Trees

Their Natural History

SECOND EDITION

Peter A. Thomas

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Second Edition

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Trees: Their Natural History

Second Edition

Trees are familiar components of many landscapes and have been vital in determining the ecology of our planet as well as the development of human cultures and communities. Yet how much do we really understand about how they work? This updated and revised edition provides a comprehensive introduction to all aspects of tree biology and ecology, and presents the state-of-the-art discoveries in this area.

The wonders and mysteries of trees are explored throughout the book and questions such as why leaves turn spectacular colours in the autumn, how water reaches the top of the tallest trees or why the study of genetics has caused so many name changes in trees are all brilliantly answered.

Written with a non-technical approach, this book will be a valuable source of reference for students and those with a less formal interest in this fascinating group of plants.

Peter Thomas is Senior Lecturer in Botanical and Environmental Science at Keele University, UK with 30 years of experience in ecological aspects of trees and forest ecology in the UK, North and Central America, Europe, Africa, Russia and Australasia. He has written two other books for Cambridge University Press: *Ecology of Woodlands and Forests* (Thomas and Packham, 2007) and *Fire in the Forest* (Thomas and McAlpine, 2010).

But blessed is the man who trusts in the Lord, whose confidence is in him.
He will be like a tree planted by the water that sends out its roots by
the stream.
It does not fear when heat comes; its leaves are always green.
It has no worries in a year of drought and never fails to bear fruit.

Jeremiah 17: 7–8

Your ghost will walk, you lover of trees,
(If our loves remain)
In an English lane

De Gustibus

Robert Browning (1812–1889)

Preface

A lot has happened in the tree world since this book was first written. Some previously unanswered questions can now be addressed, and some things we thought we knew have proved to be wrong or not the whole story. These have been put right. Our understanding of trees has also made huge leaps in areas such as the role of genetics and genetic engineering, effects of climate change, hydraulic engineering (including the bitter debate over how water gets up a tree), factors limiting tree height and why trees have colourful leaves in the autumn. New material has been added on all these and in many other areas where new discoveries have been made. This ranges from the surreal (did you know that cosmic radiation and the ocean tides appear to affect tree growth?) to the practical (why have artificial wine bottle corks proliferated?). Many of the problems faced by trees are caused by us humans, so there is also a new chapter on our interactions with trees looking at just why they are good for us and therefore worth preserving. I hope you have as much fun reading this as I had writing it.

Following comments on the first edition, the number of references at the end of each chapter has been increased to help those who want to dig deeper. To keep the text flowing, however, I've only included reference to these in the text where it is not clear which source is being used. Also following reader feedback, more scientific names of trees have been included with the common names, which I hope you won't find too intrusive.

In addition to those thanked in the first preface, I am most grateful to the following for help in gathering data and clarifying ideas: Richard Hobbs, Leif Kullman, Norm Kenkel, Janet Sprent, Andy Hirons and Duncan Slater. Andy Lawrence did a wonderful job in drawing the new diagrams. Alan Lacey is also thanked for kindly providing access to his years of research on the sycamore.

The first stirrings of this second edition began during a Bullard Fellowship at Harvard University and the help this gave me is very gratefully acknowledged.

The collection of leaf data from Honduras that was used in Chapter 2 was kindly made possible by Operation Wallacea, and the following huge team are thanked for their help in braving the often inclement conditions to gather the data: Kelly Barber, Natalie Gérardy, Catherine Dieleman, Alex Rupp, Cassidy van Rensen, Stephanie Ryan, Heather Crochetiere, Nicole Meneses, Maja Goschorska, Matthew Levan, Amy Stypa, Sarah Jupp, Sophie Cunningham, Carlós Carias, Edwardo Antunez, Christie Rajtar, Matthew Sargeant, Yacyi Mi, Refika Mustafa and in particular Leanne Meadows, Amy Rushton, Nigel Taylor, Karly Harker and Gurjot Malhi for their stamina and fortitude. The canopy

access guys in Honduras – Waldo Etherington, Cameron Alexander and Jim Fenn – are also heartily thanked for their good company, their help in collecting samples and safely getting me up and down.

All photographs are my own except where indicated otherwise.

Note: In the text sp. and spp. are used as shorthand for one or more species, respectively. Units used are hopefully self-explanatory but it might help to know that a micrometre (μm) is a thousandth of a millimetre, and ppm are parts per million (1000 ppm = 0.1%).

Preface to the first edition

Why write a book on trees? The motivation for me came from the frustration of trying to teach a subject where much is known but is scattered over a huge range of journals and books from many countries. There are so many fascinating stories to be told about the ways in which trees cope with the world and the problems of being so large and long-lived: they are extremely well designed. *Someone* had to write this book!

My goal was to draw together strands of information to create a readable book that would answer common questions about trees, set right a number of myths and open up the remarkable world of how trees work, grow, reproduce and die. It is for you, the reader, to judge whether I have been successful. Please do let me know where you find errors or would wish to argue with the logic.

I am indebted to all those who helped with this book, especially Roger Davidson and Bill Williams who read and commented on the whole manuscript and numerous colleagues who commented on parts. Val Brown, Barry Tomlinson, Colin Black and K. J. Niklas kindly provided detailed information. Maria Murphy and Lynn Davy at Cambridge University Press are to be congratulated for their extreme patience with a faltering author. And, of course, my wife and sons are thanked for putting up with my pet project.

The following are gratefully acknowledged for their help with the diagrams: Ian Wright, Lee Manby (who drew Figures 4.2 and 7.1–7.14) and John Stanley (for drawing Figure 3.7).

May 1999

Contents

Chapter 1: An overview

What is a tree?

Everyone knows what a tree is: a large woody thing that provides shade. Oaks, pines and similarly large majestic trees probably come immediately to mind. Such big trees are characterised by the enormous changes in size from seed to mature tree: a mature giant sequoia (*Sequoiadendron giganteum*) is a billion, billion times heavier than the seed it came from (that's 1 with 12 zeros after it). A stricter, but more inclusive, botanical definition is that a tree is any plant with a self-supporting, perennial woody stem (i.e. living for more than 1 year). The first question that normally comes back at this point is to ask what then is a shrub? To horticulturalists, a 'tree' is defined as having a single stem more than 6 m (20 ft) tall which branches at some distance above ground, whereas a shrub has multiple stems from the ground and is less than 6 m. This is a convenient definition for those writing tree identification books who wish to limit the number of species they must include. In this book, however, shrubs are thought of as being just small trees since they work in exactly the same way as their bigger neighbours. Thus, 'trees' cover the towering giants over 100 m through to little sprawling alpine willows no more than a few centimetres tall.

Some plants can be clearly excluded from the tree definition. Lianas and other climbers are not self-supporting (although some examples are included in this book), and those plants with woody stems which die down to the ground each year, such as asparagus, do not have a perennial woody stem. Bananas are not trees because they have no wood (the trunk is made from leaf stalks squeezed together). Nor are bamboos since they are just hardened grasses even though they can be up to 25 m tall and 25 cm thick (see Box 1.1).

There are estimated to be 100 000 species of tree in the world, about 25% of all living plant species. An interesting feature of all these trees is how unrelated they are. It is usually easy to say whether a plant is an orchid or not because all orchids belong to the same family, have a common ancestor and share a similarity in structure (especially the flowers). This is true of most plant groups such as grasses and cacti (in their own families) and chrysanthemums (all in the same genus). But the tree habit has evolved independently in a wide range

Box 1.1 The range of trees found in different plant groups

Ferns (Pteridophytes):	Tree ferns: mostly in the families of Cyatheaceae and Dicksoniaceae; rarely branched, no true bark and with a trunk containing woody strands; need frost-free shaded habitats
Seed plants:	Contains the Conifers and the Flowering plants. The ferns above produce spores but not seeds and so are not included here
Conifers and their allies (Gymnosperms): This term means 'naked seeds' (as in gymnasium where the Greeks exercised naked); the seeds are exposed to the air and can be seen in the cone or fruit without having to cut anything open	Conifers: 630 species in eight families • Cupressaceae: cypress, junipers, and now including the former Taxodiaceae: redwoods • Araucariaceae: including monkey puzzle (*Araucaria araucana*), kauri (*Agathis australis*) and the Wollemi pine (*Wollemia nobilis*) • Podocarpaceae: more than 150 species in the southern hemisphere including the podocarps (*Podocarpus* spp.) and rimu (*Dacrydium cupressinum*) • Pinaceae: pines, spruces, larches, hemlocks, firs, cedars • Cephalotaxaceae: 11 species of *Cephalotaxus*, plum yews/cowtail pines • Phyllocladaceae: 4 species of *Phyllocladus*, celery-pines • Sciadopityaceae: only *Sciadopitys verticillata*, Japanese umbrella-pine • Taxaceae: yews Ginkgo: 1 species • Ginkgoaceae: the ginkgo or maidenhair tree (*Ginkgo biloba*) Cycads: palm-like with stiff leathery leaves Gnetales: a strange group with a few interesting woody plants • *Welwitschia mirabilis*: single species in SW Africa • *Gnetum* spp.: mostly tropical climbers • *Ephedra* spp.: 30+ low shrubs of dry deserts

Box 1.1 (cont)	
Flowering plants (Angiosperms): This means hidden seeds: contained inside a fruit	Dicotyledons (two 'seed leaves' in the seed): The main group of trees such as oaks, birches, etc. Around 75 of the world's 180 families contain trees. Monocotyledons (one 'seed leaf'): A wide ranging set of trees concentrated in a few families • Palmaceae (Arecaceae): palms; mostly tropical, a few temperate; nearly 3000 species • Asparagaceae: a large family with a number of trees Dragon trees (*Dracaena* spp.); mostly N African Cordyline palms (*Cordyline* spp.); Australia and New Zealand European butcher's brooms (*Ruscus* spp.) Yuccas (including the Joshua tree, *Yucca brevifolia*) • Pandanaceae: screw pines (*Pandanus* spp.); Old World Tropics; stilt roots supporting a stout forked trunk • Xanthorrhoeaceae: grass trees (*Xanthorrhoea* spp.) from Australia with short trunk with forked branches and long narrow leaves, and aloes (*Aloe* spp.) from Southern Africa • Sterlitziaceae: traveller's palm (*Ravenala madagascariensis*) **Monocotyledons that are not trees** • Musaceae: bananas (*Musa* spp.); the trunk is made from leaf stalks squeezed together • Poaceae: bamboos (e.g. *Dendrocalamus* spp.) – are just hardened grasses with no wood

of plants: at least 20 families in temperate areas and so probably hundreds worldwide. Given this wide range it is not surprising that the only common feature of trees is having a perennial woody skeleton. Box 1.1 illustrates how many major groups have evolved the tree habit. This is a superb example of 'convergent evolution' where a number of unrelated types of plant have evolved the same answer – height – to the same problem: how to get a good supply of light.

On the whole, this book is concerned with the two biggest groups of trees. These are the **conifers** and their allies, and the **hardwoods** like oak, birch and so on. (As you can see from Box 1.2 the terminology can be confusing so throughout this book we will stick to conifers and hardwoods as shorthand for gymnosperms and dicotyledon angiosperms.) The monocotyledon trees such as palms and dragon trees are mentioned in passing but on the whole they grow in a different way from conifers and hardwoods and the book can only be so long. Purists might indeed argue that since the trunks of these trees contain no real 'wood' (Chapter 3) they are not trees anyway. Tree ferns (Box 1.1) come into the same category.

A short history of trees

Back in the Silurian, over 400 million years ago, the first vascular plants (those with internal plumbing) appeared on the earth. Initially this plumbing was just for conducting water up the plant with no structural strength. The tree habit took off once a way of making the plumbing (particularly the xylem; see *Parts of the tree* below for a definition of this) thicker and stronger had evolved; this was the cambium (again see below for a definition). The first trees (protogymnosperms) evolved in the early Devonian around 390 million years ago, capable of living for several decades and reaching up to 30 m tall and a metre wide. Within 100 million years, the coal-producing swamps of the Carboniferous (360–290 million years ago) were dominated by lush forests. We would have recognised the tree ferns from today's forests but the others – giant horsetails and clubmosses – have long since disappeared, leaving us just a few small relatives. The horsetails such as *Calamites* were up to 9 m tall and 30 cm in diameter but the clubmosses (notably *Lepidodendron*) must have been magnificent at up to 40 m high and a metre in diameter. In these forests the first primitive conifers appeared around 300 million years ago and by around 250 million years ago (the late Permian) trees such as cycads, ginkgos and monkey puzzles were recognisable: the sort of trees found fossilised in the petrified forest of Arizona from the late Triassic, 200 million years ago (Figure 1.1). The pines were not far behind, probably evolving around 180–135 million years ago (Jurassic) to share the earth with the dinosaurs. And by the end of the Cretaceous around 65 million years ago all the modern families of conifers had evolved.

Conifer domination was long and illustrious, from around 245 till 67 million years ago, but the early hardwoods were diversifying during the early Cretaceous around 120 million years ago. The hardwoods probably

Box 1.2 Definitions that go with the two main groups of trees

Throughout this book the terms **Conifers** and **Hardwoods** will be used as shorthand for Gymnosperm and Angiosperm trees.

Gymnosperms	Angiosperms

As explained in Box 1.1, these are the proper botanical terms but a little hard to digest. Both are seed plants but the angiosperms are also flowering plants; gymnosperms have no proper flowers.

Conifers and their Allies	All other trees

As you can see from Box 1.1 the gymnosperms include more than just the conifers but they are the major component.

Softwoods	**Hardwoods**

The problem with these descriptive terms (which stem from the timber industry) is that although most gymnosperms *do* produce softer wood, there are many exceptions, and many hardwoods can be physically soft. Yew (*Taxus baccata*, a Softwood) produces very dense and hard wood whereas some Hardwoods, like balsa (*Ochroma pyramidale*), are very soft and easily broken or indented with a fingernail.

Evergreens	Deciduous trees

It is often considered that conifers are evergreens and hardwoods are deciduous, losing all of their leaves at some point in the year. Exceptions can be found here as well. The dawn redwood (*Metasequoia glyptostroboides*), the swamp cypress (*Taxodium distichum*) and larches (*Larix* spp.), for example, are deciduous gymnosperms. In contrast, European holly (*Ilex aquifoilium*), rhododendrons and many tropical angiosperms are evergreen.

Needle trees	Broad-leaved trees

Most conifers do indeed have needle-shaped leaves but again there are exceptions. The ginkgo tree (*Ginkgo biloba*) and monkey puzzle (*Araucaria araucana*) have definite broad flat leaves (admittedly these trees are easily identified oddities). Cycads, which are primitive gymnosperms, have long divided leaves that resemble palms. Some angiosperms have reverted to needle leaves or have largely lost their leaves and use their needle-like branches as leaves, e.g. gorses (*Ulex* spp.) and brooms (*Cytisus* spp.).

Figure 1.1 Sections of petrified tree (in this case about 1 m in diameter) in the Petrified Forest National Park, Arizona, USA. These trees were growing in the late Triassic (200 million years ago) and became buried under river sediments which prevented rotting. Water flowing through the sediments deposited silica into the wood's tubes with other colourful minerals, such as iron, manganese and copper, and so preserved the original wood structure.

evolved from a now extinct conifer group that had insect-pollinated cones. The magnolias are some of the earliest types of hardwood that we still have around. During the Cretaceous period and into the early Tertiary (65–25 million years ago) the hardwoods underwent a massive expansion displacing the conifers, undoubtedly helped by the warm humid global climate of the early Tertiary. But further changes to the climate came to the rescue of the conifers with the development of polar ice caps at the end of the Eocene (35 million years ago), which allowed the northern pines to diversify, spread and take over the boreal forest. This was not without a price; others such as the dawn redwood (*Metasequoia glyptostroboides*), which had been very extensive around the world including on Axel Heiberg Island in the Arctic (79 °N) 60–50 million years ago, became severely limited in its distribution, now found natively only in eastern Asia.

At the end of the Permian period, around 250 million years ago, most of the earth's land masses were squashed together into the super-continent of Pangaea. By the time the hardwoods had evolved, Pangaea had broken into Laurasia (which gave rise to the northern hemisphere continents) and Gondwanaland (containing what is now Australia, Africa, S America, India and Antarctica) trapping the pines primarily in the northern hemisphere.