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Section 3: The Flora

The Aquatic Flora

Terrestrial Wetlands and Waterplants S.W.L.Jacobs

Mangroves P.Bridgewater

Marine D.I.Walker

THE AQUATIC FLORA

Certain preconceptions accompany any thoughts of the Australian flora. Our minds generally settle on visions of towering *Eucalyptus* forests, or *Banksia* heathlands, or the fields of colourful wildflowers that signal the onset of Spring. It is a natural – and entirely understandable – human response to appreciate the big and the brightly coloured. But as a result a significant portion of the Australian flora is often ignored. One group of plants that falls into this category is that which inhabits the aquatic environment. These plants are constantly or periodically immersed in either fresh or salt water, and as a result are largely hidden from view. With a few exceptions, their flowers are small and cryptic and do not make a great impression on the casual observer. Yet the aquatic environment hosts a vast diversity of plant species and their communities are of great ecological significance.

The aquatic environment is the ancestral home to all plants and, by and large, remains the domain of the algae. The algae found in Australian waters will be the subject of a independent series, the *Algae of Australia*, that will follow the *Flora of Australia* in general format, and, as such, will not be discussed here. The present chapter is concerned with the vascular aquatic plants and their habitats. Traditionally these have been studied as terrestrial systems (rivers, lakes, swamps and marshes) on the one hand, or marine systems (seagrass beds) on the other. In between, the transitional plants, the mangroves, have had their own suite of researchers. In practice, of course, such sharp distinctions do not, in many cases, exist on the ground, with one system merging gradually into another.

TERRESTRIAL WETLANDS AND WATERPLANTS

Surrey W.L. Jacobs[1]

Aston (1973) considers aquatic species 'to be those adapted to growing in or on permanent water, either completely submerged or emergent, and having a definite life form (habit, structure) related to this aquatic environment.' Sainty & Jacobs (1981) define waterplants as 'species which thrive in water or on wet land.' Mangroves can be either excluded (Aston, 1973) or included (Sainty & Jacobs, 1981), the decision usually being made on practical grounds. By convention, alpine plants are nearly always excluded from treatments of waterplants, simply because they are usually treated separately as a group of species defined by another set of ecological criteria (Costin *et al.*, 1979). These criteria are not mutually exclusive so usually there is a pragmatic decision made on membership of either category. Defining any group of species on ecological criteria is fraught with difficulty and may result in either pages of qualifications or exceptions.

A wetland is is 'land permanently or temporarily under water or waterlogged' (Jacobs & Brock, 1993), modified after Paijmans *et al*. (1985). Adam (1992) provides an insight into the kind of aspects/arguments involved in defining wetlands and both Alper (1992) and Stone (1995) provide good examples of the ecological chaos that can be perpetrated when law makers and benders start playing with words without understanding the significance of what they do. Pressure may be applied for stricter definitions but history tells us that any more specific definition of a wetland that does not incorporate consideration of its catchment or water source could well be abused. The most useful approach is to work on a very general definition and modify it as required to the particular project.

Ecological information on Australian wetlands has been reviewed for tropical Australia by Finlayson & Oertzen (1993) and for temperate Australia by Jacobs & Brock (1993). The conservation of Australian wetlands has been reviewed by McComb & Lake (1988) while preliminary analyses of the biogeography of Australian waterplants have been undertaken by Jacobs & Wilson (1996).

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[1] National Herbarium of New South Wales, Royal Botanic Gardens, Mrs Macquaries Rd, Sydney, New South Wales 2000.

Composition of the aquatic flora

This, of course, is dependent on the definition of 'aquatic' used. Jacobs & Wilson (1996) record 553 species in 139 genera in 56 families for Australasia. Aquatic bryophytes are few and mainly temperate. Ferns are present in about the same proportion as in terrestrial floras (Clarkson & Kenneally, 1988) and fairly evenly distributed with the exception of the south-west of Western Australia where there has been a proliferation of *Isoëtes*. There are no aquatic gymnosperms recorded for Australasia. The big difference between terrestrial floras and aquatic floras is in the proportion of monocotyledons: in regional aquatic floras the proportion of monocotyledons ranges from 50% to 70%, approximately twice the proportion represented in the total floras (20% to 30%). These are mostly in the families Cyperaceae and Poaceae, but there are also several specialised families of aquatic monocotyledons, such as Potamogetonaceae, Hydrocharitaceae, Nymphaeaceae, and others.

Adaptations to an aquatic environment

An aquatic environment imposes unusual conditions on plants. For example, waterlogging of root systems is common to all aquatic environments, and has engendered a range of adaptations; saline environments require adaptations to levels of sodium and choride ions that are fatal to most plants; and pollination in submerged or barely emergent flowers also requires different strategies to those found in terrestrial plants.

General adaptations to an aquatic environment

For many species of waterplants, the adaptations or complex of adaptations that allow them to have a competitive advantage in what can be a difficult environment are only now becoming understood. Problems not normally faced by terrestrial species, but which affect aquatic plants, include stability in a substrate not suited for strong root systems, photosynthesis where light energy levels are frequently low and leaf exposure to light may be limited by high flow rates, turbidity, floods and/or epiphytes, and pollination in an environment quite different from their ancestors. Sculthorpe (1967) supplied a comprehensive account of anatomical and morphological characteristics of waterplants while Jacobs (1985) provided a shorter summary. Falkowski & Raven (1997) discussed some of the physiological adaptations involved in photosynthesis in an aquatic environment, Carter *et al*. (1996) showed the effect of limiting light to submerged waterplants, Cook (1982) provided a fascinating discussion of some of the pollination mechanisms of the family Hydrocharitaceae, and den Hartog (1970) the pollination of seagrasses. Les *et al*. (1997) provided a survey of the incidence of hydrophily (water-moderated pollination mechanisms) and a cladistic study of the evolution of the trait(s), with particular reference to the Alismatidae.

Special adaptations to a saltmarsh environment

Saltmarsh species live in an extreme environment, although perhaps not as extreme as is sometimes imagined. Under 'dry' conditions the soils certainly contain extremely high levels of sodium and chloride ions. Most growth, however, takes place when the marsh is flooded by tides or floods. As the majority of saltmarshes are in estuaries, even tidal flushing can be with water substantially less saline than seawater. When saltmarshes are inundated by floods (as for example the large saltmarshes of tropical coasts), the water is often quite fresh.

Nevertheless, saltmarsh species have to survive long periods with high soil salinity. A very few species manage to avoid this by growing as ephemerals after inundation. This is most common in the tropics where seasonal flooding in the wet season allows species such as *Salsola kali*, *Sclerolaena* spp. and *Trianthema* spp. to complete their life cycles without being exposed to extremes of salinity.

Perennials are more common than annuals in saltmarshes, and most perennials use a combination of strategies that allow them a competitive advantage over other species in this environment.

The physiological variations that help in survival are discussed by Adam (1990). Examples include excretion (e.g. *Atriplex* spp., *Sporobolus* spp., *Zoysia* spp. and *Cynodon* spp.), variations in photosynthetic pathways, especially in the Chenopodiales (Carolin *et al*., 1975, 1978, 1982; Chapman & Jacobs, 1980) and grasses (Carolin *et al*. 1973; Brown, 1977), and tolerance of high levels of sodium and chloride ions. Frequently, ecotypes from a saltmarsh are able to tolerate higher levels of salinity than other ecotypes of the same species.

Succulence is often claimed to be of significance as an adaptation to salinity, but, as Adam (1990) pointed out, succulence is difficult to define and covers a multitude of characters. A certain level of succulence is induced by increasing salinity. It is sometimes suggested that this increase in succulence is to allow isolation of sodium and chloride ions in the vacuole, or to allow the accumulation of other compounds that help maintain an osmotic balance or pH balance (Adam, 1990). Succulence is often also associated with other features (for example Crassulacean Acid Metabolism (CAM)), and it is not clear how it directly relates to enhanced survival in saline conditions.

Special adaptations to a marine environment

The adaptations of mangroves to an intertidal environment, and of seagrasses to a subtidal environment, are discussed separately below, by Bridgewater and Walker respectively.

Classification

Systematics

Aquatic plants occur in many families and there are more species in non-specialised aquatic families than in specialised aquatic families. While the taxonomy of waterplant groups is about as stable as that for many other groups, there are problems that are unique to some strictly aquatic families. The highly reduced and modified flowers of species of Zosteraceae, Najadaceae, Zannichelliaceae and others means that the interpretations of the floral structure vary. As this is often important in understanding relationships, it is the increasing understanding of floral structure that has been primarily responsible for changes in classification between, for example, den Hartog (1970) and Dahlgren *et al*. (1985). The system used in the *Flora of Australia* for the aquatic monocotyledon families is that of Cronquist (1981). This differs slightly from the more recent classification of Dahlgren *et al.* (1985) in that Cronquist recognises Ruppiaceae as distinct from Potamogetonaceae, includes Scheuchzeriaceae in Juncaginaceae, includes Butomaceae in Limnocharitaceae, and places Aponogetonaceae in Order Najadales instead of Order Alismatiflorae. There is no 'final' classification on the horizon. The process of increasing knowledge means that pre-existing classifications will be modified periodically as data accumulate. Classifications of this type are a method of storing and retrieving information and, usually, constructed to reflect evolution and hypothesised relationships. They are hypotheses in their own right and are testable.

Wetlands classification

Ecological classifications are of a different nature to taxonomic classifications. They are usually based on comparatively simplistic characteristics of either the plant (e.g. growth form), physical habitat or climate. There are no evolutionary connotations in such classifications and they are usually constructed with a specific project in mind. They are usually not established as hypotheses and are therefore not testable. It is often assumed from experiences with terrestrial vegetation and plant communities that all plant communities are stable entities. While this is not even strictly true for all terrestrial communities (e.g. the so-called 'fire-weeds'), it is certainly not true for aquatic plant communities.

The simplest ecological classification of wetland plants is based on growth form and behaviour, and includes character combinations such as:

(i) rooted, submerged, flowers submerged;

(ii) rooted, submerged, flowers emergent;

(iii) free-floating submerged, flowers submerged;

(iv) free-floating on surface;

(v) rooted, leaves floating, flowers emergent;

(vi) rooted, leaves emergent, flowers emergent;

(vii) woody trees or shrubs.

There are many examples of these and the number of categories usually depends on the number of species in each category for each study. Such a classification is useful for easy grouping prior to species identification or habitat categorisation. Examples of the use of such a system are in Sainty & Jacobs (1981, 1994).

Australian wetlands have also been classified on the basis of geographical and/or physical features (Jacobs, 1983; Riley *et al.*, 1984; Paijmans *et al.*, 1985), the structure of the vegetation (Briggs, 1981; Blackhall, 1986) or a mixture of both (Riggert, 1966; Beadle, 1981; Norman & Corrick, 1988). Reviews of classification systems are provided by Jacobs & Brock (1993), Sainty & Jacobs (1994) and Finlayson & Oertzen (1993).

Most classifications were developed as part of localised studies, often within political rather than phytogeographical boundaries, and hence they tend to rely heavily on characteristics important to that particular study. For example, many studies of birds concentrate on vegetation structure as the basis for habitat classification (e.g. Blackhall, 1986) whereas De Deckker (1982) uses the relative suitability of wetlands as sites for palaeolimnological investigations.

Classifications of wetlands relying on vegetation structure and floristics are often difficult to adapt to larger scale studies. The degree of precision involved when genera or species, or percentage cover or growth form are involved in the definitions, means a lack of flexibility that often requires change in the classification of a particular wetland after flood, drought or fire (all common in the Australian climate). Most wetland vegetation types are subject to more frequent change than most dryland types. In many ways they are more similar to ephemeral dryland plant communities than to more perennial types.

The number of final categories in the classification is also important for practical reasons. Briggs (1981) has 45, Paijmans *et al.* (1985) has 55 and Beadle (1981) 58. Riley *et al.* (1984) produced a precise geomorphological hierarchical classification for the wetlands of New South Wales. With seven levels in the hierarchy and more than 1500 possible final categories it is far too finely divided to use for biological data. Even if only the top five levels of the hierarchy could be used there are about 150 categories.

The system used here (Jacobs, 1983) is based on geographical and physical characteristics and is one of the simpler systems. It was developed as a means of summarising data from numerous different sources and is especially useful for Australian wetlands and as a base for elaboration for detailed studies. References and more detail are in Jacobs & Brock (1993) and Finlayson & Oertzen (1993), and references included below are additional to those in the earlier publications. The classification is:

1. Coastal wetlands

(a) upland swamps

(b) rivers and tributaries

(c) floodplain swamps and billabongs

(d) coastal lagoons and lakes

(e) estuaries

(i) mangroves

(ii) seagrass meadows

(iii) salt marsh

2. Mountain lakes and swamps

(a) perennial lakes

(b) perennial swamps

(c) ephemeral lakes/swamps

3. Inland rivers

(a) rivers

(i) perennial, including anabranches

(ii) ephemeral

(b) billabongs and floodplains

(c) swamps – overflow or terminating

4. Inland lakes

5. Mound springs

6. Man-made storages, canal systems, dams, channels, drains, bores, bore-drains, farm storages, rice fields, storage swamps.

Descriptions of wetland types

1. Coastal wetlands

(a) Upland swamps

Upland swamps are most common along the eastern Great Dividing Range but are also found in the Kimberley, Western Australia, and other upland areas. They are situated at the heads of the coastal rivers. Many often do not have free-standing water but may absorb large volumes of water in the peat-like accumulations of organic matter. This water is released slowly, helping to maintain flow in tributaries. These upland swamps differ from the rest of the wetlands, often being described simply as wet heaths and having more in common with the surrounding dryland vegetation and fauna than with that of other wetlands. The vegetation of the swamps includes a large proportion of monocotyledonous genera from the families Cyperaceae and Restionaceae, commonly including *Baumea*, *Gahnia*, *Lepidosperma* and *Gymnoschoenus* (Cyperaceae) (Fig. 114), and *Leptocarpus* and *Lepyrodia* (Restionaceae). Other components include species of *Melaleuca* and *Leptospermum* (Myrtaceae), *Hakea* and *Banksia* (Proteaceae), and *Epacris* and *Leucopogon* (Epacridaceae). Stricker & Stroinovsky (1995), and Stricker & Wall (1995) provide recent assessments of some of these wetlands around Sydney, New South Wales.

(b) Rivers and tributaries

There are rivers all along the coast except for areas of Western Australia. Although water from the Murray-Darling System reaches the coast, the rivers and tributaries of this system are classified as inland rivers. Where the flow rate is high there is usually little characteristic vegetation in or around the channels. The vegetation of the banks is mostly dependent on the local soil type and the rainfall of the country through which the rivers flow. As the river channels broaden, the slope lessens, the flow rates decrease, more alluvium is deposited and the nutrient content of the water increases.

Typical submerged plant species in these rivers include *Blyxa* spp. and *Hydrilla verticillata* in the north, along with *Vallisneria* spp. and various species of *Potamogeton*. Free-floating species or species with floating leaves are not common. River banks are frequently lined with emergent species such as *Phragmites australis*, *Bolboschoenus fluviatilis*, *Schoenoplectus mucronatus*, *S. validus*, *Triglochin* spp. and *Persicaria* spp. The banks themselves are frequently heavily wooded with rainforest-like fringing woodlands or *Melaleuca* spp.

Australia's only two species of Podostemaceae (*Tristicha* and *Torrenticola*) grow as submerged plants in fast-flowing upper reaches of a few rivers in Queensland, Northern Territory and Western Australia.

(c) Floodplain swamps and billabongs

These wetlands are the most diverse in both the structure and composition of their vegetation. The word billabong is of Aboriginal origin and is used in Australia to describe permanent or semi-permanent areas of open water on riverine floodplains. On inland rivers they are often oxbows.

Many floodplains and billabongs have been modified or completely obliterated by alteration of water level, grazing, draining, and reclamation. They also receive increased nutrient loads from urban and rural developments in their catchments and support a large number of introduced species.

The shallow wet areas of these lowlands are often dominated by trees of *Melaleuca* spp. with an understorey dominated by sedges (Cyperaceae) and species of Restionaceae. Common understorey genera include *Caustis*, *Fimbristylis*, *Schoenus*, *Baumea*, *Callistemon* and *Banksia*. Northern billabongs frequently have a rich flora in deeper water including *Nymphaea* spp. and the Lotus, *Nelumbo nucifera*, as well as several grasses (e.g. *Pseudoraphis* spp., *Leersia* spp., *Oryza* spp.), *Nymphoides* spp., *Marsilea* spp. and *Eleocharis* spp. (Figs 119, 120).

Submerged plants of *Utricularia* spp., *Hydrilla verticillata* and *Vallisneria* spp. are common in the north, with *Vallisneria americana* and *Potamogeton* spp. common in the south.

Floating plants of the two species of *Azolla* and several species of Lemnaceae (in the genera *Lemna*, *Wolffia* and *Spirodela*) are common over most of Australia. *Pistia stratiotes*, now introduced elsewhere in Australia, was previously only common in the large floodplain swamps of the Northern Territory.

(d) Coastal lagoons and lakes

Several different types of lakes are identifiable depending on how they were originally formed. They are not very common in the tropics. Lagoons or lakes that are frequently open to the sea have a submerged vegetation of *Zostera capricorni* which, in the south, is replaced by *Z. muelleri*. Other lagoons in the south usually have *Ruppia* spp., charaphytes (e.g. *Chara* spp. *Nitella* spp., *Lamprothamnion* spp.) or, along the southern coasts, species of *Lepilaena*. The edge communities, when present, usually consist of emergents such as *Phragmites australis*, *Juncus kraussii*, *Bolboschoenus* spp. and *Schoenoplectus* spp.

(e) Estuaries

Estuaries have been reasonably well-studied and the vegetation can be divided into: (i) saltmarshes, (ii) mangroves, and (iii) seagrass meadows.

i. Saltmarshes. Saltmarshes are frequent on low-lying areas near saline water or mangroves. Coastal saltmarshes are usually subjected to periodic flooding, often by tides. They differ from mangroves in generally not being dominated by trees, but Australian temperate saltmarshes may have quite substantial numbers of *Casuarina* spp, which are not normally regarded as mangroves. Good general accounts of saltmarshes can be found in Beadle (1981), Adam (1981) and Hutchings & Saenger (1987).

While there has not been the same detailed study of the biogeography of Australian saltmarsh species as there has been for other aquatic plants (Jacobs & Wilson, 1996), there seems to be an obvious distinction in species content between tropical and temperate saltmarshes. This is masked to some extent by the almost ubiquitous *Sporobolus virginicus*, which becomes even more common in tropical saltmarshes. Common temperate saltmarsh species include *Sarcocornia quinqueflora*, *Halosarcia* spp., *Zoysia macrantha*, *Samolus repens*, *Suaeda australis*, *Juncus kraussii*, *Selliera radicans*, *Tetragonia tetragonioides* and *Triglochin striata*. Grasses are relatively uncommon in our temperate saltmarshes, but *Distichlis distichophylla*, *Puccinellia stricta* or *Austrostipa stipoides* may be locally common. *Casuarina glauca* (in the east) or *C. obesa* (in the west) may grow in and/or on the landward margins of the marsh. South Australia has very large areas of coastal saltmarsh that merge into more inland saline communities dominated by species of Salicornieae and other chenopods, and some genera of Aizoaceae such as *Disphyma*, *Carpobrotus* and *Gunniopsis*.

Tropical saltmarshes can be harder to define than their temperate counterparts. The mangroves may be much more intermittent and there may be large saline flats that are only rarely inundated and then mainly by floodwater. Some of these saline flats may seasonally support large stands of grasses such as *Xerochloa* spp. and be bare for much of the year, or have occasional shrubs of *Halosarcia* spp. More regularly inundated sites may be dominated by the grass *Sporobolus virginicus*. Other common species include *Suaeda arbusculoides*, *Tecticornia* spp., *Sesuvium portulacastrum*, *Sclerolaena bicornis*, *S. glabra*, *Salsola kali*, *Trianthema* spp. and *Zaleya* spp.

ii. Mangroves. Mangrove communities are tidal forests, occupying the boundary between land and sea. They cover about 11 550 sq km of the Australian coastline, with the main areas found in the tropics (Galloway, 1982). Species richness is also greatest in the tropics, declining to a monospecific community (*Avicennia marina*) in the south of the continent, in Victoria, South Australia and Western Australia. No mangroves extend to Tasmania. In north-eastern Queensland on the other hand, there are about 30 mangrove species, with the genera *Bruguiera* (5 spp.), *Rhizophora* (4 spp.), *Sonneratia* (4 spp.), *Lumnitzera* (3 spp.), *Xylocarpus* (3 spp.), *Avicennia* (2 spp.) and *Ceriops* (2 spp.) supplying the largest numbers of taxa (Busby & Bridgewater, 1986). Numbers decline steadily with increasing latitude (and decreasing mean temperature). Mangrove communities are typically devoid of an understorey, although on their landward side they frequently grade into saltmarsh. Mangrove communities are discussed in more detail in this volume by Bridgewater (below), and by Adam (1994).

iii. Seagrass meadows. Australia has about 30 of the world's 58 species of seagrasses, as well as some of the most extensive seagrass meadows. All six families (Hydrocharitaceae, Posidoniaceae, Cymodoceaceae, Zannichelliaceae, Ruppiaceae and Zosteraceae) are represented here, as well as 13 of the 14 genera. Seagrass meadows occur from tropical to cool-temperate regions, and are characteristic of calm, sheltered, shallow waters such as embayments and lagoons. They are discussed in more detail in this volume by Walker (below).

2. Mountain lakes and swamps

(a) Perennial lakes

Australia has comparatively few upland perennial lakes and these rarely develop a characteristic flora. The lakes are mostly shallow and subject to large fluctuations in area and depth. Consequently, most have few submerged species and those that do grow are adapted to seasonal water-level fluctuations. The most common species in the lakes are *Ruppia megacarpa*, *Vallisneria* spp., *Lepilaena* spp. and *Myriophyllum* spp. Marginal emergent vegetation is not well-developed and is usually restricted to the hardiest species, such as *Phragmites australis*, *Typha* spp., and members of the Cyperaceae, possibly because of wave action. Algal blooms are common in such lakes, especially where they are surrounded by agricultural land. Most of these lakes are found in the south-east, the Murray-Darling Basin, and in Tasmania. Benson & Jacobs (1994) have surveyed and classified the perennial and ephemeral lakes of the Monaro region of New South Wales. The lakes in the tropics are mostly a result of volcanic activity and usually have a rich sedge flora (e.g. *Eleocharis* and *Cyperus*) and species of *Nymphaea* and *Nymphoides*.

(b) Perennial swamps

Perennial swamps in the higher country are similar to coastal swamps in species composition but generally support more species of the families Cyperaceae and Juncaceae as well as species of *Ranunculus*, *Villarsia*, *Glossostigma*, *Limosella*, *Myriophyllum*, *Lythrum* and *Montia*. They occur along the Great Dividing Range and adjoining high altitude areas. In the tropics, where they are common, they are usually surrounded by species of *Melaleuca*, and have a species-rich understorey of grasses and sedges. Any areas of deeper water have floating-leaved emergent species of *Nymphaea*, *Nymphoides* or *Marsilea* and submerged species of *Vallisneria*, *Blyxa* or *Utricularia*.

(c) Ephemeral lakes/swamps

These wetlands can be difficult to distinguish from their more perennial counterparts. Many are ephemeral on a long term cycle (e.g. 10–15 years) and the dry period is probably an important factor in determining differences between their communities. The longer-cycle ephemeral wetlands are superficially similar to their perennial equivalents; the short-cycle ones usually support more plant species, although sometimes the whole area is largely covered with one species of *Amphibromus*, *Eleocharis*, or species of the family Cyperaceae. Occasional aquatic species are often present all year but if the area is heavily grazed (as is frequently the case) then the composition of the vegetation may differ dramatically at different periods of inundation. Ephemeral swamps in the tropics often have scattered trees of *Melaleuca* spp. (frequently *M. viridiflora*) and a sedge- and grass-rich understorey. Common genera include *Eriachne*, *Sacciolepis*, *Fuirena*, *Scleria* and *Drosera*.

3. Inland rivers

There are three types of inland riverine systems: (a) rivers, (b) billabongs, and (c) swamps. Three Drainage Divisions (Murray-Darling, Bulloo-Bancannia, and Lake Eyre) (Australian Water Resources Council, 1976) have rivers whose origins are in areas of comparatively high rainfall and then flow inland through areas of lower rainfall. Only from the Murray-Darling does some water actually reach the sea.

(a) Rivers

(i) Perennial rivers, including anabranches. Only the Murray-Darling Drainage Division includes true perennial rivers although the Lake Eyre Division has some that are perennial in their headwaters. Towards their source, perennial rivers are lined with *Casuarina cunninghamiana* and support submerged aquatics like *Vallisneria* spp. or *Potamogeton* spp. Emergents including *Typha* spp., *Phragmites australis*, *Triglochin* spp. or *Eleocharis* spp. grow in protected sites. After the rivers meet the plains, the channels are characteristically lined with *Eucalyptus camaldulensis, E. microtheca s. lat.* or *Melaleuca* spp., with a scattering of *Acacia stenophylla* or *E. largiflorens*. The water becomes turbid from suspended soil particles and dissolved organic matter by the time it reaches the plains. The reduction in light penetration, coupled with fluctuating levels and flows, means that few submerged aquatic species grow in the river channels. The anabranches, with their less rapidly fluctuating flows, may support sparse populations of submerged aquatics like *Vallisneria* spp., *Myriophyllum verrucosum* or *Potamogeton* spp., as well as patches of emergents such as *Typha* spp. and *Phragmites australis*. There is some circumstantial evidence that changes to the riverine environment caused by European man have been responsible for the rapid spread of European Carp and large decreases in the amount of submerged macrophytes.

(ii) Ephemeral rivers. Many ephemeral rivers only carry water for short periods after rain, with a few shallow pools persisting longer. Others, with catchment heads in higher rainfall areas, have almost permanent headwaters, but are ephemeral for the majority of their length with occasional more perennial waterholes. The channels are usually lined with *Eucalyptus camaldulensis* (Fig. 100), *E. microtheca*, or *E. largiflorens*. Aquatics are confined to the more permanent pools. The more permanent the pool the greater the range of aquatic species. As in perennial rivers, *Potamogeton* spp., *Myriophyllum* spp. and *Vallisneria* spp. are the more common submerged aquatics, but there is usually a greater range of emergents with

species of *Cyperus*, *Eleocharis*, *Persicaria* and *Juncus* in addition to those found in perennial rivers. Algal blooms are common when nutrient levels rise as the water levels fall.

(b) Billabongs and floodplains

Billabongs of inland areas are oxbows or river bends. They are often quite deep, fill during floods, and dry slowly. Plant species are similar to those of the main rivers but emergents are more common. *Muehlenbeckia florulenta* often grows on the banks. If domestic stocking rates are not too high, *Ottelia ovalifolia* or one of the floating-leaved species of *Potamogeton* may grow in the shallow water. Edge communities of species such as *Damasonium minus*, *Marsilea* spp., *Crinum flaccidum*, *Sporobolus mitchellii*, and strand species such as *Heliotropium curassavicum* or *Glinus lotoides* may also establish.

(c) Swamps – overflow or terminating

Some inland rivers only flow right through to the next channel during major floods; most of the time they terminate in ephemeral lakes, large swamps or playas. Others may overflow in large floods, inundating huge areas (sometimes in excess of 100 km^2). Normally the Lachlan River terminates in the Great Cumbung Swamp in southern New South Wales, the Macquarie River in the Macquarie Marshes in western New South Wales, and the Bulloo River before the Bulloo Overflow on the New South Wales/Queensland border. The Bulloo Overflow fills only occasionally and the water may take ten years or more to disappear. When full, many swamps have large expanses of turbid, shallow water and wave action and turbidity usually limit submerged vegetation. As the water levels drop, a ground cover of species of *Marsilea*, *Cyperus*, and *Eleocharis* develops with *Atriplex* spp. and *Eragrostis australasica* in the marginal depressions. Stands of *Muehlenbeckia florulenta*, *Eucalyptus microtheca* or *E. largiflorens*, or *E. camaldulensis* develop along the deeper channels.

4. Inland lakes

Inland lakes are mostly ephemeral. Some are seasonally ephemeral, others flood irregularly and some may remain full for many years before drying. Some perennial lakes occur in the wetter regions of the south.

Many of the lakes are terminating (endorheic); some form the source of rivers (exorheic). They range from fresh to quite saline. Wave action and fluctuating water levels limit the vegetation in larger lakes but species of *Ruppia*, *Lepilaena*, and *Lamprothamnion* are reasonably widespread. The immediate areas draining into these lakes usually support swamp species such as *Eucalyptus camaldulensis*, *Muehlenbeckia florulenta* or *Eragrostis australasica* if the salinity levels are not too high, and species of Chenopodiaceae (especially Salicornieae) and sometimes *Muehlenbeckia coccoloboides* for lakes of higher salinity.

These lakes are varied, including crater lakes, spring-fed lakes, and lakes fed from local run-off. The last group may start as essentially fresh, becoming increasingly saline as the season progresses; others are only ever saline but their salinity increases as the water level falls.

The Lake Eyre Drainage Division has the largest, most spectacular, and most intermittent of the inland saline lakes. On the rare occasions when these lakes fill they support abundant life until the salinity levels increase. When partially full the salinity levels are often too high for plant and animal life but apparently the salinity can be quite variable.

5. Mound springs

Mound springs form a minute percentage of wetlands yet they represent (or represented) the only permanent and reliable water source in much of the drier regions of the Murray-Darling, Bulloo-Bancannia, and Lake Eyre Drainage Divisions. Other mound springs, not all associated with the Great Artesian Basin, occur in Western Australia. The South Australian mound springs have been surveyed by Greenslade *et al*. (1985). Mound springs are natural outlets of the Great Artesian Basin, one of the largest artesian basins in the world with an area of about 1.8 million km^2. They are usually associated with fractures and fault lines and often have mounds of various sizes. Some of the extinct springs have mounds of several square kilometres. The mounds are built up from the minerals precipitated from the springs; the weaker the spring the larger the mound tends to be. The salinity of the water varies, as does the rate of flow. Most of the springs are used by stock, feral and native animals, and well-developed vegetation and larger surrounding wetlands were common before artesian bores were drilled and stock introduced. Uncontrolled artesian bores have apparently been responsible for lowering the water levels and pressures in the Basin, thereby reducing the amount of water reaching the surface. Rates of flow in mound springs are decreasing, and many have ceased flowing altogether. Recent moves to cap and control the flow from bores does seem to be having some positive effects for mound spring flows. The southern mound springs characteristically have species such as *Cyperus gymnocaulos*, *C. laevigatus*, *Schoenoplectus pungens*, *Typha domingensis* and *Phragmites australis*, with a few other species appearing less commonly. A few species are endemic to mound springs, including *Eriocaulon carsonii* and an undescribed species of *Utricularia*.

6. Man-made storages, canal systems, channels, drains, bores, bore-drains, farm storages, rice fields, storage swamps

Positive effects of man-made storages include the increase in numbers of large kangaroos since European settlement, largely due to the installation of a much more reliable network of watering points across the country. The range of a number of native plants have extended by colonisation of dams and other artificial water storages. Examples are *Myriophyllum verrucosum* in arid Australia (Orchard, 1986) and *M. variifolium*, *M. simulans*, and related species in wetter areas of south-eastern Australia. On-farm storages also provide habitats for waterbirds. Those species that are hunted are undoubtedly aided by an increase in number and dispersion of suitable habitats. The waterbird populations on artificial waterbodies depend largely on the age, size, and depth of the wetland. The types and extent of particular habitats are important. Those with an array of depths and plant communities have rich invertebrate communities and more waterbird species (Broome & Jarman, 1983).

The plants in these artificial wetlands, which occur all over the country, vary greatly. The species composition reflects both geographical region and the management of the particular wetland. Although many different species grow in man-made storages, less common plant species rarely seem to benefit. For example, *Eriocaulon carsonii* and *Utricularia* sp., endemic to mound springs, have not yet been recorded from any artesian bore or bore drain.

Biogeography

Jacobs & Wilson (1996) investigated the biogeography of Australasian waterplants and concluded that there is a major disjunction between the temperate and tropical aquatic floras. This distinction is more clearly defined at the species and genus levels than at the family level. A second important determinant in the differences/similarities appears to be the distance between the wetlands, although there also appears to be a strong relationship with the migratory flight paths of trans-equatorial birds (Lane, 1987).

Jacobs & Wilson suggest that Australia's aquatic flora has developed through a combination of distance dispersal, vicariance and local speciation. Climate is thought to be the most significant vicariance barrier at the species level. The geographically closer the areas are within either the tropical or temperate zones the more similar their floras are. This similarity is maintained by distance dispersal of species. At the generic level the climatic and distance barriers seem to have been about equally important. At the family level the situation is less clear, but it appears that the physical barriers have been more important than the climatic ones.

The similarity between aquatic floras of different continental areas has been noted and commented on by others. Thorne (1972) notes that more than half of his 'subcosmopolitan' category of genera are aquatic and, of the very few species that can be described as subcosmopolitan, nearly all are aquatic. Kloot (1984) notes that 61 of the 98 native species considered to have disjunct natural distributions between southern Australia and other temperate regions of the world are aquatic (the largest group of the remainder represent taxonomic errors).

The decline of wetland quality

In the past 100 000 years Australia has gone through wet and dry periods, presumably with corresponding fluctuations in waterplant populations. During this same period, Aborigines used fire to change the populations of dryland plants but, apart from harvesting some species for food, probably had relatively little impact on the waterplants. In the last 200 years European colonisation has had an enormous impact on vegetation in Australia.

Although we can be reasonably sure of the composition of the terrestrial vegetation around the watercourses at the time of European colonisation, we have very little idea of what was in the rivers themselves. By talking to people with long associations with waterways and collating their stories with what we see today, we can develop theories or hypotheses. Unfortunately these cannot be tested easily, only compared with future observations.

The deterioration of waterplant numbers and water quality started at Botany Bay. By the early 1800s the seagrasses in the bay were reduced by disturbance of the bed during harvesting of mud oysters. The Cooks River, a stream that now enters Botany Bay by an artificial route near the main runway of Kingsford Smith airport, Sydney, was classed as polluted and unfit for human use by the mid-1800s (McGuinness, 1988; Sainty & Jacobs, 1994). Since then many other streams, estuaries and wetlands have deteriorated or been destroyed.

The causes of deterioration are many. Land clearance for agriculture caused erosion and increased run-off, bank vegetation diminished and stock had increased access to streams causing further erosion. Dams were built, water stored and released at different times of the year and at different temperatures to natural flows. Concrete 'creeks' were built to speed water on its way, adding to its velocity and erosive capacity. Cities and towns grew and government, industry and agriculture often allowed or deliberately directed effluent to discharge into wetlands, streams, bays, estuaries and the sea. Sainty & Jacobs (1994) estimate that, for example, less than 5% of the wetlands of south-east South Australia are untouched by a drainage system and more than 70% of the once extensive wetlands of the Swan Coastal Plain of Western Australia have been altered or obliterated in the last 150 years.

One of the symptoms of the changes, a direct response to the increase in nutrient levels, is the 'bloom' phenomenon. Any species can 'bloom' but the term is normally associated with a free-floating species that is suddenly able to colonise in large numbers areas that it was unable to occupy previously. Examples include the growth of the free-floating *Salvinia molesta* over 330 ha of Lake Moondara, Queensland (Finlayson & Oertzen, 1993) and the floating-attached *Alternanthera philoxeroides* on the Georges River, New South Wales (Sainty & Jacobs, 1981).

Public attention has been drawn to blooms because of the involvement of one group of organisms in particular, the blue-green algae or Cyanobacteria, that are capable of producing offensive odours and/or toxins poisonous to humans and stock. Blue-green algal blooms have always been a part of the Australian environment. In areas where water levels naturally dropped through evaporation and consequently nutrient concentrations increased, blooms were to be expected. These conditions were often met in our inland rivers and billabongs. By decreasing the amount of water now reaching these systems, and increasing the amounts of nutrients entering the systems, we are now seeing an increase in frequency, duration and distribution of blooms. Entwisle *et al*. (1997) gives a good entry into distinguishing different types of freshwater algae and their characteristics, with references. Jones (1994) provided a discussion on blue-green algae or Cyanobacteria, and the conditions thought to lead to blooms.

Increasing salinity in the basins of the inland rivers is having an adverse effect on some wetlands and waterplants. The problem is not new and was predicted, in part, by Baldwin *et al*. (1939) from a study of irrigation in northern Victoria. Unfortunately their prediction was ignored.

Salinity problems are often divided into dryland and non-dryland salinity. The division is artificial. The problem is a result of rising water tables, the commonest causes of which are:

- the clearing of deep-rooted perennial dryland vegetation and replacing it with shallow-rooted short-lived pasture species or annual crops;
- continued application of irrigation water over a comparatively small area, especially in places that historically have been subjected to naturally low levels of rainfall; and
- failure to return excess irrigation water to rivers, but leaving it to evaporate and/or add to the water table.

In practice, none of these factors operate in isolation. Macumber (1990) provides a good summary of current problems and Close (1990) describes the significance of the prehistory of the Murray-Darling Basin in making it particularly susceptible to salinity problems.

Ecological and environmental importance

Waterplants have often become a management and/or environmental issue where streams or waterbodies have been modified or created. The absence or presence of waterplants, including algae, can be used for assessing the health and status of the waterbody. The role of waterplants in maintaining ecosystems, the consequences of disturbance of the natural balance, and some suggested remedies, are discussed in detail in Sainty & Jacobs (1994).

Submerged waterplants:

(i) reduce erosion by:

(a) reducing flow rates

(b) trapping suspended sediment;

(ii) add dissolved oxygen that supports much of the aquatic fauna and speeds the killing of harmful pathogens;

(iii) provide food either directly or indirectly for aquatic animals (including invertebrates) and a large number of terrestrial animals;

(iv) strip nutrients from water, and compete with bloom-forming algae for nutrients;

(v) provide a suitable physical habitat for the breeding of some aquatic animals;

(vi) help maintain habitat diversity and, therefore, total species richness.

Emergent, bank and floating plants:

(i) stabilise stream and lake banks;

(ii) provide food and shelter for aquatic animals;

(iii) provide habitats for the micro-organisms that improve water quality;

(iv) in some circumstances reduce evaporation;

(v) help to strip nutrients from water and sediments;

(vi) reduce turbidity by slowing flow, causing suspended matter to settle;

(vii) impart visual appeal to a waterbody.

Wetlands as a whole do all of the above. They also lower water velocities, thus reducing erosion and decreasing the height and velocity of a flood, but increasing its duration. In addition they provide:

(i) habitats for animals that live there;

(ii) water and food for animals from surrounding habitats;

(iii) refugia for animals that normally live under drier conditions;

(iv) staging areas for migratory or nomadic animals, especially waterbirds.

Economic Importance

The economic importance of wetlands is directly related to some of their attributes listed above. For sustainable long-term maintenance of agriculture and urban areas it will be necessary to carefully manage our biological resources. For most of Australia, and in particular those areas contributing the most to agriculture and with the greatest population, water is a major limiting resource. Australia has reached a stage where water exploitation by some user groups is having a deleterious effect on other user groups. Traditionally in Australia major (short-term) economic considerations have prevailed, but the importance of managing our resources sustainably, and the consequences of not doing so, mean that wetlands are beginning to receive recognition appropriate to their economic importance. This is true for things like water quality for both irrigation and drinking, reducing erosion, maintaining habitat diversity and species richness, and meeting some of our obligations to future generations in terms of sustaining both long-term agriculture and habitat diversity. Inventories of existing wetlands are being made, and their conservation status assessed (Usback & James, 1993; Australian Nature Conservation Agency, 1996).

In fact, the pendulum is now swinging in the opposite direction, with the role of wetlands in improving water quality becoming a fashionable touchstone. This has led to a proliferation of constructed wetlands, often built with unreasonable expectations. Sainty *et al*. (1994) provide a brief outline of some of the potential of consructed wetlands as water purifiers and common mistakes made in their construction and operation, Jacobs *et al*. (1995) assess performance of some of the species commonly used, Hunter & Claus (1995) describe some of the better early results that may be expected, and the papers published by the Queensland Department of Primary Industries (1995) outline the current range of attempts and results being achieved in this area. There are still very few records showing long-term benefits to water quality of constructed wetlands in Australia, but these may be expected as techniques improve.

Conservation

While it will never be possible to return all wetlands to their 'original' state, we can protect some of the remaining best examples and modify our actions to reduce adverse impacts on others. Some of the simpler remedies are listed below, and are considered in more detail in Sainty & Jacobs (1994):

(i) Increase main stream flows and limit diversions, aiming for a reduction of no more than 10%. More water must be allocated for the stream itself; a realistic whole catchment approach is the only hope for many of our river systems.

(ii) Modify old dams to allow water to be taken from different levels (to minimise the impact of cold water from the bottom of the storage on communities downstream). Newer dams often have the capacity for draw-down from different depths.

(iii) Reduce the amount of water extracted and increase efficiency in both on-farm storage and water use so that there is less loss from evaporation and less waste water.

(a) Drip or spray irrigation are good options for many crops, rather than more wasteful flood irrigation.

(b) Excess water should be re-used or treated and cleaned before being returned to the main stream.

(iv) Terminal 'swamps' or evaporating basins should be abandoned unless coupled with a managed system for physical salt removal, as they remove water from the main streams and add substantial amounts to the groundwater, exacerbating salinity problems.

(v) Buffer zones along streams can be built and maintained by fencing and controlling stock access.

(vi) Increased efforts are required to control European carp which increase turbidity and prey on native fish and other fauna.

Conservation has to be synonymous with total catchment management. It is not useful to isolate, even in thought, individual wetlands and streams from the total catchment (including groundwater). Although much lip service is paid to the concept, not enough happens yet in a practical sense, most catchments having several different facets controlled by different government agencies or departments. Catchment trusts are being formed (for example in Western Australia on the Swan Coastal Plain, on several major streams in Victoria, and the Hawkesbury-Nepean catchment Management Trust near Sydney). McComb & Lake (1988), Usback & James (1993) and Australian Nature Conservation Agency (1996) assess the conservation situation and provide information on the 'more important' wetlands (including Werribee Sewage Farm near Melbourne, Victoria!). Many of the remaining wetlands are physically protected (in quantity and quality), but the water supply of many of them is not.

MANGROVES

Peter Bridgewater[1]

Mangroves have long fascinated ecologists interested in coastal communities. There are perhaps 50 species of mangrove in Australia, and less than 200 world-wide. Yet there is little agreement on which plants are mangroves, and which are not. Workers in Australia have variously cited 45 taxa (Bunt *et al.*, 1982), 38 species (Busby & Bridgewater, 1986), 40 species (Smith & Duke, 1987) and approximately 30 species of trees and shrub (Hutchings & Saenger, 1987). Using a slightly broader definition, Wightman (1989) recognises 48 species for the Northern Territory. The problem stems from mangroves being a group of plants growing at the land/sea interface, with their roots literally in the water. Depending on the author, climbers, ferns and chenopods may or may not be included.

Mangrove forests (better described as mangal, following the pioneering work of Macnae, 1968) are highly productive ecosystems (Figs 121, 122), of major ecological significance for their nursery role in fish and invertebrate populations. Litter from mangal systems is also an energy source for benthic systems immediately off-shore. Galloway (1982) estimates the coverage of the Australian coastline by mangal to be 11 550 square kilometres.

Mangroves have a variety of unusual strategies to deal with their unusual environment. Because they are typically found in waterlogged anoxic soils, and are buffeted by tides which have large daily ranges (up to 9 m in north-western Australia), mangrove species have developed a variety of specialised root systems. These include the pneumatophores of the genus *Avicennia*, where roots grow upwards from the radial root system, and are alternately bathed in seawater, or exposed to air. *Bruguiera* species typically have 'knee' roots, where the

[1] Environment Australia, PO Box E305, Kingston, Australian Capital Territory 2604.

root emerges, but then returns below substrate level. *Rhizophora* species have both pneumatophores and a system of stilt roots, which perform both a supporting and aeration role. Species typical of the landward part of the mangal, such as *Ceriops*, *Heritiera* and *Xylocarpus* have the typical buttressed root systems of rainforest species. All these root systems have a large amount of aerenchyma tissue, which is assumed to help aerate the underground root systems (Crisp *et al.*, 1990; Tomlinson, 1986).

Growing in waterlogged conditions, with tidal flows, also poses problems for seedling establishment. A number of different strategies are exhibited by the seeds of mangal species. The most common feature of seaward species is vivipary. Here the seed typically germinates on the plant, producing a long tapered and fleshy root. Initial growth rates are also strong, with the early establishment of an extensive root system. Species from more landward situations often have corky or rounded fruits which appear to withstand prolonged immersion, and are able to float considerable distances. While the development of dartlike seedlings from vivipary would suggest a mechanism for survival, Tomlinson (1986) notes a range of sources which discount this. Indeed, the value to the plant of the precociously germinated seedling may be more related to a dispersal mechanism (Crisp *et al.*, 1990).

Physiological mechanisms to combat hypersaline conditions are widespread through mangal species. Three Australian genera (*Avicennia*, *Aegialitis* and *Aegiceras*), all frequently found in hypersaline situations, possess salt secreting glands which help in the general process of excluding and excreting salt. All genera have physiological mechanisms to exclude salt intake, in common with most halophytes. Salt secretors, however, have the extra mechanism of maintaining relatively high salt concentrations in their xylem. The salt is secreted as sodium chloride crystals from specially modified salt glands at the edges and apex of the leaves.

Diversity and distribution

Mangrove species come from rather few families. Many of the more 'typical' species are from the Rhizophoraceae. Other families with a number of species, or key species, are Sonneratiaceae, Combretaceae, Bombacaceae, Verbenaceae, Myrsinaceae, Myrtaceae, Acanthaceae, Meliaceae and Malvaceae. Key genera in the Australian mangal are, in declining order of significance, *Avicennia*, *Rhizophora*, *Aegiceras*, *Ceriops*, *Bruguiera*, *Sonneratia*, *Excoecaria*, *Camptostemon*, *Xylocarpus*, and *Heritiera* (see Bunt *et al.*, 1982; Bridgewater, 1989).

The last three genera contain the tallest tree mangroves in Australia, reaching their best in Queensland. *Heritiera* and *Bruguiera* are also found as tall trees on the elevated limestone terraces of Christmas Island in the Indian Ocean (Du Puy, 1993). Although not directly marine, this situation provides a fascinating example of how species which are typically marine can adapt. Beard (1967) notes an example in Western Australia of *Avicennia* growing over 40 km inland from the coast, and there are many examples around the coastline of *Avicennia* growing in apparently dry dunes. The local hydrography may provide an answer here, with underground marine inflow, or brackish outflow, providing the conditions normally experienced at the land-sea interface.

Present-day global distribution of mangal and its component species suggests that the Indo-Malayan region was the focus for mangrove evolution. Fossilised pollen and wood from south-western Australia (Churchill, 1973) indicates that some genera (*Nypa*, *Sonneratia*, *Avicennia*) were present in the mid-Eocene. The mangrove flora of this region today has only one species (*Avicennia*), indicating changes in climate and water temperature, but this evidence, coupled with further fossil data showing continuous mangrove vegetation from the lower Tertiary in Sulawesi, suggests a possible origin of mangrove flora and mangrove habit in the Australian region.

Despite this, the current suite of mangrove species in Australia contains only one endemic, *Avicennia integra* (Duke, 1988), which appears restricted to northern Australia, although some species are regionally restricted (*Osbornia octodonta*, *Aegialitis annulata* and *Bruguiera exaristata*). Biogeographic analyses of the mangal have largely been cursory. A significant analysis of the Western Australian coastline was made by Semeniuk *et al.* (1978). These data were re-presented, with data for the eastern states, by Hutchings & Saenger (1987). A more detailed analysis was made for southern and western Australia by Bridgewater (1989). A re-interpretation of available data for Australia is made for this volume, and appears as Fig. 89.

Figure 89. Biogeographic regions of mangroves in Australia. The divisions are a combination of climatic conditions and major or significant mangrove genera. In Western Australia a transitional area occurs with little mangal development except at Shark Bay. There the presence of halophytes typical of both the arid tropical and mediterranean regions suggests a transitional nature to this zone.

Ecology

Why is mangal important ecologically? Like saltmarshes, mangrove forests are important buffers between land and sea – highly dynamic systems that can change extent and composition over quite short periods, and show quite marked changes over decades (Bird & Barson, 1975; Crisp *et al*., 1990).

Zann (1995) notes that Australia has the third largest area of mangal for any one country in the world. Only Brazil and Indonesia have larger areas. Australia also has the unusual feature of coastlines where mangrove and salt-marsh merge in both a Mediterranean climate (Bridgewater & Cresswell,1993) and Temperate climate (Bridgewater, 1982a, 1982b).

Zann (1995) also stresses the important ecological role that mangroves play: 'providing habitats and nurseries for many fish, [they] form a buffer for estuaries from sediments and for coastlines from storm waves, are natural nutrient filters, and are critical habitats for many birds and other wildlife'. Such views are echoed by Hutchings & Saenger (1987).

Most mangrove species are tall trees and shrubs, and are home to many vertebrate species. These include 13 species of birds (although up to 250 species are thought to associate with or visit mangal systems), fruit bats (*Pteropus* spp), crocodiles, skinks, sea snakes, other snakes (including the venomous black-bellied swamp snake) and around 150 species of fishes. The invertebrate fauna is even more diverse, although mainly dwelling in the sediments (Clough *et al*., 1982).

Some species (e.g. *Sonneratia alba*) grow where the tide covers the lower third of their stems daily. Other species (e.g. *Ceriops tagal*) are found growing in hypersaline conditions, with irregular tidal inundation. Yet others (e.g. *Xylocarpus granatum*) are found only where freshwater flows are sufficiently strong to significantly reduce the salinity of the seawater. For those authors who adopt a wide view of mangal, the range of habitats is much wider, including those of chenopods and even salt-tolerant grasses which occur with shrubs along the northern and western coastlines.

The mangal is a complex series of plant communities, often defined by only a few species. Communities are graded or zoned on the shoreline depending on the local coastal geology, hydrology and climate. Australia has the most southerly occurrence of a mangrove species, near Corner Inlet, in southern Victoria. There, fully fertile individuals of *Avicennia marina* between 0.5 and 0.75 m in height occur. This population represents the highest latitude reached by mangrove species in either Hemisphere. Around the southern coast of Victoria, South Australia and Western Australia extensive mangal occurs in suitable estuaries. This community is monospecific: *Avicennia marina* occurs as a shrub or tree to 2–3 m in height. Landward saltmarshes frequently occur, dominated by such species as *Sarcocornia quinqueflora*, *Suaeda australis* and *Samolus repens*. These communities are widespread in the region of Australia typified by a Mediterranean climate type (Bridgewater, 1982b).

On the western coastline of Australia mangal is relatively scarce, occurring in suitable habitats as a thin band between the sea and the highly arid interior. On the east coast of the continent mangal is more frequent, with species richness increasing towards lower latitudes.

The most extensive and biodiverse areas of mangal occur along the northern coastline of Australia, from the Gulf Country of Queensland to the Kimberley region of Western Australia. This is also the most richly textured mangal landscapes. In terms of diversity, the 25–26°S region is a major point of change in Australia. Northwards, the mangal is more species-rich, whatever the climate (see Bunt *et al*., 1982; Wightman, 1989). While not as diverse as that of the north coast, the tallest mangal is to be found along the east coast of Cape York Peninsula, north of Cairns.

Threats and conservation

Australia has had a relatively good record of conservation of mangal, surpassing that of many other countries. This is partly due to lower population densities in Australia, but more importantly, because much of the Australian mangal is in isolated areas. Unlike many other countries with substantial mangrove areas, Australia has no traditional human occupation and use of such areas, and little development of aquaculture facilities. However, mangal is now threatened by many human activities, particularly the filling and draining of coastal wetland systems, and the development of port and marina infrastructure.

The most affected mangal is that south of 32°S, where industrial and residential development have taken their toll. There is also a threat from the introduced grass, *Spartina* × *townsendii*, which was originally introduced to control silting in estuaries, but now has the potential to damage stands of mangal in Victoria (Rash *et al*., 1996).

While other vegetation types, particularly other wetlands, have suffered degradation and species extinction in the last 200 years, it appears unlikely that any species of mangrove, or species associated with mangal, has become extinct in Australia, or is especially endangered. It is interesting that Aboriginal Australians appear to have relatively few uses for mangroves, in contrast to other indigenous cultures in the region. For the future, careful management and monitoring of remaining mangal and its hinterland will be critical to ensuring a relatively intact community remains.

THE MARINE ANGIOSPERMS

Diana I. Walker[1]

The Australian marine environment occupies some 11 million km^2, stretching from the 50 000 km of coastline outwards for a distance of 200 km (the Australian Exclusive Economic Zone), to depths of thousands of metres. Much of this environment is, however, unsuitable for photosynthetic organisms, which rely on sufficient light being available to support net photosynthesis (Kirk, 1994). The surface layers of the oceans are occupied by phytoplankton (micro-algae), but this is a very thin layer (tens of metres) relative to the depth of waters off the continental shelf (Price, 1990). The shallow waters along coastlines where land and sea meet are the most productive and diverse environment for marine macrophytes (Mann, 1982), both seaweeds (algae) which occur mainly on rocky shores, and seagrasses (marine angiosperms) found mainly on soft sandy or muddy bottoms. This section focuses on the marine angiosperms in Australian waters.

The seagrasses are a specialised group of only 58 species which evolved from terrestrial angiosperms about 100 Mya (den Hartog, 1970; Waycott & Les, 1996). The lack of species diversity and the antiquity of species suggest an extremely slow rate of evolution within the group (den Hartog, 1970; Les, 1988; Larkum & den Hartog, 1989). Terrestrial angiosperms had evolved mechanisms to cope with life on land, developing adaptations such as thick cuticles to prevent water loss, stomata for gas exchange, support tissues and conducting vessels (Raven, 1985). In recolonising maritime habitats seagrasses needed to develop mechanisms to cope once more with a submerged aquatic existence, in particular, tolerance of a saline medium while submerged completely, an anchoring mechanism, and underwater pollination (Arber, 1920).

Seagrasses have creeping rhizomes with roots (Tomlinson, 1982) that anchor the plants in the sediment in a turbulent environment. This rhizome bears upright shoots which can be ribbon-like (e.g. *Posidonia*) or with lignified erect shoots with terminal leaf clusters (e.g. *Amphibolis*). They do not possess stomata and have only a very thin cuticle (Kuo, 1983)

[1] Department of Botany, University of Western Australia, Nedlands, Western Australia 6907.

which facilitates gas exchange. Seagrasses have unusual floral structures and both pollen and stigmas show adaptations to their saline medium (McConchie, Ducker & Knox, 1982; McConchie, Knox, Ducker & Pettitt, 1982). Approximately 75% of seagrasses are dioecious, having separate male and female plants (den Hartog, 1970; Pettitt *et al.*, 1981; Les, 1988; Cox & Humphries, 1993) compared to only 4% of angiosperms as a whole (Richards, 1986).

Seagrasses have their greatest species richness in Australia, where there are also some of the largest meadows (Walker & Prince, 1987). This chapter explores this richness and distribution. The ecological significance of seagrasses are described, as well as the large scale losses that have resulted from human activities.

Diversity and distribution

The Australian coastline has 30 of the 58 species of seagrass that occur worldwide (Table 28) (Kuo & McComb, 1989) (Figs 123, 124). These come from 11 of the 12 worldwide genera, and all four families (Hydrocharitaceae, Posidoniaceae, Cymodoceaceae, Zosteraceae) from two orders (Hydrocharitales and Najadales) (Tomlinson, 1982). These species occur in shallow, relatively clear water around Australia, from tropical to cool-temperate waters.

The distributions of seagrass species (Table 28) fall into two main types. Sixteen species are endemic to Australia, and confined mainly to temperate southern Australian. Two other temperate species of Zosteraceae are more widespread, one occurring only in Australia and New Zealand, the other only in Australia and Chile. A further 12 species are tropical, and found throughout the Indian Ocean and tropical Pacific region. These distributions reflect the length and diversity of Australian coastal habitats and the comparative isolation of the Australian temperate zone. The pattern of circulation of water around Australia (Fig. 90) reveals some of the potential links to the Indo-West Pacific Region (Jeffrey *et al.*, 1990).

In tropical areas of Australia, seagrasses often occur as mixed assemblages (Poiner *et al.*, 1989) with biomass values of c. 200 g/m^2 and very rapid rates of turnover (Brouns, 1984, 1985, 1987a, 1987b; Brouns & Heijs, 1986). These seagrasses are often associated with coral reef environments where they occur in the shelter of lagoons, although they are also found in embayments such as in the Gulf of Carpentaria (Poiner *et al.*, 1989). They are important as food for dugongs and turtles (Lanyon *et al.*, 1989)

In southern Australia, particularly Western Australia and South Australia, there are large, mainly monospecific meadows of southern Australian endemic species. These meadows have high biomasses (500–1000 gC/m^2) and high productivities (>1000 $gC/m^2/yr^1$) (Hillman *et al.*, 1989). Southern Australian seagrasses are unusual in that they occur in water bodies exposed to levels of water movement only slightly reduced from open ocean environments (Walker & McComb, 1992). Where seagrasses occur elsewhere in the world they are confined to protected water bodies such as estuaries and lagoons. Australian species do require some protection and most seagrasses occur in habitats with extensive shallow sedimentary environments, sheltered from oceanic swells, such as embayments (e.g. Shark Bay and Cockburn Sound, Western Australia; Spencer Gulf, South Australia; Westernport Bay, Victoria), protected bays (e.g. Botany Bay, New South Wales; Jervis Bay, Australian Capital Territory; Geographe Bay and Frenchman's Bay, Western Australia) and lagoons enclosed by fringing reefs, both tropical (associated with coral reef environments) and temperate (e.g. the Western Australian west coast from Bunbury to Kalbarri) (see Larkum *et al.*, 1989, for full descriptions).

Table 28. List of species of marine angiosperms reported from Australia, with their biogeographic distribution (adapted from Kuo & McComb, 1989).

Species	Distribution
HYDROCHARITACEAE	
Enhalus acoroides (L.f.) Royle	Indo-West Pacific
Halophila decipiens Ostenf.	Indo-West Pacific, Caribbean
Halophila minor (Zoll.) Hartog	Indo-West Pacific
Halophila ovalis (R.Br.) Hook.f.	Indo-West Pacific
Halophila spinulosa (R.Br.) Asch.	Indo-West Pacific
Halophila australis Doty & Stone	Australian endemic
Halophila tricostata Greenway	Queensland endemic
Thalassia hemprichii (Ehrenb.) Asch.	Indo-West Pacific
POSIDONIACEAE	
Posidonia australis Hook.f.	Southern Australian endemic
Posidonia angustifolia Cambridge & Kuo	Southern Australian endemic
Posidonia denhartogii Kuo & Cambridge	Southern Australian endemic
Posidonia sinuosa Cambridge & Kuo	Southern Australian endemic
Posidonia coriacea Cambridge & Kuo	Western Australian endemic
Posidonia kirkmanii Kuo & Cambridge	Western Australian endemic
Posidonia ostenfeldii Hartog	Western Australian endemic
Posidonia robertsoniae Kuo & Cambridge	Western Australian endemic
CYMODOCEACEAE	
Amphibolis antarctica (Labill.) Sond. & Asch. ex Asch.	Southern Australian endemic
Amphibolis griffithii (J.M.Black) Hartog	Southern Australian endemic
Cymodocea angustata Ostenf.	Tropical Western Australian endemic
Cymodocea rotundata Ehrenb. & Hempr. ex Asch	Indo-West Pacific
Cymodocea serrulata (R.Br.) Asch. & Magnus	Indo-West Pacific
Halodule pinifolia (Miki) Hartog	Indo-West Pacific
Halodule uninervis (Forsk.) Asch.	Indo-West Pacific
Syringodium isoetifolium (Asch.) Dandy	Indo-West Pacific
Thalassodendron ciliatum (Forssk.) Hartog	Indo-West Pacific
Thalassodendron pachyrhizum Hartog	Western Australian endemic
ZOSTERACEAE	
Heterozostera tasmanica (Asch.) Hartog	Southern Australia, Chile
Zostera capricorni Asch.	Australia, New Zealand
Zostera mucronata Hartog	Southern Australian endemic
Zostera muelleri Irmisch & Asch.	Southern Australian endemic

The suitability of habitats on the south-western Australian coast for seagrasses has been attributed to these protected lagoonal systems and to water temperature (Kirkman & Walker, 1989). Kirkman & Kuo (1990) describe the processes affecting these communities.

South-western Australia in particular has the highest diversity of *Posidonia*, with seven of its eight species occurring in this region (Cambridge & Kuo, 1979; Kuo & Cambridge, 1984). The only non-Australian species of *Posidonia* (*P. oceanica)* occurs in the Mediterranean. This speciation seems related to the more exposed nature of this part of the coast where the five members of the more leathery *P. ostenfeldii*-group are found (Kuo & Cambridge, 1984).

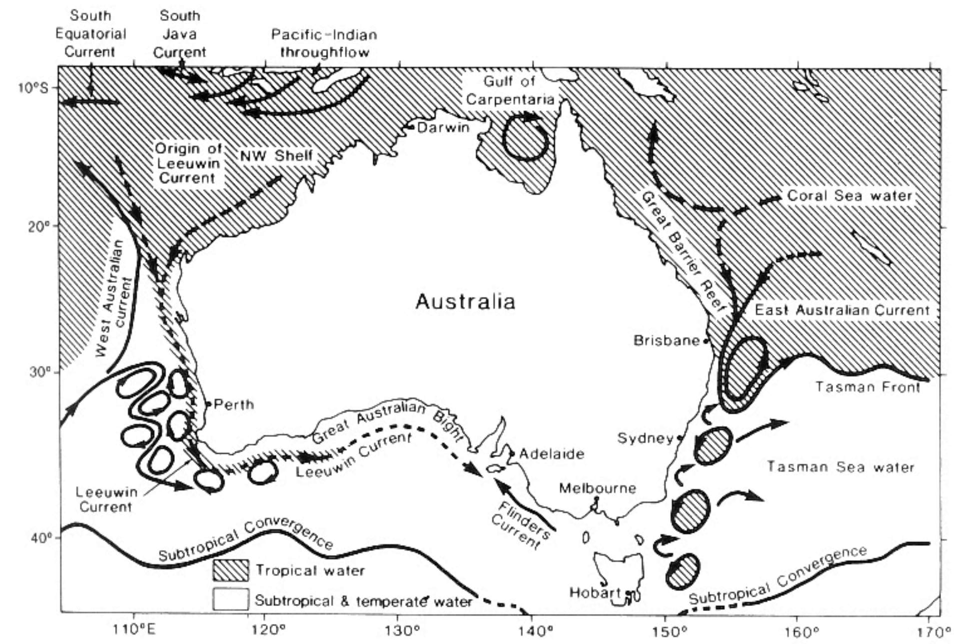

Figure 90. Australia's ocean circulation patterns (adapted from Jeffrey *et al*., 1990).

Ecological importance

Seagrasses provide a stabilising third dimension in an otherwise unstable environment. They are capable of colonising areas unavailable to macroalgae, most of which require a hard substratum for attachment. The presence of seagrasses changes the seabed from a two-dimensional structure of unconsolidated sediment into a complex three-dimensional structure incorporating the leaves, stems, rhizomes and roots of the seagrass themselves, plus extensive populations of epiphytic algae and invertebrate fauna. Many of the functional roles that seagrasses play depend on this three-dimensional structure.

Seagrasses lack the variety in habit that characterises terrestrial vegetation. Most seagrasses have long strap-like leaves, therefore biomass and leaf area are useful measures of complexity at small scales. The obvious exceptions to this are genera such as *Amphibolis* and *Thalassodendron*, with perennial woody stems, clusters of leaves, and large epiphytic algae growing on the stems.

Physical attributes

Water flow within a seagrass canopy encounters frictional resistance, therefore the current velocity drops (Fonseca & Fisher, 1986; Fonseca & Cahalan, 1992). As current velocity drops, the particle-carrying capacity of the water also decreases, which results in the deposition of fine particles within the meadow. Calcium carbonate, from epiphytic coralline algae (Walker & Woelkerling, 1988) and invertebrates such as molluscs (Hutchings *et al.*, 1991), and organic material produced within the seagrass meadow are also trapped (Walker & McComb, 1985). Furthermore, velocity-reduction by the canopy, in combination with the binding properties of the seagrass root and rhizome system, acts to stabilise the sediments. The net effect of seagrass meadows on sedimentation processes may be summarised as: less sediment erosion; increased sedimentation rates; a higher proportion of fine particle sizes and changes in the levels of organic matter and calcium carbonate. However, under conditions of orbital swell, as occur on much of the southern Australian coast, this increased sedimentation may not occur due to the more extreme physical environments (Walker *et al.*, 1996).

Chemical attributes

Compared to unvegetated areas, seagrass meadows represent considerable accumulations of carbon, nitrogen and phosphorus, particularly in the nutrient-poor environments they typically occupy (Hillman *et al.*, 1989; Fourqurean *et al.*, 1992). To maintain their high growth rates seagrasses also need large amounts of nutrients (nitrogen and phosphorus), and their requirements are met partly by uptake of nutrients from the sediments by the roots and rhizomes, and partly by uptake by the leaves from the water column (Hemminga *et al.*, 1991). It has been suggested that most seagrass nutrients are derived from the (largely bacterial) recycling of organic material within the meadows plus efficient internal recycling of nutrients: nutrients are withdrawn from senescing plant material before it is shed (Dennison *et al.*, 1987; Caffrey & Kemp, 1990; Yamamuro *et al.*, 1993; Erftemeijer & Herman, 1994). Bacterial populations both in the water column and in sediments associated with seagrass meadows are far higher than in unvegetated areas, and bacteria also occur as epiphytes on seagrass leaves (Moriarty & Boon, 1989). The growth of these microbial populations is supported by the organic carbon compounds that are exuded from live seagrass material and those released from the breakdown of the organic matter accumulating in seagrass meadows (Moriarty & Boon, 1989; Blum & Mills, 1991).

Biological attributes

Seagrasses are an important source of primary productivity on sandy substrata. Most research on seagrass ecology in Australia has been carried out on the large temperate genera *Posidonia* (Cambridge, 1975; Larkum, 1976; Kirkman & Reid, 1979; Kirkman *et al.*, 1979; Cambridge *et al.*, 1986; Silberstein *et al.*, 1986; Larkum & West, 1990; West, 1990) and *Amphibolis* (Walker, 1985; Walker & McComb, 1988, 1990; Walker & Cambridge, 1995), although a recent monograph has been published on *Halophila ovalis* (Hillman *et al.*, 1995). *Zostera capricorni* has also been the subject of detailed studies (Kirkman *et al.*, 1982; Larkum *et al*., 1984; Abal *et al.*, 1994).

Algae epiphytic on seagrasses also contribute substantially to productivity. Cambridge (1975) and Silberstein *et al.* (1986) have documented algae on *Posidonia australis* and *P. sinuosa*, while epiphytes on *Amphibolis* have been studied extensively (Kendrick *et al.*, 1988; Borowitzka & Lethbridge, 1989; Borowitzka *et al.*, 1990). These epiphytes are more easily broken down and form a more palatable food source than seagrass tissue which is very fibrous.

Many invertebrate animals are found in association with seagrasses. Often these animals use the leaf canopy only for shelter, and only consume epiphytic algae. It is often suggested that seagrass meadows form a 'nursery' for juvenile invertebrates and fishes, a refuge from predation. The refuge value and the amount of habitat available to the fauna inhabiting seagrasses are frequently correlated with the 'complexity' of the habitat, as measured by plant biomass and/or plant surface area (Stoner, 1983; Virnstein & Howard, 1987a, 1987b; Ansari *et al.*, 1991; Mellors & Marsh, 1993; James & Heck, 1994).

Relationships between the abundance of plants and animals remain more or less constant for different species of seagrass and for different sites within the same general area (e.g. Virnstein & Howard, 1987a, 1987b; Howard *et al.*, 1989). Faunal assemblages rarely associate with particular seagrass species; rather they respond to a large number of environmental factors that differ between sites. Thus many animal species are common to adjacent beds of different seagrass species, but the fauna of a bed of any particular species of seagrass may be quite different to that of the same species growing elsewhere. This has been demonstrated in Western Australia for the invertebrate fauna of both subtropical seagrass meadows (Edgar, 1990; Edgar & Robertson, 1992) and temperate seagrass meadows (Hutchings *et al.*, 1991). Australian studies in temperate and tropical seagrass meadows have also demonstrated strong relationships between faunal abundance and the density of seagrass leaves, as measured by biomass (Howard *et al.*, 1989; Humphries *et al.*, 1992; Mellors & Marsh, 1993).

Fish diversity in and near seagrass beds varies enormously with depth, spatially, and with seagrass species (Ferrell *et al.*, 1993; Blaber *et al.*, 1995). Bare sand has been found to have fewer species of fish, (Bell & Pollard, 1989; Connolly, 1994), with only one or two species (as opposed to 39 in seagrass). Fish population density is also lower (Burchmore *et al.*, 1984).

Seagrasses provide foraging grounds for the largest single-species fishery in Australia, that of the Western Rock Lobster (*Panulirus cygnus* George). The catch has an annual value of about $A200 million and is largely taken between latitudes 28–32°S on the west coast (Phillips *et al.*, 1991).

Seagrass loss

The decline of seagrass meadows is a world-wide phenomenon (Walker & McComb, 1992). This may result from natural events such as 'wasting disease' (den Hartog, 1987) or high energy storms (Patriquin, 1975), but most seagrass loss has resulted from human activities, such as nutrient enrichment leading to eutrophication (Orth & Moore, 1983; Bulthuis, 1983; Cambridge & McComb, 1984; Neverauskas, 1987), or land reclamation and changes in land use (Kemp *et al.*, 1983). These studies have documented changes in ecology and some ecosystem processes, but there is still a need for greater understanding of these processes, in order to manage these ecosystems effectively.

The major man-induced declines of seagrass in Australia and their suggested causes are summarised by Walker & McComb (1992). They are discussed in more detail by Shepherd *et al.* (1989). Although many factors may interact, most cases of seagrass decline have resulted from a decrease in light reaching seagrass chloroplasts, hence reducing net effective seagrass photosynthesis. This may result from increased turbidity from living or non-living particulates in the water, increased shading by the deposition of silt or from the growth of epiphytes on leaf surfaces or stems. Seagrass meadows occur between an upper limit imposed by exposure to desiccation or wave energy, and a lower limit imposed by penetration of light at an intensity which allows net photosynthesis. A small reduction in light penetration through the water results in elimination of seagrass at the lower edge of a meadow, while particulates on leaves reduce meadows over extensive areas of shallower water.

The turbidity of the water column above seagrasses can increase through discharge or resuspension of fine material in the water column (e.g. sludge dumping, dredging). Increased nutrient concentrations, from discharge of sewage and industrial wastes, or agricultural activity in catchments, may stimulate phytoplankton growth, significantly reducing light penetration through the water column (Chiffings & McComb, 1981; Lukatelich & McComb, 1986).

Nutrient enrichment can also result in greater growth of macroscopic and microscopic epiphytic algae on leaf surfaces. Macroalgae dominate over seagrasses under conditions of marked eutrophication. This effect is due to the growth of epiphytes (both microscopic and macroscopic), and associated loose-lying species (e.g. *Ulva*, *Cladophora*, *Enteromorpha*, *Ectocarpus*) which may originate as attached epiphytes. The effect of such epiphytes on the health of seagrass beds has been demonstrated in Cockburn Sound, Western Australia (Cambridge & McComb 1984, Silberstein *et al*., 1986).

Physical removal of seagrass is also a major threat. Boat moorings around Australia can cause localised damage (Walker *et al.*, 1989). Harbour and groyne construction, which change the wave energy regime, can also affect seagrass growth. Increased wave or current energy may increase sedimentary erosion and lead to fragmentation of seagrass beds and loss of the rhizome mat. The dredging of Botany Bay, New South Wales, appears to have precipitated this effect in the *Posidonia* beds there (Larkum & West, 1990). If the wave energy regime is decreased by man-made structures then increased deposition of sediment is probable (Harrison, 1987).

Conservation value

Australia's seagrass beds have the world's greatest species richness with a high level of endemism, as well as being some of the most extensive (Walker & Prince, 1987). In addition, they support rich communities of algae, invertebrates and vertebrates. These communities rely on the stable three-dimensional structure of the seagrass canopy. Seagrass beds thus provide a large contribution to biodiversity on sandy bottoms. Their vulnerability to development pressures on Australia's coastal environment means that effective management will be needed if Australia is to retain these rich plant communities.

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