^c}(x-a)^{c-1}\exp\left[-\left(\frac{x-a}{b}\right)^c\right]$$

and where a, b, and c are parameters.

Wet deposition: The transfer of atmospheric pollutants from the air to terrestrial ecosystems by rain, fog or snowfall.

Wet end: Part of a paper machine system where fibers are suspended in water.

Wet strength: The ability of paper to retain part of its strength after rewetting.

Wet strength resin: A synthetic material which is incorporated in paper and board to improve its strength when wet.

Wetting: The achievement of intimate molecular level contact when a liquid is deposited on solid surface. Wetting is favorable when liquid/solid adhesive forces are greater than the cohesive forces within the liquid.

Wetting agents: Surface active molecules which are commonly added to aqueous adhesives and which improve wetting (lower the contact angle) by reducing the surface energy of the liquid adhesive. Wetting agents are also known as surfactants or surface active agents because they tend to concentrate at the liquid/air and liquid/solid interfaces.

Wheatfield regeneration: Simultaneous germination of large quantities of seed resulting in a wheatfield-like appearance.

Wildfire: (1) Any unplanned and uncontrolled wildland fire which regardless of ignition source may require suppression response, or other action according to agency policy. (2) Any free burning wildland fire unaffected by fire suppression measures which meets management objectives (cf. wildland, wildland fire, prescribed natural fire, prescribed fire).

Wildland fire: Any fire occurring on wildland regardless of ignition sources, damages or benefits (cf. wildland, wildfire, residential/wildland interface).

Windthrow: Uprooting and blowing down of trees by the wind.

Wireframe: A wireframe model is a 3D computer model that does not have a solid surface, but rather a transparent wire grid is stretched over the surface to indicate its shape. The wire grid shows where the edges of the model are, but the model is not represented as a solid or textured form; linear forms such as trees or towers may be represented as single lines or simple geometric symbols. Modern versions of geometric models may represent solid surfaces with a grid pattern which has a similar abstract, wireframe appearance.

Wood flour: Wood pulverized to finely divided particles, approximately the same as those of cereal flours in size, appearance, and texture and passing a 40 to 100 mesh screen.

Wood gasification: The process of heating wood in an oxygen-starved chamber until volatile pyrolysis gases (e.g., carbon monoxide, hydrogen, and oxygen) are released from the wood. The gases emitted are lower- or medium-energy gases that can be combusted in various ways that include the operation of internal combustion engines.

Wood I-joist: An I-shaped structural member consisting of dimension lumber or laminated veneer lumber flanges and plywood, oriented strand board, or dimension lumber webs.

***Wood nematodes*:** Parasitic nematodes normally survive in roots; however, wood nematodes are unique in surviving in woods and in being mycophagous.

Wood preservation: The treatment of wood, or products made from wood, with biocide-containing systems, or other processes such as heat treatment, to prevent degradation by living organisms or fire.

Wood preservative: The combination of a biocide(s), other inert ingredients, and carrier in a commercial system used to treat wood.

Wood rat middens: Assemblages of plant material collected and amassed by wood rats or other rodents within caves or rocky burrows of arid regions of the American Southwest; these plant materials can generally be dated and identified to provide a record of plants growing in an area with records dating back 40,000 years or more.

Wood ray: See Ray.

Wood-free pulp: A pulp containing no more 5% mechanical woodpulp.

Woodland: Scattered tree formation or simply a small area of forest <25 ha'.

Writing paper: Any grade of paper that is specially sized so that it can be satisfactorily used for pen and ink writing purposes.

***x*:** The basic chromosome number, i.e., the number of different chromosomes that make up a single complete set. For a diploid, x is equal to the number of chromosomes in a gamete.

Xeric: dry.

Xeromorphic: Possessing morphological adaptations for a dry environment.

Xerophilous: Adapted to water deficiency.

Xylem cavitation: Breaks in the water column of the xylem are caused by tension and freezing in the column and are filled with water vapor or air at atmospheric pressure.

Xylometer: Direct volume measurement of irregularly shaped objects, particularly wood samples, is carried out using a xylometer, which is essentially a water tank in which the wood is submerged. The principle of water displacement requires that the xylometer is equipped or used with a suitably graduated volume scale. The cubic volume of wood equals the volume of water and wood minus the volume of water. Pycnometry requires that the wood is weighed before and during submersion, for example on a scale beam or in a sieve bucket. The cubic volume of wood equals the apparent difference in mass.

Yankee dryer: A large diameter, steam-heated pressurized dryer used on a paper machine to produce a glazed finish on one side of the sheet of paper.

Yield table: Table showing timber volume by age for a given species and size index.

Zygomorphic: Bilaterally symmetrical. Capable of being divided into only two equal parts by a line drawn through the middle that results in a mirror image of the part on one side of the line to the part on the other side, e.g., the flower of species of *Lecythis*.

Zygote: The fertilized egg cell that has fused with a pollen nucleus to become the diploid cell from which the seed embryo and ultimately the free-living tree develops.

INDEX

Abbreviations

EFPs – edible forest products
FAO – Food and Agriculture Organization
NWFPs – non-wood forest products
UNCED – United Nations Conference on the Environment (UNCED) (Rio 1992)

Notes

Cross-reference terms in italics are general cross-references, or refer to subentry terms within the main entry (the main entry is not repeated to save space). Readers are also advised to refer to the end of each article for additional cross-references – not all of these cross-references have been included in the index cross-references.

The index is arranged in set-out style with a maximum of three levels of heading. Major discussion of a subject is indicated by bold page numbers. Page numbers suffixed by T and F refer to Tables and Figures respectively. *vs.* indicates a comparison.

This index is in letter-by-letter order, whereby hyphens and spaces within index headings are ignored in the alphabetization. Prefixes and terms in parentheses are excluded from the initial alphabetization.

A

C

D

E

F

G

H

I

J

K

L

M

N

O

P

Q

R

S

T

U

V

W

X

Y

Z