FLORA OF AUSTRALIA

Volume 1 Introduction

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Section 3: The Flora

Present Vegetation Types

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PRESENT VEGETATION TYPES

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Australian vegetation types are the result of interaction between a wide range of factors, some major, some minor. The most important determinant is rainfall, both its total amount and its distribution throughout the year: summer-incident in the north and winter-incident or all-year-round in the south. Closely related to rainfall as a determinant of vegetation type is temperature, which influences available water. Of lesser influence, but still often important at a regional or local level are such factors as soil type, drainage, nutrient level, salinity, grazing pressures, exposure and of course, fire, whether natural or human-induced. All of these factors act upon a flora which has been shaped over many millions of years by changing climates and geomorphology, as well as by evolution and recruitment from other regions. For details see chapters in this volume by Frakes (climate & geomorphology); Hill *et al*. (palaeobotany); and Crisp *et al*. (biogeography).

Several attempts have been made to classify and name Australian vegetation types. Aboriginal peoples recognised many associations and their terms for distinctive vegetation such as brigalow, kwongan, mallee, mulga and wallum have been taken into general parlance. Subsequent attempts, dating from the time of Banks in 1770, used more Europocentric terms, either in relation to some vegetation types (e.g. 'heath') or to some dominant genera, such as 'box'-barked eucalypts or 'wattles' (*Acacia* spp.). Some terms still in current use, such as 'dry' and 'wet' sclerophyll forests, add environmental descriptors to the terminology, which can be confusing.

More recent attempts to classify present Australian vegetation have usually been based on a mixture of structural and floristic attributes; such a mixture is still used and appropriate because of the predominance of *Eucalyptus*, the phyllodineous spineless group of *Acacia* species, and *Triodia* in many Australian plant communities. In those vegetation types where the above genera do not occur and in which there is high floristic diversity, e.g. some closed-forests, usually only structural attributes have been used (see e.g. Webb *et al*., 1976), although even here descriptions based on floristics have been used (e.g. in heath vegetation).

The system of classification most commonly used in Australia currently is the structural one of Specht (1970); it is a subsequent modification to this system (see Table 24) which is employed throughout most of this chapter. This simple system of a two-dimensional matrix uses life-form and foliage projective cover of the tallest stratum to characterise most major vegetation types. Specht's system, with the modification to it of the floristics of the over- or under-storey, has been used subsequently to successfully map Australian vegetation at both regional and continental scales (Beard, 1976; Carnahan, 1976, 1977, 1990) (Fig. 82).

This chapter describes the distribution across Australia of five major vegetation types — closed-forests (both tropical and temperate), open-forests, woodlands, shrublands and grasslands. The vegetation types in some regions of extreme conditions, such as alpine or coastal vegetation, will not be described except in passing (but see relevant chapters in Groves, 1994 for further detail). Regional patterns that operate at different scales to modify the distribution of these five major vegetation types over the continent are outlined towards the end of the chapter.

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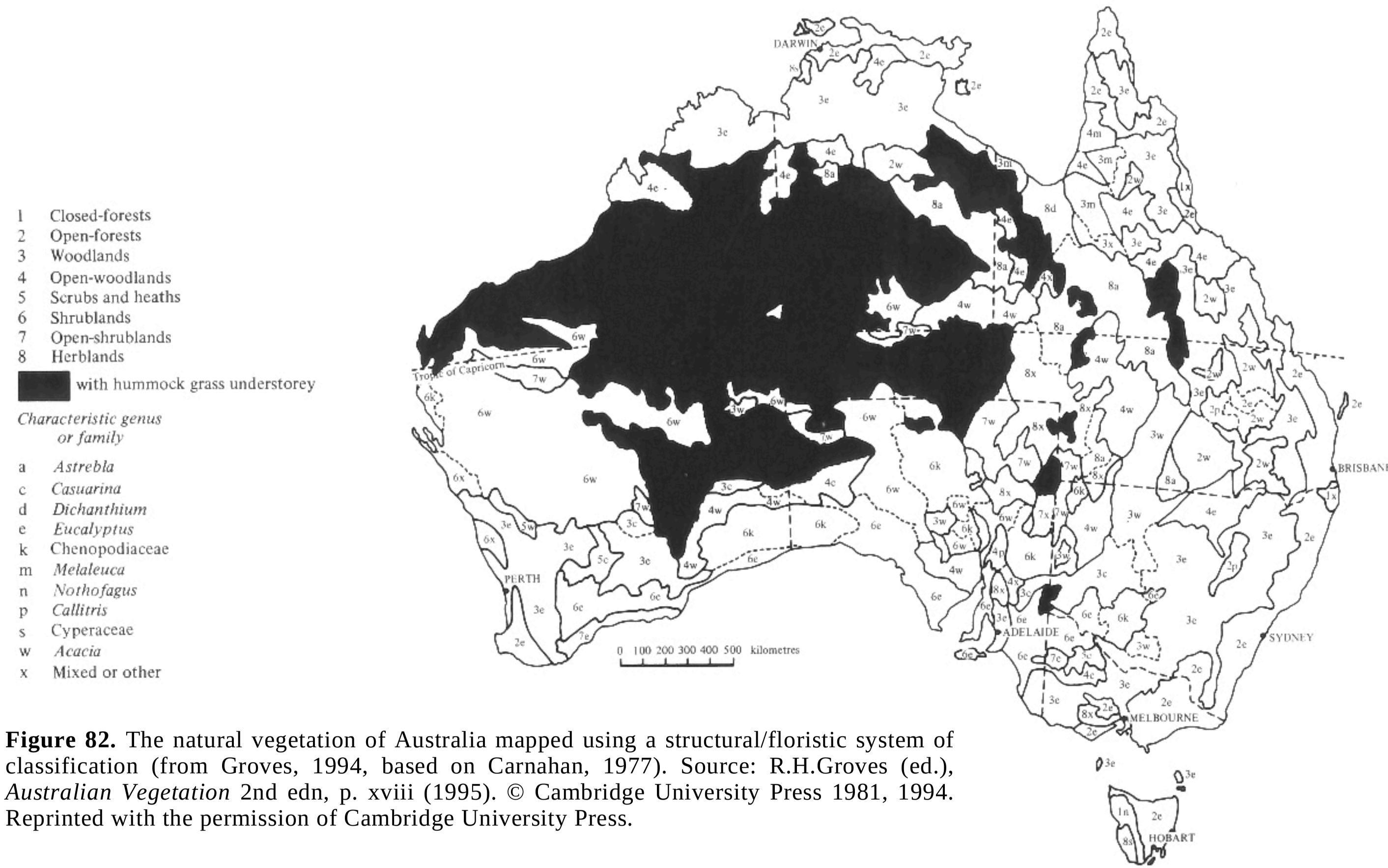

Figure 82. The natural vegetation of Australia mapped using a structural/floristic system of classification (from Groves, 1994, based on Carnahan, 1977). Source: R.H.Groves (ed.), *Australian Vegetation* 2nd edn, p. xviii (1995). © Cambridge University Press 1981, 1994. Reprinted with the permission of Cambridge University Press.

Table 24. Structural formations in Australia and their percentage area (adapted from Specht *et al*., 1974).

Life form and height of tallest stratum	Foliage projective cover of tallest stratum					
	100–70%		70–30%		30–10%	<10%	
Trees> 30m.	Tall closed-forest		Tall open-forest 1.64%		(Tall woodland)	(Tall open-woodland)	
Trees 10–30 m.	Closed-forest	0.92%	Open-forest	3.61%	Woodland 17.84%	Open-woodland	5.80%
Trees <10m	Low closed-forest		Low open-forest		Low woodland 4.81%	Low openwoodland	
Shrubs >2m	Closed scrub		Open scrub 7.69%		Tall shrubland 9.89%	Tall open-shrubland 0.22%	
Shrubs 25 cm–2m	Closed-heath		Open-heath 1.47%		Low shrubland 4.00%	Low open-shrubland 14.39%	
Shrubs <25 cm	–		–		Fell field	Open-fellfield	
Hummock grasses <2 m	–		–		Hummock grassland 3.95%	Open-hummock grassland 14.71%	
Graminoids, herbs, ferns, etc.	Closed-grassland		Grassland 1.13%		Open-grassland 6.69%	Ephemeral herbland	

Major vegetation types

Closed-forests (tropical and temperate rainforests)

In recent geological times, the total area of closed-forest, sometimes called rainforest, has been relatively small (less than 1% of the continental surface) and discontinuous. Pockets of closed-forest cover more than 30 degrees of latitude along the east coast, from Cape York to southern Tasmania (Fig. 83). Webb & Tracey (1994) referred to these pockets as 'islands' in a 'sea' of sclerophyll vegetation, which follows Herbert's earlier analogy of an 'archipelago of habitats' (Herbert, 1967). Such a pattern of discontinuity and fragmentation of closed-forest types is more pronounced in the drier inland areas of northern Australia (Webb & Tracey, 1994) and in closed-forests ('temperate rainforests') in southern Australia (Busby & Brown, 1994).

Figure 83. Distribution of Australian closed-forest types. Shaded area = rainforest; dotted line = 800 mm rainfall isohyet; solid line = limit of closed vine thickets. Redrawn (P.McCarthy) from L.J.Webb & J.G.Tracey, The rainforests of northern Australia, *in* R.H.Groves (ed.), *Australian Vegetation* fig. 4.1 (1994).

Wherever closed-forests occur, and however discontinuous and fragmented their distribution may be, they always have a closed canopy (greater than 70% foliage projective cover; see Table 24) with trees densely spaced. Closed-forests in tropical climates are characterised by a complex mixture of species (Figs 5, 6, 7, 23) with no one species or genus dominant and usually an array of certain life-forms, such as angiosperm epiphytes, lianes and trees with buttresses (see Fig. 84 for a profile through a sample of a type of closed-forest called 'simple

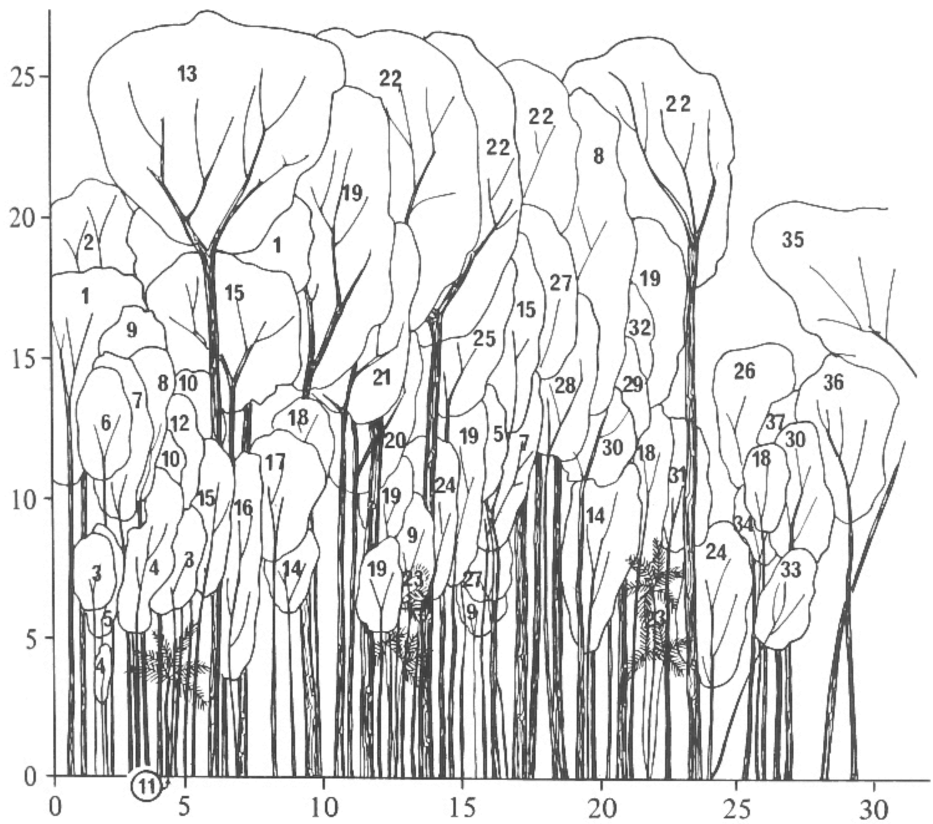

Figure 84. A profile diagram illustrating a simple notophyll vine-fern forest, a structural type of tropical closed-forest. 1. *Elaeocarpus largiflorens*; 2. *Polyscias murrayi*; 3. *Pullea stutzeri*; 4. *Rhodomyrtus trineura*; 5. *Apodytes brachystylis*; 6. *Opisthiolepis heterophylla*; 7. *Cryptocarya densiflora*; 8. *Ceratopetalum virchowii*; 9. *Sarcopteryx martyana*; 10. *Cryptocarya corrugata*; 11. *Orania appendiculata*; 12. *Cinnamomum laubatii*; 13. *Prumnopitys ladei*; 14. *Rapanea achradifolia*; 15. *Carnavonia* sp.; 16. *Guettardella tenuiflora*; 17. *Syzygium endophloium*; 18. *Acmena hemilampra* spp. *orophila*; 19. *Sphalmium racemosum*; 20. *Endiandra montana*; 21. *Symplocos cyanocarpa*; 22. *Flindersia pimenteliana*; 23. *Laccospadix australasicus*; 24. *Rhodamnia blairiana*; 25. *Garcinia brassii*; 26. *Syzygium cormiflorum*; 27. *Planchonella obovoidea*; 28. *Cryptocarya angulata*; 29. *Diospyros* cf. *hemicycloides*; 30. *Goniothalamus australis*; 31. *Beilschmiedia collina*; 32. *Sphenostemon lobosporus*; 33. *Wilkiea macooraia*; 34. *Aceratium ferrugineum*; 35. *Alphitonia petriei*; 36. *Planchonella macrocarpa*; 37. *Elaeocarpus stellularis*. Source: L.J.Webb & J.G.Tracey, The rainforests of northern Australia *in* R.H.Groves (ed)., *Australian Vegetation*, 2nd edn, fig. 4.6d (1994). © Cambridge University Press 1981, 1994. Reprinted with the permission of Cambridge University Press and the authors.

notophyll vine-fern forest'; Webb & Tracey, 1994). On the other hand, the southern closed-forests that occur at either higher latitudes or altitudes in climates characterised by frequent frosts and some snow are simpler floristically, with the Gondwanan genus *Nothofagus* dominant, although several other genera may also be dominant locally. The southern closed-forests are distinguished from their tropical counterparts by the absence of significant buttressing at the tree bases and lack of woody lianes. Epiphytes in southern closed-forests are mainly ferns, bryophytes and lichens with only two species of epiphytic angiosperms (Busby & Brown, 1994).

Visually striking sharp boundaries usually separate closed-forests from the adjoining and more widespread sclerophyll vegetation. Sometimes, however, such edges between the two vegetation types may be diffuse, depending on fire characteristics and history. Most closed-forest species are evergreen, although some winter-deciduous species may occur, especially in dry northern sites.

Classification of the different sub-types of closed-forests has resulted in an enhanced understanding of the ecological factors that may control their distribution. Such classification has also established a more rational basis for a system of reservation of different types of closed-forest in eastern and northern Australia (Webb *et al.*, 1973) and Tasmania (Brown *et al.*, 1990).

Based largely on numerical analyses of floristic data collected over the entire latitudinal range of distribution, Webb & Tracey (1981) subdivided closed-forests into many types. These floristic types, at the species level, could be correlated with climatic types, such as 'tropical wet', 'tropical dry' and 'subtropical and temperate wet' provinces, but at the generic level no such correlation was possible (Webb *et al.*, 1984; Webb & Tracey, 1994). While similar floristic subdivisions are possible in southern closed-forest (e.g. that between *Nothofagus* and *Athrotaxis* alliances in Tasmania; Busby & Brown, 1994), most analytical effort has been in northern closed-forests, and especially in the canopy species of those forests, because of their greater floristic diversity at the species level. To illustrate this floristic difference, Beadle (1981) cited data from one site in north-eastern Queensland with 105 tree species listed in the upper canopy, of which 77 were found only in one plot, 15 occurred in two plots and only 1 tree species occurred in more than 5 plots, each plot being 0.5 ha. This floristic richness contrasts with the situation in southern closed-forests in which the canopy may comprise no more than 3 or 4 species, while occasionally there is only one (Busby & Brown, 1994).

The complex classifications developed by the workers above reflect the latitudinal and climatic range over which closed-forest is found, and the taxa of which they are composed. The taxonomic content of closed-forest is not uniform in number or in content, nor is it entirely clinal, however. Closed-forest communities contain a number of centres of species richness and endemism, particularly in the Cape Tribulation and Atherton Plateau areas of Queensland, the 'Macleay-McPherson Overlap' region on the border of Queensland and New South Wales, and in Tasmania.

The floristic composition of the closed forests of the north-eastern Queensland region (Figs 5, 9) have often been compared to (or even thought to be derived from) those of Indo-Malaya. This view, however, has been contested by the results of more recent work which suggests that many of the taxa in these communities are derived from an ancient Gondwanan flora (Webb *et al.*, 1986; Truswell *et al.*, 1987; Barlow & Hyland, 1988). The north-eastern closed-forests contain a number of 'primitive' Magnolialian and Lauralian groups such as *Bubbia* and *Tasmannia* (Winteraceae), *Galbulimima* (Himantandraceae), *Eupomatia* (Eupomatiaceae), *Austrobaileya* (Austrobaileyaceae) and *Idiosperma* (Idiospermaceae). Vines are common, particularly in the lowlands, and include *Flagellaria indica*, *Rhaphidophora* spp., *Bambusa moreheadiana*, *Smilax* spp., *Faradaya splendens*, and climbing palms such as *Calamus* spp. Arborescent palms (Arecaceae) such as *Archontophoenix alexandrae*, *Licuala ramsayi*, *Orania appendiculata* and *Linospadix* spp. are common emergents or subcanopy taxa. Epiphytic ferns such as *Asplenium* spp., (Fig. 7) and *Platycerium* spp., orchids such as *Dendrobium* spp. and *Bulbophyllum* spp. and strangling figs (*Ficus*) are also abundant. Canopies and sub-canopies contain a range of endemic or near endemic tree genera, including *Doryphora* (Monimiaceae), *Ceratopetalum* (Cunoniaceae), *Darlingia*, *Cardwellia*, *Buckinghamia*, *Musgravea* (all Proteaceae), *Backhousia* and *Lindsayomyrtus* (Myrtaceae) and *Blepharocarya* (Anacardiaceae), and other more widespread genera like *Castanospermum* (Fabaceae). The gymnosperms *Araucaria* spp. (Fig. 10) and *Agathis* spp. are distinctive emergents in places (Beadle, 1981; Busby & Brown, 1994).

Further south, the numbers of vines, palms and epiphytes progressively decreases. In New South Wales the closed-forests are often dominated by *Doryphora sassafras* (Monimiaceae) and *Ceratopetalum apetalum* (Cunoniaceae). In some areas other species such as *Acmena smithii*, *Tristania laurina*, *Syzygium* spp. (all Myrtaceae), *Argyrodendron* spp. (Sterculiaceae) and various taxa of Lauraceae, Simaroubaceae, Rutaceae, Meliaceae and *Nothofagus* spp. may be major components (Beadle, 1981, Busby & Brown, 1994).

The cool temperate closed-forests of Tasmania are largely dominated by *Nothofagus cunninghamii* (Figs 11–14). In western Tasmania this species may form virtually monospecific forests with a sparse understorey of terrestrial ferns. More commonly it forms a mixed canopy with *Atherosperma moschata* (Atherospermataceae) and *Phyllocladus asplenifolius* (Podocarpaceae), with a range of genera such as *Eucryphia*, (Eucryphiaceae) *Anodopetalum* (Cunoniaceae), *Cenarrhenes*, *Agastachys*, *Orites*, *Telopea* (all Proteaceae), *Richea* (Fig. 15), *Archeria*, *Cyathodes* (all Epacridaceae), *Anopterus* (Grossulariaceae), *Pittosporum* (Pittosporaceae) and *Tasmannia* (Winteraceae) represented in the understorey. A more restricted closed-forest type is that dominated by *Athrotaxis cupressoides* (Cupressaceae), found only at high-altitude sites (Fig. 16) (Busby & Brown, 1994; Read & Brown, 1996).

Open-forests

Open-forests are a much more diverse group of vegetation types, occupying between 5% and 14% (depending on definition) of Australia in pre-European times. They are defined as those forest types with between 30% and 70% foliage projective cover of the dominant stratum and range from tall open-forest (>30 m tall) to open-heath (25 cm to 2 m tall). Pre-European Australian vegetation was made up of about 1.64% tall open-forest, 3.61% medium to low open-forest, 7.69% open-scrub and 1.47% open-heath (Specht *et al*., 1974). Open-forests are found mainly in a coastal band up to 250 km wide extending from near Darwin in the north around the east coast to the vicinity of Melbourne, with isolated pockets extending further inland in southern Queensland, in the eastern half of Tasmania, and in south-western Western Australia (Fig. 82).

In higher rainfall areas of eastern Australia open-forest species rely on some particular frequency or intensity of fire to maintain their dominance, and it is this which determines whether a particular area remains as open-forest or closed-forest. For example, in parts of Tasmania a fire occurring more frequently than once in about every 400 years will maintain the dominant eucalypts and exclude dominance of closed-forest species such as *Nothofagus cunninghamii* (Gilbert, 1959; Howard, 1973, 1981; Busby & Brown, 1994). Fire frequencies of between about 80 and 400 years may lead to a 'mixed' forest of *Eucalyptus*-dominated tall open-forest and other communities in which closed-forest floristic elements will be present to varying degrees in the understorey, such as can be found in moist areas of southern Victoria and Tasmania (Busby & Brown, 1994).

Another common feature of open-forests is the omnipresence of species of eucalypts in the upper stratum of such forests (*Eucalyptus s. lat.* was recently divided by exclusion of the bloodwoods as the genus *Corymbia* (Hill & Johnson, 1995). The vernacular descriptor 'eucalypts' is still usually applied to *Eucalyptus s. str.* + *Corymbia* + (sometimes) *Angophora*), however. A mixture of two or more species from different subgeneric groups of *Eucalyptus* may dominate some open-forests (Florence, 1981). Ashton & Attiwill (1994) commented aptly that tall open-forests 'are the supreme expression of the genus *Eucalyptus sensu lat*.'. Other genera, however, may be dominant in some open-forests. In some coastal open-forests, such as those near Sydney, *Angophora* species may be codominant. *Acacia* species, such as *A. harpophylla*, may form open-forests in south-eastern Queensland; they will be described briefly below (see Johnson & Burrows (1994) for further detail).

Many open-forest types have been recognised in both tropical and temperate Australia, depending primarily on tree height and species composition (Beadle, 1981; Ashton & Attiwill, 1994). Generally, subcategories of open-forests may be differentiated on the height of the dominant tree layer: as either tall (>30m), medium (10–30m) or low (>10m), but always with a foliage projective cover of between 30 and 70% (Table 24). While some closed-forest species may occur as an understorey to the eucalypt canopy, more usually the understorey species are shrubs or small trees with or without a ground stratum of grasses and/or ferns and mosses. Leaves of the understorey shrubs in tall open-forest are usually mesomorphic compared with the more xeromorphic leaves typical of the understorey species of lower forests. Tall open-forests generally occur in areas of higher rainfall and on soils of relatively higher fertility than the open-forests of medium or low heights, although there are local exceptions depending on fire history, substrate and microclimate.

While the distribution of closed-forests is confined to the more humid areas of eastern, and to a lesser extent, northern Australia, that of open-forests includes not only eastern and southern Australia, but also a relatively well-watered triangle between Perth and Albany in south-western Western Australia (Fig. 82). Though the same structural vegetation type occurs in the two regions, there is nonetheless a marked floristic discontinuity between the eucalypt species dominant in Western Australia and those in the east. It is some of these species dominant in tall open-forests in either region (Mountain Ash, *Eucalyptus regnans*, in south-eastern Australia; Karri, *E. diversicolor*, and Jarrah, *E. marginata*, in south-western Australia) which are among the tallest trees of the world; they can exceed 80 m (Ashton & Attiwill, 1994). What is more, in the case of *Eucalyptus regnans*, half of this final mature height may be achieved in the first 25 to 35 years following fire (Ashton & Attiwill, 1994).

Open-forests may be subdivided into different floristic types depending on either the species of *Eucalyptus* which dominates the tallest stratum (Beadle, 1981) or on the dominant species in the understorey. Ferns provide a pertinent example. In eastern Australia tree ferns of the genera *Cyathea* (Cyatheaceae) and *Dicksonia* (Dicksoniaceae) are often present in tall open-forests and may dominate the understorey, although they never occur in analogous south-western forests. Ground ferns may occur in the understoreys of both regions, however. A further floristic difference between the open-forests of east and west is the absence of closed-forest species in the lower strata of Western Australian tall open-forests.

The eucalypt species characteristic of the canopy of tall open-forests are usually fire-sensitive and lack a lignotuber; they regenerate as a cohort of even-aged seedlings from canopy-stored seed under the conditions of high light, high nutrient availability and changed soil microflora that inevitably follows a fire of high intensity. Only in the understorey species of tall forests are lignotubers represented, for example, in *Olearia argophylla* and *Bedfordia arborescens* (both Asteraceae), which also store their seed in the soil. On the other hand, eucalypts characteristic of open-forests of medium or low height generally possess lignotubers and their canopies may recover from fire by development of buds located on either the lignotuber or as epicormic buds beneath the generally thicker bark of the bole and major branches. Such forests may be much more 'mixed' in terms of age classes, as well as in species composition, than their taller counterparts.

Beadle (1981) recognised 10 alliances of eucalypt communities in the tropics, 10 alliances of tall eucalypt forests in the eastern coastal lowlands, 7 alliances of eucalypt woodlands and forests on soils of low fertility, mainly on the eastern coastal lowlands, 18 alliances of eucalypt communities of cooler climates of the eastern highlands, lowland Victoria and Tasmania, 4 alliances of Ironbark forests and woodlands of the east (Cape York Peninsula to Victoria), 13 alliances of Box woodlands of the east and south-east, 18 alliances of mallee and marlock communities, and 11 alliances of eucalypt forests and woodlands in the south-west, a total of 91 alliances. Most of these had a number of sub-alliances. It is therefore very difficult to generalise about floristic and ecological characteristics.

Very tall open-forests are found in two widely disjunct areas: the relatively wet margins of closed forest communities in south-eastern Australia (Victoria and Tasmania) (Figs 17, 18), and in south-western Western Australia in those areas where soil of good texture and reasonable fertility exists. The south-eastern forests, dominated by *E. regnans*, occur on rich, well-drained loamy soils, and reach heights of up to 90 m. They are fire-sensitive and thus tend to occur in stands of even-aged trees. Little or no eucalypt recruitment occurs in the understorey, because of low light levels. Instead, a sparse to moderately dense understorey of shade-tolerant shrubs and small trees such as *Bedfordia salicina* (Fig. 17), *Olearia argophylla*, (both Asteraceae), *Pomaderris apetala* (Rhamnaceae) and some *Acacia* species (e.g. *A. melanoxylon*). Tree ferns, particularly *Dicksonia antarctica* may be locally abundant (Fig. 18), and ferns of shorter stature such as *Blechnum* (Blechnaceae), *Histiopteris* and *Hypolepis* (both Dennstaedtiaceae), sedges and rushes may also be common. A successional shift in these very tall open-forests towards closed forest communities may occur over time, as such species as *Nothofagus cunninghamii* establish and replace smaller shrubs. Fire frequencies of less than 50–100 years favour *E. regnans*, frequencies of more than 350 years favour succession to closed-forest (Gilbert, 1959). The influence of fire is discussed in more detail later in this chapter. In the south-west of Western Australia the lack of tree ferns and adjacent closed-forest communities give the very tall forests a different facies. The tallest communities (Karri, *E. diversifolia*) grow to 70–85 m tall, with an often dense understorey of mesomorphic or semi-xeromorphic shrubs 3–7 m tall. The dominant understorey shrub is often *Trymalium spathulatum* (Rhamnaceae), with various species of *Acacia*, *Paraserianthes*, (both Mimosaceae), *Allocasuarina* (Casuarinaceae), *Agonis* (Myrtaceae), *Banksia*, *Persoonia* (both Proteaceae), Rutaceae, and Fabaceae (Beadle, 1981; Beard, 1990).

The medium to tall open-forests on both sides of the continent present superficially similar appearances. With varying degrees of fire-tolerance, they tend to be more mixed-age, and this provides a better-lit forest floor than the very tall forests (Figs 4, 19, 20). Consequently the understorey tends to be more diverse, and varies locally with conditions of water, light, nutrients, disturbance, fire frequency and other factors. Understorey shrubs come particularly from the Proteaceae (e.g. *Persoonia*, *Grevillea*, *Hakea*, *Banksia*, *Dryandra*), Fabaceae (e.g. *Pultenaea*, *Daviesia*, *Bossiaea*, *Gompholobium*), Myrtaceae (e.g. *Leptospermum*, *Agonis*, *Melaleuca*), Casuarinaceae (*Casuarina*, *Allocasuarina*), and Mimosaceae (*Acacia*) (Beadle, 1981; Beard, 1990).

Floristic composition of the understorey in medium and low open-forests is complex. Gill (1994) noted that there are numbers of genera which are common to both eastern and western Australia, such as shrubs of *Acacia* (Mimosaceae), *Daviesia* (Fabaceae), *Hakea* (Proteaceae), *Hibbertia* (Dilleniaceae), *Leptospermum*, *Leucopogon* (Epacridaceae) and *Pultenaea* (Fabaceae), the herbaceous genera (all rhizomatous) *Dianella* (Liliaceae), *Lepidosperma* (Cyperaceae) and *Lomandra* (Xanthorrhoeaceae), and the ferns *Adiantum* (Adiantaceae) and *Pteridium* (Dennstaedtiaceae). Furthermore, there are numerous discontinuities in species distributions between eastern and western open-forest floras, especially within the Orchidaceae (Green, 1964). There are also some obvious species disjunctions within eastern Australia, for instance on either side of Bass Strait.

The open-forests of Australia are complex floristically and ecologically. The predominance of *Eucalyptus* in all these open-forest types imparts a superficial uniformity to what is really a complex of vegetation associations and species which are often subtly adapted to local conditions. Interactions of soil types, patterns of water use and fire regimes are only recently coming to be understood for some open-forest types. Much still needs to be learned about this 'important and conspicuous element of the Australian landscape' (Gill, 1994: 219).

Woodlands

The foliage projective cover of Australian woodlands varies widely from 0.1 to 70 per cent; such woodlands may also vary in height but they are always over 2 m tall (Table 24). Defined in this way, woodlands cover about 25 per cent of Australia, in a band of varying width (up to 500 km) on the 'arid' (usually inland) side of the open-forest communities, and extend northwards into southern Papua New Guinea. They occur in all mainland Australian States and Territories, and on the Bass Strait Islands, but are rare in Tasmania (Fig. 82). They are dominated by perennial woody plants, usually of the genera *Eucalyptus* and *Acacia* (Figs 21, 22, 24, 25, 27, 100, 104) but occasionally of *Melaleuca* (Myrtaceae), which do not have their crowns touching; usually they have a grassy understorey (Gillison, 1994). Because of the latter characteristic, they have sometimes been referred to as 'savanna' woodlands in the past.

Of the c. 700 species of eucalypts so far described, about 80 per cent of them occur in woodlands (Gillison, 1994). In northern Australia where annual rainfall is less than 600 mm *Acacia* spp. tend to replace eucalypts. *Melaleuca* spp. may dominate woodlands in areas where seasonally fluctuating watertables are pronounced (Figs 8, 26). While the majority of woodlands are evergreen, some of the northern woodlands have genera present in the overstorey which may be winter-deciduous. These genera include *Terminalia* (Combretaceae) and *Bauhinia* (Caesalpiniaceae).

Woodlands are characterised not only by the form and spacing of the dominant trees but also by the presence of a grassy understorey, in contrast to the sclerophyll shrub understoreys typical of most open-forests. The grassy understorey of such woodlands has undergone considerable floristic change over the last 200 years in many regions. Such changes have arisen primarily because of the effects of continuous grazing by introduced animals, with often complex interactions between grazing and changed fire regimes, nutrient enrichment and plant species introductions, leading to a diversity of understorey types. The understorey to some woodlands, such as those in south-eastern Australia dominated by *Eucalyptus melliodora,* is now composed nearly entirely of annual species of Mediterranean origin, because few indigenous species can persist under such a continuous grazing regime (Table 25) (Moore, 1970). In this instance, even the dominant eucalypts fail to regenerate unless protected from grazing and the entire plant community disappears, as has happened over large areas of central New South Wales and northern Victoria.

In terms of surface soil nutrients, woodlands are usually less impoverished than the adjoining open-forests with a sclerophyll shrub understorey. The corollary to this difference is that, about 200 years ago, not only did such woodlands have a grassy understorey suitable for grazing, but they were initially easier to clear and more productive to graze; the resultant changes in understorey composition were accordingly greater. Remnants of the original understorey flora now exist in only a few cemeteries or roadside verges in southern Australia. Similar changes to the understoreys of northern Australian woodlands have occurred more recently as they are utilised increasingly for grazing.

A unique type of vegetation in southern Australia known as 'mallee' may be both a tall shrubland or a low woodland; as such, it sits between the broad subdivisions of woodland and shrubland used in this chapter. The word 'mallee' is an Aboriginal term for a eucalypt with lateral roots close to the soil surface from which drinking water could be obtained. Mallee vegetation is dominated by mature eucalypts which possess not only water-yielding roots but also a strongly developed lignotuber that develops at the base of the main stem. From this lignotuber arise numerous stems of more or less equal size, either as part of the inherent growth form, or as the result of sprouting of buds from the lignotuber when the main stem loses apical dominance as a result of drought, fire, frost or herbivore damage. (Figs 28, 99). Depending on the height of the regrowth, a woodland or a tall shrubland results. The same vegetation dominated by certain eucalypts, such as *Eucalyptus oleosa*, has been mapped as either woodland or shrubland by different individuals and provides one reason why the all-encompassing aboriginal term has been retained.

Different types of mallee vegetation are usually characterised by the taxonomic identity of the multi-stemmed eucalypt species (see, e.g. Noble & Bradstock, 1989; Parsons, 1994). Of the total number of *Eucalyptus* species described, about one fifth are mallees, with the greatest number occurring in south-western Western Australia (Parsons, 1994). What is more, the extent to which the multi-stemmed character is expressed in response to adverse site factors varies within a species, so that the same eucalypt taxon may have mallee and non-mallee forms (e.g. *Eucalyptus cladocalyx*). In semi-arid Western Australia vegetation occurs which is characterised by low single-stemmed eucalypts similar to mallees but which lack or have only a poorly developed lignotuber; these eucalypts are termed 'marlocks' – another

Table 25. Species changes resulting from grazing in herbaceous communities of *Eucalyptus melliodora–E. blakelyi* woodlands of the Southern Tablelands of New South Wales (after R.M.Moore (1970), with names updated).

Themeda triandra-Austrostipa aristiglumis-Poa caespitosa s. lat.
(Tall warm-season perennial tussock grasses)
GRAZING

↓

Austrostipa arisriglumis-Poa caespitosa s. lat. -Austrosripa scabra subsp. *falcata*

↓

Austrostipa scabra subsp. *falcata-Austrodanthonia carphoides-Austrodanthonia auriculata*
(Short cool-season, perennial grasses)

↓

Austrodanthonia carphoides-Austrodanthonia auriculata
(Short cool-season perennials)

↓

INTRODUCTION OF NATIVE SPECIES FROM MORE ARID COMMUNITIES
Enneapogon nigricans, *Chloris truncata*,
Tripogon loliiformis, *Panicum effusum*,
Vittadinia triloba, *Euphorbia drummondii*,
Convolvulus erubescens
(Short warm-season species)
GRAZING

↓

Austrodanthonia carphoides-Austrodanthonia auriculata

INTRODUCTION OF MEDITERRANEAN ANNUALS
Trifolium glomeratum, *Vulpia bromoides*,
Bromus spp., *Hordeum leporinum*,
Asreraceae, *Erodium cicutarium*,
Aira caryophyllea
(Exotic cool-season annuals)

Enneapogon nigricans, *Chloris truncata*, *Panicum effusum*,
Vittadinia triloba, *Eragrostis brownii*
(Short warm-season perennials)
GRAZING AND SUPERPHOSPHATE

↓

Vulpia bromoides, *Bromus diandrus*, *Erodium cicutarium*, *Trifolium glomeratum*, *Cirsium vulgare*
(Exotic cool-season annuals)

Chloris truncata, *Eragrostis cilianensis*, *Chenopodium carinatum*, *Polygonum aviculare*
(Warm-season species)

(Parameters: — Soils: Solodised solonetz. ph 5.9 (1:5 suspension). Rainfall: 584 mm per annum, distribution uniform. Altitude: 610 m above sealevel)

Aboriginal term still in use to describe a regional vegetation type. The genera *Acacia*, *Casuarina/Allocasuarina* and *Callitris* may be co-dominant with *Eucalyptus* in some areas of mallee vegetation.

The understorey to mallee vegetation may comprise either the sclerophyll shrubs or the chenopod shrubs to be described in the next section. In other cases, the understorey is more sparse and ephemeral with a high cover of litter and/or bare ground. In yet other cases, the hummock grass genus *Triodia* may characterise the understorey.

While mallee vegetation is typical of a large part of semi-arid southern Australia, the subalpine woodlands in the high-rainfall, montane areas of south-eastern Australia have the same form and structure (Williams & Costin, 1994). Just as mallee vegetation tends to be the most arid of the eucalypt-dominated communities of temperate Australia (but see Parsons, 1981, for some exceptions), so the subalpine woodlands are the most cold-tolerant of the tree communities; beyond the treeline in colder sites the woodland trees with a mallee form are replaced by alpine shrublands or grasslands. Subalpine woodlands of south-eastern mainland Australia are dominated by *Eucalyptus* species (particularly *E. niphophila* and *E. pauciflora*). In Tasmania other *Eucalyptus* species such as *E. coccifera* and *E. subcrenulata* form the treeline, often in association with or replaced by gymnosperms such as *Athrotaxis cupressoides*, *A. laxifolia*, *A. selaginoides* (Cupressaceae) and *Phyllocladus lawrencii* (Podocarpaceae), temperate rainforest stragglers such as *Nothofagus cunninghamii*, *Anopterus glandulosus*, *Persoonia gunnii* and *P. muelleri*, and some specialist subalpine taxa such as *Richea pandanifolia*, *R. scoparia* (Epacridaceae) and *Nothofagus gunnii* (Fagaceae).

A similar blurring of the distinction between low woodland and tall shrubland is evident for some vegetation dominated by *Acacia*, as occurs for analogous eucalypt-dominated mallee vegetation. Species of *Acacia* dominate some low woodlands and tall shrublands (and even some open-forests) in all regions of Australia generally too dry to support eucalypts (Johnson & Burrows, 1994). Some *Acacia* woodlands may also occur in more mesic areas, such as the *Acacia harpophylla* (brigalow) woodlands of south-eastern and central Queensland (Fig. 24). In general, the *Acacia* species characteristic of more arid regions, e.g. Mulga, *A. aneura* (Figs 104, 105) cope with water stress both physiologically and anatomically (e.g. by having photosynthetic phyllodes instead of leaves; thickened cuticles, etc) as well as by spatial patterning of the vegetation, whereby the *Acacia* occurs in thickets that receive run-off water from the sparsely vegetated inter-thicket areas (Johnson & Burrows, 1994). In general, different species, and even different Sections of the genus *Acacia*, occur in the canopy of woodlands on different soil types, but with past history also having an effect on species distributions (see Johnson & Burrows, 1994, for further detail). The complexities in patterning in *Acacia* species in semi-arid and arid regions rival that in *Eucalyptus* species characteristic of woodlands in more mesic Australia.

Other low woodland or tall shrubland communities are dominated by genera such as *Banksia* (Proteaceae), *Callitris* (Cupressaceae) and *Casuarina/Allocasuarina* (Casuarinaceae). *Banksia* woodland/tall shrubland is particularly well developed on parts of the coastal sand plain north of Perth, where *Banksia menziesii* and *B. attenuata* dominate woodlands and scrub heaths. Woodlands 4.5–6 m tall, dominated by *B. ashbyi*, are found fringing the arid zone from Freycinet Estuary to the Murchison River area. On the southern coastal sandplain of Western Australia, various *Banksia* species are major components of shrub-heaths, and near the coast *B. grandis* and *B. ilicifolia* may locally form woodlands or dense scrubs to 2–3 m tall (Figs 3, 103) (Beadle, 1981; Beard, 1990). In the east, species such as *B. serratifolia*, *B. aspleniifolia*, *B. robur* and *B. ericifolia* form similar coastal assemblages in Queensland and New South Wales, either as dominants or co-dominants with species of *Leptospermum*, *Casuarina/Allocasuarina*, and other taxa. *Callitris*, particularly *C. glaucophylla*, forms woodlands of limited extent in mallee regions of southern Australia, extending into central Australia (Fig. 21). In the tropics *C. glaucophylla* is replaced by *C. intratropica*, and in Western Australia the related genus *Actinostrobus* fills a similar niche (Beadle, 1981; Beard, 1990). Like *Callitris*, species of *Casuarina* and *Allocasuarina* are common components of eucalypt woodland almost throughout the country. In some areas they may form pure stands, as for example, woodlands of *Casuarina cristata* and *C. glauca* in eastern Queensland and New South Wales, *C. equisetifolia* in tropical coastal areas, and *Allocasuarina verticillata* in south-eastern Australia (Wilson & Johnson, 1989).

Shrublands

In Australia, two main types of shrublands have been recognised. Sclerophyll shrublands contain the same or similar species to those which comprise the understorey to open-forests of medium or low height (see above). This sclerophyll shrubland type is usually called 'heath' (Specht, 1994) but in Western Australia the Aboriginal term 'kwongan' has been used (Figs 3, 103) (Pate & Beard, 1984). Sclerophyll shrublands are distributed discontinuously in an arc around the coastal regions of southern and eastern Australia from Kalbarri in Western Australia to Cape York in north-eastern Australia, with outliers of the same community (and sometimes even the same genera) in upland areas of eastern Indonesia. Sclerophyll shrublands always occur on soils highly deficient in available phosphorus and nitrogen (Specht, 1994); the depth of infertile sand to the clayey subsoil varies from several centimetres to greater than 2 m depending on the previous geomorphological history of particular regions.

As with other vegetation types, many subtypes of sclerophyll shrublands can be distinguished on the basis of height (between 0.25 and 2 m) and foliage projective cover (Specht, 1994). The majority occur as patches of varying areal extent close to the present or previous coastline. Sclerophyll shrublands are species-rich communities (especially in south-western Western Australia) with no one taxon dominant; the families Epacridaceae, Myrtaceae, Fabaceae, Restionaceae, Rutaceae and Proteaceae and the genera *Acacia* (Mimosaceae), *Allocasuarina* (Casuarinaceae) and *Xanthorrhoea* (Xanthorrhoeaceae) are common. The structural and floristic features of coastal shrublands (Figs 2, 3, 103) are matched by other shrublands of lesser extent occurring in exposed montane regions and by those above the treeline in alpine environments (Figs 117, 118) (Costin, 1981).

The high floristic diversity of sclerophyll shrublands is matched by diverse responses to different fire frequencies and intensities, as exemplified by a diversity of regeneration mechanisms in the plant community (Gill & Groves, 1981). Another strongly developed feature of such shrublands is their diverse array of nutrient-uptake or nutrient-conservation mechanisms that enable them to grow and survive on nutrient deficient sands (Lamont, 1982).

The second major type of shrubland is that dominated by shrubs of the family Chenopodiaceae — the 'chenopod shrublands' (Leigh, 1994). They occupy about 7 per cent of inland Australia (Fig. 85) on sodium-rich soils with generally a higher clay content in the surface soil than that underlying sclerophyll shrublands. While the latter shrublands are comprised of many genera within a large group of families, the chenopod shrublands are dominated by the genera *Atriplex* and *Maireana* within the one family Chenopodiaceae, as their name implies (Fig. 106). An open-shrubland of sclerophyll species is structurally similar to one dominated by chenopods but the species diversity of the latter is always less and the influence of sodium ions always greater.

Chenopod shrublands are composed of xeromorphic halophytes which are drought- and salt-tolerant (Leigh, 1994). The height of such shrublands may vary from 0.5 m to 3 m (the latter in the case of *Atriplex nummularia)* and with usually low values for foliage projective cover (between 10 and 30%, but sometimes below 10%). Because of this relatively low cover, indigenous and naturalised species of annual and perennial grasses and some forbs typically occur under or between the dominant shrubs. Various admixtures of species of *Atriplex* and *Maireana* occur in different regions mainly in response to different soil types, and in the case of *Maireana*, different species are distributed according to the proximity of the limestone layer to the soil surface (Leigh, 1994).

Grazing of the 'saltbush' (*Atriplex*) country commenced early in the period of European settlement of Australia; while grazing of the dominant shrubs may occur in times of drought, grazing animals prefer to concentrate on the more palatable inter-shrub grasses and forbs. This differential pattern of grazing according to relative palatabilities began a process of degradation of the floristic diversity (and the grazing value) of these chenopod shrublands

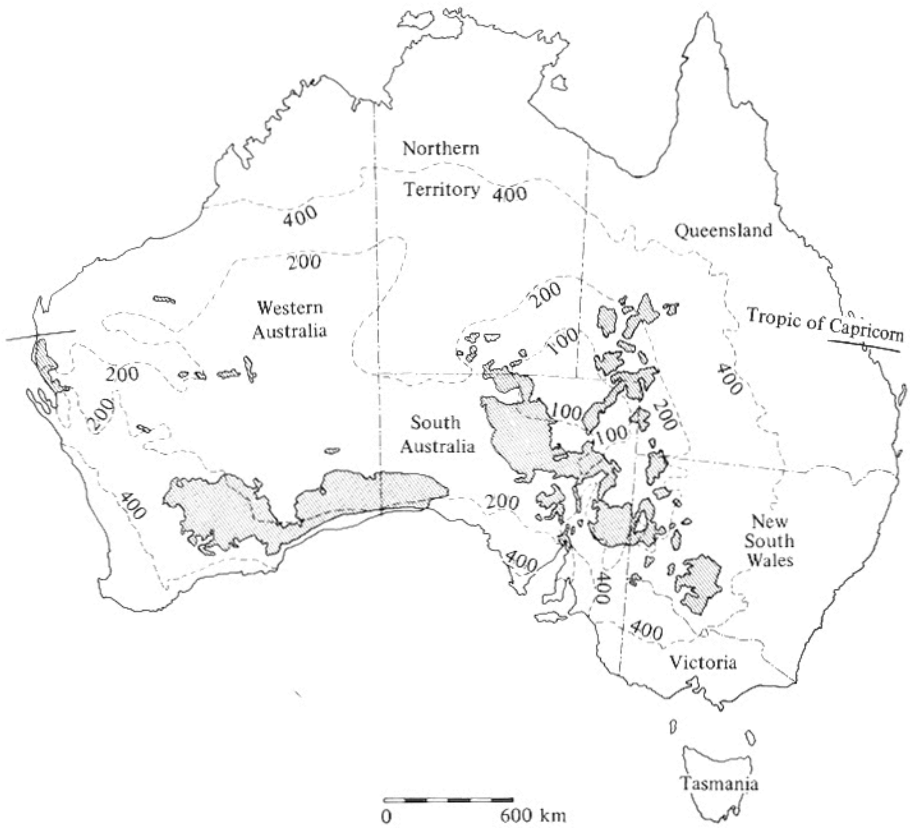

Figure 85. Distribution of chenopod shrublands in relation to the isohyets representing mean annual rainfalls of 100, 200 and 400 mm (dashed lines). Source: J.H.Leigh, Chenopod shrublands, *in* R.H.Groves (ed.), *Australian Vegetation*, 2nd edn, fig. 12.1 (1994). © Cambridge University Press 1981, 1994. Reprinted with the permission of Cambridge University Press and the author.

that has continued. In the worst instances, where the chenopod shrubs are defoliated and/or their stems trampled, only bare areas ('scalds') remain, and these are very difficult to revegetate. In other instances, stable ('disclimax') communities of perennial grasses have replaced the chenopod shrubs and an increase in grazing capacity has resulted, as on the inland riverine plains of New South Wales (Leigh, 1994).

Grasslands

Grasslands are treeless communities dominated by indigenous perennial grasses, usually with some annual grasses and introduced species present (Mott & Groves, 1994).

There are four basic types of grassland in Australia. By far the most widespread are the arid hummock grasslands of central Australia (Fig. 86). These cover as much as a third of the continent in areas with less than 200 mm average annual rainfall which can be either summer- or winter-incident. The arid hummock grasslands are dominated by the genera *Triodia* (Fig. 109) and *Plectrachne* which are referred to as 'hummock' grasses, in that individual clumps are usually large and hemispherical in form.

Areas with a higher rainfall (between 200 and 500 mm/annum) and a predominant pattern of summer rainfall support *Astrebla* species as dominants in what are called arid tussock grasslands (Fig. 108), with *Astrebla* characteristically forming a tussock, i.e. a more or less vertical clump.

The third type is made up of the coastal grasslands of tropical northern Australia. These are dominated by species of *Sporobolus* and *Xerochloa,* and rainfall is again summer-incident.

The fourth type, the subhumid grasslands of eastern Australia, comprises three recognised subtypes. In areas of eastern and northern Queensland with summer rainfall, genera such as *Dichanthium* (Fig. 110) and *Eulalia* form tropical subhumid grasslands, whereas in south-eastern Australia with a predominantly winter or year-round rainfall, temperate grasslands are characterised by tussock grasses belonging to the genera *Themeda, Poa* and *Stipa s. lat.* (now mainly included in *Austrostipa*, see Jacobs & Everett, 1996) (Fig. 112). The third subtype, the subalpine tussock grasslands of cold and wet tableland or montane regions of southern Australia (Fig. 111), is dominated by the genera *Poa* and *Danthonia s. lat.* (comprising *Austrodanthonia, Notodanthonia* and *Rytidosperma*).

The four basic types of grassland described above represent the natural grassland cover present in different regions of Australia. While some types are extensively distributed, such as the arid hummock grasslands, other grasslands currently exist in south-eastern Australia only as small remnants and were never as widespread as their arid equivalents (Fig. 86).

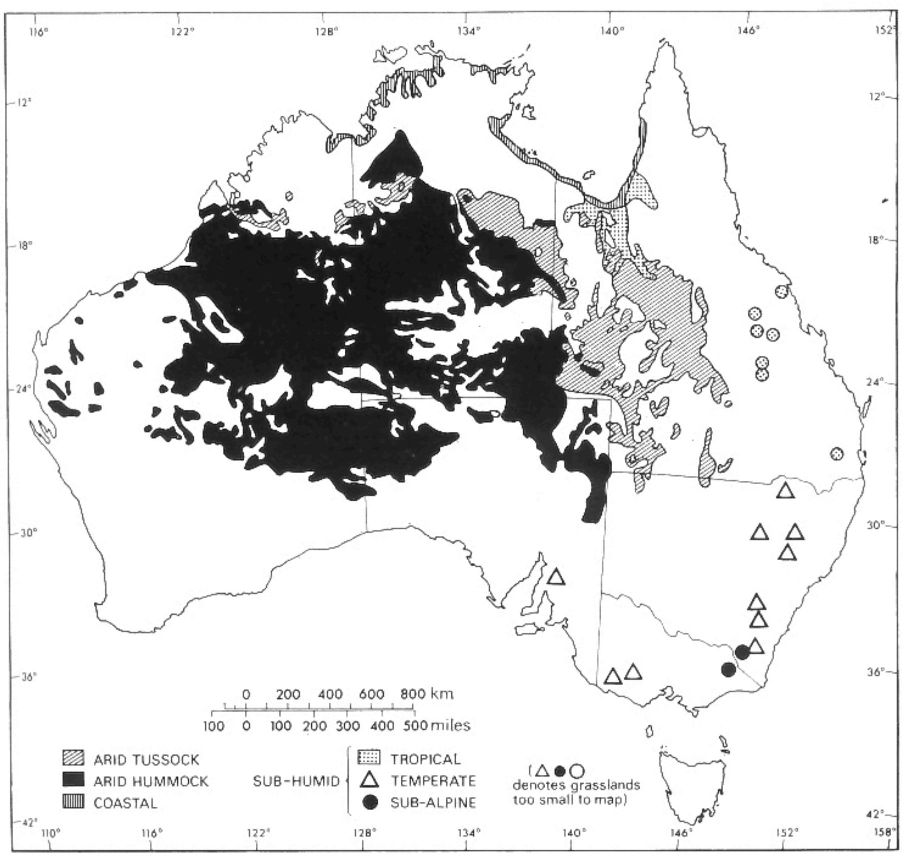

Figure 86. Distribution of major grassland types in Australia. Source: R.H.Groves, fig. 1 (1979). Reproduced with permission.

In addition to these present areas of natural grassland, large areas of derived grasslands now exist in both northern and southern Australia, representing the grassy understorey to the open-woodlands, as described above. Over large areas the overstorey trees have been cleared or thinned and derived or secondary grasslands result. In the north, the grass genera once present in the understorey and now dominant in the derived grasslands include *Themeda* (Fig. 113), *Sorghum* and *Heteropogon*; in south-eastern Australia they are *Themeda, Danthonia s. lat.* and *Poa*, all of which are perennial tussock grasses. In areas of south-eastern Australia with lower rainfall and a history of more intensive sheep grazing, derived grasslands now consist largely of annual grasses and forbs introduced from mediterranean Europe. In such grasslands the indigenous element may be entirely absent.

A range of ecological factors exclude woody vegetation from natural grasslands, even in the absence of grazing. For derived grasslands in relatively humid areas as described above, trees will regenerate naturally provided there is a seed source and protection from grazing and frequent fires. For natural grasslands, inadequate soil moisture seems to be a primary cause of treelessness. While trees will continue to grow adequately from seedlings planted into some treeless areas, they rarely if ever establish naturally. In some instances, as on the Basalt Plains of south-western Victoria, tree seedlings seem unable to establish because the clay soil on which most grasslands occur cracks deeply on drying and there is inadequate moisture for early root growth. Below an average annual rainfall of about 250 mm, as in at least a third of Australia, both establishment *and* growth of trees are prevented. Only in the localised cases of inverted treelines ('frost hollows') in subalpine regions does soil moisture seem not to be implicated. In these situations a short exposure to winter temperatures lower than usual may kill even established seedlings of *Eucalyptus pauciflora*.

If soil moisture limits tree seedling establishment in natural grasslands, the interaction between grazing and fire seems especially important in maintaining the herbaceous character of derived grasslands. If grazing occurs soon after a fire and continues, then the regenerative capacities of some grasses are so severely depleted that botanical composition of the grassland changes. In southern Australia this change usually favours the grass genera having a C3 photosynthetic pathway such as *Danthonia s. lat.* and *Stipa*, at the expense of the C4 *Themeda* element. But the same interaction seems to influence the balance between *Heteropogon* and *Themeda* (both C4 grasses) in grazed and regularly burnt grasslands in tropical Queensland. In the arid hummock grasslands of north-western Western Australia, burning and deferred grazing restricts the growth of *Triodia pungens*, a relatively undesirable species for animal production, and promotes the growth of other, more desirable *Triodia* species (Suijdendorp, 1981). The proportions of the dominant species in both types of grasslands may also change in relation to other ecological factors, of which soil nutrient status and temperature are the main ones (see Moore, 1970, and Groves & Williams, 1981, for further examples).

Floristic classification of Australian vegetation

The classificatory basis for Australian vegetation of Specht (1970), Beard (1976), Carnahan (1976, 1977, 1990) and many others is structural, and this approach has a considerable following. However, another approach to describing vegetation is floristic, a recent example being that of Bridgewater (1994).

Bridgewater (1994) recognised and mapped 26 Divisions, and a further 11 Divisions were defined on an ecological basis without being mapped. Each Division was defined by a suite of 'character genera'. The geographically-defined Divisions are shown in Fig. 87. Characteristics of the Divisions are shown in Table 26 (note that some of the 'genera' are in fact subgenera or 'Alliances' of *Eucalyptus* and these are shown in quotation marks in Table 26).

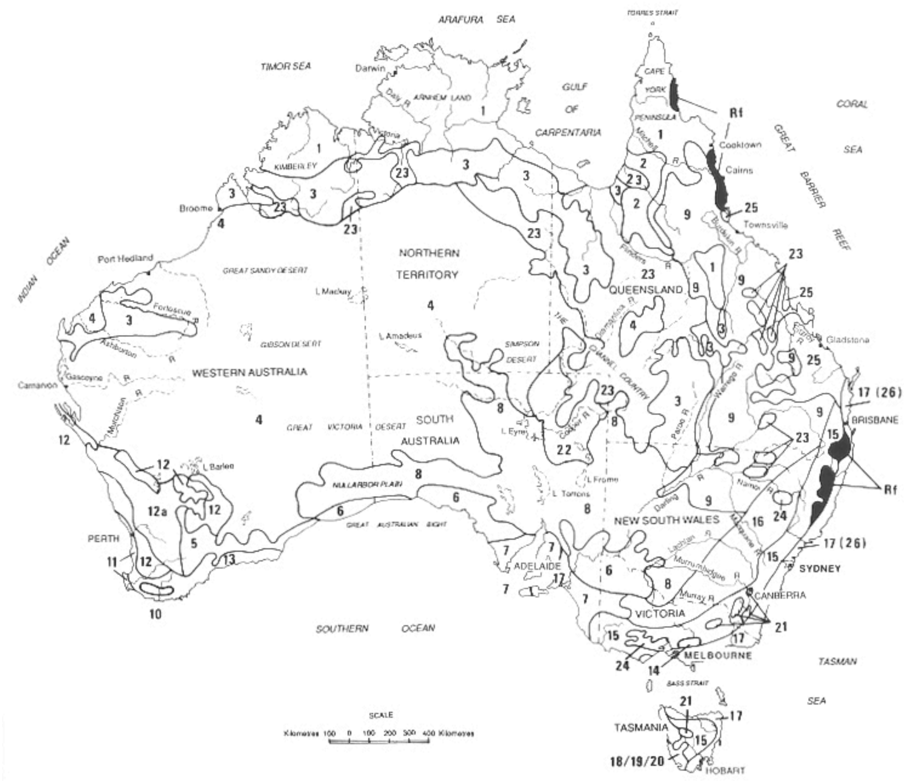

Figure 87. Floristic vegetation Divisions for Australia. The numbers refer to the Divisions as described in Table 26. Rf = areas where rainforest patches dominate the landscape. Reproduced with permission.

Table 26. The floristic divisions, character genera, structure and distribution of the Australian flora (after Bridgewater, 1994).

Division	Character genera	Structure & distribution
1. Blakella-Gardenia Division	'*Blakella*', *Corymbia*, '*Symphyomyrtus*', '*Eudesmia*', *Livistona*, *Adansonia*, *Gardenia*, *Erythrophleum*, *Terminalia*, *Buchanania*, *Xanthostemon*, *Grevillea*, *Callitris*, *Themeda*, *Aristida*, *Eriachne*, *Heteropogon*, *Mnesithea*, *Cymbopogon*, *Sorghum*	Forest to open woodland in tropical northern Australia. Often *Eucalyptus* species and genera of the Indo-Malayan monsoonal forest with a tall grass understorey
2. Melaleuca-Sorghum Division	*Melaleuca*, *Sorghum*, *Chrysopogon*, *Heteropogon*, *Pandanus*, *Terminalia*, *Bauhinia*, *Xerochloa*, *Alphitonia*, *Barringtonia*	Open savannah around the Gulf of Carpentaria, dominated by *Melaleuca* with a tall grass understorey; inundated in wet season
3. Acacia-Triodia Division	*Acacia*, *Corymbia*, '*Symphyomyrtus*', *Owenia*, *Calytrix*, *Erythrophleum*, *Grevillea*, *Solanum*, *Verticordia*, *Jacksonia*, *Terminalia*, *Pityrodia*, *Callitris*, *Triodia*, *Plectrachne*, *Eriachne*	Open woodland with stunted *Eucalyptus* and *Acacia* species, a (hummock) grass understorey and occasional low shrubs
4. Duboisia-Triodia Division	*Duboisia*, '*Eudesmia*', '*Symphyomyrtus*', *Allocasuarina*, *Santalum*, *Codonocarpus*, *Tribulus*, *Zygophyllum*, *Hakea*, *Grevillea*, *Dodonaea*, *Eremophila*, *Senna*, *Abutilon*, *Triodia*, *Aristida*, *Plectrachne*	Hummock grasslands of central and central-western Australia with tree shrub cover of variable density
5. Eudesmia-Banksia Division	'*Eudesmia*' '*Symphyomyrtus*', *Banksia*, *Chamaelaucium*, *Chorizema*, *Lambertia*, *Leucopogon*, *Lysinema*, *Xanthorrhoea*, *Petrophile*, *Allocasuarina*, *Jacksonia*, *Dryandra*, *Templetonia*, *Verticordia*, *Stirlingia*, *Kennedia*, *Loxocarya*, *Mesomelaena*, *Anarthria*, *Stylidium*	The western mallee, with an understorey of sclerophyllous shrubs
6. Symphyomyrtus-Sclerolaena Division	'*Symphyomyrtus*', *Sclerolaena*, *Maireana*, *Senna*, *Eremophila*, *Myoporum*, *Santalum*, *Melaleuca*, *Zygophyllum*, *Dodonaea*, *Calytrix*, *Lycium*, *Triodia*	Mallee, on solonised soils, with many halophytic shrubs in the understorey
7. Symphyomyrtus-Danthonia Division	'*Symphyomyrtus*', *Leptospermum*, *Grevillea*, *Thysanotus*, *Pultenaea*, *Lasiopetalum*, *Dampiera*, *Astroloma*, *Acrotriche*, *Baeckea*, *Goodenia*, *Melaleuca*, *Danthonia s. lat.*, *Austrostipa*	The eastern mallee, with a mixed shrub and grass understorey

Table 26 continued

Division	Character genera	Structure & distribution
8. Maireana-Sclerolaena Division	*Acacia*, *Maireana*, *Sclerolaena*, *Chenopodium*, *Halosarcia*, *Nitraria*, *Lycium*	Low shrublands of eastern and central-southern Australia, dominated by Chenopodiaceae, with occasional *Acacia*; soils often saline or alkaline
9. Geijera-Paspalidium Division	*Geijera*, *Flindersia*, *Carissa*, *Eremophila*, *Eremocitrus*, *Capparis*, *Sclerolaena*, *Enchylaena*, *Sida*, *Terminalia*, *Acacia*, *Atalaya*, *Heterodendron*, *Chloris*, *Paspalidium*, *Sporobolus*, *Aristida*, *Cymbopogon*, *Eragrostis*	Open woodland with a dense grass understorey, and including a number of monsoon forest genera in the tree layer. Now heavily impacted by grazing. Northern Queensland to northern New South Wales, west of the Great Dividing Range
10. Allocasuarina-Trymalium Division	'*Symphyomyrtus*', *Allocasuarina*, *Paraserianthes*, *Trymalium*, *Thomasia*, *Mirbelia*, *Phebalium*, *Banksia*, *Chorilaena*, *Burtonia*, *Chorizema*, *Crowea*, *Veronica*, *Stylidium*, *Leucopogon*, *Agonis*, *Clematis*, *Bossiaea*, *Hovea*, *Tremandra*, *Persoonia*, *Podocarpus*	Wet sclerophyll, well stratified forest of south-western Australia (Karri or Tingle forest). Fire normally absent, and trees regenerating from seed rather than coppicing if burnt
11. Acacia-Leucopogon Division	'*Symphyomyrtus*', '*Monocalyptus*', '*Eudesmia*', *Acacia*, *Leucopogon*, *Dryandra*, *Pimelea*, *Hakea*, *Jacksonia*, *Hibbertia*, *Conospermum*, *Melaleuca*, *Phyllanthus*, *Xanthorrhoea*, *Scaevola*, *Templetonia*, *Spyridium*, *Calothamnus*, *Diplolaena*, *Myoporum*, *Olearia*, *Lomandra*, *Lepidosperma*, *Conostylis*, *Mesomelaena*, *Austrostipa*	A complex of low shrubland with some tall forest, on recent calcareous sands in a narrow coastal zone of south-western Australia
12. Banksia-Nuytsia Division	'*Monocalyptus*', *Corymbia*, '*Symphyomyrtus*', *Acacia*, *Banksia*, *Nuytsia*, *Actinostrobus*, *Xylomelum*, *Hybanthus*, *Gompholobium*, *Burchardia*, *Stirlingia*, *Persoonia*, *Melaleuca*, *Conospermum*, *Verticordia*, *Hypocalymma*, *Allocasuarina*, *Hibbertia*, *Leucopogon*, *Eremaea*, *Dryandra*, *Hakea*, *Grevillea*, *Jacksonia*, *Lechenaultia*, *Stylidium*, *Anigozanthos*, etc	A complex of forests and shrublands, generally on sands and laterites, in south-western Australia

Table 26 continued

Division	Character genera	Structure & distribution
13. Agonis-Persoonia Division	*Corymbia*, '*Monocalyptus*', *Allocasuarina*, *Agonis*, *Adenanthos*, *Banksia*, *Hakea*, *Leucopogon*, *Persoonia*, *Regelia*, *Synaphea*, *Verticordia*, *Oxylobium*, *Burtonia*, *Gompholobium*, *Styphelia*, *Hypocalymma*, *Boronia*, *Melaleuca*, *Petrophile*, *Isopogon*, *Grevillea*, *Lechenaultia*, *Patersonia*, *Xanthorrhoea*, *Kingia*, *Dasypogon*, *Anarthria*, *Loxocarya*, *Macrozamia*	An extremely species-rich complex of forest, shrubland and coastal communities on nutrient-poor soils
14. Bedfordia-Pomaderris Division	'*Symphyomyrtus*', *Bedfordia*, *Pomaderris*, *Coprosma*, *Lomatia*, *Olearia*, *Atherosperma*, *Hedycarya*, *Clematis*, *Dicksonia*, *Australina*, *Lepidosperma*, *Gahnia*, *Tetrarrhena*, *Cyathea*, *Microsorium*	Well stratified wet sclerophyll forest dominated by very tall *Eucalyptus* (especially *E. regnans*) with a tree understorey of Monimiaceae and Asteraceae. Dominant taxa fire-susceptible and regenerating from seed, not coppicing
15. Cassinia-Daviesia Division	'*Symphyomyrtus*', '*Monocalyptus*', *Cassinia*, *Daviesia*, *Leucopogon*, *Viola*, *Coprosma*, *Tetratheca*, *Prostanthera*, *Epacris*, *Xanthorrhoea*, *Astroloma*, *Lissanthe*, *Pimelea*, *Platylobium*, *Banksia*, *Platysace*, *Dillwynia*, *Stylidium*, *Persoonia*, *Correa*, *Hibbertia*, *Caustis*, *Dichelachne*, *Danthonia s. lat.*, *Themeda*, *Austrostipa*, *Lomandra*, *Lepidosperma*, *Microlaena*, *Dianella*, *Hypolaena*, *Cladium*	The 'damp sclerophyll' forests of south-eastern Australia, largely on, but not confined to, the Great Dividing Range
16. Astroloma-Bursaria Division	'*Symphyomyrtus*', '*Monocalyptus*', *Astroloma*, *Acrotriche*, *Lissanthe*, *Callitris*, *Bursaria*, *Dichelachne*, *Lomandra*, *Hydrocotyle*, *Dichondra*, *Brachychiton*, *Gonocarpus*, *Indigofera*, *Wahlenbergia*, *Dodonaea*, *Poa*, *Themeda*, *Echinopogon*, *Austrostipa*	Forest on the drier western slopes of the southern Great Dividing Range, with a range of understoreys. Now much disturbed by Aboriginal and European burning practices and agricultural use
17. Banksia-Leptospermum Division	'*Monocalyptus*', *Corymbia*, *Angophora*, *Banksia*, *Leptospermum*, *Telopea*, *Epacris*, *Monotoca*, *Persoonia*, *Dillwynia*, *Dampiera*, *Melaleuca*, *Sprengelia*, *Lambertia*, *Darwinia*, *Baeckea*, *Westringia*, *Lasiopetalum*, *Allocasuarina*, *Pultenaea*, *Hakea*, *Xanthorrhoea*, *Kunzea*, *Xylomelum*, *Patersonia*, *Doryanthes*, *Lepidosperma*, *Leptocarpus*, *Tetrarrhena*, *Hypolaena*, *Caustis*	A complex of forests and shrublands on a range of soils, from dry sandstone to permanently wet peats, in diverse habitats, from the Mt Lofty Range and Kangaroo Island in the west to the vicinity of Brisbane in the east, and south to Tasmania

Table 26 continued

Division	Character genera	Structure & distribution
18. Nothofagus Division	*Nothofagus, Atherosperma, Anodopetalum, Polystichum, Eucryphia, Prionotes, Cenarrhenes, Tasmannia, Phyllocladus, Dacrydium, Doryphora, Elaeocarpus, Ceratopetalum, Cyathea, Dawsonia, Blechnum, Microsorium, Grammitis, Dicksonia, Tmesipteris*	Rainforest pockets from Tasmania to Queensland
19. Athrotaxis-Tasmannia Division	*Athrotaxis, Agastachys, Orites, Tasmannia, Cyathodes, Richea, Monotoca, Astelia, Trochocarpa, Podocarpus, Nothofagus, Oreomyrrhis, Epacris, Hydrocotyle*	Low forest and shrubland of the high country of central and western Tasmania
20. Gymnoschoenus Division	*Gymnoschoenus, Sprengelia, Schoenus, Xyris, Tetrarrhena, Epacris, Gleichenia, Comesperma, Lepidosperma, Empodisma, Sphagnum*	Tall tussock sedgeland on peaty plains of western Tasmania
21. Poa-Ranunculus Division	*Poa, Ranunculus, Danthonia s. lat., Viola, Plantago, Luzula, Acaena, Asperula, Epacris, Oreobolus, Celmisia, Craspedia, Pentachondra, Leucopogon, Baeckea, Pultenaea, Wahlenbergia, Wittsteinia, Gaultheria, Restio, Astelia, Empodisma, Carex, Deyeuxia, Sphagnum*	Shrublands and grasslands in alpine regions of south-eastern Australia
22. Zygochloa-Acacia Division	*Acacia, Atriplex, Psoralea, Solanum, Sclerolaena, Zygochloa, Aristida, Eragrostis*	The true 'desert' communities dominated by canegrass (*Zygochloa*), on red sands in very low rainfall areas
23. Astrebla-Dichanthium Division	*Hibiscus, Sida, Psoralea, Crotalaria, Chenopodium, Atriplex, Astrebla, Dichanthium, Bothriochloa, Eulalia, Cymbopogon, Aristida, Eriachne, Eragrostis*	Grasslands of northern Australia. Subject to heavy grazing pressure in many areas, and threatened in places by the introduced *Acacia nilotica*
24. Themeda-Stipa Division	*Themeda, Austrostipa, Danthonia s. lat., Eryngium, Leptorhynchos, Plantago, Schoenus, Helichrysum s. lat., Tricoryne, Geranium*, Orchidaceae	Now mainly reduced to remnant patches, often invaded with introduced genera
25. Angophora-Syncarpia Division	*Corymbia*, '*Symphyomyrtus*', '*Monocalyptus*', '*Idiogenes*', *Angophora, Elaeocarpus, Tristaniopsis, Cupaniopsis, Backhousia, Archontophoenix, Syncarpia, Ceratopetalum, Toona, Dendrocnide, Trema, Ficus, Rhodomyrtus, Wickstroemia, Culcita, Doodia, Cyathea, Blechnum, Themeda, Imperata*	Coastal forest, with some inland extensions, in Queensland north of the Tropic of Capricorn

Table 26 continued

Division	Character genera	Structure & distribution
26. Syncarpia-Ceratopetalum Division	*Syncarpia*, *Ceratopetalum*, *Angophora*, '*Symphyomyrtus*', *Corymbia*, '*Monocalyptus*', *Lophostemon*, *Backhousia*, *Acmena*, *Doryphora*, *Livistona*, *Notolaea*, *Rapanea*, *Callicoma*, *Phebalium*, *Doodia*, *Culcita*, *Todea*, *Gahnia*	Dense forest with a fern-rich understorey, on the eastern slopes of the Great Dividing Range, and intermixed with Division 17
27. Allosyncarpia Division	*Calophyllum*, *Carpentaria*, *Pouteria*, *Syzygium*, *Podocarpus*, *Xanthostemon*, *Alstonia*, *Flagellaria*, *Fimbristylis*	Patchy, perhaps relictual, in Arnhem Land of the Northern Territory
28. Muehlenbeckia Division	*Muehlenbeckia*, *Echinochloa*, *Eragrostis*, *Chenopodium*, *Trigonella*, *Cyperus*, *Scirpus*, *Carex*	Found in flood channels of river beds of the 'Channel Country' of Queensland and South Australia
29. Spinifex-Cakile Division	*Spinifex*, *Tetragonia*, *Zoysia*, *Distichlis*, *Cakile*, *Arctotheca*	Sand dune community of the southern coasts
30. Canavalia-Ipomoea Division	*Canavalia*, *Ipomoea*, *Boerhavia*, *Spinifex*	Sand dune community of the tropics
31. Baumea Division	*Baumea*, *Cladium*, *Schoenoplectus*	Emergent vegetation in freshwater wetlands of southern Australia
32. Baumea-Leptocarpus Division	*Baumea*, *Leptocarpus*, *Gahnia*, *Lepidosperma*, *Restio*, *Chorizandra*	A range of associations, found in fresh or brackish swamps in southern Australia
33. Phragmites Division	*Phragmites*, *Typha*, *Scleria*	Vegetation of freshwater swamps or lagoons in tropical or temperate areas, where there is flowing water
34. Typha Division	*Typha*, *Azolla*, *Spirodela*, *Eleocharis*	Vegetation of standing or flowing eutrophic waters in coastal and inland areas
35. Hymenachne-Oryza Division	*Hymenachne*, *Oryza*, *Eleocharis*, *Cyperus*, *Leersia*, *Pseudoraphis*, *Panicum*, *Nymphaea*, *Polygonum*, *Nelumbo*	Vegetation of lagoons and flood plains in the coastal tropics. Can be inundated for 3–4 months of the year
36. Heterozostera-Amphibolus Division	*Heterozostera*, *Amphibolis*, *Posidonia*	Seagrass beds of shallow estuaries of southern and south-western areas
37. Halophila-Cymodocea Division	*Halophila*, *Cymodocea*, *Thalassia*, *Thalassodendron*	Seagrass vegetation north of the Tropic of Capricorn. Overlaps with Division 36 near Shark Bay, Western Australia

Patterns at regional scales

The structural description of present vegetation in Australia given earlier omits some specialised vegetation types, such as those in which either saline or fresh water, coastal salt-laden winds or low temperatures play a major role (but see Adam, 1994; Brock, 1994; Clarke, 1994; and Williams & Costin, 1994, respectively for details of the vegetation of these extreme habitats, and the chapter on aquatic vegetation in this volume). The five major structural vegetation types described above have been categorised on the basis of plant height and foliage projective cover. Some aspects of floristic variation and the ecological factors controlling such variation within these categories have been mentioned briefly. Vegetation rarely falls into neat categories, however; instead, it usually varies along a continuum or gradient in which many factors interact in a highly complex way. The following section describes the regional patterning of vegetation types along transects in several different parts of Australia, in order to present something of the ecological complexity and the dynamic nature of present Australian vegetation. Many other examples could have been given, but consideration of these is beyond the scope and capacity of this volume. For more details see Groves (1994).

Aridity gradient

A transect from the coastline towards the centre of the continent is characterised by an increase in aridity. The concentric pattern of decrease in total annual rainfall, from as much as 3500 mm to as little as 125 mm, irrespective of its seasonal incidence (Fig. 88), broadly matches the concentric distribution of the major vegetation types shown in Fig. 82. Closed-forests typical of high rainfall areas close to the eastern coast (1000–2500 mm) merge into tall open-forests of the coastal mountains which in turn grade into low open-forests or tall woodlands typical of drier, inland areas (sometimes occurring as tablelands), and especially if they are the inland 'slopes' of the coastal mountain chain. Further inland still, low woodlands of mallee eucalypts (in the south) or of acacias (in the north) may be intermixed with chenopod shrublands in regions having an annual rainfall of between 500 and 250 mm. In the arid centre, these vegetation types may persist in special ecological situations, but generally hummock grasslands dominated by *Triodia* species, of yet lower stature, become more common in regions having an annual rainfall below about 200 mm. Physiographic complexity, especially in the arid zone (Mabbutt, 1969), together with the distribution of soil types, may singly or together modify this general pattern of vegetation induced by aridity. Only in two regions – that abutting the Nullabor Plain in South and Western Australia, and the central west coast of Western Australia – do arid communities occur at the coastline proper.

The gradient in aridity from coast to inland is accompanied by a gradient in rainfall variability, in which coastal rainfall is generally much less variable on average than that in the inland. This variability increases with increasing aridity and the vegetation shows adaptations to such variability, especially by the 'desert ephemeral' element in the arid zone vegetation complex. For example, for the annual flora of the arid Murchison region of Western Australia (less than 200 mm annual rainfall, which can occur at any time of the year), winter rainfall leads to a predominantly dicotyledonous flora, whereas the flora germinating after summer rains is largely made up of monocotyledons, especially grasses (Mott, 1972). This difference could be related to the different temperatures required for seed germination – the summer flora requiring a higher temperature for germination than the winter flora (Mott, 1972). The further along the gradient in aridity then the more likely it seems to be that the vegetation is adapted to irregular episodic events, rather than to the 'average' rainfall amounts as shown in Fig. 88.

At the moist end of the gradient, the land on which closed-forests and tall open-forests grow is an important source of potable water for Australian cities as well as for hardwood timber of high quality. On the east coast much of the land formerly covered by closed-forest has been cleared for crops such as sugar (in the north) or for dairy pasture. The low open-forests and woodlands further inland have mostly been greatly modified and are now used for

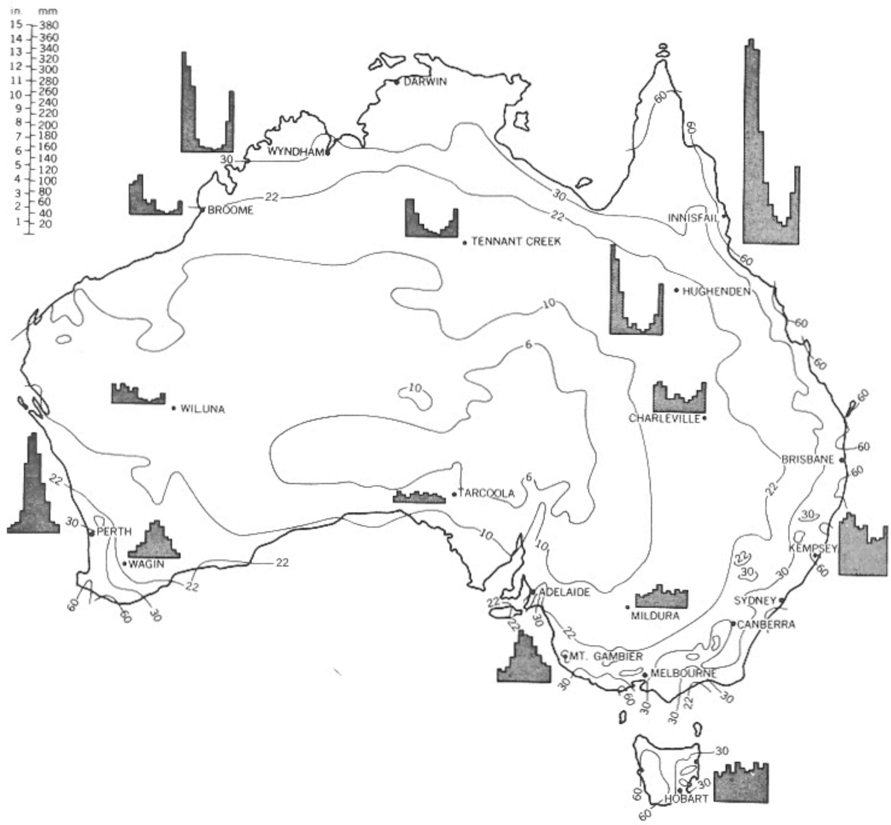

Figure 88. Mean monthly rainfall of selected recording stations with the mean annual rainfall (in./mm) being recorded under each diagram. Source: adapted from Climate and Meteorology of Australia, Bulletin no. 1 (reprint from official Year Book of Commonwealth of Australia, 1965). Reproduced with permission.

grazing and/or cropping. Chenopod shrublands are extensively grazed by sheep, while the mosaic of more arid vegetation types in central Australia is grazed by cattle or sheep as well as by feral animals. All the vegetation types have value for nature conservation although the grassy woodlands and grasslands are least well represented in the total system of conservation reserves.

Nutrient gradient

Australian soils are in general poor in nutrients, especially nitrogen and phosphorus, and much of the native flora has evolved in this regime. In fact, additional nitrogen and phosphorus, at the levels usually employed in agriculture and horticulture, can be toxic to many native plants. As a consequence of the depauperate nutrient levels of natural soils, few examples of major nutrient gradients affecting vegetation patterns can be found. The following is one case study.

The Sydney Basin region on the central east coast of the continent comprises three main Series of Triassic rocks. Wianamatta shales overlie sandstones of the Hawkesbury Series which in turn overlie Narrabeen shales and sandstones. Below all three types of parent rock lie Permian coal-containing sandstones. Uplift of these strata subsequent to their deposition has led to complex physiographic patterning of the landscape in areas such as the Blue Mountains west of Sydney. Furthermore, remnants of Tertiary basalt flows are found on some areas of the uplifted tablelands, as at Mount Wilson. Such complex geologic and physiographic patterning is matched by an equally complex mosaic of vegetation types.

Results of ecological studies in the Sydney region date back almost 100 years to Cambage (1907) and Andrews (1916); collectively, the results show that the different vegetation types in the region are distributed predominantly along a soil nutrient gradient – specifically soil phosphorus and/or nitrogen gradients – which in turn reflect the phosphate status of the parent rock type (see e.g. Beadle, 1954, 1962; Hannon, 1958). Typically, low woodlands and sclerophyll shrublands occur on the Hawkesbury sandstones which are lowest in soil phosphorus. Low open-forest occurs on lateritic soils with somewhat higher soil phosphorus levels, while tall open-forests and small areas of closed-forest ('rainforest') are confined to soils higher in phosphorus derived from Narrabeen shales and sandstones. The closed-forests occur on those soils highest in phosphorus, and especially when they are derived from Tertiary basalts (see Beadle, 1962, for typical soil phosphorus levels).

More recent findings of Burrough *et al.* (1977) show that factors other than soil nutrients may also be significant in accounting for the mosaic of vegetation types in the Sydney region. They showed that the patterning of open-forest, woodland, sclerophyll shrubland and sedgeland – which all occur on Hawkesbury sandstone – could be explained primarily by soil moisture differences, expressed either as mean annual rainfall or as different levels of impedance of soil drainage (in the case of shrublands and sedgelands).

The complex distribution pattern of a range of present vegetation types of the Sydney region thus may be partly accounted for by differences in soil nutrient levels. From the findings of Burrough *et al.* (1977), however, it becomes clear that the same vegetation types may be distributed along gradients of other factors such as soil moisture. Whether the soil nutrient gradient is primary remains to be clarified for this and other regions. The physiographic complexity of the Sydney Basin will probably always complicate any simple explanations based on single ecological factors and their influence on the distribution of present vegetation types.

Fire

The role of fire frequency in distinguishing closed- from open-forests has already been referred to above. In summary, in high rainfall areas of Tasmania and southern Victoria, a fire occurring more frequently than once in about every 400 years will prevent the dominance of the closed-forest species *Nothofagus cunninghamii* and maintain dominance of eucalypts, such as *Eucalyptus regnans.* A fire frequency of between about 80 and 400 years will be associated with an overstorey of characteristic tall open-forest eucalypts with some closed-forest floristic elements in the understorey. At fire frequencies less than 80 years *Acacia* species, such as *A. melanoxylon*, will be prominent; at frequencies less than about 20 years, treeless shrub- and sedge-grasslands will be perpetuated (Jackson, 1968; Ashton 1981). Thus variation in fire frequency may play a major role in determining vegetation patterning in this region of south-eastern Australia.

A fire regime is composed not just of fire frequency, however, but also of fire intensity and season of fire (Gill, 1975). Differences in the latter two components may also influence the distribution of present vegetation types. Around the area of Darwin in the Northern Territory, a native grass *Sorghum intrans* occurs as a dominant understorey species in eucalypt woodland. In many areas, this grass has now been replaced by the introduced species *Andropogon gayanus* (Gamba grass) and *Pennisetum polystachion* (Mission grass), which together produce fuel loads three to four times that of the native species which they have replaced (Anderson, 1997). Furthermore, the introduced grasses dry out later in the season when fire danger may be higher. When fire occurs, it is of a higher intensity and later in the season than if the native grass still dominated the understorey. Two components of the fire regime are thus changed as a result of the invasion by introduced grasses, with a consequent increase in fire hazard and a reduced value of the vegetation for nature conservation.

The influence of fire on Australian vegetation types operates at the level of individual taxa, and some Australian plant genera show specific adaptive responses to fire regimes. For instance, some geophytes (including several orchids) and the genera *Xanthorrhoea* and *Kingia* are usually stimulated to flower or flower more heavily after a fire, although their need for fire might not be obligate. Some species of *Banksia*, *Casuarina/Allocasuarina* and *Eucalyptus* may be stimulated to release seed from their woody aerial fruits in response to heat and/or desiccation The seeds thus land on an ash-bed that is more favourable in terms of nutrient levels and absence of competitors than a pre-fire microsite. For other genera, such as *Acacia* and many other leguminous shrubs, which store their seed not aerially but in the soil, fire may stimulate germination of those soil-stored seeds. The extent of germination will depend mainly on fire intensity and how deeply the heat from the fire may penetrate the soil profile. After a fire, light intensity will be higher and this increase together with endogenous hormonal changes may result in bud development being stimulated. This response is shown by many genera which have epicormic buds buried in their stem tissue or have aggregations of such buds at their base as lignotubers. This latter response is shown by the 'sprouters' in the Australian flora, of which many species in the genera *Eucalyptus* (Fig. 99), *Hakea*, *Grevillea* and *Banksia* are good examples.

Gill (1981) has classified these responses into seven different categories (Table 27). Gill's scheme separates firstly the plants killed by fire (non-sprouting) from those that recover from the effects of fire by sprouting. Such a primary difference is not diagnostic of different genera, however, and species within the same genus can respond differently. Some genera (e.g. *Hakea*, see Barker *et al*., in press) can contain species exhibiting almost all sprouting/non-sprouting types. Most communities of Australian plants show a mixture of these different adaptive responses.

Table 27. A simple classification of adaptive responses to fire in vascular plants (table 2 of Gill, 1981).

Reproductive Strategy	Response Type
A. Plants in the reproductive phase just subject to 100% leaf scorch by fire die (non-sprouters)	
(a) Seed storage on plant	I
(b) Seed storage in soil	II
(c) No seed storage in burnt area	III
B. Plants in the reproductive phase just subject to 100% leaf scorch by fire recover (sprouters)	
(a) Subterranean regenerative buds	
(i) Root suckers, horizontal rhizomes	IV
(ii) Basal stem sprouts, vertical rhizomes	V
(b) Aerial regenerative buds	
(i) Epicormic buds grow out	VI
(ii) Continued outgrowth of active aerial prefire buds	VII

While the general responses of many Australian plant genera and species to fire have been described, it is important to recognise that particular fire regimes are but one of the many environmental stresses on Australian plants. Other stresses may include water deficit or excess, extreme cold, herbivore attack, and their interactions.

Fire has been a major ecological factor influencing Australian vegetation types for a long time, at least since the Tertiary period (Kemp, 1981). The different species or species groups comprising those vegetation types have evolved a range of adaptations to its incidence (Gill, 1975). Because of variation in intensities and frequencies, as well as in seasonal occurrence, fire regimes are often unique and few generalisations may be tenable on which to base future management of present Australian vegetation types. The gap between existing knowledge of fire effects and the widespread implementation of management practices, such as prescribed burning, remains considerable, although it is gradually closing.

Grazing

Grazing by domesticated stock over a period as long as 200 years has induced floristic changes in many Australian vegetation types, but none more so than in the woodlands and grasslands of south-eastern Australia. A general change from perennial grass cover to a shallower-rooted annual one has already been noted above. One such sequence of species changes that is well documented has occurred in *Eucalyptus melliodora/E. blakelyi* woodlands on the Southern Tablelands of New South Wales (Table 25). Moore (1970) considered that this sequence was also representative of the changes resulting from grazing other woodlands dominated by *E. camaldulensis* and *E. leucoxylon* in both western Victoria and South Australia.

The discovery of routes across the Great Dividing Range from 1812 onwards enabled grazing of the inland temperate woodlands by sheep and cattle to commence. As grazing intensified the tall warm-season perennial tussock grasses (mainly *Themeda triandra* and *Stipa aristiglumis*) that originally dominated the understorey to these woodlands were replaced by predominantly shorter cool-season grass species of *Danthonia s. lat.* and *Stipa s. lat.* This change was in turn followed by an increasing dominance of cool-season annual legumes and other herbs, usually of Mediterranean origin. Because this stage of the sequence was usually of higher nutritional quality, especially through winter, it was subsequently maintained and even promoted by regular applications of superphosphate fertilizer, which in turn led to dominance of the introduced annual legume *Trifolium subterraneum* and elimination of *Danthonia s. lat.* and other native perennials. Although there are regional variations, especially according to the relative incidence of summer- and winter-rainfall, this general pattern applies over much of south-eastern Australia.

Recognition of the acidifying effect of repeated superphosphate application, together with increases in fertilizer cost, have subsequently led to reductions in the levels of fertilizer applied to these areas of former woodland. This has been accompanied by a reversion of some grazed grasslands back to those dominated once again by native cool-season perennial grasses, such as species of *Danthonia s. lat.* Novel and more sustainable systems of grazing management are now having to be developed to accommodate these recent floristic changes.

Almost 200 years of grazing by sheep and cattle have been accompanied by significant floristic changes to the understoreys of eucalypt woodlands in south-eastern and south-western Australia. So complete have these changes been in most areas that representative samples remain of the original understorey only in a few cemeteries and some travelling stock routes and roadsides. On all grazed areas, the trees are over-mature and few in number. Thus the conservation status of these long-grazed woodlands and grasslands is now precarious and increasingly uncertain in the future.

Salt gradient

In south-western Western Australia, a transect inland from the west coast close to Perth moves in general from sclerophyll shrubland or low open-forest dominated by *Banksia* on the Swan coastal plain to open-forests of low or medium height dominated by various species of

Eucalyptus along the Darling Escarpment. This change in vegetation type corresponds with an increase in annual rainfall and a change in substrate from deep sand to a lateritic podzol, both soil types being relatively low in available nutrients. Further eastwards eucalypt woodlands predominate, with the mallee habit becoming more prominent as rainfall decreases with increasing distance from the west coast. Further eastwards still, chenopod shrublands may occur intermixed with eucalypt woodland.

Clearance of the deep-rooted eucalypt woodlands on the eastern face of the Darling Range and the growing of either cereals or equally shallow-rooted annual pasture species have led over time to an increasing local problem of salting of both agricultural land and surface water in the region. Saunders & Hobbs (1992) cited data for this region which showed that nearly 3 per cent of cleared land was already affected by salinity and that this level could increase to more than 15 per cent in the next 30 years. Such increased salinity in this inland region has serious implications for the ever-increasing need for either surface- or ground-water of potable quality for the city of Perth, the inland salted region being the 'catchment' for much of the surface-water on which Perth depends. Only retention of the remaining natural vegetation and strategic replanting with deep-rooted tree species in this catchment area can ameliorate the increasing salinization of Perth's drinking water. In this instance it is the gradual change over about 150 years from perennial, deep-rooted native vegetation to annual, shallow-rooted herbaceous crops and pastures which has induced the long-term change in salinity levels. Whether reversion to something resembling the original vegetative state will halt the further degradation in water quality is for the future to discover.

The consequences of the change from native perennial vegetative cover to introduced annual vegetation described above applies even more so to the entire south-eastern Australian region, where it has been exacerbated by the development of irrigation schemes along the Murray and Darling Rivers. In this large region the effects of clearance of native vegetation have taken longer to express themselves, but a similar ecological scenario is developing, with equally dire consequences for continued agricultural land use and the provision of potable water for large cities such as Adelaide.

Introduced plants

About 15 per cent of the total Australian vascular flora has been introduced from outside Australia, with the proportion varying according to the degree of disturbance of the natural vegetation. The proportion is highest on islands such as Norfolk (viz. 60%) and lowest in the Northern Territory and in the Kimberley region of Western Australia (about 5%) (see table 2.1 of Humphries *et al.*, 1991). For the last 100 years, it seems that the average rate of naturalisation of these introduced plant species has been about six species per year in each of the southern States (Specht, 1981). Many of these species have seemingly little effect on the natural vegetation, while a significant minority of the total are major weeds in that they affect human well-being in some deleterious way. Such weeds may reduce production of crops or pastures, either directly or indirectly. Other introduced plants may affect human health in diverse ways. Yet other introduced plants – those known collectively as 'environmental weeds' – may reduce native plant or animal biodiversity and thereby affect the functioning and conservation of natural vegetation.

The vegetation types most affected by introduced plants are probably the coastal vegetation, temperate grasslands and woodlands of south-eastern Australia. For instance, the ground stratum of much of Australia's eucalypt woodlands has in many cases been either completely or substantially replaced by introduced plants, with drastic consequences for the conservation of some native animal groups such as insects and reptiles. In instances where the introduced plants are legumes able to fix atmospheric nitrogen, soil nitrate levels will be raised, ecosystem function changed and fire regimes permanently altered. For example, the leguminous shrub *Mimosa pigra*, introduced from central America, is capable of increasing soil nitrogen levels in the wetlands of the Northern Territory as well as changing the habitat for waterbirds, such as the magpie goose (Braithwaite *et al.*, 1989). The introduced tree *Tamarix aphylla* or Athel Pine has changed river physiography and water flow of the Finke River in central Australia over about 20 years, since a major flood in 1974; this species is able to reduce regeneration of the native riverine vegetation and by accumulating salt *Tamarix* may permanently change the ecosystem (Griffin *et al.,* 1989). Many other examples could be given: Boneseed (*Chrysanthemoides monilifera*) from South Africa in coastal sand-dune communities, Rubber vine (*Cryptostegia grandiflora*) from Madagascar in Queensland watercourses, vine thickets and open-forest, and European blackberries (*Rubus fruticosus* agg. and other species) in open-forest gullies and along waterways of south-eastern Australia.

Introduced plants affect numbers of native plant species, floristic composition or the functioning of native vegetation in many ways. While there are many well-documented instances of introduced plants reducing economic value of agricultural products, there are only a few for introduced plants deleteriously affecting native plant biodiversity, ecosystem function and vegetation structure. It is a subject in urgent need of more research.

Plants do not need to be introduced from outside Australia to be weedy in natural vegetation, however. There are now many instances of indigenous plants becoming weedy when they move beyond their native range. The native shrub *Pittosporum undulatum* is indigenous to some subtropical moist gullies on the south coast of New South Wales and far eastern Victoria. Because of its perceived horticultural value, and especially its scented flowers, it has been widely planted beyond its fairly localised native range (Gleadow & Ashton, 1981). The increased rate of propagation of the shrub, its shade tolerance and the fact that its seeds are bird-dispersed has led to *P. undulatum* spreading widely; it is now a common and sometimes dominant species in many vegetation types in southern Victoria and South Australia where it never occurred 200 years ago.

A number of species naturally restricted in their distribution to Western Australia are now occurring as environmental weeds in eastern Australia, especially in coastal vegetation (for example, the plant known as Cape Wattle, Crested Wattle or Cape Leeuwin Wattle, *Paraserianthes lophantha*), and the reverse situation is equally common (for example, Tasmanian Blue Gum, *Eucalyptus globulus*). This enhanced admixture of native plant species has consequences for hybridisation within genera of Australian plants and untold effects on native plant function and survival.

Summary and conclusions

Australia is a vast continent that spans more than 30 degrees of latitude, over which average annual rainfall varies from less than 100 mm to more than 2000 mm and from summer- to winter-incident as latitude increases. Geologically, it is an old continent with nutrient-impoverished soils in many regions. This chapter has described the five major types and some subtypes of natural vegetation that occur over this diverse continent. Some of the ecological factors that may account for the patterning of those vegetation types have been discussed for different regions of Australia.

The present distribution of the different vegetation types is in no way constant over time, however, and never has been. As the continent separated from Gondwana and drifted northwards, shifts in palaeoclimates changed distribution patterns of vegetation types (Frakes, this volume). The arrival of Aboriginal people and their use of fire changed vegetation patterns in ways that we are only gradually becoming aware of. More recent clearance of native vegetation in many parts of Australia has often been excessive and ecologically disastrous; in southern Australia, at least, it has resulted in a general shift from deep-rooted perennial vegetative cover to one dominated by annuals, usually with shallower root systems. After 200 years of European exploitation, further clearance of natural vegetation has only recently been outlawed over most of Australia. Past utilisation of native vegetation, whether for grazing by domesticated stock or for timber, over the same period, has drastically reduced habitat for many native plant and animal species, with consequent loss of biodiversity, not all of which we even know about. Clearance and grazing along with ecologically inappropriate use of fire have together changed entire landscapes and rendered those landscapes susceptible to weed and pest invasion as well as to increased salt levels in surface- and ground-water. Urbanization of coastal regions progresses with seemingly few checks and balances, producing homogenisation of localised areas of natural vegetation and planted European-style gardens in the 'bushland' around the major Australian cities.

On the above basis, the scenario for the future of Australian vegetation is grim unless human population pressure on the land can be reduced. There are, however, some grounds for optimism. An increased percentage of land under reservation could lead to wiser land management, including the conservation of representative samples of the vegetation types and subtypes described above. Recently, there has been an increase in knowledge of these vegetation types and their dynamics, on which management programs for their conservation can be based. Whether this increase in knowledge translates into wiser land management remains to be seen. Increase in knowledge of the Australian flora should be accompanied by similar increases in knowledge of the unique Australian vegetation types and their variants. Given this more optimistic basis, conservation of a representative sample of such vegetation types should follow and lead thereby to an enrichment of the quality of life for future generations.

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