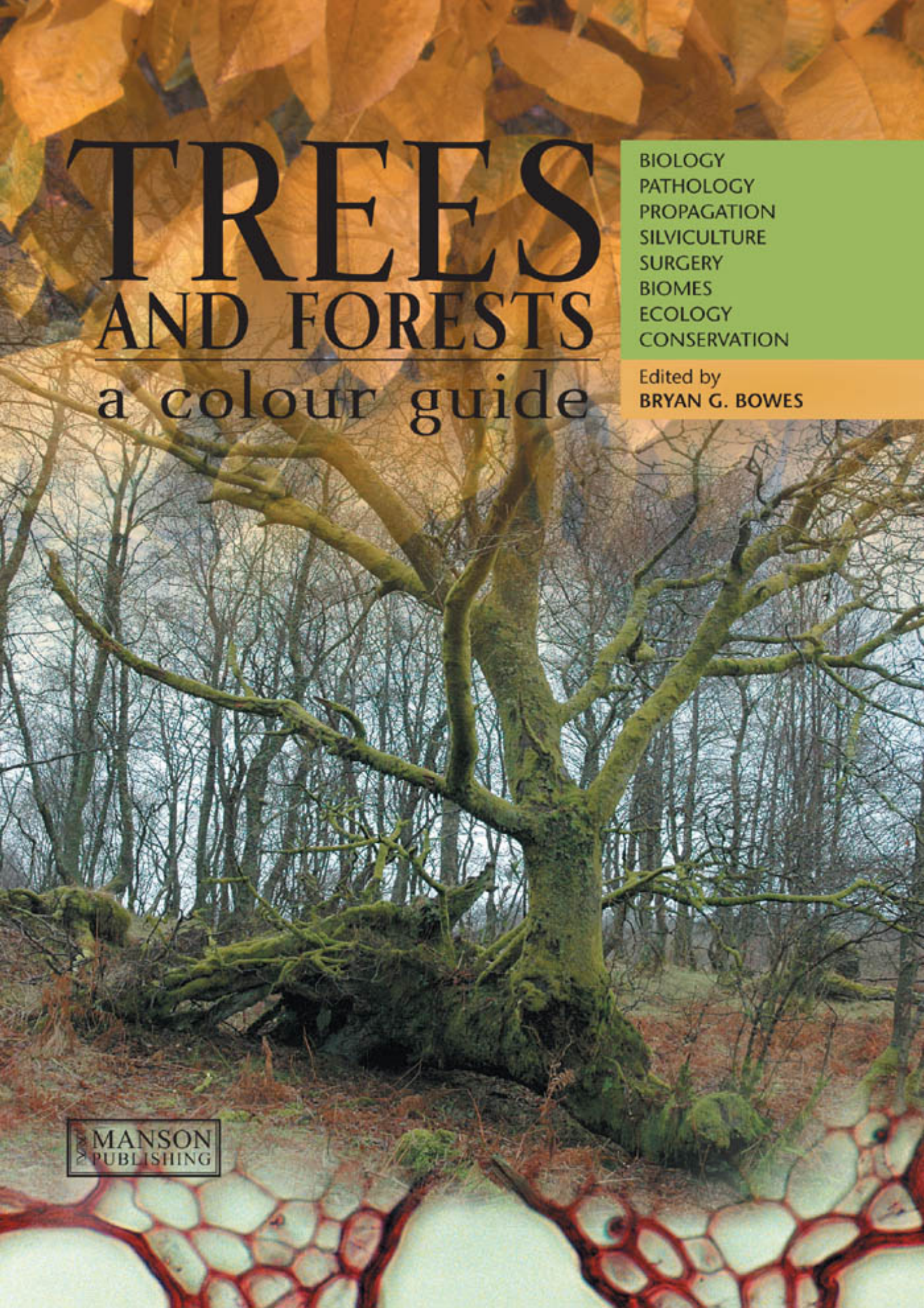
TREES
AND FORESTS
a colour guide
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TREES AND FORESTS

A Colour Guide

Biology, Pathology, Propagation, Silviculture, Surgery, Biomes, Ecology, Conservation

Edited by
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Contents

Preface

> A grove of sequoias [*Sequoiodendron giganteum*] – occupy an area of perhaps less than a hundred acres – The perfect specimens not burned or broken are singularly regular and symmetrical – showing infinite variety in general unity and harmony; the noble shafts with rich purplish brown fluted bark, free of limbs for one hundred and fifty feet or so, ornamented here and there with leafy rosettes; main branches of the oldest trees very large, crooked and rugged, zigzagging stiffly outward seemingly lawless, yet unexpectedly stooping at the right distance from the trunk and dissolving in dense bossy masses of branchlets, thus making a regular though greatly varied outline, – a cylinder of leafy, outbulging spray masses, terminating in a noble dome, that may be recognised while yet far off upheaved against the sky – the king of all conifers, not only in size but in sublime majesty of behaviour and port.
>
> (John Muir, *My First Summer in the Sierra,* September 17th 1869)

A reverence and respect for trees, such as are exhibited in Muir's scientific but beautiful prose describing his experiences in the Californian Sierra Nevada is deeply embedded in the human psyche. A sacred oak (*Quercus*) was at the centre of the Greek oracle at Dodona founded in about 1800 BP; while Artemis, the goddess of woodlands, and Apollo (her twin brother) were said to be born under a date palm. For the Pehuenche Amerindians of Chile, the monkey puzzle tree (*Araucaria araucana*) is holy, Buddha is believed to have attained enlightenment while sitting under the bodhi tree (*Ficus religiosa*), while ginkgo (*Ginkgo biloba*) is almost extinct in the wild of China but has survived as a sacred tree in temple gardens.

Sadly, for the last century or more, such respect for trees has generally been forsaken. Today, environmentally detrimental logging and forest clearances still continue, either illegally or by official connivance, driven by world population growth, industrialization, market globalization, and the pursuit of maximal (but patently unsustainable) commercial profits.

The principal aim of this present volume is to bring together and review a number of features of forests, trees, their development, natural environments, and ecology, which are usually disparately considered. These topics are expertly treated by scientists from various countries and presented in a format in which, as an integral part of each chapter, numerous high-quality colour illustrations complement the concise but clearly written text.

This Guide will be of importance and interest to anyone studying plant science, forestry, or ecology and of practical and theoretical use to conservationists, foresters, tree propagators, and tree surgeons working in the field. The 16 contributing authors, based in Britain, the USA, Australia, and Italy, reflect a wealth of expertise, which will help ensure that this volume is of value and use for students and interested amateurs in countries throughout the world.

Bryan G Bowes

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Abbreviations

BP	before present
B.t.	*Bacillus thuringiensis*
B.t.k	*Bacillus thuringiensis* var. *kurstaki*
CWD	coarse woody debris
DED	Dutch elm disease
DON	dissolved organic nitrogen
E	east
HRGPs	hydroxyproline-rich glycoproteins
IBA	indolebutyric acid
IUCN	International Union for Conservation of Nature
IPM	integrated pest management
MUS	Malayan Uniform System
MVP	minimum viable population
mya	million years ago
NEP	net ecosystem productivity
NPP	net primary productivity
PGA	polygalacturonic acid
PME	pectin methyl esterase
PRPs	pathogenesis-related proteins
REGUA	Reserva Ecologica Guapi-açú
RG-I	rhamnogalacturonan-I
RG-II	rhamnogalacturonan-II
SMS	selective management system
W	west
TDF	temperate deciduous forest
TEF	temperate evergreen forest
TSS	tropical shelterwood system

Note: all sectioned specimens were photographed under the light microscope except where designated TEM (transmission electron micrograph). Abbreviations: LS, longitudinal section; RLS, radial longitudinal section; TS, transverse section; TLS, tangential longitudinal section.

Dedications

To the Editor's family

With great love to my dear, supportive, and forbearing wife Diane; in warm memory of my late wife Ruth; with all love and affection for our children Tanya and Adrian; and to my six bright, creative, and affectionate grandchildren – Sean, Aidan, Declan, Cian, Myles, and Marcus.

To William Shakespeare

The quality of mercy is not strain'd;
It droppeth as the gentle rain from heaven
Upon the place beneath. It is twice blest:
It blesseth him that gives and him that takes.
'Tis mightiest in the mightiest; it becomes
The throned monarch better than his crown;
His sceptre shows the force of temporal power,
The attribute to awe and majesty,
Wherein doth sit the dread and fear of kings;
But mercy is above this sceptred sway,
It is enthroned in the hearts of kings,
It is an attribute to God himself

(*The Merchant of Venice*)

SECTION 1 INTRODUCTION TO WOODY HABITAT

CHAPTER 1

Survey of trees: their global significance, architecture, and early evolution

Bryan G Bowes

INTRODUCTION

Most trees – apart from those growing in plantations, horticulture, arboreta, parks, or urban settings – are distributed in various biomes, or major regions, of the terrestrial world (**1**; Packham *et al*., 1992). Each biome is characterized by its own range of animal and plant life. Chapters 2–5 of this Guide consider the various natural regions populated by trees, while Chapters 10 and 14 emphasize the vital role of trees in the complex web of life.

According to Jane (1970), there are some 20,000 species of woody plants but, more recently, Oldfield *et al*. (1998) estimated that there are possibly up to 100,000 tree (arborescent) species: these were defined as single-stemmed species growing to at least 2 m in height at maturity. However, this definition seems unduly restrictive, since it would apparently exclude some natural multi-stemmed species of

1 Overview of the Blue Mountains *Eucalyptus* forest near Sydney, Australia. This forest is dominated by eucalypts, with some 90 arborescent species of *Eucalyptus* and other members of the family Myrtaceae occurring here.

2 Multi-stemmed specimen of *Sorbus aucuparia* (mountain ash, rowan tree), which shows no evidence of a coppice origin.

3 Multi-stemmed specimen of *Eucalyptus gregsoniana* growing in Australia.

4 Foliage of the recently discovered *Wollemia nobilis* (Wollemi pine) growing in the Royal Botanic Gardens, Sydney, Australia.

5 Conical canopy of *Araucaria araucana* (monkey puzzle) bearing ripening female cones. This specimen is growing in Scotland, but the tree is endangered due to over-logging in its native southern Chile.

common trees such as *Salix* (willow), *Sorbus*, and *Eucalyptus* (**2**, **3**), as well as various palms and other taxa.

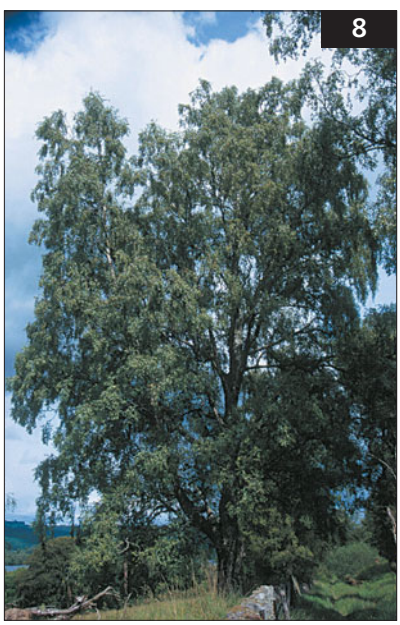
In any case, more species of tree are very likely to be discovered, or sometimes just await accurate scientific recognition and description. For example, *Wollemia nobilis* (Wollemi pine, **4**) is a relic of the extensive araucarian flora existing in the early Cretaceous period, 116 mya (million years ago). However, the Wollemi pine was only discovered in 1994; having survived until then, as a small population of conifers growing within the protective walls of a narrow, deep canyon located only 150 km from Sydney, Australia. Various new *Eucalyptus* species (Chapter 4) were only recently recognized in Western Australia.

Oldfield *et al.* (1998) concluded that, worldwide, some 8,500 tree species are classified as threatened (**4**, **5**). Of these, over 4,500 are endangered or critically endangered in their native habitats, due in

6 Specimen of the tree fern *Cyathea* sp. growing in its native temperate rain forest habitat in Queensland, Australia.

7 Tall specimen of the palm *Woodyetia bifurcata* growing in an Australian botanic garden.

large part to over-logging of natural forests, or their clearance for cultivation (Chapters 2–5 and 14). However, the continued widespread occurrence of tree cover was recently confirmed by the UN Food and Agriculture Organization, which estimated that about one third of the Earth's land surface currently remains as forest (**1**; Lamb, 2002). Nevertheless, these calculations were probably overly optimistic, since the term 'forest' was applied to tree cover of as little as 10% on any land over half a hectare in area.



8 Tall specimen of *Betula pendula* (silver birch) growing in the wild in Scotland.

TYPES OF TREES

To many European and North American observers, it is perhaps surprising that some 300 species of ferns, principally in the genera *Cyathea* and *Dicksonia*, are arborescent. Tree ferns mainly grow in tropical mountainous regions, but are also found in temperate Australasia and elsewhere. Several species of *Cyathea* may reach 20 m in height, while *Dicksonia antartica* grows up to 10 m tall. The normally unbranched trunk of the tree fern rarely exceeds 30–40 cm in diameter and bears a terminal crown of very large compound fronds (leaves), which may be several metres long (**6**).

However, almost all tree species are angiosperms, commonly termed flowering plants (**7**, **8**), or gymnosperms (**4**, **5**). The seeds of gymnosperms are naked (not enclosed within a fruit) and are usually borne in obvious cones (**9**).

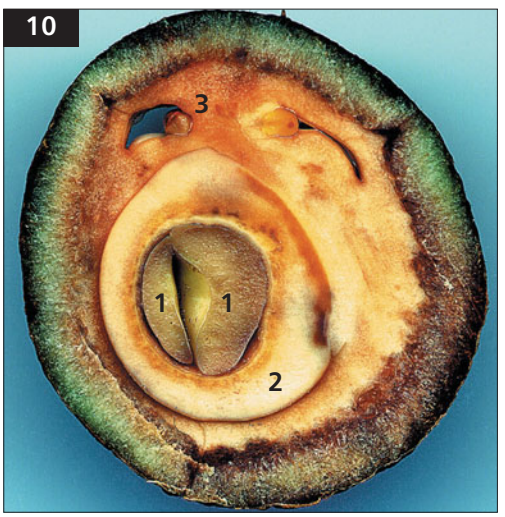
By contrast, the seeds of angiosperms are enclosed

9 Large cones of the conifer *Abies procera* (noble fir) native to northwestern America but growing in Scotland.

within a fruit (**10**), which develops from the carpel (pistil) on a flower (**11**).

Gymnosperms are almost entirely arborescent. Taxonomists give varying estimates of their present-day numbers, but it seems reasonable to conclude that at least 500 conifer (**12, 13**) and 200 cycad species (**14, 15**) are still extant plus a single species of *Ginkgo biloba* (maidenhair tree, **16**). Of the three gnetophyte genera, only *Gnetum gnemon* is a tree. Pollination in the gymnosperms is mostly effected by wind, but beetle vectors may be involved in cycads.

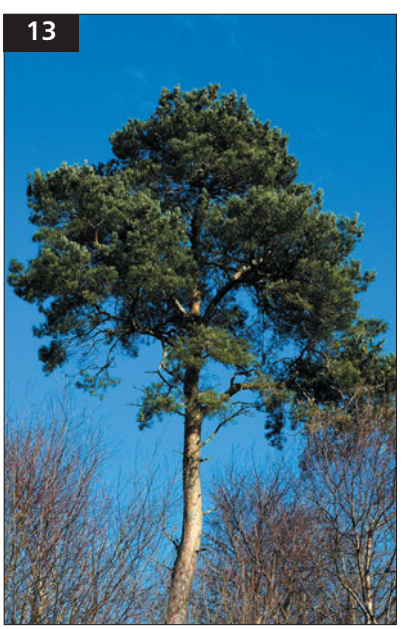
The latter are tropical/sub-tropical in distribution and bear large compound fronds (**15**). These xerophytic leaves have thick, waterproof cuticular coverings and sunken pores, or stomata, concerned with gaseous exchange from the internal leaf tissue to the outside air (**17**). Cycads are generally rather squat (**15**), although *Macrozamia hopei* may attain 20 m in height (Foster and Gifford, 1974). They bear either male or female cones on separate individuals, and generally these cones are massive (**14**). The trees undergo only very limited woody (secondary)



10 TS of an immature fruit of the dicot tree *Aesculus hippocastanum* (horse chestnut) showing two cotyledons (1) within the ovule (2). Fruit wall (3).

11 LS hermaphrodite flower of the arborescent dicot *Magnolia.* Note the numerous basal stamens, while abundant green carpels are inserted above on the flower axis.

12 Tall specimen of *Sequoia sempervirens* (coastal redwood and native to California) but planted in the mid-1800s in a botanic garden in Scotland.



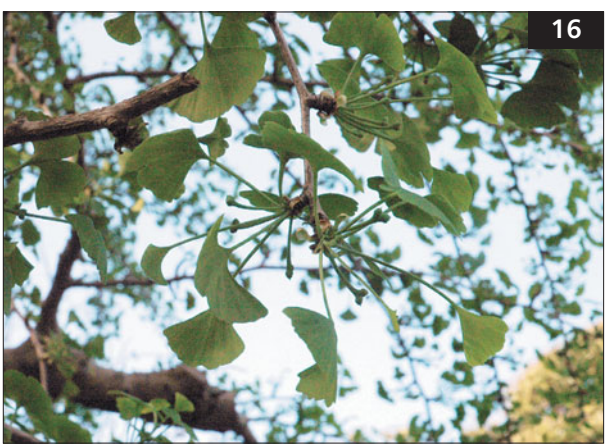
13 Tall specimen of *Pinus sylvestris* (Scots pine) growing wild on an exposed site in Scotland. Note the long trunk (devoid of branches) but with a terminal rounded canopy.

thickening but their trunks are strengthened by the covering of persistent fibrous leaf bases (**15**).

Conifers commonly have needle-like leaves as in *Larix* (larch), *Abies* (fir), *Picea* (spruces), and *Pinus* (pines, **18**). However, some have scale-like leaves, as in species of *Cupressus* (cypress) and *Chamaecyparis lawsoniana* (Lawson cypress), or spiny leaves, as in *Araucaria araucana* (monkey puzzle). Like the cycads,

14 Massive male cone of the tropical gymnosperm *Cycas circinalis*, but growing in a botanic garden in Scotland.

15 Large specimen of the African cycad *Encephalartos altseinii* growing in an Australian botanic garden.



16 Newly expanding foliage of the deciduous *Ginkgo biloba* (maidenhair tree) growing in an Australian botanic garden.

17 TS of a leaflet of *Cycas revoluta* showing its thick epidermal cuticle (stained dark blue) and sunken stomata confined to the lower epidermis.

18 Foliage of *Pinus caribaea*, which is native to the Caribbean region, but is here growing in an Australian botanic garden.

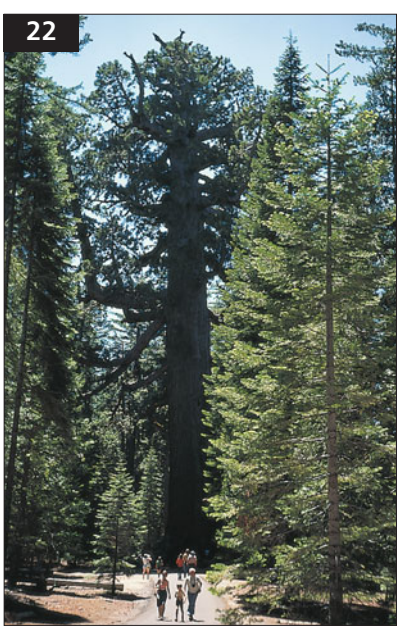
conifer leaves are generally xerophytic with several modifications, such as thick, waxy cuticules and sunken stomata, to minimize water loss. Most conifers occur in the boreal, montane, and temperate rain forests of the northern hemisphere (Chapters 2 and 3). The numerous species of *Pinus* (pine, **13**) are mostly indigenous to the northern hemisphere, but *P. caribaea* (Caribbean pine, **18**) occurs in its extreme south. Conifers such as species of *Fitzroya*, *Podocarpus*, and *Araucaria* (**5**) are indigenous to the southern hemisphere (Chapter 4). With some exceptions, such as *Larix* (larch) and *Metasequoia glyptostroboides* (dawn redwood, **19, 20**), most conifers are evergreens. Their leaves are generally shed over only a few years, while the large spiny leaves of *Araucaria araucana* (monkey puzzle, **5, 21**) last up to 30 years.

Conifers often grow into very large individuals (Chapters 2 and 3) and many are extremely long-lived, as is demonstrated in the famous Mariposa Grove in the Sierra Nevada of California. Here, there are many giant trees of *Sequoiadendron giganteum*

19 A specimen of *Metasequoia glyptostroboides* (dawn redwood), a deciduous conifer native to southwest China, in its winter aspect growing in England.

20 New foliage of the deciduous conifer *Metasequoia glyptostroboides* (dawn redwood).

21 Young specimen of the conifer *Araucaria araucana* (monkey puzzle) showing its spiny, long-lived leaves on the main stem and branches.



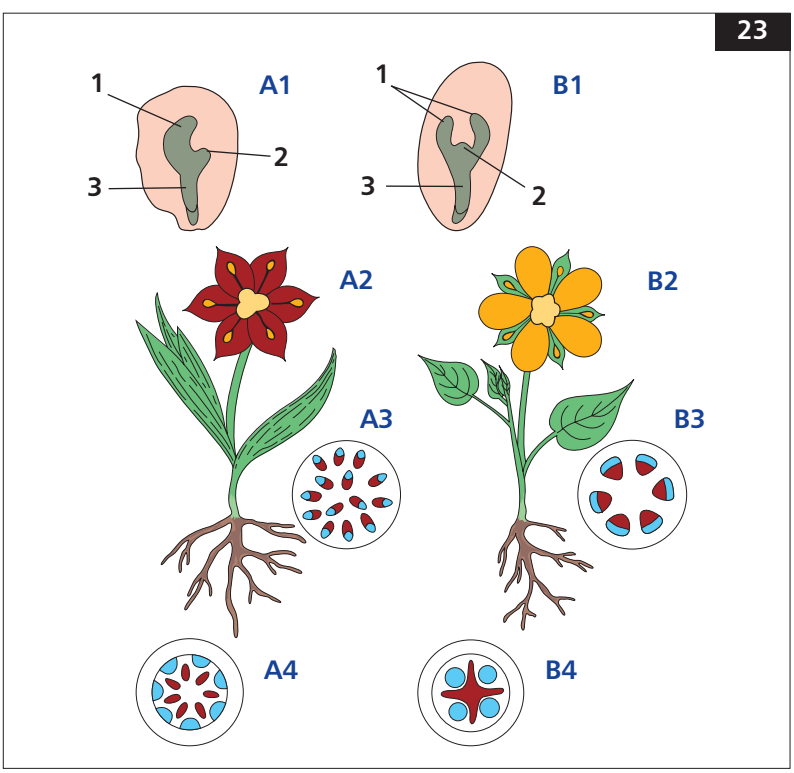
22 Massive ancient specimen of *Sequoiadendron giganteum* (big tree, Welligtonia) growing in its native habitat at Mariposa Grove, California, USA.

(big tree, Wellingtonia, **22**). A 3,500-year-old specimen of this tree (known as 'General Sherman') is ca. 83 m tall, with a basal diameter of some 11 m. On the Californian coast, a specimen of *Sequoia sempervirens* (coastal redwood) is 111 m in height, while other North American conifers such as *Abies procera* (Noble fir), *Pseudotsuga menziesii* (Douglas fir), and *Pinus monticola* (western white pine) may be 70 m or more tall. The oldest, accurately dated living tree is a nearly 4,770-year-old specimen of *Pinus longaeva* (the bristlecone pine 'Methuselah'), growing at about 3,000 m elevation in the White Mountains of California (Anonymous, 2003). A Scottish specimen of *Taxus baccata* (yew) is estimated to be 5,000 years or more old; but it is impossible to accurately date the relicts of such a large-diametered, but now much-fragmented specimen, which has none of its heartwood remaining (Lewington and Parker, 1999).

Flowering plants (trees, shrubs, and herbs) dominate most terrestrial habitats, except for the northern biomes of the moss- and lichen-rich tundra, and the conifer forests (Chapter 2). Angiosperms are divided into two main taxa (groups), the monocots and the many more numerous species of dicots, which display a number of different vegetative and floral characteristics (**23A, B**).

Monocots are mainly herbaceous and generally bear flower parts in threes or multiples of three. Their leaves are frequently long and narrow, with their main veins running lengthwise along the blade (**23A, 24**). Although most species are not woody, *Dracaena draco* (dragon tree) and some other monocots (Chapter 6) undergo an unusual form of woody secondary thickening and may form large trees. Many palms may also become tall trees (7) and some species live for more than a century (Tomlinson, 2003). Palms do not undergo secondary thickening, but instead increase in thickness by a process of diffuse secondary growth throughout the living tissues of the trunk (Esau, 1965).

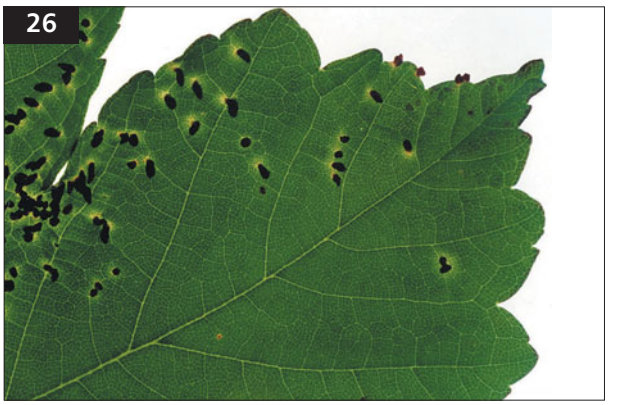
By contrast, in dicots the flower parts usually occur in fives or fours, or are indefinite in number (**11, 23B**) and most species show some degree of



24 Leaf of a large-leaved bamboo showing the arrangement of parallel veins in its leaf, which is typical of the venation in a monocot.

23A–B Idealized diagrams illustrating the salient differences between mono- (series **A**) and dicotyledonous (series **B**) flowering plants. **A1/B1**: LS seeds; cotyledon (1), plumule (2), radicle (3). **A2/B2**: Leaf and floral differences. **A3–4/B3–4**: distribution of the primary xylem (red) and phloem (blue) in the young shoots (**A3/B3**) and roots (**A4/B4**).

25 Leaves of *Firmiana malayana* (family Sterculiacea); although a tropical dicot tree, it is deciduous, shedding its leaves after a dry period and remaining bare for up to three months.



26 Leaf of the dicot *Acer pseudoplatanus* (sycamore) showing its branched veins which terminate in a reticulum of fine veinlets. Note also the numerous insect galls.

27 Newly expanding foliage from a breaking bud of *Aesculus hippocastanum* (horse chestnut) in spring.

28 Stump of the conifer *Pinus sylvestris* (Scots pine) clearly showing its annual rings.

woody thickening (Chapter 6). The leaves are generally relatively wide, and hence a dicot tree is commonly termed broadleaved (**25**). From the main vein(s) of the leaf, prominent side veins arise and further branch with the ultimate veinlets, forming a closed network in the leaf blade (**26**). On average, some 25–30 different broadleaved species occur per hectare of temperate forest, whereas the number of tropical tree species is much greater, with up to 300 present per hectare (Thomas, 2000; see also Chapter 5). Pollination of broadleaved trees is primarily effected by insects and, to a lesser extent, by birds and mammals, but wind pollination is common in species native to higher latitudes.

Temperate broadleaved trees are usually deciduous (Chapter 3), producing new leaves when the buds burst in spring (**27**). The foliage senesces and drops in autumn (the fall), with the accompanying dormancy of the tree. In seasonally dry tropical climates, trees such as *Firmiana malayana* (**25**) may shed their leaves during the dry season. However, most tropical species are evergreen (Chapter 5), and the woody thickening of their trunks and branches usually proceeds without abrupt interruption (Longman and Jenik, 1987). By contrast, in temperate broadleaved species, and also most coniferous trees, the annual growth rings mark the cessation of woody thickening at the end of the growing season in late summer/early autumn and its resumption in the following spring (**28**; see also Chapter 6).

IMPORTANCE OF TREES FOR CIVILIZATION

Trees and timbers have been used all over the world, both prehistorically and in historical times, in the construction of shelter and housing (**29, 30**). Today timber – together with a large variety of wood products – is used worldwide, both for domestic housing and for larger-scale constructions. Wooden-framed buildings (**31**) house more than 70% of the populations of Australia, Japan, North America, and Scandinavia. Such construction is much less popular in the UK but, even here, in a typical brick-built modern family house, wood is used for the rafters, trusses, joists, stairs, doors (and often the window frames), while the floors are either of timber or wood composites (Lewington, 2003). In developing countries of the tropics, smallholder farmers utilize agroforestry and cultivate various species of trees, as well as harvesting plants from the wild. These provide fruit, animal fodder, timber, poles, firewood, livestock fences, and shade, all in combination with the nurture of their livestock and food crops (Longman and Jenik, 1987).

In Burkina Faso (West Africa) the tree *Bombax costatum* (locally known as li-suoli) provides a profusion of edible or other useful products for the villagers. The flowers attract bees, which provide honey, the dried outer parts of its flowers make a mineral-rich sauce, the fruit is used in brewing, the floss around the seeds gives kapok; the bark yields a brown dye, the leaves provide animal fodder; and the timber is used for the fishermen's canoes. Among other species harvested from local trees for food are the leaves of *Adansonia digitata*, *Balanites aegyptica*, and *Commiphora africana*, and fruits from *Tamarindus indica* and *Saba comorensis* (Anonymous, 2005).

Many species of both conifers and broadleaved trees yield important commercial timbers. Conifer woods lack thick-walled hard fibres and are classed as softwoods. This term is somewhat misleading, since the water-conducting cells (tracheids) in the wood are often thick-walled and tough (Chapter 6). *Taxus baccata* (common yew), for instance, possesses a very strong, durable, and even-textured wood. Yew branches were used extensively in the Middle Ages for the production of the English longbow, while the hard wood is excellent for use in

29 Reconstruction of wooden crannoch (communal dwelling) built for the protection of its inhabitants over the margins of a loch, as used in the late Bronze/early Iron Age of Scotland.

30 The interior of the Great Hall of Stokesay Castle in England, which still retains some of the original massive oak trusses holding up its roof.

31 Exterior of a modern wooden-framed bungalow in Queensland, Australia (courtesy of Molly Miller). Despite the danger from termites, wood is still a very popular building material for Australian housing.

turnery. Broadleaved trees usually contain a large proportion of tough, thick-walled wood and fibres (Chapter 6), and hence are termed hardwoods. However, the soft, light, and easily carved wood of the tropical broadleaved *Ochroma pyramidale* (balsa wood) provides an obvious exception.

In the boreal (taiga) forests of the northern hemisphere across the far northwest of Europe, Russia, and North America, huge areas of natural conifer forests still exist (Chapter 2) but many have been very heavily logged. In Scandinavia and Finland most of the original conifer trees are now replaced by commercially managed secondary forests, and in northern Europe large areas of conifers such as *Picea abies* (Norway spruce), *P. sitchensis* (Sitka spruce), and *Pseudotsuga menziesii* (Douglas fir) have been planted. In the northwestern USA, plantations of *Abies* (firs), *Picea glauca* (white spruce), *Pinus* (pines), *Tsuga heterophylla* (western hemlock), *Pseudotsuga menziesii* (Douglas fir), and other conifers are widely established and provide very valuable commercial timbers. In the southern hemisphere various conifers, including *Araucaria araucana* (**5**), *Fitzroya cupressoides*, and species of *Agathis* and *Podocarpus*, have been logged for timber, sometimes to near extinction in the wild (Chapter 3). In addition to timber for construction, a vast quantity of conifer wood pulp, mainly from *Picea* (spruces), is processed into newsprint, cardboard, fibreboard, and rayon.

Several broadleaf trees provide important temperate and tropical hardwood timbers (Chapters 3–5). Some may attain great heights and *Eucalyptus diversicolor* (Karri), formerly an extensively logged native of southwest Australia but now protected, grows up to 87 m tall and 4 m in trunk diameter. In Tasmania, a 350-year-old specimen of *E. regnans* (called 'El Grande') was discovered in 2002. It was 79 m tall, with a girth of 20 m and an estimated volume of some 439 cubic metres (Anonymous, 2004). The tree was accidentally fire-killed (but still remains standing) by a mismanaged forestry regeneration burn, which spread from an adjacent logged area. In Tasmania this magnificent tree species is still being cut down to provide woodchip for the paper industries in Japan and elsewhere.

There are numerous other important hardwood trees, with some further examples being various species of *Carya* (hickories), *Dryobalanops* (kapur, camphor wood), *Fagus* (beech), *Fraxinus* (ash), *Grevillea* (silky oak), *Juglans* (walnut), *Khaya* (African mahogany), *Liquidambar* (satin walnut), *Magnolia* (magnolia), *Populus* (cotton wood, poplar), *Quercus* (oak), *Swietenia* (American mahogany), *Tectona grandis* (Asian teak), *Tilia* (lime, linden), and *Ulmus* (elm). Such trees provide very valuable timber and are extensively used for buildings/joinery, furniture, and sculpturing (**30, 32**). Smaller trees and branches are also harvested to provide poles, fuel, and charcoal (**33**). Finer branches from species such as *Betula* (birch), *Corylus* (hazel), *Salix* (willow), and other genera, often from trees which have been pollarded or coppiced (**34, 35**), are used for brooms, baskets, and fencing (**36**).

32 16th century carved limewood (*Tilia* sp.) altar piece from southern Germany.

33 Demonstration of a charcoal kiln in a national park in southern Spain.

34 Ancient pollard of the broadleaved *Salix* sp. (willow) growing along the river Cam in England.

35 Young coppice branches growing from a stool of the broadleaved tree *Acer pseudoplatanus* (sycamore).

36 Demonstration of a wicker fence, woven from coppice branches of *Corylus avellana*, at a crannoch reconstruction in Scotland (see also **29**).

Many broadleaved trees provide valuable foods and spices for human consumption (**37–42**). Some important examples from temperate and tropical regions are *Artocarpus* spp. (breadfruit and jackfruit), *Bertholletia excelsa* (Brazil nut), *Carica* spp. (papaws, mountain papaw), *Castanea* spp. (sweet chestnut, Chinese chestnut), *Cinnamomum verum* (cinnamon), *Coffea* spp. (Arabica, robusta, and liberica coffees), *Citrus* spp. (grapefruit, lemon, lime, tangerine, and orange), *Ficus carica* (edible fig), *Garcinia mangostana* (mangosteen), *Malus* × *domestica* (apples, in a large variety), *Mangifera indica* (mango), *Nephelium lapaceum* (rambutan), *Olea europea* (olive), *Pistacia vera* (pistachio), *Prunus* spp. (apricot, cherry, damson, nectarine, peach, and plum), *Syzgium aromaticum* (clove), and *Theobroma cacao* (cocoa).

In addition to such broadleaved trees, the monocot palm family, which is mainly confined to the tropics and sub-tropics, contains a number of trees which provide very important foods. Coconuts are gathered from *Cocos nucifera* (**43**), dates from

37 Crop of *Citrus aurantium* (Seville orange) growing on a southern Spanish street.

38 Tropical breadfruit on the small broadleaved tree *Artocarpus*.

39 Apple tree (*Malus* x *domestica*) bearing ripe fruit in an English autumn.

40 Fruits of *Juglans nigra* (black walnut) – a broadleaved tree native to North America but here growing in England.

Phoenix dactylifera (**44**), and sago from the trunk of the *Metroxylon sagu*. *Metroxylon rumphii* and the fruits of *Elaeis guineensis* yield both palm oil and palm kernel oil. Various palm species are also tapped for their sugary sap, which may be used as a sweetener or fermented into toddy. Palm hearts (terminal buds) are harvested from various palms, and provide a vegetable delicacy. Many palms are also of importance for housing, with their trunks used for beams and flooring, and the leaves for roofing and weaving. Species of *Pandanus* (screw pines, another tropical family) yield large fruits (**45**), which are roasted and their seeds eaten by the Australian Aborigines. The long fibrous leaves of *P. utilis* are also used in thatching and to make Manila

41 Fruits of the tropical broadleaved evergreen tree *Garcinia mangostana* (mangosteen) – some fruits have been opened to show their white arils containing the edible seeds.

42 Fruits of the tropical broadleaved tree *Nephelium lapaceum* (rambutan) with some fruits opened to show their edible arils.

43 Crop of coconuts borne among the terminal crown of palm leaves on the arborescent monocot *Cocos nucifera*.

44 Crop of edible date fruits from the tropical palm *Phoenix dactylifera*.

45 Fruit of the arborescent monocot *Pandanus* sp., which provides a food sometimes eaten by the native (aboriginal) Australians.

46 Edible seeds and fan-shaped foliage of the gymnosperm *Ginkgo biloba* (maidenhair tree).

47 Mature seeds of the shrubby cycad *Cycas circinalis*. The seeds are highly toxic (as are all cycad seeds) but after prolonged leaching in water they can be safely eaten.

hats. The long, hollow, and very strong stems of several tall tree-like bamboos, such as *Dendrocalamus* spp., are used extensively to build houses and bridges, for scaffolding in building construction, and also as water pipes. The newly emerged shoots of bamboos, such as species of *Bambusa*, *Dendrocalamus*, and *Phyllostachys*, are harvested when about 15 cm long and, after removal of their enclosing leaf sheaths, are widely cooked as a vegetable in Asia.

The seeds of a number of conifers and some other gymnosperms are edible. Examples include various species of *Pinus*, *Araucaria* (bunya-bunya pine, monkey puzzle, and parana pine), *Gnetum gnemon* (gnetum), and *Ginkgo biloba* (ginkgo, **46**). In some Pacific Island countries, and also Australia, the indigenous people gather starchy seeds of *Cycas* (**47**) and other cycads such as *Lepidozamia peoffsykana*. After prolonged leaching in water, the seeds can be ground into flour. However, the fresh untreated seeds are very poisonous for humans (Chapter 4).

Several plant commodities are derived from the bark of trees; such as cork from *Quercus suber* (**48**), fabric and rope from *Adansonia* spp., and rubber from *Hevea brasiliensis*. Various drugs and medicines are also sourced from trees. Quinine is derived from the bark of *Cinchona officinalis*, while an extract from the bark of the *Prunus africana* is used to treat prostatic disorders. The latter species is slow-growing and classified as endangered due to over-felling in the wild. In Kenya, a single tree may fetch around £100 for its bark (Lewington, 2003). Many other trees yield a variety of medicines. Aspirin was originally isolated from *Salix alba* (white willow), while various antiseptics are also derived from trees, for example tincture of witch hazel from *Hamamelis virginiana*, tea tree oil from *Melaleuca alternifolia*, and eucalyptus oil from species of *Eucalyptus*. Recently, the drug Taxol has been isolated from *Taxus brevifolia* and *T. baccata* (Pacific yew and common yew, **49**) and is used in the treatment of breast and ovarian cancers.

Trees and forests are very important as amenities, particularly in the developed world, for activities such as walking, hunting, riding, picnicking, and general relaxation. In the past, and still to some

48 Stacked cork from the bark of the evergreen broadleaved tree *Quercus suber* (cork oak), after harvesting in Spain.

49 Foliage and 'berries' of *Taxus baccata* (common yew). The foliage and red 'berries' are sometimes eaten by cattle with fatal results but the foliage contains a potent anticancer compound which, when extracted, is marketed as Taxol.

50 Specimen of a large evergreen broadleaved tree *Ficus* sp. (fig) – this is regarded by Buddhists as a sacred tree, as indicated by the ribbons tied around its trunk and small figures of Buddha embedded in its roots.

extent today, trees have had deep spiritual/religious significance for humans. In Europe, oaks (*Quercus robur* and *Q. petraea*) were important in Germanic and Norse mythology, while in Britain the Celts believed oak trees to be sacred. Also, throughout Europe, the evergreen, long-lived, and highly poisonous common yew (*Taxus baccata*, **49**) must have been of great significance to our ancestors. Ancient specimens grow in many churchyards, and it is likely that some of these churches were established on what were originally pagan religious sites (Lewington and Parker, 1999). The relic yew, still just surviving in the church graveyard at Fortingall in Scotland, greatly pre-dates the coming of Christianity to Scotland. In Asia, several species of fig, in particular *Ficus benghalensis* (banyan tree) and *F. religiosa* (bodhi tree), are revered. Buddha is believed to have gained enlightenment while sitting under a specimen of the latter tree. Such figs still often have images of Buddha embedded in their spreading roots, while the trunk is bound round with yellow and red ribbons (**50**). *Ginkgo biloba* (ginkgo, **46**) still exists in the wild, but as an endangered species, in a mountainous area of Zhejiang, China. However, it has also survived in Chinese, Korean, and Japanese temple gardens, having been planted there and tended by Buddhist monks. In Chile, *Araucaria araucana* (monkey puzzle, **5**) is a sacred tree for the Pehuenche Aborigines, with its nutritious seeds forming a staple of their diet.

TREE ARCHITECTURE

Trunk and canopy of the aerial tree

In most trees it is estimated that the trunk (**51**) makes up 40–60% of their mass, while the aerial canopy (which bears the foliage, cones, flowers, and fruit; **5, 8, 25, 37**) contributes another 20–30% (Thomas, 2000). Frequently, the height of a tree is approximately 100 times its trunk diameter, but there are various exceptions to this rule of thumb (**52**). Many conifers retain a single main trunk, from which arise regular rings of branches (**53**). The mature conifer tree canopy often retains a regular pyramidal form (**12, 19**), due to its continued growth from a dominant terminal bud. Boreal and montane conifers (Chapter 2) often have branches that slope downwards and from which the snow tends to slide off, while some species of *Abies* (fir) and *Picea* (spruce) have broad canopies when growing in deep shade or at treeline level (Thomas, 2000). Tree architecture often changes with age. For example, *Pinus sylvestris* (Scots pine) is more or less conic when young but, particularly in exposed sites, many of its lower branches have been lost by the time it attains maximum height. Its long trunk is often then left bare, except for its terminal canopy (**13**).

Palms and some other arborescent monocotyledons frequently show an unbranched trunk bearing a terminal tuft of large, elongated leaves (**7, 43**). The natural form of broadleaved trees is very variable, and their canopies may range from somewhat spherical to broadly spreading (**1**). The latter shape is commonly seen in European temperate species (**8**). In marked contrast, some broadleaved trees are narrowly or broadly columnar, with examples seen in *Fagus sylvatica* 'Fastigiata' (Dawyck beech, **54**), *Populus nigra* 'Italica' (Lombardy poplar), *Nothofagus cunninghamii* (myrtle beech), and *Chrysolepis chrysophylla* (golden chestnut). *Polyalthia longifolia* (Indian mast tree) has a weeping habit. Various 'architectural models' have been proposed to encompass the extensive range of tree forms, but it seems that each species conforms to one of 25 possible characteristic branching patterns (Bell, 1991).

According to Thomas (2000), the shape of a tree is also a compromise between various factors, such as the overall exposure of the foliage to optimize photosynthesis, reproduction (the display of flowers for pollination and subsequent seed dispersal), the most 'cost-effective investment' by the tree in growing its large wooden skeleton, and the response of the tree to its immediate physical surroundings. Hence, in addition to its basic 'architectural model', the shape of a tree is often greatly modified by external environmental factors, such as grazing and wind (**13, 55–57**), disease (**58**; see also Chapters 8 and 9), and pruning/tree surgery (**34, 35, 51**; see also Chapter 12).

51 Massive ancient pollarded specimen of the broadleaved deciduous tree *Quercus robur* (English oak) growing in the wood pasture of Hatfield Forest, England.

52 Huge swollen trunk of the broadleaved sub-tropical tree *Brachychiton rupestris* growing in an Australian botanic garden.

53 Trunk of *Pinus sylvestris* (Scots pine) showing how several side branches all originate in whorls at the same level from the trunk.

54 Specimen of the broadleaved *Fagus sylvatica* 'Fastigiata', which in 1860 originated as a sport in the woodland at Dawyck, Scotland.

55 Group of wind-trimmed conifers ('Krumholz') exposed to fierce gales on the tree line at Libby Flats, Wyoming, USA.

56 Grazed and wind-trimmed miniature specimen of *Fraxinus excelsior* (ash) growing in a gryke of the limestone pavement on the Burren Region of western Ireland.

57 Major branch breakage on a large specimen of *Quercus petraea* (sessile oak) growing in native mixed woodland in Scotland.

58 Canopy of *Pinus sylvestris* (Scots pine) with a huge foliage gall probably caused by infection with the fungus *Taphrina*.

Underground root system of the tree

Tree roots generally lie underground and hidden from view, unless exposed by erosion in a wind-blown tree or on a very shallow soil over bedrock (**59, 60**). Nevertheless, the complexly branched root system is a vital component of the tree. Water and nutrients are absorbed from the soil via the roots, and anchorage for the aerial trunk and canopy is also provided by the root system. In thickened roots, an outer layer of impermeable cork is present, but the lenticels are channels through which gaseous exchange with the soil atmosphere can occur (**61**). In many trees, the root system is estimated to make up 20–30% of the tree mass, but the figure may be as little as 15% in some tropical trees and up to 50% in trees growing in very dry conditions (Thomas, 2000).

A tree root system generally shows a central plate of framework roots (**60**), which then spread laterally as far as the margins of the aerial leaf canopy, where they are much narrower and are primarily concerned with the absorption of water and its dissolved minerals. At their origin from the trunk, the framework roots may be 30 cm or so thick, and frequently graft together where they cross each other, so producing a rigid root plate which binds the associated soil and stones together (**59, 60**). The swollen root bases often produce a prominent collar at the base of the trunk which, even in temperate trees, may flare into small buttresses (**62**). However, in many tropical trees, this is much more marked and the root buttresses may extend several metres up the trunk and slope for some distance obliquely into the soil (**63**).

According to Rackham (2004), most trees in England are shallow-rooted, with the tap root not persisting after early seedling growth. This is also frequently likely to be the case in Europe and elsewhere, with such trees very susceptible to gales. In the woodlands of western Scotland many wind-thrown, prostrate, but living trees still survive after gales from some decades earlier. These continue to grow actively but with only very limited root contact with the soil (**64**). A similar situation occurs when a standing tree is root pruned (as in site clearance for construction or road building). It is estimated that in many cases a tree may survive when only a quarter (sometimes less) of its root system still remains (Rackham, 2004). However, although such a restricted area of roots may be sufficient for the water requirements of the tree, it will often be insufficient for its role as a stabilizing support for the aerial tree. In areas with only a thin soil cover, the root plate lies superficially (**59**), and the expansion of these roots that accompanies secondary thickening helps to fragment and weather the surface of the underlying bedrock (**65**). In deeper soils the root plate may be situated a metre or more beneath the surface, while sinker roots may further grow down to a deeper lying water table.

59 Underside of the root plate of a wind-felled specimen of *Fraxinus excelsior* (ash) growing in mixed native woodland in Scotland.

60 The root plate of *Quercus petraea* (sessile oak) felled by wind-blow, and then exposed after flooding by the waters of Loch Lomond, Scotland.

61 Detail of a main root of *Quercus petraea* (sessile oak), exposed after flooding/soil erosion, showing numerous lenticels in its bark.

62 Young specimen of the deciduous broadleaved tree *Fagus sylvatica* (beech), demonstrating that even temperate trees may develop root buttresses.

63 Massive root buttresses on the tropical broadleaved tree *Parkia javanica*.

64 Large wind-blown specimen of *Quercus petraea* (sessile oak) in Scotland, which was probably felled by the devastating gales of 1987/1990, now showing the transformation of a side branch into a large vertical new trunk despite its meagre root connection to the soil via the original root plate.

65 Part of the exposed root system of *Fraxinus excelsior* (ash) growing in rock fissures and helping to break up the bedrock.

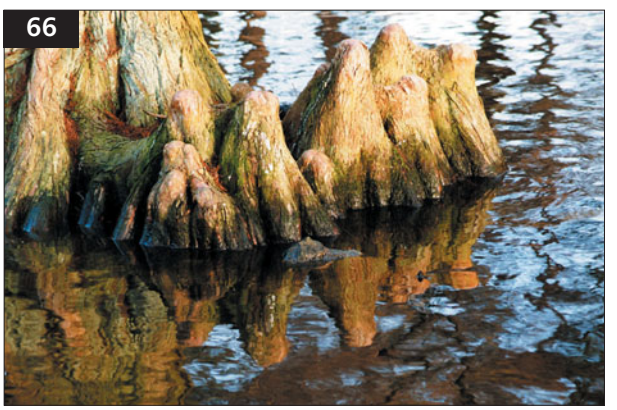
Accessory roots on the aerial tree

Some trees develop trunk- or branch-borne adventitious roots. As well as providing an increased aerating and absorbing surface (**66, 67**), these may serve as an additional anchorage/support to the trunk, as in species of *Ficus* and *Pandanus* (**68, 69**), and also facilitate the spread of the tree following branch rooting (**70**).

Tidal mangroves have various anchorage and aeration devices, such as the complex stilt (prop) roots of *Rhizophora* spp., the upright peg roots of *Avicennia* spp., and the knee roots of *Bruguieria* spp. (**67**). At low tide, atmospheric oxygen diffuses through the lenticels into the well-developed cortical intercellular space system of the subterranean roots. Knee roots also develop in the gymnosperm *Taxodium distichum* (swamp cypress, **66**).

Pillar and strangler root systems occur in a number of species of fig (*Ficus*, **69, 71**). A specimen of *F. benghalensis* (banyan tree), planted in 1782 in Calcutta, now forms a tree grove comprised of some 1800 separate pillars (trunks), which originated as branch-borne adventitious roots (Thomas, 2000). The roots of the strangler figs originate from a seed(s) germinating in the canopy of a host tree. These roots repeatedly branch and anastomose as they grow down the trunk and eventually reach the soil. The host trunk often becomes completely enclosed ('strangled'), dies, and then rots away. The shell of fused *Ficus* spp. roots remains (**71**) and these thicken to form an independent hollow-trunked fig tree.

Many old trees are hollow, and very commonly the growth of internal adventitious roots within the trunk allows recycling of nutrients released from the rotting heartwood. In the UK this is especially common in ancient pollards of tree such as *Fagus sylvatica* (beech, **72**), *Fraxinus excelsior* (ash), and *Carpinus betulus* (hornbeam). In other trees, the rooting of low branches (layering) may eventually



66 Knee roots of the conifer *Taxodium distichum* native to swampy areas of the southern USA.

67 Breathing roots in tropical broadleaved trees. Knee roots of *Bruguieria gymnorhiza* and upright air roots of *Avicennia marina* exposed at low tide in the coastal mud flats of Queensland, Australia.

68 Prop roots of the arborescent monocot *Pandanus pedunculatus* growing along the sandy coast of New South Wales, Australia.