

Chapter 2

AUSTRALIAN VEGETATION

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The woody plants of Australia have been noted for their uniqueness from the time of their discovery and study by European botanists. How different they are is a matter of interpretation, but a degree of uniqueness derives from the fact that some 75% of the species are endemic to Australia and the woody vegetation over most of the continent is dominated by two large genera, *Eucalyptus* and *Acacia*. At a higher taxonomic level, almost all angiosperm families in Australia occur widely in other parts of the world. In this sense, the Australian flora is a typical segment of the world flora and the special character of Australian plants has to be explained in terms of the geography and environment in which they have evolved (Barlow 1981).

Prolonged isolation of Australia following the break-up of the southern super-continent of Gondwana has contributed greatly to the distinctiveness of the vegetation. Australia has been isolated from other continents and even from its near neighbour, New Zealand, for at least 60 million years. During this long period great changes occurred in the climate and soil, which were important in the evolution of the modern flora.

EVOLUTION OF THE MODERN FLORA

The most significant events shaping the evolution of Australian flora took place during the Tertiary period (3–65 million years ago) and the Quaternary period (present to 3 million years ago). During the early Tertiary it is probable that Australia was uniformly humid with a warm seasonally-wet climate, a set of conditions that favoured the development of lateritic soils on the already highly-weathered land surface over much of the continent. These laterites still persist in tropical areas and on mesa formations in the arid zone. Laterisation reduced an already low soil fertility level by progressively fixing phosphorus in insoluble iron and aluminium complexes. Infertile sands derived from

weathered laterites were dispersed across the continent and added to similar poor sandy soils derived from sandstone and granite.

Land movements and volcanic activity in the late Tertiary provided some soils of higher fertility in eastern Australia but overall soil fertility appears to have declined in the period leading up to the present. Beadle (1966, 1981) suggests that such soil changes were responsible for the primary evolutionary directions within the Australian flora; many elements of the modern flora have adaptations that enable them to survive and grow on nutritionally very poor soils.

Evidence from fossils indicates that mesophytic communities dominated by temperate rainforest covered much of Australia, including the interior, in the early Tertiary. Major climatic changes occurred in the remainder of the Tertiary, possibly due to the northwards drift of the continent into drier latitudes. It has been postulated that about 10 million years ago the north of Australia became arid or semi-arid and that these conditions moved progressively southwards. The moist temperate climate contracted southwards, except in the eastern ranges, and the northern leading edge of the continent entered the moist humid tropics. The scenario, with significant fluctuations during the Quaternary including several glacial periods, suggests that there has been a major increase in the extent of arid areas in Australia in the last 15 million years.

The increased aridity and greater climatic variability would have fragmented the temperate rainforests established in the relatively stable, humid climate of the early Tertiary. These formations became generally restricted to moister enclaves in eastern and southern Australia, although remnants adapted to drier conditions are now represented in so-called 'softwood scrubs' by species such as *Brachychiton populneus*, *Flindersia maculosa* and *Geijera parviflora*.

Expansions and contractions of communities in response to climatic fluctuations have left disjunct, relict

species and populations amongst the present vegetation associations. Many of the species in the modern flora have experienced a variety of environmental conditions and clearly have needed a wide ecological amplitude to survive. The gene pools must have undergone considerable sorting and selection during these vicissitudes leading to the evolution of new species and a high overall genetic variability in the more-widespread species.

Many Australian species have specialised adaptive traits for survival and reproduction that suggest that fire has been a major influence in their evolution (Gill 1981a). It seems likely, however, that long-term evolution of the flora has been influenced more by changes in climate and soils and that the major effect of fire has been relatively recent. Singh et al. (1981) suggest that the use of fire by Aboriginal people in the past 40 000 years, probably resulting in more frequent and less intense fires than in pre-Aboriginal times, has been at least partially responsible for the dominance of *Eucalyptus* and other fire-adapted genera over large areas of Australia. This situation appears to be very different from the more distant past when fire-sensitive plants seem to have been more widespread.

VEGETATION TYPES

Each plant species has a range of environmental conditions in which it is able to grow. Some species with wide ecological tolerances tend to be widely distributed while those with a narrow range tend to be restricted to specific habitats. Species with similar requirements occur in associations or communities, which together constitute the overall vegetation.

Different types of vegetation can usefully be characterised by criteria such as life form, height and leaf size.

There have been various attempts to devise a classification to accommodate satisfactorily the distinctive vegetation of Australia. The system most widely recognised at present was drawn up by Specht (1970) and defines structural forms of vegetation in terms of life form and projective foliage cover of the tallest stratum (Table 2.1). The use of foliage cover rather than canopy cover in classifying Australian vegetation takes special account of the open nature of *Eucalyptus* crowns. Trees and shrubs are involved in 20 structural forms defined by five life forms and four classes of projective foliage cover.

In the classification, a tree is defined as a woody plant more than 5 m tall, usually with a single stem. A shrub is a woody plant less than 8 m tall, frequently with many stems arising at or near the base. Projective foliage cover is the percentage of area covered by foliage, measured by a vertical point quadrat technique. The categories include six types of forest ranging from tall closed-forest to low open-forest. They encompass the older and still commonly used terms of 'rainforest,' 'wet sclerophyll forest,' and 'dry sclerophyll forest'.

The broad vegetation types have been mapped by Carnahan (1977) to show their probable distribution immediately prior to European settlement 200 years ago (Figure 2.1).

The following brief accounts of major Australian vegetation types include only those structural forms of vegetation in which woody perennials over 2 m in height are prominent. Heaths, low shrublands, hummock grasslands and herblands are therefore not covered.

Closed-forests

Such forests are commonly known in Australia as 'rainforests'. They are tree-dominated communities, almost

Table 2.1. Structural forms of vegetation in Australia (based on Specht 1970).

Life form and height of tallest stratum	Projective foliage cover of tallest stratum			
	Dense (70–100%)	Mid-dense (30–70%)	Sparse (10–30%)	Very sparse (< 10%)
Trees > 30 m	Tall closed-forest	Tall open-forest	Tall woodland	Tall open-woodland
Trees 10–30 m	Closed-forest	Open-forest	Woodland	Open-woodland
Trees 5–10 m	Low closed-forest	Low open-forest	Low woodland	Low open-woodland
Shrubs 2–8 m	Closed-scrub	Open-scrub	Tall shrubland	Tall open-shrubland
Shrubs 0–2 m	Closed-heath	Open-heath	Low shrubland	Low open-shrubland

always with a 'closed' canopy, and usually characterised by broadleaved evergreen species lacking adaptations to dry conditions. A closed canopy means the crowns of the trees touch or overlap so that little sunlight penetrates to the forest floor. Tree and shrub components occur in at least two layers. Closed-forests at one time covered much of the landmass of Australia and provided the primitive stocks that gave rise to the bulk of the modern Australian flora.

The closed-forest communities occur primarily in eastern Australia from tropical northern Queensland to cool temperate Tasmania at altitudes from near sea level to 1200 m or more. Small outliers occur along the tropical coasts of the Northern Territory and Western Australia. Fragments of closed-forest derived from ancient communities are also found in gorges and other specialised environments within the arid and semi-arid zones of tropical and subtropical Australia. The total area of closed-forest at the time Europeans began clearing for agriculture was less than 1% of the land area and is estimated at 6–8 million ha, of which about 2 million ha remain (Webb and Tracey 1981). According to Baur (1989), there is 1.2 million ha of

rainforest in Queensland and 0.7 million ha in Tasmania. The biodiversity of rainforest formations is much more than might be expected from its limited area, for they include perhaps half of the total terrestrial biota of Australia (Bell 1981).

Closed-forest formations usually occur in areas with a mean annual rainfall in the range 1200–2500 mm but the drier types may extend to regions with 600–800 mm. Four main types have been recognised: tropical, subtropical, warm temperate and cool temperate. These closely approximate to the mesophyll vine forest, notophyll vine forest, microphyll fern forest and nanophyll moss forest of Webb (1959). The main differences between the tropical and temperate closed-forests are the greater structural complexity and the larger number of tree species present in a given area of the former type. A closed-forest (rainforest) is strictly defined to exclude species that do not regenerate within a well-developed or only slightly disturbed canopy (Webb and Tracey 1981). This definition excludes all species of *Casuarina*, *Eucalyptus* and *Melaleuca* and all but a few species of *Acacia*, *Lophostemon* and *Tristania*. Acacias such as *A. aulacocarpa*, *A. bakeri*, *A. cincinnata*, *A. fasciculifera*, *A. hylonoma*, *A. mangium*

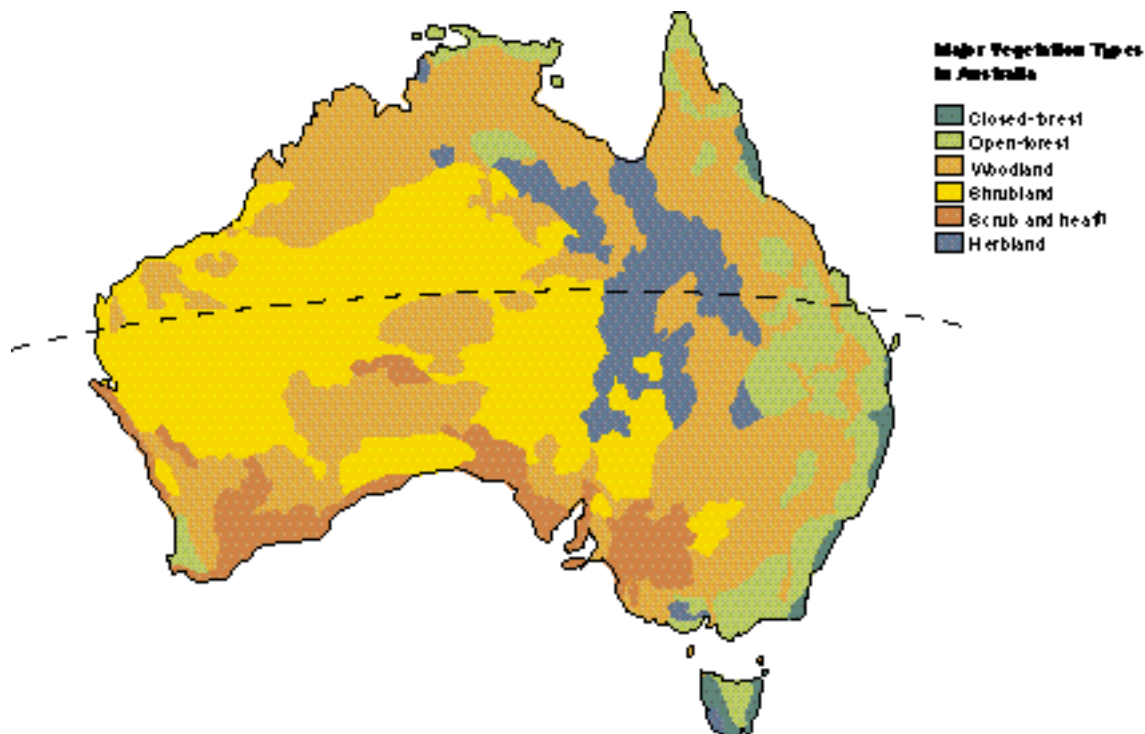


Figure 2.1. Major vegetation types in Australia (from Carnahan 1977).

and *A. melanoxylo*n may be regarded as components of closed-forest but are more often found in marginal communities or in more extensive disturbances within the closed-forest, usually where the soils are of low fertility.

The complex pattern of closed-forest and eucalypt open-forest within climatically suitable regions of eastern Australia is primarily related to soil nutrient status (Webb 1969) or to the influence of topography on soil properties. Closed-forests occur on the more fertile soils and have only a limited occurrence on soils derived from acidic rocks such as rhyolites, sandstones and some shales. Soil physical properties are of lesser importance, although closed-forests in higher rainfall areas typically grow on well-drained soils. The ecological balance between the eucalypts and acacias on one side and rainforest species on the other is much more precarious on soils of lower fertility than on highly fertile soils. Frequent fires may maintain a eucalypt or acacia community on a soil of somewhat low nutrient status, which in the absence of fire would support closed-forest. Similarly where soils are temporarily or permanently waterlogged, closed-forest may give way to open-forest dominated by *Melaleuca* species.

Many trees of the closed-forest formations are relatively slow-growing, intolerant of poor soils and sensitive to fire. They commonly provide fine timbers but are of little value for the rapid production of posts, poles and fuelwood now so much in demand in developing countries. It is on the margins of closed-forest where fires are frequent or the soils are of lower fertility that fast-growing, adaptable species with a high potential for planting are to be found. Well-known, successful species such as *Acacia mangium*, *Eucalyptus grandis* and *Melaleuca leucadendra* typically occur in such situations.

Several specialised forms of closed-forest exist in particular habitats and these communities have the potential to provide useful trees and shrubs for planting. They include forests designated semi-evergreen vine forest, softwood scrub, gallery rainforest and mangroves.

Semi-evergreen vine forest, sometimes called 'monsoon forest', occurs in northern Australia where the mean annual rainfall of 1300–1500 mm is concentrated in a short summer wet season and there is little effective rainfall in the remainder of the year. In drier areas these forests may extend along watercourses or

occupy sites receiving runoff water from higher ground. They occur on a wide range of soils including lateritic red earths, lateritic podzols and even dune sands. They include such species as *Acacia auriculi-formis*, *A. aulacocarpa* and *Alphitonia excelsa*. Where water availability is limiting during the dry season, the canopy is lower and dominated by deciduous species such as *Bombax ceiba* and *Terminalia sericocarpa*. In many inland and coastal vine forests of the Northern Territory up to 90% of species may be seasonally deciduous. While many of these species tolerate seasonal drought, it appears that they possess neither the physiological capabilities nor the regenerative capacities which enable eucalypts to compete so effectively in a fire-prone environment (Brock 1988).

Another interesting group of communities occurs sporadically in semi-arid and sub-humid zones of northern Australia. It includes species of genera that otherwise occur in wetter closed-forest. These species are shrubs or trees that form distinctive communities referred to as 'softwood scrubs' in some localities or occupy the understorey in eucalypt forest or are found as scattered individuals in *Acacia* shrubland. These dry closed-forest taxa include species of potential value for fuelwood and agroforestry such as *Acacia shirleyi*, *Brachybiton* spp., *Lysiphyllum cunninghamii*, *Terminalia oblongata* subsp. *volucris* and *Ventilago viminialis*.

Gallery rainforests are closed-forests that fringe watercourses. They may occur within the general closed-forest complex and include species such as *Grevillea robusta*, *Melia azedarach* var. *australasica* and *Toona ciliata*. Elsewhere they extend as ribbons into drier country where they may be dominated by *Syzygium floribundum*, *Grevillea robusta*, *Casuarina cunninghamiana* or *Nauclea orientalis* sometimes in association with *Eucalyptus camaldulensis* or *E. tereticornis*.

Mangrove communities are found on many parts of the Australian coast and in structural terms vary from tall to low closed-forests to open shrublands. They can therefore be regarded as rainforest. Adam (1992) treats mangroves as just one of many rainforest formations even though some occurrences are on climatically dry coasts or have a shrubland structure.

In general, mangrove communities occur in the intertidal zone on the coast or in river estuaries and range in height from over 30 m to less than 5 m.

Globally, about 80 species in several genera are regarded as mangroves and the Australian flora includes about 40 species in 15 families. The canopies of mangroves have few species and in many stands there is only a single species. Mangrove species have characteristics which are regarded as adaptations to growing in saline and waterlogged environments. Some produce root adaptations, pneumatophores, which facilitate gaseous exchange, especially of oxygen. *Avicennia marina* produces thin pencil-like pneumatophores from long cable roots while in *Bruguiera* species they are thick and knee-like.

More detailed accounts of Australian closed-forest can be found in Beadle (1981), Webb and Tracey (1981), Figgis (1985), Werren and Kershaw (1987), Brock (1988) and Adam (1992).

Open-forest

In Australia open-forests are usually dominated by *Eucalyptus* trees, although in drier areas species of *Acacia* and *Callitris* may assume dominance. The projected foliage cover is 30–70%, so that the penetration of the main canopy by light may be substantial, and the trees usually develop a forest form with flat crowns and trunks greater in height than the depth of the crowns.

Extensive areas of open-forest cover a broad geographical range from the tropics to temperate regions with great variation in canopy height and structural complexity. Open-forest extends across the northern part of the Northern Territory and to the coastal and highland regions of northern Queensland, southwards through coastal New South Wales, eastern Victoria and Tasmania. The formation is also common in the south-western corner of Western Australia.

The open-forest formation has been divided into three subformations, viz. 'tall open', 'open' and 'low open' (Table 2.1). In ecological and forestry literature tall open-forest has commonly been referred to as 'wet sclerophyll forest' and open- and low open-forest as 'dry sclerophyll forest'. Tall open-forest covers 126 000 km², principally in New South Wales (55%) but with substantial areas in Victoria (21%) and Tasmania (17%). Open-forest extends over 217 000 km² and is prominent in Western Australia (22%) although the main areas are in New South Wales (42%) and Victoria (26%) (Specht et al. 1974).

A striking feature of the open-forests of Australia is dominance by species of the genus *Eucalyptus*. Typically two or three eucalypt species grow together as co-dominants in the same stand. Only in a few forest types, mainly in drier or cooler areas, is a single species dominant. For example, some of the more significant tall open-forests are dominated by *E. camaldulensis*, *E. delegatensis*, *E. diversicolor*, *E. grandis*, *E. pilularis* and *E. regnans*. Throughout these forests two habitat factors, water availability and the level of soil fertility, strongly influence species composition and growth. The interplay of these factors and the great number of eucalypt and acacia species give an unusual character to the open-forests. Because the dominant eucalypts, and to some extent the acacias, are very sensitive to habitat conditions, the species change more frequently and rapidly than in open-forests elsewhere in the world (Ovington and Pryor 1983). The structure and composition of the understorey of open-forest change with rainfall, soil type, fire frequency and latitude. In tall open-forest of the wetter areas (over 1000 mm annually) there is usually a dense understorey including tree ferns and tall shrubs, but as rainfall decreases the amount of understorey also becomes less. *Acacia* species are prominent in the understorey of these forests and in the drier areas, or on particular soil types, may assume dominance.

1 Tall open-forest

Tall open-forest is capable of developing on most closed-forest sites under appropriate fire regimes, but elsewhere it is extensive in mountain areas where the annual rainfall is in the range 1000–1500 mm. Temperature conditions range from cool, with frosts and snowfalls, in the mountainous areas of southeastern Australia to mild and warm in coastal Queensland and southwestern Western Australia. Exceptionally tall *Eucalyptus* trees, often over 60 m, are characteristic of this subformation. In the subtropical areas of New South Wales and Queensland the tall open-forests are dominated by *E. pilularis*, *E. microcorys*, *E. saligna* and *E. grandis*; the more temperate southeastern forests by *E. obliqua*, *E. viminalis*, *E. fastigata*, *E. delegatensis*, *E. nitens* and *E. globulus*; and in southwestern Western Australia *E. diversicolor*, *E. calophylla*, *E. jacksonii* and *E. guilfoylei* are common (Ashton 1981). Associated

smaller trees and shrubs include *Acacia dealbata*, *A. binervata*, *A. melanoxylon* and *Allocasuarina torulosa*.

Fire plays a major role in the maintenance of the tall open-forest as in its absence many eucalypts are unable to regenerate in the dim light of the forest floor (Ashton 1981). Some of the dominant eucalypts, such as *E. grandis* and *E. regnans*, are fire-sensitive and are killed in an intense fire. However, dense regeneration from seed usually follows rapidly after fire and tall open-forests are typically even-aged. Acacias regenerate and grow very quickly after fire and in some instances temporarily outgrow the eucalypts.

2 Open-forest and low open-forest

The open-forest subformation sometimes includes the same dominant tree species as tall open-forest, but usually the species and the structure of the understorey change as the tree height decreases. On very infertile soils a layer of dense low shrubs, 2 m tall or less, with hard, small leaves is present. On more fertile soils, especially where there is a high fire frequency, the understorey is largely composed of grasses and herbs with few shrubs. There are many open-forests with understoreys intermediate between these two extreme types.

Eucalypt open-forests often with an understorey of grasses are prominent in the north of the Northern Territory, where *E. tetradonta* and *E. miniata* are dominant, either singly or in combination, and in eastern Queensland where *E. drepanophylla* extends over large areas and the mean annual rainfall is 1000–2000 mm.

Open-forests of *Acacia* tend to develop in areas where the mean annual rainfall is 400–1000 mm. *Acacia harpophylla* is the major component of many open-forests in southeastern Queensland where there are relatively fertile clay soils. *Acacia cambagei* and *A. argyrodendron* assume importance on similar sites where rainfall is 450–650 mm. In drier areas of Queensland and the Northern Territory, acacias such as *A. shirleyi* and *A. aneura* form open-forest and low open-forest on acidic, sandy and gravelly soils (Johnson and Burrows 1981).

Considerable areas of tropical and subtropical Australia with a mean annual rainfall of 500–1200 mm and sandy soils are dominated by open-forests of *Callitris intratropica* and *C. columellaris* (including *C. glaucophylla*). In tropical and subtropical coastal areas on seasonally-inundated sites and along river banks, *Melaleuca leuca-*

dendra and *M. cajuputi*, occasionally exceeding 40 m in height, are important in open-forest formations (Stocker 1972; Brock 1988).

In contrast to the situation in tall open-forest many tree species in the drier forests are fire-resistant and recover from damage by shoot regeneration from epicormic buds on the trunk and branches. Many understorey species survive fire by shooting from underground root stocks, or regenerate readily from seed. *Acacia harpophylla* (brigalow) is one species that has the ability to produce root sucker shoots vigorously, a habit that enables it to recover from fire damage and to resist clearing for agriculture.

Low open-forests often comprise depauperate forms of communities that may exist as open-forest. The canopy level does not exceed 10 m and these low open-forests frequently occupy marginal habitats where their height growth is restricted by aridity, waterlogging, low fertility or low temperatures throughout the year (Specht 1970). *Acacia harpophylla* forms extensive areas of this subformation in the drier parts of southeastern Queensland, while in cool temperate montane areas *E. pauciflora* occurs in a similar form before grading into a woodland formation.

Woodland and open-woodland

Woodland and open-woodland are widespread in Australia and dominated by trees of *Eucalyptus*, *Acacia*, *Allocasuarina*, *Callitris*, *Casuarina* and *Melaleuca*. About 80% of all *Eucalyptus* species and most Australian acacias occur in these formations (Gillison and Walker 1981). Woodland trees project a foliage cover of 10–30% and usually have rounded crowns and trunks shorter in length than the depth of the crowns. Tree height in woodlands is more restricted than in open-forest being mainly 15–25 m in moister areas and 5–15 m in drier parts. Dominants rarely exceed 30 m tall so that few species are found in the tall woodland subformation. In general terms, open-woodlands may be regarded as an extension of woodlands into arid, infertile or fire-prone environments only marginally suitable for tree growth. They have an open canopy, with a projective foliage cover of less than 10%, and comprise scattered low trees, usually less than 10 m tall.

Large areas of inland Australia are covered by woodland and open-woodland. They are the most

common formations in inland Queensland and New South Wales, and are extensive in northern parts of Western Australia and the Northern Territory. There are also substantial areas in Central Australia and southwestern Western Australia.

Eucalyptus species dominate woodlands in northern Australia in areas receiving more than 600 mm annual rainfall but are replaced by *Acacia* species in drier habitats. Eucalypt woodlands occur widely in more temperate parts of southern and eastern Australia to where the annual rainfall declines to 400 mm or less. Eucalypt woodlands characterised by a grassy understorey are very prominent on the heavier and more fertile soils and on alluvial flats along rivers in northern and eastern Australia. *Eucalyptus camaldulensis*, *E. tereticornis*, *E. drepanophylla*, *E. populnea*, *E. tetradonta* and *E. alba* are common dominants in this type of woodland. On somewhat less fertile soils or where rainfall is low the eucalypt woodland may have an understorey of low trees or tall shrubs of *Acacia*, *Casuarina* or *Callitris* species.

Woodlands dominated by acacias or casuarinas usually have a lower canopy height than eucalypt woodland and where it does not exceed 10 m the association is referred to as low woodland. The structure of low woodlands is variable, consisting generally of an open low-tree layer 3–6 m in height, a sparse low-shrub layer of 1–2 m and a ground layer of ephemeral herbs or grasses. Both the size and the form of species vary with site conditions so that a species may be either a small tree or tall shrub according to the habitat.

In eastern Australia dominant species of the low woodland formation are *Acacia cambagei*, *A. excelsa*, *A. harpophylla*, *A. pendula* and *Casuarina cristata* (Johnson and Burrows 1981). The seasonally dry solodic floodplains around the Gulf of Carpentaria have extensive areas of low woodlands of *Melaleuca*, of which the most common species are *M. nervosa* and *M. viridiflora*. The woodlands to the southeast of the Gulf grade into a mixed low woodland with a wide range of dominants including *Atalaya hemiglauca*, *Lysiphyllum cunninghamii* and various *Terminalia* species.

The most abundant open-woodland type is low open-woodland in which widely-spaced small trees of *Eucalyptus* or *Acacia* grow in association with shrubs, hummock grasses or tussock grasses. A vegetation type known as 'pindan', which occurs on the sandy plains of

northwestern Western Australia, is an example of low open-woodland with tall shrubs in the understorey. It is characterised by scattered eucalypts, mainly *E. dicbro-mophloia* and *E. setosa*, over a dense layer of tall shrubby acacias including *A. ancistrocarpa*, *A. eriopoda* and *A. tumida*. Pindan communities are subject to regular burning and, while the eucalypts tolerate the fire, many acacias are killed or severely damaged and regenerate from seed or roots.

Low open-woodlands with an understorey of hummock grasses are associated with skeletal soils of rocky hills or the sandy soils of sand plains or dunes. They are usually in areas with a mean annual rainfall from 600 mm to less than 300 mm. The hummock grasses include a wide range of *Triodia* species, with *T. pungens* prominent in the north and *T. basedowii* in the south. *Plectrachne schinzii* predominates on deep, coarse sands. In typical hummock grassland the individual plants are from 1 to 6 m in diameter and 0.5 m high. Each plant branches repeatedly into a great number of culms that intertwine to form a hummock with rigid sharp leaves.

Across northern Australia low open-woodland of *E. brevifolia*, or a closely-related species, extends over large tracts of rocky, hilly country with siliceous, acidic and low fertility soils between the 350 and 650 mm isohyets. In the Northern Territory shallow or rocky soils may support stunted eucalypt communities with a dense grass layer. The canopy is often 7 m in height and dominated by *E. foelscheana*, *E. tectifera* and *E. clavigera*. On the red sand plains and dunes of Central Australia *E. gongylocarpa* reaches the remarkable height of 8–13 m in very arid conditions. It occurs as isolated trees, sometimes with the mallee *E. youngiana*, or as small pure stands with an understorey always dominated by *Triodia* hummock grasses. Also on the arid, sandy plains of the Central Australian deserts is the impressive and picturesque desert oak, *Allocasuarina decaisneana*. It is often present as small groves at the base of sand dunes in some of the hottest and driest country in Australia.

Many species of *Acacia* are found in hummock grassland but few reach a large size. In the subtropical arid and semi-arid zones *A. aneura* is the most common acacia in low open-woodland but further north species such as *A. coriacea*, *A. cowleana* and *A. holosericea* become prominent.

Open-woodland with an understorey of tussock grasses, including *Astrebla* in northern Australia and *Danthonia* species in the south, are widespread in lower rainfall areas. *Eucalyptus coolabah* subsp. *coolabah* and *E. microtheca* are a characteristic species of grassy open-woodland on the heavier clay soils of seasonally inundated country in northern and inland Australia. In western Queensland, grassy low woodland of *A. cambagei*, *A. harpophylla*, *A. excelsa*, *A. pendula* and *Casuarina cristata* give way on drier sites to low open-woodlands dominated on the heavier calcareous soils by *A. georginae* and on the more acidic sandy soils by *A. aneura*. In other parts of northern Australia grassy open-woodland and low open-woodland with *Melaleuca viridiflora* and *M. nervosa* occur on swampy, nutrient-deficient sites.

The life span and leaf features of woodland species suggest an adaptation to environmental pressures of which water stress, nutrient deficiency and fire incidence are paramount. The prominence of phyllodinous acacias and casuarinas with reduced leaves, and the deciduous species of *Terminalia* and *Lysiphyllum*, are examples of traits linked to water stress. Eucalypts and melaleucas have well-developed lignotubers, thick protective bark and the ability to produce epicormic shoots, which ensure survival and recovery after fire. Some acacias will tolerate fire but others such as *A. aneura* are relatively sensitive and can be killed by a hot burn. The more sensitive species generally produce abundant seed at an early age and the substantial bank of hard-coated seed in the surface layers of the soil ensures their regeneration after fire.

The multitude of species in woodlands and open-woodlands include trees and shrubs highly tolerant of very adverse habitats. An understanding of the different adaptive strategies they use to cope with a variety of stress conditions is important if the most appropriate species are to be selected and brought successfully into cultivation. There is, for example, a clear need to separate the opportunistic fast-growing, short-lived species, such as *A. holosericea*, from more persistent, very hardy and usually slower-growing species.

Shrublands and scrub

Shrublands are defined as having an upper stratum of shrubs with a foliage cover of 10–30%. They may be

separated into tall shrublands (individuals exceed 2 m tall) and low shrublands (less than 2 m tall). The tall shrublands have *Acacia* and *Eucalyptus* as the principal genera, with *Banksia* and *Grevillea* of local importance. Low shrublands are dominated by the family Chenopodiaceae, especially the genera *Atriplex*, *Bassia* and *Maireana* (*Kochia*). They are very important rangelands but produce little woody biomass and are not considered further in this account.

Scrubs are tall shrubs with a foliage cover over 70% (closed-scrub) or in the range 30–70% (open-scrub). Closed-scrub formations, usually of *Melaleuca* or *Leptospermum* species in swamps or on coastal sand dunes, are relatively rare. Open-scrub dominated by *Acacia*, *Allocasuarina* and *Eucalyptus* species is more frequent, especially in southern Australia. Species occurring in these open-scrubs are usually also found in adjacent shrublands.

Tall shrublands dominated by *Acacia* species extend over 1.5 million km² of inland Australia. They are widespread in tropical areas where the mean annual rainfall is ca 400 mm but further south extend into localities where the annual rainfall is less than 150 mm. They occur on diverse soils ranging from deep siliceous sands to heavier red duplex soils. Soil reaction tends to be alkaline in southern shrublands and acid to neutral in northern occurrences.

Acacia shrublands occur in conjunction with low woodlands with some species, such as *A. aneura*, common to both formations. *Acacia aneura* is dominant in many shrublands of Central Australia but in Western Australia it is replaced by *A. grasbyi*, *A. lino-phylla*, *A. ramulosa*, *A. sclerosperma* and other species, largely in response to topographic and edaphic factors. The trees and shrubs in the arid shrublands of Western Australia are described by Mitchell and Wilcox (1994). *Acacia cambagei* shrubland is a typical formation in the clayey interdune areas of the eastern Simpson Desert, while further to the southeast in Queensland and northern New South Wales, *A. ligulata* and *A. tetragono-phylla* form sparse shrubland. Other acacias prominent in the tall shrublands include *A. brachystachya*, *A. georginae*, *A. holosericea*, *A. kempeana*, *A. papyrocarpa*, *A. pendula*, *A. victoriae* and *A. xiphophylla*.

Tall shrublands of *Acacia* are largely used for extensive grazing by sheep or beef cattle. *Acacia aneura*

shrublands are by far the most important associations utilised commercially and *A. aneura* is Australia's most important fodder shrub, not because it is the most nutritious, but because it is palatable, widespread and abundant (Johnson and Burrows 1981). In some places overgrazing, especially in severe droughts, has resulted in virtually complete destruction of the ground vegetation and the edible shrubs followed by widespread soil erosion (Chartres et al. 1982).

Eucalyptus tall shrublands have a wide distribution in southern Australia, especially between latitudes 30° and 36°S where the mean annual rainfall is in the range 200–450 mm and has a predominantly winter incidence. The eucalypts in this formation exhibit a 'mallee' form, having many stems arising from a large, underground woody swelling ('lignotuber') composed of stem tissue. Eucalypt tall shrublands are frequently referred to simply as 'mallee'. The mallee eucalypts are usually 3–9 m tall but exceptionally reach heights to 18 m (Parsons 1981). There are about 100 mallee eucalypts with most occurring in the south of Western Australia. Environmental factors may be important in inducing the multi-stemmed characteristic as many species also occur occasionally as single-stemmed trees.

Mallee formations are extensive on the somewhat undulating topography in southern and southwestern Australia on grey-brown calcareous soils and red-brown earthy sands. Soil nutrient levels and water availability are generally low and the incidence of fire is high. In southeastern Australia dominant mallees include *E. socialis*, *E. oleosa*, *E. gracilis*, *E. incrassata* and *E. viridis*. In arid areas of Western Australia the mallee formation is dominated by *E. pyriformis*, *E. kingsmillii* and *E. oleosa*. The mallees tolerate a variety of soil conditions but rainfall seems to be the most important factor influencing overall distribution. Eucalypt tall shrubland can be regarded as occupying the most arid habitat of the eucalypt-dominated communities in temperate Australia. There are, however, a few eucalypts with the mallee habit, such as *E. odontocarpa*, *E. pachyphylla* and *E. normantonensis*, growing in drier tropical localities.

The mallee eucalypts have been used for fuel and farm timbers in Australia for many years but have not been at all widely planted as exotics. It may be that the special attributes of these eucalypts will enable plantings of them to contribute to solving the wood

shortage in some of the harsher environments of the warm temperate and subtropical areas of the world. However, those species that have been tried have generally been slow-growing and unappealing for large-scale cultivation.

ADAPTIVE TRAITS

The more recent evolution of the Australian flora has frequently taken place under environmentally stressful conditions of which water scarcity, low nutrients, recurrent fires and high levels of salinity appear to have been paramount. The woody perennial vegetation has in consequence acquired adaptive traits that facilitate survival and reproduction under the various natural environmental stresses. Although apparent adaptive characteristics are often discussed in isolation it is evident that they may have evolved in response to several environmental stresses. Many plants occurring in dry regions or in wetter regions on soils of low fertility or high salinity exhibit xeromorphic features including small hard leaves, thick cuticles, sunken stomates, hairiness, rolled leaves and in some cases succulence (Beadle 1981). Xeromorphism is also seen in alpine plants so it appears to be a response to one or a combination of environmental extremes, viz. reduced water supply or low fertility or both.

Australian woody plants adapted to a range of harsh habitats have potentially a very valuable role in revegetating environments modified by human action to such a degree that species native to the area are unable to thrive. The account that follows is intended to highlight salient biological features of Australian trees and shrubs rather than be a comprehensive review of adaptive strategies.

Water stress

Australia is often described as the world's driest continent outside the Polar regions with about 50% of the land area receiving 300 mm or less of rain annually. Marked seasonal variation in rainfall can considerably reduce soil moisture availability through evaporation and transpiration in the dry season, in winter in the north and summer in the south. Rainfall may vary considerably between years; in the drier areas of Australia variability is about 10% greater than the

global mean for regions having the same average rainfall (Williams 1979), and long droughts are common.

The effect of transpiration is to reduce the leaf water content and potential. The balance is restored by drawing water from soil through the roots. If the soil water is not replenished, insufficient water reaches the leaves and irreversible damage to the leaf tissues can occur. As far as is known there is nothing fundamentally different in the way native Australian species cope with water stress (Cowan 1981) but the great extent of arid and semi-arid areas in Australia has meant most species in the country exhibit a high tolerance to periodic severe moisture stress.

Growing plants cope with water deficiency by either minimising internal water deficits by various mechanisms such as stomatal closure, and/or by having the ability to tolerate much reduced water potential in their tissues. Australian woody plants have a wide range of mechanisms that enables them to avoid or tolerate drought conditions. Many of the life forms and leaf features of plants suggest xeric influences acting in concert with low soil nutrient levels. Sclerophylly is well developed in many woody genera in the form of thickened cuticles, increased glaucousness, rolled leaf margins, dense indumentum, high specific leaf weight and an increase in the volatile oils (Walker and Gillison 1982). Eucalypt leaves are commonly pendulous and isobilateral with a high oil content; *Casuarina* and *Allocasuarina* have highly reduced leaves and photosynthetic cladodes; Australian acacias are principally those that develop phyllodes, and phyllode-like leaves are a feature of *Melaleuca* species. Reduced leaf size is characteristic of plants in arid zones and in the seasonally very dry regions of northern Australia a deciduous habit exists in some species of *Acacia* (subgenus *Acacia*), *Eucalyptus*, *Erythrina*, *Lysiphyllum* and *Terminalia*.

Acacia is the dominant genus in the drier zones with eucalypts often restricted to moister habitats along watercourses and around depressions. The distribution suggests that acacias are generally better adapted to withstand extremes of water stress than are eucalypts. Large areas of open-forest, woodland and shrublands of inland Australia are dominated by *A. aneura* and *A. harpophylla*. Both possess phyllodes that exhibit extreme resistance to desiccation (Tunstall and Connor 1975), exceeding that of eucalypts (Connor et al. 1977). *Acacia harpophylla* will

form forests on heavy-textured soils with adverse water relations and some salinity or alkalinity in the profile.

Acacia aneura has hairy, resinous, compact phyllodes held vertically to minimise heat absorption and water redistribution. The plants stop growth when drought occurs and may even shed some of their phyllodes during the greatest stress, but they can rapidly resume growth when water becomes available. Rainwater often flows along their phyllodes and stems so that it is concentrated at the base of the trunk (Slatyer 1965). In the more arid parts of its range *A. aneura* frequently occurs in groves that receive runoff water from sparsely vegetated intergrove areas, and many of the *A. harpophylla* stands are in areas where the microrelief inhibits runoff and accumulates surface moisture. The development of extensive root systems by acacias to tap both surface water and that accumulating at depth above the hard pan assists in sustaining the plants during drought periods (Winkworth 1983).

In general, the Australian arid zone is well vegetated and even areas classed as desert almost always possess a plant cover of some kind. Despite its great extent the Australian arid zone is not as arid as some parts of the world, with even the driest localities having a mean annual rainfall of about 100 mm, and hence the flora of these areas has attributes enabling it to tolerate and/or avoid the corresponding level of water stress.

Low nutrient availability

There is probably no continent with soils so critically low in essential plant nutrients as Australia and in consequence a large part of the indigenous flora is likely to be adapted in one way or another to cope with these deficiencies (Bowen 1981). Instances of extreme nutrient deficiencies are especially common on acidic light sandy podzolic soils derived from siliceous rocks, sandstones and quartzites or lateritic residues. Information on nutrient concentration ranges and critical nutrient concentrations is very limited for Australian trees and shrubs. Diagnosis of nutrient disorder from visual symptoms can be verified by chemical analysis of affected plant tissue (Dell et al. 1995). Typically phosphorus and nitrogen are lacking, and most known specialised mechanisms of nutrient uptake are related to these elements.

Nutrient uptake and the subsequent nutrient use by the plant are key stages in mineral relations of

plants. The sources of plant nutrients are organic and inorganic materials in the soil and, in some plant groups, atmospheric nitrogen. The production of fine roots with well-developed root hairs may be adequate for some plants to obtain nutrients in a soil of moderate fertility, but this is unlikely to be the case in less fertile soils. Where nutrients are scarce, some species enhance uptake by allocating a much greater proportion of their assimilate to root growth, thereby tapping a larger volume of soil. However in the very infertile Australian soils many trees and shrubs increase their access to nutrients by altering their root morphology, usually in association with microorganisms such as mycorrhizal fungi or soil bacteria.

1 Nitrogen fixation

Leguminous plants, such as *Acacia*, *Albizia* and *Casua* spp., and some non-legumes, especially the family Casuarinaceae, overcome the problem of limited nitrogen availability by forming symbiotic nitrogen-fixing associations with bacteria. The bacterial symbiont is *Rhizobium* or *Bradyrhizobium* for the legumes and the filamentous soil actinomycete, *Frankia*, for the casuarinas. Roots are infected by the soil bacteria and form specialised lobes on the root surface called 'nodules'. Plant sugars are utilised by the bacteria, which convert atmospheric nitrogen (N₂) to ammonium nitrogen. This symbiotic relationship is widespread in leguminous subfamilies of Mimosoideae and Papilionoideae but is much less common in Caesalpinoideae (Allen and Allen 1981; Halliday 1984). In Casuarinaceae the association with the actinomycete genus *Frankia* appears to be much better developed in the genus *Casuarina* than in *Allocasuarina*, possibly related to moister sites that *Casuarina* species usually occupy.

The rate of nitrogen fixation varies according to species and environmental conditions. Estimates of nitrogen fixation from the atmosphere are often unreliable because the figures quoted frequently include the contribution of soil nitrogen. Nitrogen fixation rates within the range 20–50 kg/ha/year appear to be reasonable and are comparable with estimates for herbaceous annuals (MacDicken 1994). Orchard and Derby (1956) calculated that a dense stand of *A. mearnsii* in South Africa fixed 180 ± 40 kg N/ha/year but studies of small native acacias in Australia have indicated fixation at

rates from 3 to 16 kg/ha/year (Langkamp et al. 1979). In Senegal, the annual rate of accumulation of nitrogen under plantations of *Casuarina equisetifolia* was estimated at 12–80 kg N/ha depending on water availability (Dommergues et al. 1990)

Australian acacias and casuarinas when grown as exotics have generally formed nodules from bacteria present in the soil but the question as to whether these associations are as effective as could be achieved by inoculation with selected symbionts remains unresolved. Research suggests that selected *Frankia* will be beneficial in improving the early growth of *Casuarina* species.

2 Mineral uptake

Mycorrhizas are symbiotic associations between plant roots and soil fungi that provide a means of improving nutrient absorption from the soil. It is likely that most Australian native plants, including *Acacia*, *Casuarina*, *Eucalyptus*, *Melaleuca* and others, are mycorrhizal (Bowen 1981). The fungi hyphae are narrower, longer and more flexible in their direction of growth than root hairs, providing greater access to the nutrient-holding soil pores and particles. Most mycorrhizal studies have pointed to the crucial role of mycorrhizas in phosphate uptake but they appear to also improve the availability of poorly mobile ions of zinc, copper, molybdenum, and possibly ammonium.

There are two major types of mycorrhiza: the general vesicular arbuscular (VA) and the host-specific ericoid, orchid or ecto-mycorrhizas. The VA mycorrhizas are the most widespread. They infect and enter plant roots and form intracellular structures so are collectively known as endomycorrhizas. Many plant species have VA mycorrhizas although they are notably rare or absent in Proteaceae (e.g. *Banksia*, *Hakea*, *Persoonia*) (Malajczuk et al. 1981). The ectomycorrhizal fungi form a sheath around the rootlets of the host; they grow between the root cells but rarely penetrate them. In the Australian flora ectomycorrhizas are found mainly on woody species including *Acacia*, *Allocasuarina*, *Casuarina*, *Eucalyptus*, *Leptospermum* and *Melaleuca*, most of which also form endomycorrhizal associations.

Large differences occur between strains of ecto- and endo-mycorrhizal fungi in the extent of their stimulation of plant growth on particular soils. The

differences may be due to different strains of fungi being less effective for the host species on that site (Bowen 1981). Such observations suggest there is considerable scope for the selection and matching of efficient fungal strains with hosts. More comprehensive accounts of the role of mycorrhizal fungi are provided by Bowen (1981), Lamont (1984), Reddell and Warren (1987) and Malajczuk et al. (1994).

An alternative mode of enhancing nutrient uptake is provided by bunches of hairy rootlets produced on the root systems of some plant groups. Several types of root 'clusters' are recognised with the best known being the proteoid roots. In this type a very large number of rootlets are packed in rows along the parent root providing a surface area at least five times that of 'normal' roots (Lamont 1984). Proteoid roots form dense mats of lateral rootlets generally in the upper 10 cm of the soil. They are induced by soil microorganisms and enhance the absorption of ions such as phosphate from phosphorus-deficient soils (Lamont 1982). Most species in the family Proteaceae and some in the genus *Casuarina* have proteoid roots (Bowen 1981; Diem and Arahou 1996). Under cultivation many proteaceous species (e.g. *Banksia*, *Grevillea*) are sensitive to phosphorus toxicity caused by excessive fertilizer application, a situation possibly due to the inability of the proteoid roots to exclude the over-abundant ions (Reddell 1984). (Additional information on nitrogen-fixation and mineral uptake in relation to silvicultural techniques is given in Chapter 4).

Fire

Fire caused by lightning has been a natural environmental stress in most regions of Australia for millions of years. Since Aboriginal people arrived on the continent some 40 000 years ago the fire regime has been modified to more frequent but generally less intense burns.

For woody perennials the threat of extinction by an untimely fire prior to the age of seed production is high. It is then highly probable in an environment where there have been recurrent fires for a long period that surviving species are those that evolved traits that enhance the persistence of populations when burnt. Many apparent fire-adaptive traits may however have evolved principally as a response to other selective

forces. For example, evolution of the eucalypt lignotuber may have been in response to low soil-nutrient levels (Beadle 1968). It has therefore been suggested that adaptive traits ascribed to fire may well be of multipurpose use, enabling a species to persist by tolerating various types of environmentally induced physiological stresses (Hodgkinson and Griffin 1982), such as drought or excessive competition from other plants. In practical terms the origin of the particular traits is of less importance than the fact that they exist and enable species to grow in fire-prone environments.

The survival of established trees and shrubs in a fire varies considerably according to the intensity of the fire and the stage of development of the plants. Hot summer burns can be far more damaging than those in the cooler conditions of spring, and mature plants may be highly resistant to fire but their seedlings highly vulnerable. Such variation needs to be taken into consideration when assessing the fire tolerance of any species.

The ability to coppice or resprout is an important trait that enables woody plants to survive fire damage. The degree to which individuals will recover by resprouting is partly dependent upon the extent to which vegetative buds are protected by bark or soil during the fire. Some arid zone species of *Acacia*, *Allocasuarina*, *Grevillea* and *Hakea* have thick protective bark that affords protection to buds but others such as *Acacia aneura* and *Dodonaea viscosa* subsp. *angustissima* have bark thicknesses less than 3 mm (on shrubs 2.5 m tall), which offers little protection. These thin-barked species are relatively sensitive to fire damage, although they often have the capacity to resprout readily from subsurface stem tissue when cut off at ground level (Hodgkinson and Griffin 1982).

Most eucalypts and many other species will regenerate from 'lignotubers'. These structures are particularly well-developed in the mallee eucalypts. Many eucalypts, such as *E. tetradonta*, reproduce from root suckers. However, rhizomes, root suckers and lignotubers are not confined to *Eucalyptus* but occur in many other trees and shrubs in tropical savannas. Adventitious buds on lateral roots are especially evident in acacias (such as *A. coriacea*, *A. dealbata*, *A. harpophylla* and *A. murrayana*), *Atalaya hemiglaucula* and *Ventilago viminalis* which can send up a thicket of root suckers when the main stem is fire-damaged.

Aerial buds protected by bark in the upper parts of a tree or shrub ensure rapid regeneration of the crown following fire in some eucalypts and melaleucas and to a lesser extent in casuarinas and acacias. In eucalypts, bunches of shoots emerge from epicormic buds on the trunk and major branches. Acacias as a whole appear to be better equipped than eucalypts to withstand extremes of water stress rather than fire. While many acacias such as *A. lysiphloia* and *A. monticola* are highly flammable, with some exceptions, e.g. *A. inaequilatera* and *A. hemignosta*, they lack the thick, protective bark of the eucalypts.

Species lacking vegetative traits useful to survive fire often have reproductive features to ensure rapid regeneration of their offspring. Fire triggers the release of seeds from the serotinous 'cones' of *Allocasuarina* species and from the woody capsules of many eucalypts. The release of seed from abundant crops present on *Melaleuca quinquenervia* during fires has been largely responsible for the rapid spread of this species and its weed status in Florida.

Heavy seed production and early reproductive maturity are features of many Australian species with low to moderate resprouting ability. It is not unusual for species such as *Acacia holosericea*, *A. colei* and *Dodonaea viscosa* to set viable seeds within three years of establishment. With few exceptions, Australian acacias are hard-seeded and need some sort of physical change in the seed-coat to stimulate germination. Fire is one agent that does this effectively and abundant regeneration may follow the passage of a fire through a stand of acacias. The ability of seeds of *Acacia*, *Cassia*, *Dodonaea* and other hardseeded genera to remain dormant in the soil for long periods is an adaptive trait to ensure survival in the event of loss of the parent trees due to fire, drought or other catastrophe.

The persistence of many Australian species in the face of periodic fire suggests that they may have considerable value for planting in fire-prone environments where it is necessary to retain vegetative cover. They offer good possibilities for providing cover in water catchments or on steep slopes likely to be subject to severe erosion in the event of fire. Detailed reviews of plant traits adaptive to fires and the general response of species to fire have been provided by Gill (1975, 1981b), Noble and Slatyer (1981) and Hodgkinson and Griffin (1982).

Salinity

Almost one-third of the Australian landscape has salt-affected soils. In a broad survey, Northcote and Skene (1972) estimated that there are 39 million ha of naturally saline soils and 200 million ha of sodic soils with a high level of adsorbed sodium. In addition the long coastline has salt marshes, estuarine and tidal flats, and mangroves either under regular tidal influence or subject to occasional inundation by sea water. It is reasonable to expect that vegetation that occurs naturally over such extensive areas of salt-affected lands will have acquired a significant degree of tolerance to high levels of groundwater salinity. In addition the woody vegetation of coastal sand dunes and other littoral associations above high tide level are frequently exposed to substantial amounts of salt in windborne spray.

Halophytes, i.e. plants that grow and complete their life cycles on saline soils, have evolved specialised physiological adaptations for coping with high salinity levels. Most evidence suggests that once salt enters the plant it is the control of salt transport to the leaf and the final compartmentation of salt within that leaf that are the principal factors determining salt tolerance (Winter et al. 1981). It appears that halophytes transport salt rapidly to their shoots, preferentially accumulating it in the vacuoles where it does not interfere with cytoplasmic metabolism, but contributes to osmotic adjustment. The relative importance of this particular adaptive trait in conferring salt tolerance of Australian woody plants growing on saline soils is difficult to assess but it is certainly very important in mangroves (Adam 1990).

Saline sites may have other features that make them stressful for plant growth. On many sites high salinity levels are associated with waterlogging, and thus tolerance of relatively anaerobic, saline conditions in the root zone for at least part of the year may be essential. *Casuarina glauca* and *Melaleuca* species in the brackish water of coastal swamps combine tolerance of these conditions. Not all species of *Casuarina* are salt-tolerant, but *C. equisetifolia*, and especially *C. glauca* and *C. obesa* will grow on saline sites. A similar situation prevails amongst *Melaleuca* species. *M. balmaturorum*, *M. lanceolata* and *M. styphelioides* are adapted to saline sites and will withstand moderate exposure to salt-laden winds. *Melaleuca quinquenervia* is regarded as

only moderately salt-tolerant, but will tolerate salt-laden coastal winds. In the dry interior of Australia, species such as *M. bracteata*, *M. glomerata*, *M. nervosa* and *M. pauperiflora* occur on the margins of salt lakes (Midgley et al. 1986). Other genera, including *Eucalyptus* and *Acacia*, also have a limited number of species that grow in saline environments. Salt-tolerant acacias, such as *A. ampliceps*, *A. maconochieana* and *A. stenophylla* are described in the species' digests later in this book. A more comprehensive description of trees suitable for planting on salty lands is given by Marcar et al. (1995).

REPRODUCTIVE BIOLOGY

The reproductive processes of Australian woody plants are not dissimilar to those of many species in other parts of the world, but an understanding of the reproductive biology can be important when introducing exotic species for trial. The potential of a species to set fertile seed, produce hybrids or inbreed is a significant aspect of seed collection and controlled seed production. The following brief account does no more than draw attention to the variety of mechanisms for pollination and the relative importance of inbreeding, outcrossing and hybridisation in a selection of Australian genera.

Mimosaceae

When conditions are favourable acacias produce flowers in great profusion. Flowering usually commences at an early age; *A. monticola* can flower in its first year, but many species such as *A. holosericea* and *A. simsii* flower in their second year and produce mature seed from the third year. *Acacia mearnsii* in plantations begins to flower at about age 20 months and, while providing some ripe seed from the third year, it is not until the fifth or sixth year that appreciable quantities of seed are produced (Sherry 1971).

Acacia flowers are small, regular and usually bisexual (male and female parts on the same flower). Each flower contains basically 4 or 5 sepals and petals. The sepals may be free or united into a calyx and the petals free or united into a corolla. The stamens are numerous and arise from under or just above the base of the ovary. A thread-like style protrudes beyond the stamens. The structure and histochemistry of the stigma

and style in some Australian acacias has been described by Kendrick and Knox (1981). The ovary is sessile or has a short stalk and its outer surface may be smooth or covered in minute hairs. Each flower is subtended by a small bracteole the shape of which varies according to species (Doran et al. 1983). Except in the degree of division of the calyx, degree of hairiness, or ratio of corolla to calyx, all *Acacia* flowers look very much the same.

Flower colour is mostly due to the colour of the projecting filaments of the stamens; almost all Australian acacias have white to orange-yellow flowers. The flowers are arranged in either heads (compact spherical clusters of flowers) or in spikes (compact cylindrical clusters of flowers) commonly made up of 10–50 individual flowers.

Insects are the main pollinating vectors of acacias, wind having a very minor role. It also seems likely that birds, seeking insects or attracted to extra-floral nectaries on the phyllodes or on the rachis of true leaves, play a part in pollination (Ford and Forde 1976). There is very little information available on *Acacia* pollination and, although there is a general belief that insect pollinators are nonspecific, the constancy of flower colour of most acacia species implies that there could be some pollinator specificity (New 1984).

After pollination, the ovary matures within the flower to form the pod characteristic of species in the Mimosaceae family. Although there is usually a large number of flowers in each acacia inflorescence, relatively few pods are formed. At maturity the pods usually split longitudinally along both margins to release the seed. Seed dispersal from the pod is usually by gravity or in some instances the drying pods dehisce and propel the seeds with some force. Ants may be involved in short-distance dispersal of seeds on the ground and in a few cases dispersal of seeds by birds appears to be a regular strategy. Some acacias, for example, produce seeds with bright red or orange arils which may be attractive to birds especially when they remain suspended by their funicles from open pods. Glyphis et al. (1981) report the distribution of *A. cyclops* by birds.

The breeding system appears to be one of preferential outcrossing. The mating systems have been determined for four Australian acacias (*A. auriculiformis*, *A. crassicarpa*, *A. mangium* and *A. melanoxylon*)

and in all there were high levels of outcrossed progeny. In other species high levels of self-incompatibility have been found (Kendrick and Knox 1989). However, experimentally manipulated selfs of two species from the dry zone, *A. cowleana* and *A. holosericea*, resulted in good seed set and germination of almost 100% (Moran et al. 1992). Substantial inbreeding may therefore occur and could reach high levels in some species.

Some natural interspecific hybrids are known to occur. Intermediates between *A. auriculiformis* and *A. mangium* have been observed in natural stands in Papua New Guinea and occur occasionally in plantations in Sabah. Artificial hybridisation techniques for these species have been developed by Sedgley et al. (1992). A hybrid swarm of *A. brachybotrya* and *A. calami-folia* in Victoria has been studied by Leach and Whiffin (1978) and in Western Australia fertile natural hybrids of *A. ampliceps* and *A. bivenosa* and of *A. ancistrocarpa* and *A. trachycarpa* have been reported. Natural hybrids may be a relatively common occurrence but the full extent of hybridisation and introgression in Australian acacias is not known. Most Australian acacias that have been examined are diploid with $2n=26$ (Vassal and Lescanne 1976). However, three species in the *A. holosericea* complex are diploid, tetraploid and hexaploid while *A. cowleana* is tetraploid (Moran et al. 1992).

Casuarinaceae

Casuarinas flower annually and usually begin to produce seed before they are five years old. They are mainly dioecious, but some are monoecious, and both conditions may occur in some species — the flowers are unisexual and greatly reduced. The male flowers consist of a single stamen after anthesis and occur in whorls on cylindrical spikes, which are terminal or lateral on the branchlets. The female flowers terminate short lateral shoots and form dense compact globular heads. Each flower consists of a unilocular ovary containing two ovules, only one of which forms a seed. There is no perianth. The ovary is subtended by two lateral bracteoles which form a single bract. Flower structures are described in more detail by Beadle (1980) and Barlow (1983).

The pollen is disseminated by wind and after fertilisation the inflorescence enlarges to form a woody, cylindrical fruiting body. Aspects of the floral

biology of *Allocasuarina verticillata* have been described by Moncur and Boland (1996). The individual fruit is a one-winged samara surrounded by two bracteoles ('valves') and a single bract. The samara is single-seeded and has a membranous terminal wing. It is released when the valves retract and is dispersed initially by wind, further dispersal sometimes being assisted by water and ants. Many Australian casuarinas in the genus *Allocasuarina* have serotinous fruits and fire or extreme desiccation may be necessary to release the seeds. Species in the genus *Casuarina* usually shed their seed annually (Turnbull and Martensz 1982).

As the family comprises wind-pollinated, predominantly dioecious species, the plants are primarily obligate outbreeders. The taxonomy, breeding system and genetic variation of casuarinas have been reviewed by Turnbull (1990). In *Casuarina* polyploidy has not been recorded. There are no indications of extensive hybridisation although occasional natural hybrids of *C. cunninghamiana* with *C. glauca* and *C. cristata* are known. In *Allocasuarina* polyploidy is sometimes frequent. Hybridisation between some closely related species occurs and at least one species has obligate apomixis, producing populations consisting entirely of females (Barlow 1983).

Myrtaceae

Many species of the Myrtaceae family flower prolifically and at an early age. Within the family there are many types of inflorescences including much-branched panicles and a variety of reduced forms, including umbels and spikes, down to single flowers. In *Eucalyptus* the umbel comprises 1, 3, 7, 11, 15 or more individual flowers and in some species the individual clusters form compound branching structures. *Melaleuca* and *Callistemon* flowers are arranged in a spike-like inflorescence, the 'bottlebrush', with new shoot growth often extending from the axis. Solitary flowers are found commonly in genera such as *Leptospermum*. Within the family there is a great diversity in flower appearance; in eucalypts and melaleucas the mass of stamen filaments, often brightly coloured, is the showy part, while other genera have flowers deeply enclosed within coloured bracts and yet others such as *Leptospermum* have more conventional flowers with prominent petals. Pollination is by insects, birds, or sometimes mammals including

bats and possums. Eucalypts and melaleucas with brightly coloured flowers show adaptations for bird pollination. Some species produce large quantities of nectar that attracts both insects and birds.

Eucalyptus the best known genus in the Myrtaceae, has bisexual flowers. An individual flower bud consists of a hollow receptacle, the hypanthium. This is surrounded by the operculum, which is an organ formed by the fusion of the sepals or petals or of both structures. On the rim of the hypanthium is a ring of stamens some of which may be sterile. This ring may be continuous or in the subgenus *Eudesmia* the stamens are grouped in bundles. Inside the staminal ring is a band of tissue, the disc or nectary, which descends to the top of the ovary. The ovary chambers themselves are surmounted by the style and stigma. At flowering the operculum is shed, the stamens spread and the pollen is released from the anthers. Detailed descriptions of the eucalypt reproductive cycle can be found in Boland et al. (1980).

The stigma does not become receptive until some days after the pollen is released, a sequence which impedes self-pollination. While this mechanism is largely effective in preventing self-pollination of a single flower it is less so over a whole tree because of the varying time of pollen shed in different flower clusters. There is little doubt that although eucalypts are preferential outcrossers a degree of self-fertilisation does take place. In *E. obliqua* this has been estimated as high as 24% (Brown et al. 1975) and in *E. pauciflora* 37% (Phillips and Brown 1977).

Individual interspecific hybrids between closely related species of *Eucalyptus* occur under natural conditions but are probably more common in plantations where geographic barriers to hybridisation are broken down by planting compatible species in the same neighbourhood (Eldridge et al. 1993). Large hybrid swarms or areas of introgression are found under natural conditions involving species such as *E. saligna* and *E. botryoides*, and *E. camaldulensis* and *E. tereticornis*.

After pollination the ovary matures to form a woody capsule and seed shed depends on the separation of the seed from the placenta and opening of valves on the top of the fruit. As the fruit dries out the locules open and the seed falls out under the influence of gravity and agitation by wind. Wind is probably the

only important agent of seed dispersal in eucalypts, melaleucas and the majority of the dry-fruited Myrtaceae genera. The fleshy berries of some Myrtaceae including *Acmena*, *Eugenia* and *Syzygium* species are attractive to birds and animals, and the seeds may be dispersed over long distances.

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