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ECOLOGY OF MANGROVES

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Peter Saenger

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ECOLOGY OF MANGROVES

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Foreword

Ecology is the science involved with the interactions of organisms and their physical and biotic environments. This field always has been a source of fascination to professional biologists, naturalists and conservationists. In recent years, as human population has progressively increased, environmental problems have become of vital interest and importance to the public as well. It has become imperative now that ecological principles, and the ecology of specific regions, be understood by a wide variety of people. The present series is designed to help fill this need.

It is felt that the volumes of this series will serve as a source of information for university students, teachers and the interested public who require a basic factual knowledge to broaden their understanding of ecology, and for those conservationists, agriculturists, foresters, wildlife officers, politicians, planners, engineers, etc. who may need to apply ecological principles in solving specific environmental problems. In addition, it is hoped that the series will be a valuable reference work and source of stimulation for professional ecologists, botanists and zoologists.

The study of ecology can be approached on various levels. For example, one can emphasize the biotic community and analyze the kinds and numbers of organisms living together in a particular habitat, the way they are organized in space and time and the interactions they have with each other. This type of ecology is known as synecology.

Another way of studying ecology is by systems analysis. In this method the biotic community and the physical environment, which together make up what is known as an ecosystem, are looked upon as a functioning unit. In such an approach the main emphasis is on the cycling of energy, minerals or organic materials within the ecosystem and the factors influencing these processes, rather than specifically upon the organisms themselves. Often mathematical or theoretical models are constructed and tested, frequently with the aid of computers.

Both of the above approaches are synthetic; they take an overview of entire communities or systems and do not emphasize individual species. By contrast the following two approaches, collectively known as autecology, are concerned mainly with particular species.

The population approach, often called demography, is concerned with: (1) fluctuation in the abundance and distribution of individuals of a given species in an area, (2) the contributing phenomena such as birth and death rates, immigration, emigration, longevity and survival, and (3) the influence of the physical environment and of other species on these characteristics. Of major interest are mechanisms regulating population density and factors influencing population stability.

The final approach to ecology is one primarily concerned with the effect of the environment on the individuals of a species, that is, how they are affected by temperature, moisture, light or other external factors. This approach is known variously as environmental physiology or physiological ecology. The keynote is adaptation to specific environments.

All of the above approaches are employed with varying emphasis in the volumes of this series.

Certain topics, such as ecology of grasslands, ecology of forests and woodlands, or ecology of deserts lend themselves to a community approach; grassland, forest and desert are types of communities and if studied as an entity must be approached on the community or ecosystem level. On the other hand, where specific taxa such as reptiles, birds or mammals are treated, the autecological approach is used more often. The particular aspect emphasized varies from group to group, depending on the information available.

Regardless of emphasis, in each book of this series the available information in a particular field is reviewed critically and summarized, so that the reader might be brought abreast of current knowledge and developments. Recent trends are indicated and the foundations for future developments are prepared by highlighting conspicuous gaps in knowledge and pointing out what appear to be fruitful avenues for research.

HAROLD HEATWOLE

Preface

Any book dealing with communities or ecosystems must draw information from a wide range of sources. This is especially true of one treating mangroves, for not only are both plants and animals important as in any community, but marine, terrestrial and freshwater habitats and their biotas are all involved to some extent. Detailed treatment of such a variety of conditions and organisms lies beyond the expertise of any one individual and multiple authorship of this book was essential for maintaining even-handed treatment of all aspects of the topic. Inevitably the relative contributions of the two authors varied from chapter to chapter. The first author, a zoologist, had the greatest input into those chapters treating the faunal component and the functioning of the community (Chapters 5–8) whereas the second author, a botanist with experience in management, was primarily responsible for those dealing mostly with plants (Chapters 1–4) and management (Chapter 9). However, each read, revised and re-wrote sections of the other's chapters a number of times and made suggestions for change. We are grateful to the series editor, Harold Heatwole, for assisting in the melding of ideas, styles and approaches and for writing several small sections. His input into the integration of the material was greater than that normally contributed by an editor.

We acknowledge Colin Field, Harry Recher and William Dunson who read and commented on parts of the book; they provided many helpful suggestions and criticisms.

Various people provided advice, literature, special expertise or unpublished data. They are Hal Cogger, Harry Recher, Doug Hoese, Alan Greer, Winston Ponder, Ian Loch, Bill Rudman, Paul Adam, Colin Field, James Elsol, John Tierney, Barry Clough, Roger Springthorpe, Di Jones, Fred Wells, Mike Gray, Courtney Smithers, Mabel Griffiths, Elizabeth Marks, Robert Taylor, Ron Straughan, David McAlpine, Ivor Thomas, Peter Davie, Eric Reye, Jim Davie, David Rentz, Tony Watson, Leigh Miller, Roger Kitching, Ian Common, Elwood Zimmerman, Margaret Cook, Ralph Nursall, David Reid, Norm Milward, Ron West, Rob Williams and Helen Tranter.

We are indebted to Viola Watt and Sandra Pont (Department of Zoology, University of New England) and June Adam (Australian

Museum) who patiently typed the manuscript in its various drafts and eventually put it on a word processor. They never complained about the many changes and reorganization occasioned by numerous versions of the book bouncing back and forth between authors and series editor. Some of the figures are the handi-craft of Robyne Jones and Stephen Perry. Grace Hart, Lyn Albertson and Lexie Walker checked parts of the bibliographies.

Introduction

While the term "mangrove" is generally well understood, it is difficult to define precisely what constitutes a mangrove. The word "mangrove" is used in at least two different ways. It can refer either to an individual species of plant or to a stand, or forest, of plants that contains many species. These two meanings are traditionally used interchangeably; that tradition, although perhaps initially confusing, is maintained in this book. Mangrove communities comprise plants belonging to many different genera and families, many of which are not closely related to one another phylogenetically. What they do have in common is a variety of morphological, physiological and reproductive adaptations that enable them to grow in a particular kind of rather unstable, difficult environment. On the basis of the common possession of these various adaptations, approximately eighty species of plants belonging to about thirty genera in over twenty families are recognized throughout the world as being mangroves. Different species vary in their dependence on the littoral habitat. Of the total number of species accepted worldwide as mangroves plants, fifty-nine are exclusive to the mangrove ecosystem and twenty-two are important but non-exclusive (Saenger et al. 1983).

Mangroves are the characteristic littoral plant formations of sheltered tropical and subtropical coastlines. They have been variously described as "coastal woodland", "mangal", "tidal forest" and "mangrove forest". Where conditions are suitable, they form extensive and productive forests.

Given suitable conditions for growth, propagules of mangrove species colonize and establishment begins. Species interact among themselves and respond to environmental conditions, with the result that a characteristic grouping of species, called a community, is formed. Such a community, in combination with the physical environment with which it interacts, makes up an ecosystem. It is the mangrove ecosystem which is the subject of this book.

The mangrove ecosystem occurs at the interface of land and sea. Loren Eiseley (1971) captured this essential feature in a passage of the book *The Night Country*:

> The beaches on the coast I had come to visit are treacherous and the tides are always shifting things about among the mangrove roots. . . . A

> world like that is not really natural. . . . Parts of it are neither land nor sea and so everything is moving from one element to another, wearing uneasily the queer transitional bodies that life adopts in such places. Fish, some of them come out and breathe air and sit about watching you. Plants take to eating insects, mammals go back to the water and grow elongate like fish, crabs climb trees. Nothing stays put where it began because everything is constantly climbing in, or climbing out, of its unstable environment.

This quotation illustrates graphically the mangrove ecosystem in which tides and coastal currents bring unremitting variation to the forest, and where plants and animals adapt continuously to the changing chemical, physical and biological characteristics of their environment. Many species use the environment dominated by mangroves for food and shelter during part or all of their life cycle. There is constant movement of living and non-living matter into and out of the mangrove ecosystem (Walsh 1974).

A major difficulty in delimiting the mangrove ecosystem is that, because it lies at the land–sea interface, many of the processes that regulate it have their origin elsewhere. These external processes, governing water availability, the pool of available nutrients and the stability of the habitat, often are not seen as part of the ecosystem — and if they are, then the physical boundaries of the ecosystem become virtually impossible to define. In view of the above, it seems preferable to leave the delimitation of the mangrove ecosystem rather loose. This can be justified in that there is general agreement on the suite of species which invariably characterize it.

The existence of extensive mangrove communities appears to depend on a number of basic requirements, although there is some disagreement as to the exact number. Jennings and Bird (1967) described the six most important geomorphological characteristics which affect estuaries, and in so doing provided the first summary of the main factors relating to mangrove establishment. The characteristics were: (1) aridity, (2) wave energy, (3) tidal conditions, (4) sedimentation, (5) mineralogy and (6) neotectonic effects.

Walsh (1974) identified five characteristics as essential mangrove prerequisites on a global scale, and Chapman (1975, 1977) added two others. These seven, apart from their biological slant, are very similar to the six derived from geomorphological considerations by Jennings and Bird (1967). They are: (1) air temperature within a certain range, (2) mud substrate, (3) protection, (4) salt water, (5) tidal range, (6) ocean currents and (7) shallow shores. These will be reviewed in turn.

1. Temperature: Walsh (1974) and Chapman (1975, 1977) maintained that extensive mangrove development occurs only when the average air temperature of the coldest month is higher than 20°C and where the seasonal range does not exceed 10 degrees. Also, the world distribution of mangroves (figure 1), particularly at the northern and southern limits, appears to correlate reasonably well with the 16°C isotherm for the air temperature of the coldest month (Chapman 1977). However, Barth (1981) has shown that equally good correlations can be obtained using water temperatures; the presence of mangroves seems to correlate with those areas where the water temperature of the warmest month exceeds 24°C, and the limits occur in those waters that never exceed 24°C throughout the year. The occurrences of mangroves in south-western Western Australia and Victoria and in the North Island of New Zealand appear to be exceptions regardless of whether air or sea temperatures are used; these mangroves are discussed in more detail below.

2. Mud substrate: Although mangroves are able to grow on sand, peat and coral, the most extensive mangroves are invariably associated with mud and muddy soils. Such soils are usually found along deltaic coasts, in lagoons, and along estuarine shorelines. The mangroves themselves may influence the sediment composition, even accelerating mud accretion on coral islands (Steers 1977).

3. Protection: Walsh (1974) and Chapman (1975, 1977) argued that protected coastlines are essential as mangrove communities cannot develop on exposed coasts where wave action prevents establishment of the seedlings. Bays, lagoons, estuaries and shores behind barrier islands and spits are suitable localities.

4. Salt water: While there is increasing evidence that most mangroves are not obligate halophytes, there is evidence that a number of them have their optimal growth in the presence of some additional sodium chloride (Stern and Voigt 1959; Connor 1969; Sidhu 1975a). Chapman (1977) suggested that *Rhizophora* is probably an obligate halophyte, with growth being poor or reduced in the absence of salt, and Vu-van-Cuong (1964) reported that *Ceriops tagal* and *Avicennia officinalis* would not grow in the absence of salt. However, Walsh (1974) and Chapman (1975, 1977) maintained that the real importance of salt lies in the fact that mangroves are slow-growing and that they cannot compete with faster-growing species unless these species are eliminated or reduced by salt. In this sense, they argued, salt is an essential requirement for mangrove development.

5. Tidal range: Tidal range, coupled with local topography, influences primarily the lateral extent of mangrove development. The greater the tidal range, the greater the vertical range available for

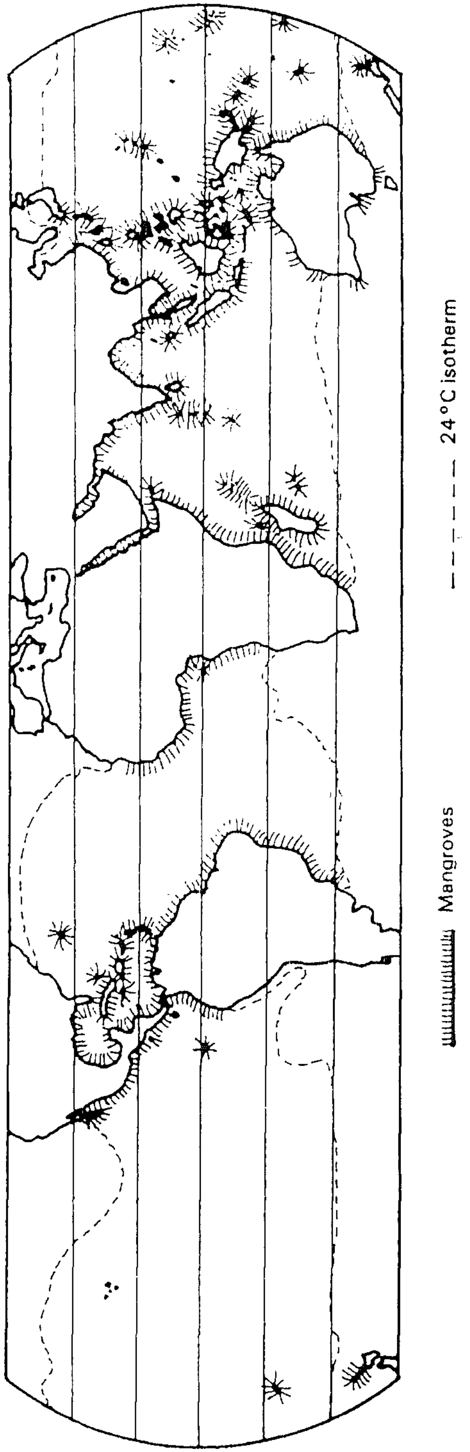


Figure 1 World distribution of mangroves in relation to the 24° isotherm.

mangrove communities. For a given tidal range, steep shores tend to have narrower mangrove zones than do gently sloping ones. Although Walsh (1974) and Chapman (1975, 1977) considered tidal range to be important, there are exceptions in Australia. For example, considerable mangrove development occurs on the microtidal coasts (mean spring range of less than 2 metres) of Cape York Peninsula and in the Gulf of Carpentaria, and Galloway (1982) has shown that similar patterns of mangrove development can exist under a wide range of tidal environments. Mangroves have been reported from tideless areas as well (Beard 1967; Stoddart, Bryan and Gibbs 1973). Although not a direct physiological requirement, tides play an important role in the functioning of the ecosystem.

6. Ocean currents: Favourable currents are essential since they disperse mangrove propagules and distribute them along coasts. Chapman (1975) noted that the southern limit of mangroves on the western coast of Africa coincides with the boundary between a southern cold-water upwelling and warm currents, and that a similar situation occurs on the western coasts of Australia and South America. Apart from the temperature of cold currents, Chapman (1975) argued that in all cases in the southern hemisphere such currents flow northwards, thereby inhibiting the southerly drift of floating propagules.

7. Shallow shores: Mangroves grow in relatively shallow water as seedlings cannot become anchored in deep water. The physical size of mangroves and their requirement of having a great proportion of their body above the water but at the same time being anchored in the soil makes occupancy of deep water impossible. Chapman (1975) maintained that the shallower the water and the more extensive the shallows, the greater the extent of mangrove development; on steeply shelving shores, where the zone of shallow water is narrow, only fringe communities develop.

Although detailed information on the prerequisites for all the individual mangrove species is lacking, the statement can be made that if certain conditions prevail, such as a protected shoreline with suitable climate, muddy substrate and suitable tidal regime, then a mangrove community is likely to develop, provided, of course, that there is a proximal source of propagules. Furthermore, this mangrove community will consist of some combination of characteristic plant species.

1. *Mangrove Biogeography*

Based primarily on floristic data, Saenger et al. (1977) divided the mangrove coastlines of Australia into twelve biogeographic zones. More recently, Semeniuk, Kenneally and Wilson (1978) subdivided one of the Western Australian zones into two, resulting in a total of thirteen (figure 2). While it can be expected that a further refinement of boundaries will occur, these thirteen zones correlate closely with certain environmental (particularly meteorological and tidal) as well as physiognomic features for both the mangrove and saltmarsh vegetation. This correlation suggests that meteorological and tidal features of the coastline are involved in the distribution and the physiognomy of the mangrove vegetation and its constituent species.

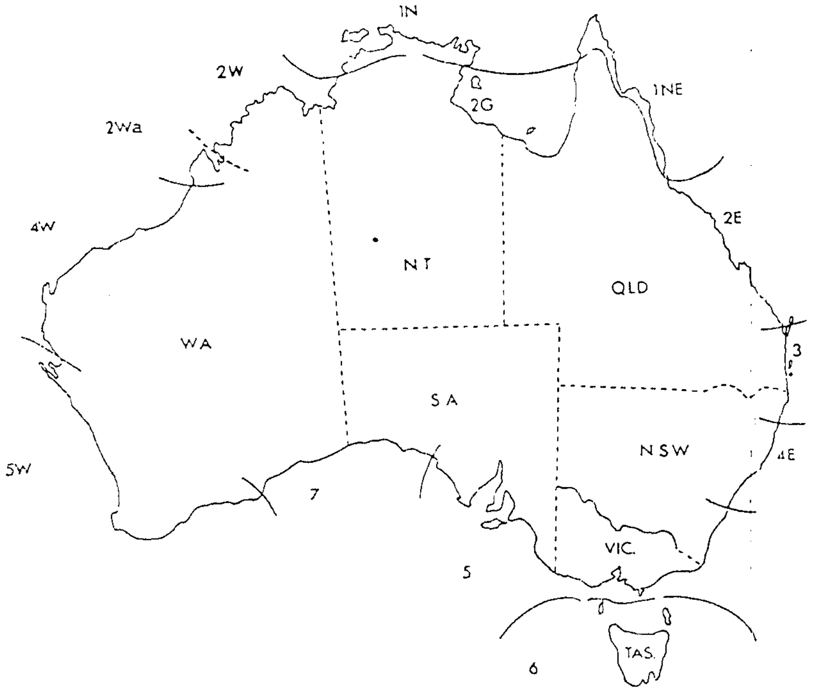


Figure 2 Australian mangrove biogeographic regions based on Saenger et al. (1977) and Semeniuk, Kenneally and Wilson (1978).

The present-day distribution of mangroves suggests that the region between Malaysia and Northern Australia was the centre of evolution of the mangrove flora (Ding Hou 1958, 1972; Chapman 1976, 1977; Specht 1981b; Mepham 1983). However, Muller (1964) demonstrated an unbroken succession of tropical mangrove vegetation from the Lower Tertiary to the Recent in northwestern Borneo, and Churchill (1973) recorded late Eocene fossils of *Nypa*, *Sonneratia*, *Avicennia* and species of the Rhizophoraceae in southwestern Australia. The geological ages of these fossils are indicated in table 1. On the basis of this fossil evidence, Specht (1981) postulated that the centre of the origin of mangroves is more likely to be the region of southwestern and northern Australia to Papua New Guinea rather than the Malayan Archipelago, and that the present-day distribution could be satisfactorily explained only if the early ancestors evolved in the Early Cretaceous (or even earlier) and were dispersed as shown in figure 3. With the later closure of the Mediterranean Sea as a dispersal route, two isolated groups of mangroves would have been formed, and this accords with the present-day situation; whereas three genera (*Avicennia*, *Hibiscus* and *Rhizophora*) are shared between the Indo-Pacific region and the New World–West African region, only four species are common to both.

Fossilized mangrove pollen and wood from southwestern Australia (Churchill 1973) indicates that tropical coastal waters extended along these shores during the Middle to Late Eocene. Several of the species recorded as fossils in southwestern Australia do not occur there today, and it appears that there has been a loss of these elements from southern Australia since the Eocene. In view of the more restricted distribution of these species today, past changes in climate and coastal conditions appear to have had a sifting effect on the Australian mangrove flora. This sifting had undoubtedly contributed to the existing species gradients, not only of the mangroves themselves but also of their associated plants and animals.

In Australia and Papua New Guinea, approximately thirty species of trees and shrubs, belonging to fourteen families of angiosperms, are generally considered to be part of the mangrove flora. None of these species is endemic to the Australian region; Macnae (1966) stated that three species appear to be purely Australian and he included *Aegialitis annulata*, *Bruguiera exaristata* and *Osbornia octodonta*. However, all of these species occur throughout the Indo–West Pacific region and *Osbornia* occurs as far north as the northern Philippines (Van Steenis 1979).

Table 1 Geological time scale of fossil mangroves in relation to other evolutionary events

Era	Period	Millions of years before present	Fossil Records
Cainozoic	Holocene	0.01	Modern man
	Pleistocene	1.8	Giant mammals
	Pliocene	5	Earliest man-like apes; earliest *Acacias* in Australia
	Miocene	24	Earliest *Eucalyptus* in Australia; earliest *Avicennia* and *Sonneratia* pollen in Borneo
	Oligocene	36	Earliest *Rhizophora* pollen in Asia, New Guinea and South America
	Eocene	54	Earliest *Nypa* pollen in Europe, Asia and Australia; earliest *Rhizophora, Avicennia* and *Sonneratia* pollen in Australia. Earliest fossils of *Nypa* fruits and hypocotyls of *Ceriops* and *Palaeobruguiera* in London Clay.
	Palaeocene	65	Earliest *Nypa* pollen in Brazil
Mesozoic	Cretaceous	140	Earliest flowering plants; Extinction of dinosours
	Jurassic	210	Earliest birds
	Triassic	245	Earliest dinosaurs
Palaeozoic	Permian	285	Diverse reptiles and amphibians
	Carboniferous	365	Earliest major coal forests; earliest reptiles and winged insects
	Devonian	415	Earliest trees and amphibians
	Silurian	440	Earliest land plants
	Ordovician	505	Earliest coral reefs and fishes
	Cambrian	570	Earliest invertebrates
Precambrian	Proterozoic	1000	Earliest algae, protozoa and sponges
	Archaeozoic	4000	Earliest bacteria

In Australia, an additional ten species from eight families have been noted as associated lianas, epiphytes, or understorey species (Saenger et al. 1977), and a further ten to fifteen species, although occasionally occurring in the mangrove community, find their greatest development away from it. A large number of other plants such as algae and seagrasses, fungi and lichens also have been recorded from mangrove communities (Saenger et al. 1977; Stevens and Rogers 1979; Cribb 1979; Stevens 1979), but most of these species are not restricted to mangrove environments (see chapter 4).

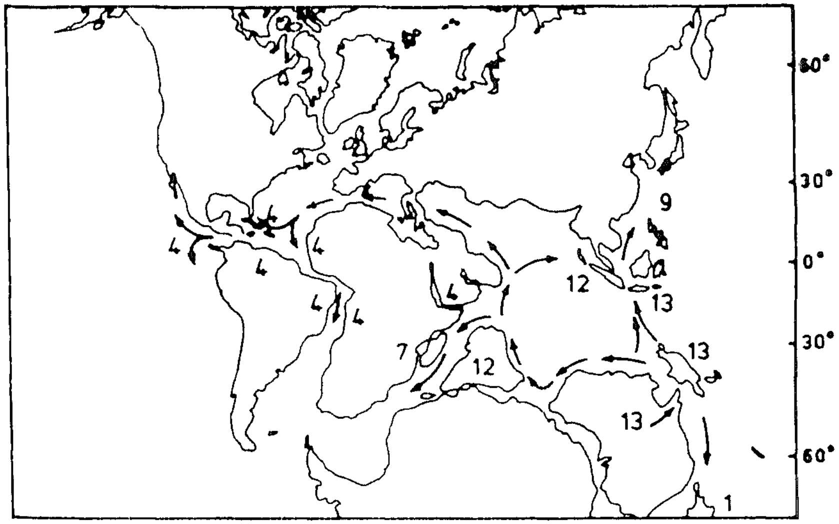


Figure 3 Geographical distribution of continents in the Early Cretaceous period, showing the probable migration routes of the mangrove flora. Number of genera recorded today in various parts of the world are also shown (redrawn from Specht 1981).

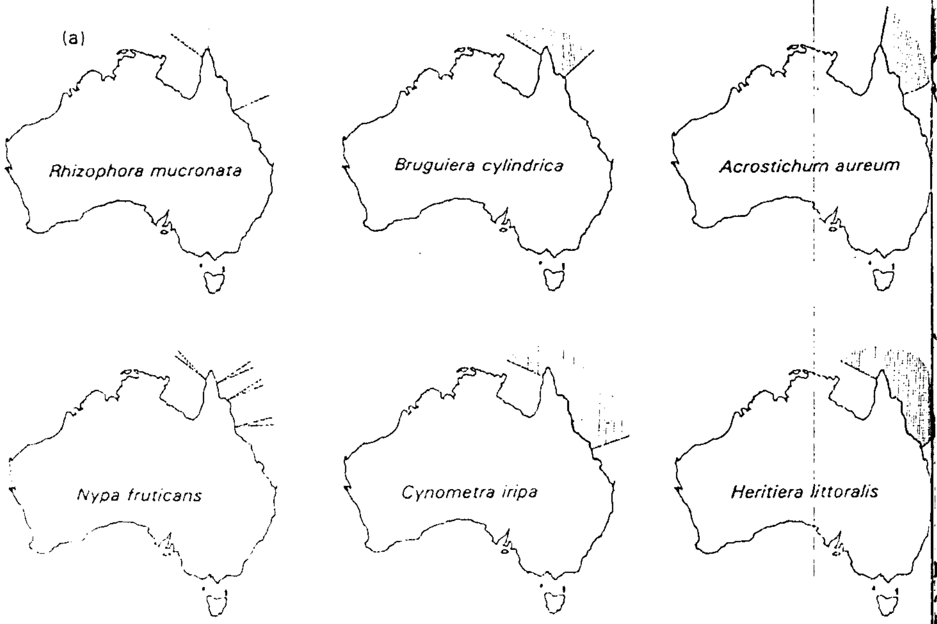
The distributions of the abundant species of mangroves around the Australian coastline are shown in figure 4. It is apparent that the largest number of species occurs on the northern and northeastern coastlines. This concentration of mangrove species and associated plants in the northeastern area of Australia can be attributed to three main factors:

1. This region was the centre of origin of mangroves and the point of their secondary dispersal into and out of Australia by virtue of its land connections with southeastern Asia (Walker 1972) during the various changes in palaeo-sealevels. This interpretation accords with other floristic elements (Burbidge 1960).
2. The climatic regime of this area is similar to that under which mangrove vegetation first developed, consequently little or no sifting of species has occurred there. In fact, Mepham (1983) argued that the northeastern coastline provides refuges for the once widespread and diverse Australian mangrove flora as it withdrew northwards with the onset of arid conditions in the Oligocene. Consequently, these northeastern mangrove forests are best regarded as relicts.
3. Coastline configuration in this region, with its numerous estuaries generally sheltered by the offshore Great Barrier Reef, provides large areas of low-energy coastline suitable for mangrove colonization and development.

The distribution of individual species of mangroves (figure 4) can be misleading, for many species show patchy occurrences within their general range. For example, several species are absent along the southern shores of the Gulf of Carpentaria (Saenger and Hopkins 1975; Wells 1982, 1983) but occur in the Northern Territory (Wells 1982) as well as in northeastern Queensland. Similarly, *Xylocarpus granatum* is absent from the mainland coast south of the mouth of Raglan Creek (lat. 23 °40'S) but small stands occur on Fraser Island (lat. 25 °20'S). In addition, some species are relatively unimportant (in terms of numbers, size, and so on) along one part of the coast but make up one of the more important constituents of the mangrove vegetation in other areas.

The explanations for these disjunctions are undoubtedly to be found in the ecological requirements of the individual species (chapter 3) but, in a broad biogeographical sense, temperature and rainfall are probably the main determinants.

Along the Queensland coastline, the most highly developed mangrove vegetation, in terms of number of species and of structural complexity, is found in those areas where the annual rainfall exceeds 1,250 mm (figure 5); these areas are generally where elevations greater than 700 metres occur in proximity to the coast. With increasing latitude, both on the eastern and western coastlines, the number of species declines rapidly. Lower water and air



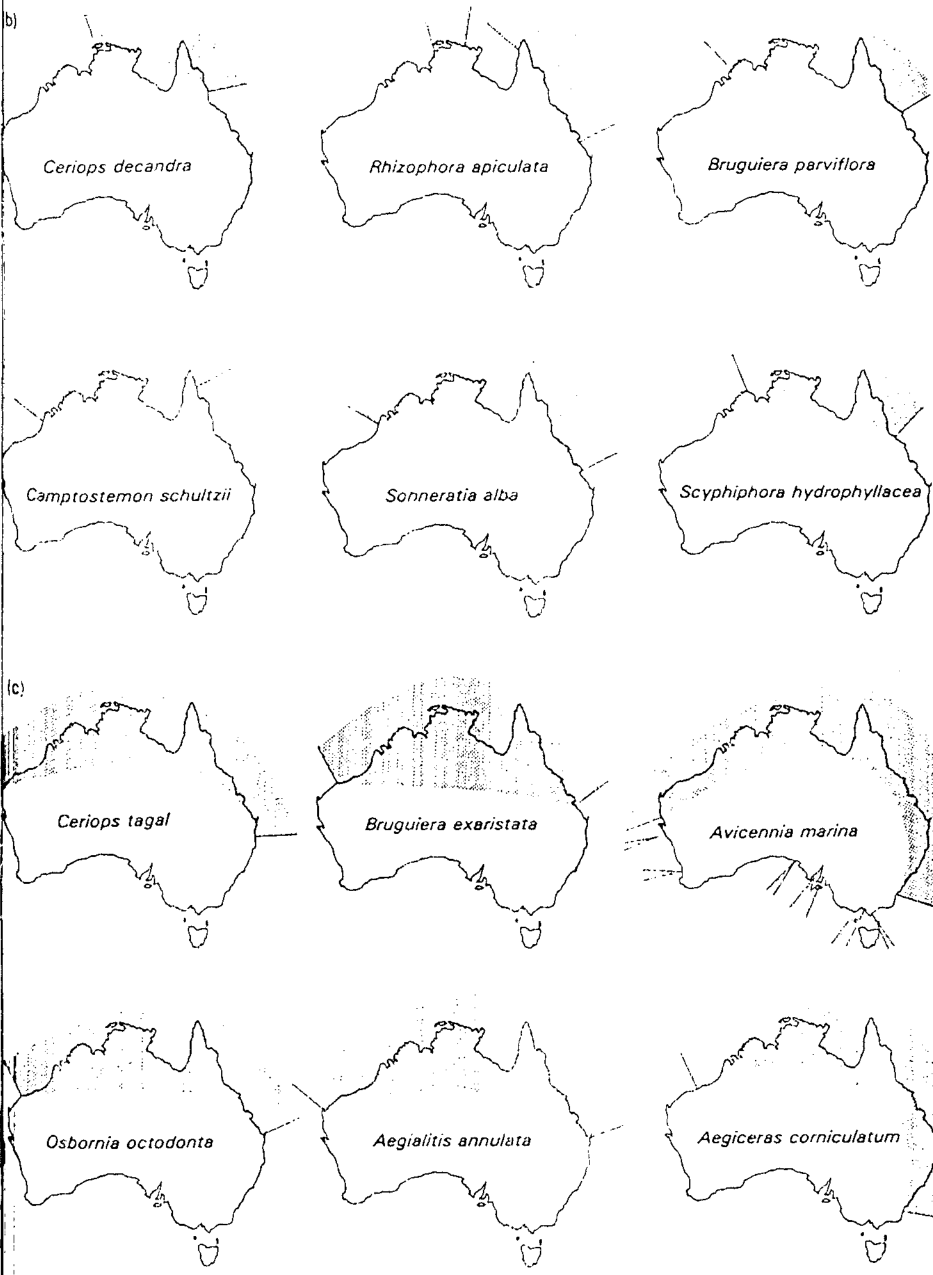


Figure 4 Australian distribution of major mangrove species: (a) species confined to northeastern Australia; (b) species occurring in northern Australia but absent from parts of the Gulf of Carpentaria and (c) species widespread around northern and eastern coastlines.

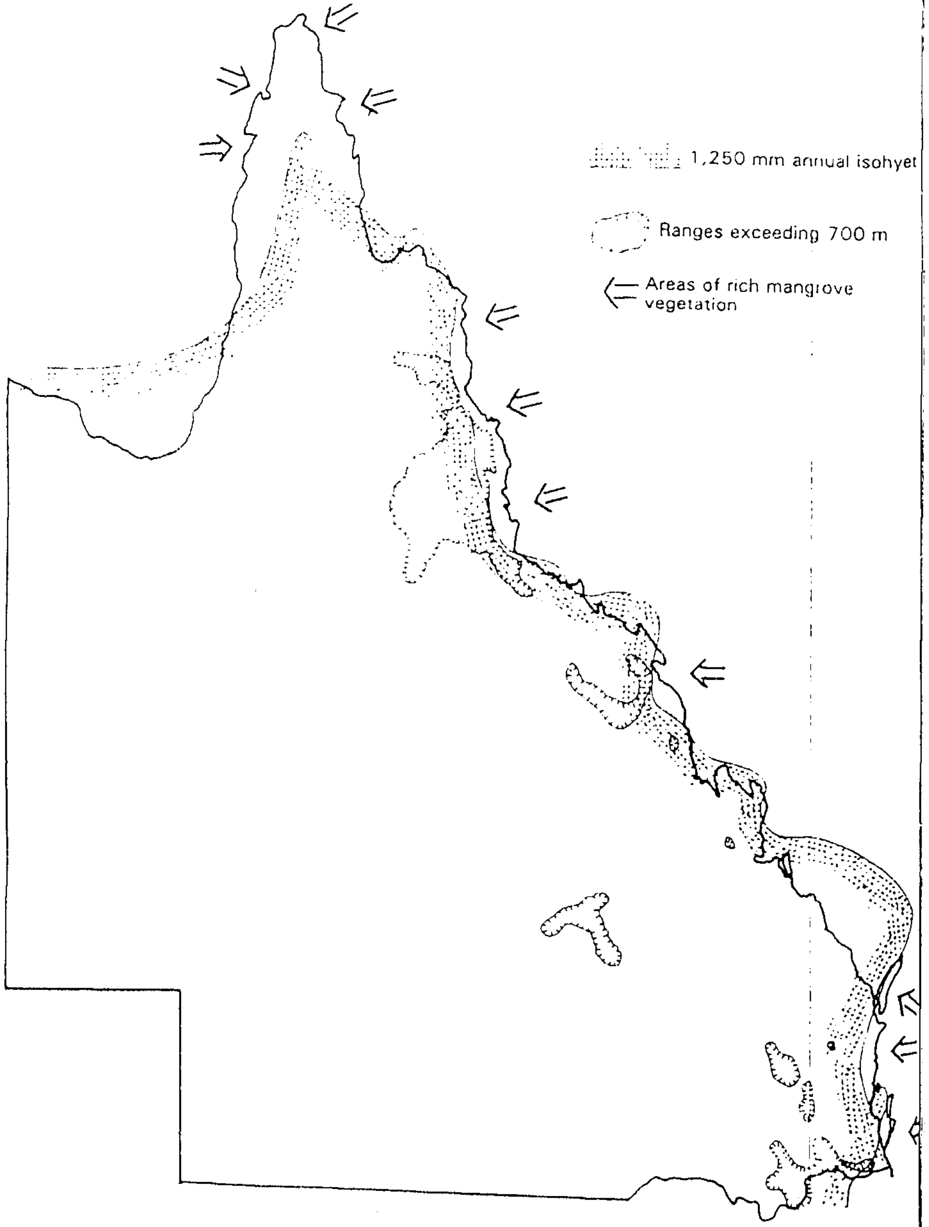


Figure 5 Relationship along the Queensland coastline between areas of rich mangrove vegetation and the 1,250 mm annual isohyet and mountain ranges exceeding 700 m in height.

temperatures as well as the predominance of winter rainfall effectively limit the southward extension of many species, reducing the southern mangrove flora to a solitary species (*Avicennia marina*) which survives as relict populations in disjunct pockets (for example, Abrolhos Islands in Western Australia, Ceduna and Spencer and St Vincent Gulfs in South Australia, and Barwon Heads, Port Phillip Bay, Westernport Bay and Corner Inlet in Victoria). In these localities, *Avicennia* grows in areas where the daily mean minimum temperatures drop to 4°C and 7°C in July (Melbourne and Adelaide respectively), and where minima of 0°C have been recorded (Macnae 1966). These data suggest that, once established, *Avicennia* can withstand low but not sub-zero temperatures. The experimental work of McMillan (1975) showed that these southern populations are hardier than more northerly populations in relation to low temperatures, even though their growth may be somewhat stunted. In southern Africa, where other factors appear to be similar, *Avicennia* occurs only in areas where the mean air temperature does not drop below 13°C (Macnae 1963).

Macnae (1966) suggested two explanations for the present-day distribution of the southerly mangrove populations: (1) transmission by ocean currents and (2) persistence of relicts of previously warmer seas. He preferred the latter explanation. From the work of Ludbrook (1963) and others, it is clear that during the Tertiary (including the Pliocene) the seas around southern Australia were warmer than they are today. The occurrence of other mangrove fossils from the late Eocene in southwestern Australia (Churchill 1973) suggests that the present-day mangrove vegetation on the southern Australian coastline is a relict from these earlier, warmer conditions which has managed to maintain itself in a few favourable localities.

2. Adaptations of Mangroves

The mangrove environment is a variable one owing to a combination of periodic fluctuations and extremes in physico-chemical parameters. Despite such variability, however, the mangrove flora has successfully colonized this environment, apparently aided by the development of numerous morphological, reproductive and physiological adaptations (Macnae 1968; Saenger 1982; Clough, Andrews and Cowan 1982). Many of these adaptations are inferred; that is, adaptations of mangrove species have generally been identified simply by comparing the characteristics of mangroves with those of species from non-mangrove environments. Experimental investigation of the efficiency of many of these adaptations remains to be carried out.

Coping with High Salt Concentrations

The abundance of salt is the single most important characteristic of the mangrove environment, and most mangroves absorb some sodium and chloride ions. Sea water, containing about 35 grams of dissolved salts per litre, has an osmotic potential of approximately -2.5 MPa, and the soil water may have an even lower (more negative) one. The fact that mangroves are able to grow in such highly saline substrates and even grow better in the presence of some salt (Connor 1969; Downton 1982) suggests that they are able to control the intake of salt and maintain a water balance which is physiologically acceptable. Although these processes are understood in general terms, reliable data are lacking on many details.

Jennings (1968) reviewed the mechanisms whereby mangroves deal with excess environmental salt. It appears that three are operative: (1) they take up highly saline water and then secrete the salt (extrusion); (2) they take up water but prevent the entry of salt (exclusion); or (3) they develop tolerance to high salt loads and allow salt to accumulate in the tissues (accumulation). Scholander et al. (1962) classified mangroves functionally into "salt-secretors" and "salt-excluders", although the various mechanisms of dealing with salt are not mutually exclusive. Some species emphasize one, others emphasize another.

Salt Secretion

Salt secretion occurs by means of salt glands (figure 6) in the leaves of *Avicennia* (Baylis 1940), *Sonneratia* (Walter and Steiner 1936), *Aegiceras* (Cardale and Field 1971), *Aegialitis* (Atkinson et al. 1967), *Acanthus* (Mullan 1931) and *Laguncularia* (Biebl and Kinzel 1965), and possibly via cork warts in the leaves of *Rhizophora* (Baijnath and Charles 1980).

Ultrastructural studies of the glands of *Aegiceras* (Cardale and Field 1971; Bostrom and Field 1973) have shown that they consist

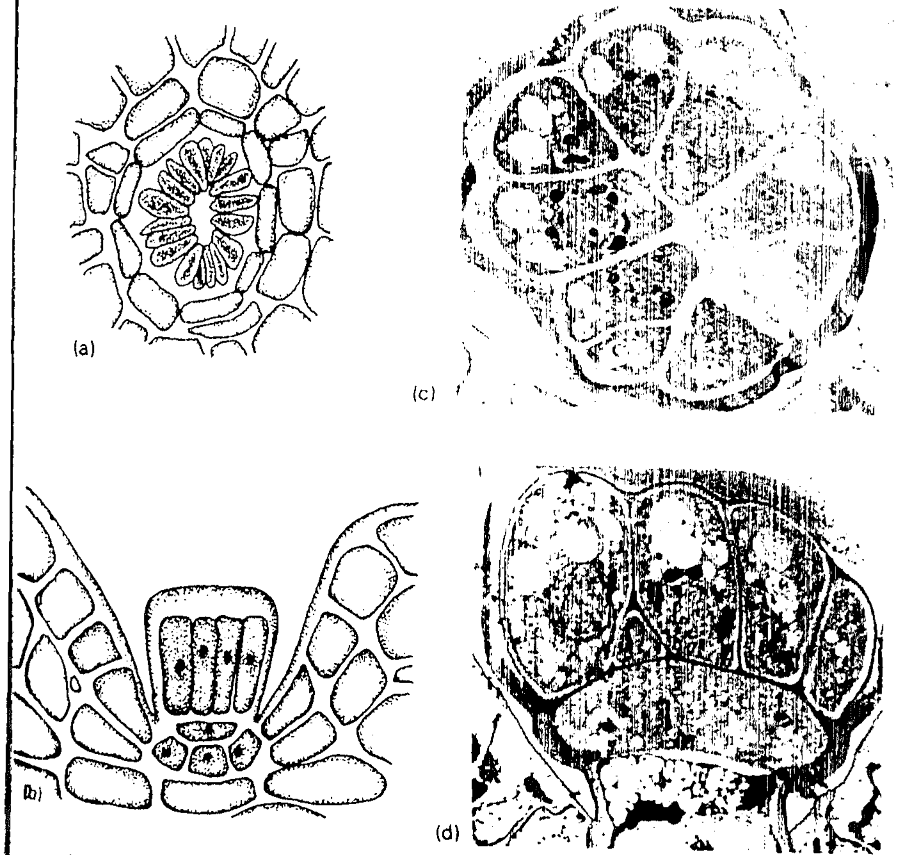


Figure 6 Salt glands in mangroves: (a) salt glands from leaves of *Aegiceras corniculatum* seen in dorsal view (mag. x 1,000); (b) salt glands of *Avicennia marina* on the upper leaf surface seen in transverse section (mag. x 1,000); (c) salt glands of *Acanthus ilicifolius* seen in transverse section (mag. x 5,000); (d) salt glands of *Acanthus ilicifolius* in transverse view (mag. x 5,000). (Figures (c) and (d) courtesy of J.E. Ong and C.H. Wong)

of 24-40 secretory cells situated over a single large, basal cell. The secretory cells are densely packed with mitochondria and other organelles, suggesting some metabolically active function. The living contents of the basal cell and the secretory cells are linked by fine cytoplasmic threads (plasmodesmata) that pass through the cell walls. On the other hand, the junction between the basal cell and the sub-basal cells, which form a layer above the palisade mesophyll, seems to be partially cutinized. Field, Hinwood and Stevenson (1984) showed, however, that there is a small slit-like opening between the cuticle of the gland and that of the leaf; it is through this slit that salt secretion occurs. The mesophyll cells contain two types of vacuoles: one type contains large amounts of an organic solute and little or no chloride whereas the other is free of organic solute but rich in chloride (Van Steveninck et al. 1976). The fluxes of Na^+, K^+ and Cl^- have been measured using radioisotopes (Cardale and Field 1975), and all of these ions are actively transported out of the parenchyma by the gland cells.

The salt glands of *Acanthus* appear to have a similar ultrastructure; the vacuoles appear to contain a fine precipitate, but nearer the epidermis this seems to be replaced by round, dark vesicles (Wong and Ong 1984). It seems likely that these two vacuolar inclusions correspond to the two types of vacuoles found in *Aegiceras* by Van Steveninck et al. (1976).

Glycinebetaine, an organic solute involved in balancing total leaf osmotic potential, has been detected in the leaves of *Avicennia marina* (Wyn Jones and Storey 1981); similar compounds also have been reported from other mangroves with salt glands. Choline-O-sulphate, another organic osmo-compensator, has been reported from *Avicennia* and *Aegialtis* and choline-O-phosphate is present in large amounts in *Aegiceras* and *Acanthus* (Benson and Atkinson 1967).

A mechanism similar to that of *Aegiceras* seems to operate in *Aegialitis annulata*; the flow-path of salt was traced using ^{36}Cl, and it was found to pass directly from the leaf veins via the palisade mesophyll to the salt glands (Atkinson et al. 1967). The mechanism of the salt pump in the salt glands is still unknown (Clough, Andrews and Cowan 1982).

In *Avicennia*, salt glands are formed only under saline conditions (Mullan 1931; Macnae 1968), whereas in *Aegiceras* they appear to be formed whether or not salt is present in the medium (Cardale and Field 1971). They are entirely absent from *Acanthus* grown in fresh water (Mullan 1931). Joshi et al. (1975) concluded that among salt-secreting species *Avicennia* is the most efficient, and consequently is able to grow in highly saline conditions, whereas the less efficient *Acanthus* and *Aegiceras* are restricted to less salty habitats.

Loetschert and Liemann (1967) found that changes in the contents of Cl, Na, K, Ca and N in *Rhizophora mangle* seedlings indicated that there is a barrier between the cotyledonary body and the peripheral tissues. The outer layer of the cotyledonary body consists of small, nearly spherical cells which according to Pannier (1962) are characterized by an increased phosphatase activity, a condition generally indicative of secretory tissues. Loetschert and Liemann (1967) concluded that the reduced salt uptake by seedlings of *R. mangle* is accomplished by the activity of this glandular tissue. Similar glandular tissue is present on the outside of the cotyledonary body in the Australian *Rhizophora stylosa* (Saenger 1982), and may be identical to the papillose layer described from *R. stylosa* and *Ceriops tagal* by Carey (1934). Highly vacuolated, metabolically active cells also have been described from the outer cotyledons of the propagules of *Avicennia marina* (Butler and Steinke 1976); these cells may have a similar regulatory role.

Salt Exclusion

Salt-excluders possess an effective mechanism, presumably an ultra-filter in the roots (Rains and Epstein 1967; Scholander 1968), whereby water is taken up and salt is largely excluded. Species found to be able to exclude salt are *Rhizophora*, *Ceriops*, *Sonneratia*, *Avicennia*, *Osbornia*, *Bruguiera*, *Excoecaria*, *Aegiceras*, *Aegialitis* and *Acrostichum*. Measurements of the osmotic potential of xylem sap in species which lack salt glands gave values of less than -0.2 MPa (Scholander et al. 1962), indicating that the concentration of soluble salts in the xylem is close to that of many plants from non-saline environments. The osmotic potential of xylem sap in salt-secreting species appears to range from -0.4 to -0.7 MPa (Scholander et al. 1966), showing that they are somewhat less efficient in excluding salt than those species without salt glands. However, Downton (1982) has shown that the osmotic potential of *Avicennia marina* is correlated with the salinity of the growth medium, ranging from -1.6 MPa at zero salinity to -3.6 MPa at full sea water. Nevertheless, salt-secreting species apparently still exclude 80–90 per cent of the salt in sea water (Scholander 1968), although the physical and biochemical basis for this is still poorly understood (Field 1984). Scholander (1968) found that neither chilling nor metabolic inhibitors caused any change in the capacity of the roots to exclude salt, and he concluded that the process was simply a passive function of the differential permeability of membranes in the root.This was supported by the absence of any obvious diurnal variation in the salt concentration of the xylem sap (Scholander et al. 1966), which suggests that the flux of salt into the root is tied closely to water uptake.

Salt Accumulation

Salt-accumulating mangroves (*Excoecaria*, *Lumnitzera*, *Avicennia*, *Osbornia*, *Rhizophora*, *Sonneratia* and *Xylocarpus*) often deposit sodium and chloride in the bark of stems and roots and in older leaves (Atkinson et al. 1967; Joshi, Jamale and Bhosale 1975; Clough and Attiwill 1975). Leaf storage of salt is generally accompanied by succulence (Jennings 1968). Joshi, Jamale and Bhosale (1975) have shown that prior to leaf fall in *Sonneratia*, *Excoecaria* and *Lumnitzera*, sodium and chloride are deposited in senescent leaves. In this way, excess salt is removed from metabolic tissue. For deciduous species such as *Xylocarpus* and *Excoecaria*, annual leaf fall may be a mechanism for the removal of excess salt prior to the onset of a new growing and fruiting season (Saenger 1982).

The movement of salt into viviparous and cryptoviviparous seedlings while still attached to the parent tree appears to be regulated in *Rhizophora*, *Ceriops*, *Bruguiera*, *Aegiceras*, *Avicennia* and *Acanthus* (Chapman 1944; Loetschert and Liemann 1967; Joshi, Jamale and Bhosale 1975). Seedlings taken from *Avicennia marina* growing on tidal mudflats had osmotic potentials more negative than sea water, yet they contained little sodium or chloride (Downton 1982). It appears that while still attached to the tree, seedlings can control the uptake of sodium and chloride, and adjust osmotically by the accumulation of organic rather than inorganic solutes (Downton 1982), but after falling they rapidly increase their salt content until their root system is capable of ultra-filtering sea water (Chapman 1944; Field 1984).

Although it is clear that the internal salt concentration in mangroves must be maintained if turgor potential is to be constant, the metabolic effects of salt are inadequately known.

Salt may influence the functioning of metabolic enzymes and therefore affect such vital processes as respiration, photosynthesis and protein synthesis. For example, Joshi et al. (1974) and Joshi, Jamale and Bhosale (1975) suggested that high salt concentrations in the cell inhibit ribulose diphosphate carboxylase, an enzyme of the carboxylation process. In addition, activity of the enzyme malic dehydrogenase was significantly lower in mangroves than in other plants, and this was attributed to salt inhibition and/or the unavailability of calcium to the metabolic tissues. Through the use of radioactive CO_2, Joshi et al. (1975) were able to show a rapid (one-hour) build-up of amino acids which was consistent with the inhibition of ribulose diphosphate carboxylase and malic dehydrogenase.

The high content of amino acids and their presence as initial products of photosynthesis suggest a large pool of readily available nitrogen in the leaf (Joshi et al. 1975). It has been known for some time that plants from saline soils have higher carbohydrate and nitrogen contents than plants from non-saline soils and that amino acids accumulate in their tissues (Udovenko and M'Inko 1966; Strogonov et al. 1970). Other experimental work showed that a disturbance of protein synthesis could be related to substrate salt levels (Kahane and Poljakoff-Mayber 1968; Hall and Flowers 1973).

Mizrachi, Pannier and Pannier (1980) tested the response of seedlings of *Avicennia germinans* (as *A. nitida*) and *Rhizophora mangle* to different salt concentrations and simultaneously determined the chloride and nitrogen content (total N, protein N and amino N) and the rate of uptake of the labelled amino acid, leucine, in both leaves and roots. The two species responded differently in some respects, but both showed a reduction in leucine uptake with increasing soil salinity, indicating reduction in protein synthesis. In *R. mangle* the amino N increased with increasing salinity, whereas in *A. marina* there was an initial increase to a salinity of 9.6 ‰ followed by a rapid decline. Amino N accumulated at all salt concentrations in the roots of both species.

These effects of salt on enzyme activity suggest that the enzymes of mangroves and saltmarsh plants do not differ from those of other plants; the enzymes probably would not function if they were directly in contact with the salt levels implied by the overall salt content of the plant. How are enzymes kept out of contact with unfavourable salt levels? One possibility is that most of the salt is contained in the vacuole and that in the cytoplasm, where enzymes are located, low concentrations of salt are maintained. However, the water potential of the cytoplasm and the vacuole must be balanced. Consequently, if partitioning of salt actually occurs, other solutes which do not adversely affect enzyme function must be in the cytoplasm at concentrations sufficient to achieve a water potential equal to that of the vacuole. Several organic compounds have been found in various halophytes which appear to function as such cytoplasmic osmoregulators. For example, glycinebetaine, a quarternary ammonium compound, has been detected in the leaves of *Avicennia marina* (Wyn Jones and Storey 1981), and Downton (1982) has calculated that if this compound occupies a cytoplasmic volume of 5–10 per cent of the cell, then its reported concentration is sufficient to balance total leaf osmotic potential. This would be consistent with the current view that halophytes successfully compartmentalize inorganic ions in a way that salt-sensitive species do not, utilizing ions from the environment to maintain vacuolar osmotic potential lower than that of the external solution, while protecting the salt-sensitive cytoplasm from dehydration and ion excess by the substitution of compatible organic solutes (Downton 1982).

Other compounds with osmoregulatory properties found in various halophytes include choline-O-sulphate, choline-O-phosphate, the amino acid proline and the sugar alcohol sorbitol. The amino N accumulation reported with increasing salt concentrations in *Avicennia germinans* and *Rhizophora mangle* (Mizrachi, Pannier and Pannier 1980) suggests that proline may be involved in these species.

Recently, studies on chloroplasts isolated from *Avicennia marina* showed that they have different and unusual properties compared with chloroplasts from species that are not tolerant of salt (Critchley 1982). The *Avicennia* chloroplasts were found to require chloride for maximal production of oxygen during photosynthesis. Similar requirements were also found in *Avicennia germinans* (Critchley et al. 1982) and in two saltmarsh species (Critchley et al. 1982; Critchley 1983), and it was suggested that these halophytes might preferentially accumulate chloride in the chloroplasts.

It should be apparent from the above discussion that, although the generally adverse effects of salt on whole plants are well documented, the metabolic basis for these effects are still speculative: nitrogen metabolism, protein synthesis, carboxylation enzyme inhibition and stimulation of photosynthetic oxygen production all appear to be involved.

Conserving Desalinated Water

The mangrove environment has frequently been described as "physiologically dry" or "physiologically arid", and this apparent contradiction must be clarified. Clearly, most mangroves have an abundant supply of water around them at all times. However, because this water is saline compared with the internal sap concentration of the mangrove, it must be taken up against an osmotic gradient. An energy cost is coupled to this process, and the real availability to the plant of water of reduced salinity is determined by the amount of metabolic energy the plant can make available for desalination. In other words, it is the high physiological cost of this water that underlies the physiological dryness of the mangrove environment.

Having obtained desalinated water at considerable cost, many mangroves display features, generally associated with plants of arid environments, which tend to conserve or retain that water; these are referred to as xeromorphic features.

Xeromorphic Features

Leaves of most mangroves exhibit a range of xeromorphic features, that is, features normally associated with plants from arid or semi-arid regions (Stace 1966), although this is disputed by some (for example Uphof 1941), and there are few experimental studies in support of the water-conserving function of such leaf characteristics (Miller, Hom and Poole 1975). The major xeromorphic features are discussed below.

All species of mangroves have a thick-walled epidermis which, at least on the upper leaf surface, is covered by a thick waxy cuticle that would seem to retard evaporative loss, or by a layer of variously shaped hairs (*Avicennia*, *Hibiscus tiliaceus*) or scales (*Heritiera*, *Camptostemon*) (figure 7). These usually cover salt glands and stomata (when present) and, presumably, reduce water loss via these apertures.

Stomata are minute pores in the leaf that can open or close. They permit the passage of gases into and out of the leaf, and it is through these that much evaporative loss occurs. With a few exceptions, stomata are restricted to the lower leaf epidermis. In terms of frequency and dimension, mangrove stomata are similar to those of plants of other habitats but many species show stomata sunk beneath the level of the epidermis — for example, *Avicennia*, *Aegiceras*, *Bruguiera*, *Ceriops*, *Lumnitzera* and *Rhizophora*. Substomatal chambers are present in *Avicennia*, *Ceriops* and *Rhizophora* (Sidhu 1975b).

Three types of stomata have been reported from mangroves, but Sidhu (1975b) was unable to attach any ecological significance to them. The stomata of mangroves show considerable variation in behaviour; Joshi et al. (1975) reported that in a number of Indian species the stomata are wide open between 4 a.m. and 10 a.m., closed in the early afternoon, and again slightly open in the evening. On the other hand, photosynthetic studies with *Avicennia* and *Rhizophora* in Australia have shown the stomata to remain open throughout the day (Attiwill and Clough 1980; Clough, Andrews and Cowan 1982). It is possible that high temperature also affects stomatal behaviour which, in turn, is reflected in transpiration rates (Lewis and Naidoo 1970; Lugo et al. 1975; Steinke 1979).

Both Stace (1966) and Sidhu (1975b) concluded that the presence of a thick cuticle, wax coatings, sunken stomata and the distribution of cutinized and sclerenchymatous cells throughout the leaf, including the epidermis, are xeric characters which probably developed in response to the physiological dryness of the mangrove environment.

Succulence, or storage of water in fleshy tissue, is a xeromorphic feature common in mangrove leaves. Based on studies of *Rhizophora* (Bowman 1921) and *Sonneratia* (Walter and Steiner 1936) growing in saline and freshwater conditions, it appears that succulence is a response to the presence of chloride. Anatomical

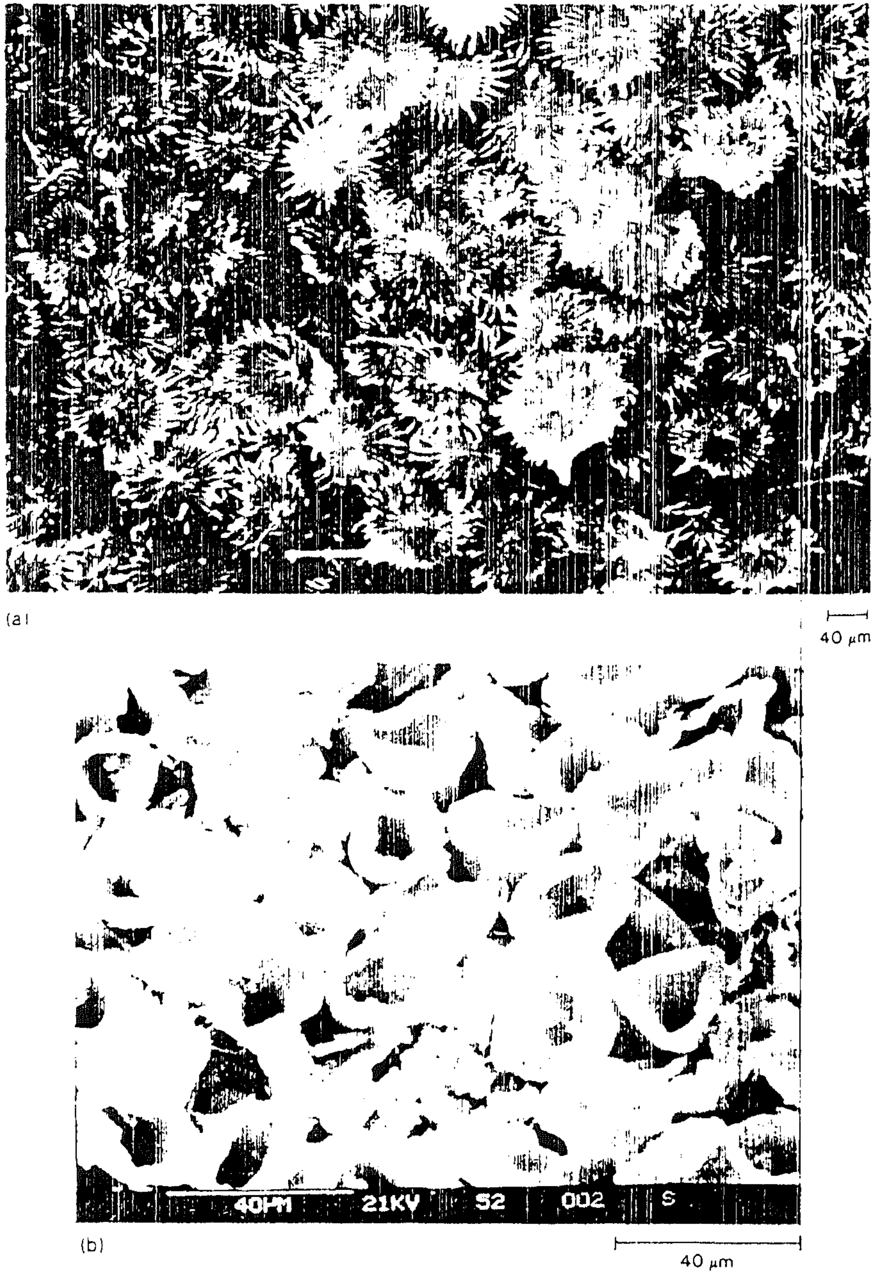


Figure 7 Leaf hairs and scales in mangroves: (a) scales on the underside of leaves of *Heritiera littoralis* (scale bar given); (b) glandular hairs on the underside of leaves of *Avicennia marina* (scale bar given).

factors contributing to succulence in leaves include the presence of a well-developed, large-celled, water-storing hypodermis, a strongly developed palisade mesophyll and generally small intercellular volumes. With the exception of *Ceriops*, those species with isobilateral leaves (upper and lower sides of the leaf the same) do not possess a hypodermis (Saenger 1982), but in several of these, large undifferentiated mesophyll cells form a central water-storing tissue (figure 8). Spongy mesophyll is absent from species with

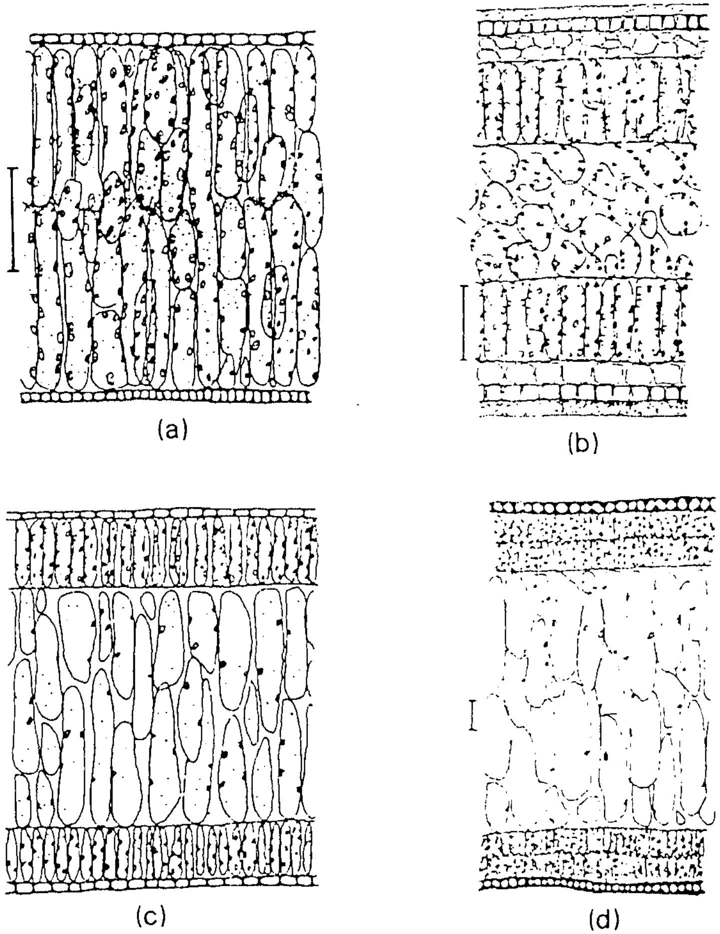


Figure 8 Transverse sections of leaves of Australian mangroves with isobilateral leaves (bar scale is μm in all sections): (a) *Aegialitis annulata*; (b) *Ceriops tagal* – note upper and lower hypodermis and enlarged spongy mesophyll; (c) the mangrove mistletoe *Amyema mackayense*; (d) *Sonneratia caseolaris*, *Lumnitzera racemosa* and *Osbornia octodonta* – note that all these species have enlarged water-storing cells.

isobilateral leaves with the exception of *Ceriops*, and it generally forms less than 40 per cent of the cross-sectional area of those species with dorsiventral leaves.

In several species, including *Avicennia*, *Bruguiera* and *Ceriops*, the ends of the vascular bundles (tissue conducting water and solutes throughout the plants) are surrounded by irregular groups of tracheid cells which are much larger than the conducting elements. Their walls bear spiral, reticulated or pitted thickenings and, since they possess a flange-like connection to the hypodermis, a water-storage function has been attributed to them (Baylis 1940). In addition to these storage tracheids, various other anatomical structures have been reported from the leaves of some species. For instance, stone cells have been reported from *Avicennia*, *Rhizophora*, *Sonneratia* and *Xylocarpus*, sclereids from *Rhizophora*, *Scyphiphora* and *Bruguiera* and mucilage cells from *Sonneratia* and *Rhizophora*. These cells undoubtedly give toughness and rigidity to the leaf, reduce damage from wilting and may be involved in conserving water (Malaviya 1963).

The anatomy of the wood of some mangroves also appears to be related to the physiological dryness of the environment. According to Janssonius (1950), mangroves possess more vessels per square millimetre, with a larger total cross-sectional area, and distinctly smaller pores than do their nearest inland relatives. Such wood modifications have been postulated to be related to resistance to water movement in the conducting tissue (Jansonnius 1950) or to reduced likelihood of rupturing the water column in narrow vessels (Reinders-Gouwentak 1953). In the Rhizophoraceae, the pitting and the perforation plates of the vessels also are modified (Marco 1935; Carlquist 1975); the latter author noted that the perforation plate arrangement seems "ideal to resist collapse in vessels under tension".

Transpiration

As indicated above, many mangroves show xeromorphic characteristics which generally are regarded as being involved in conserving water. Hence, it is not surprising that the transpiration rates of mangroves are low when compared with the rates of non-saline plants (Gessner 1967; Lugo et al. 1975; Moore et al. 1982).

At several different localities, transpiration in *Avicennia marina* reached a mid-morning maximum at approximately 10 o'clock, after which there was a steady decrease (Lewis and Naidoo 1970; Leshem and Levison 1972; Steinke 1979; Attiwill and Clough 1980). The afternoon decrease in transpiration was not influenced by tidal inundation, and it is assumed that the water potential gradient was so steep that the consequent high rate of transpiration induced an internal water deficit which resulted in the closure of the stomata (Steinke 1979). Once the stomata were closed, the continuing high temperatures prevented stomatal reopening, even when water was freely available (Steinke 1979). Attiwill and Clough (1980), however, found that in a temperate population of *Avicennia* in Westernport Bay, Victoria, there was no change in water stress during the day, even on days of sustained sunlight.

Scholander et al. (1962, 1965) suggested that rates of water loss in mangroves are related to salinity adaptations. Those plants that grow in highly saline situations tend to transpire less than those growing in less saline conditions. This is partly due to the fact that the water is supplied to the leaf at a considerable negative hydrostatic pressure potential, and the demand for water, in terms of the vapour pressure difference at the leaf and air interface, often can be high. In addition, maintenance of the osmotic potential of the xylem sap (although considerably higher than the hydrostatic pressure potential) has a high energy cost because water is taken up against an osmotic gradient. Finally, Gessner (1967) suggested that since the xylem sap of mangroves contains salt, a high transpiration rate would rapidly concentrate salt in the leaf with consequent deleterious effects.

Scholander at al. (1965) discussed some of the physiological cost of these adaptations and indicated that there is a limit to the amount of water a plant can effectively take up and transport against the osmotic gradient of its environment; this limit is reflected in lower transpiration and higher respiration rates.

Energy diverted to the uptake of water or the production of water-conserving structures such as hairs, waxy cuticles and scales is clearly not available for growth and reproduction. Consequently, a number of strategies have developed in relation to this energy cost. In some species, the energy expenditure is reduced (1) by growing in less saline conditions, (2) by reduction of transpirational water loss, or (3) by growing in bursts when fresh water is available and "marking time" during other periods. Other species have increased the efficiency of energy production by such means as leaf orientation and a large photosynthetic surface area.

Even with these strategies in highly saline situations the net productivity is decreased and dwarfing or stunting may occur. Dwarfed mangrove systems apparently use a larger portion of their energy supply for respiration and low-loss recycling mechanisms, and a correspondingly smaller proportion for growth (Lugo et al. 1975).

Root Specializations

Two of the problems affecting mangroves are waterlogged soils that are low in oxygen (anaerobic) and a semi-fluid substrate that provides little mechanical support. The root systems of many species display adaptations which aid in overcoming these problems.

Below the surface, most mangroves possess a laterally spreading cable root system with smaller, vertically descending anchor roots; the latter bear fine nutritive roots. The root system is shallow, generally less than 2 metres deep; tap roots have not been observed. Despite such shallow root systems, the ratio of below- to above-ground biomass is higher for mangroves than for other vegetation types (Saenger 1982), particularly during early developmental stages. This high biomass ratio may be an adaptation to unstable substrate conditions.

Some species do not possess a specialized root system (such as *Aegialitis*, *Excoecaria*) and their roots lie near or on the substrate surface. Since in these species only relatively small surface areas are available for the assimilation of oxygen, they tend to be found on less waterlogged soils (*Excoecaria*) or on coarser, more aerobic sediments (*Aegialitis*). However, *Nypa*, the mangrove palm, grows from an underground rhizome and yet has no specialized aerial root system; it is found in areas of frequent inundation and may occur on waterlogged soils (Tomlinson 1971).

There is an array of above-ground root types displayed by mangroves (figure 9). These include: (1) Pneumatophores — roots arising from the cable root system (for example, *Avicennia*, *Xylocarpus* and *Sonneratia*) and extending upward into the air as small conical projections; (2) Knee-roots — modified sections of the cable root which first grow upward above the substrate and then downward again (for example, *Bruguiera*); (3) Stilt roots — generally branched roots that arise from the trunk and grow into the substrate (*Rhizophora*, *Ceriops*); (4) Buttress roots — similar to stilt roots in origin but expanding into flattened, blade-like structures (*Heritiera*); (5) Aerial roots — generally unbranched roots arising from the trunk or lower branches and descending downward but usually not reaching the substrate (for example, *Rhizophora*, *Avicennia* and *Acanthus*). Most mangrove genera have one or more of these types (see table 2).

Evidence that these root structures are adaptations providing aeration for subterranean roots and which physically anchor the plant comes from a variety of sources. The most apparent is that those mangroves growing at lower tide levels and which are, consequently, more frequently inundated tend to possess the greatest array of above-ground root types. The presence of aerenchymatous tissue and numerous lenticels in most above-ground roots provides further supporting evidence. The mechanism of air uptake, through the development of a negative gas pressure, has been investigated by Scholander, Van Dam and Scholander (1955) in

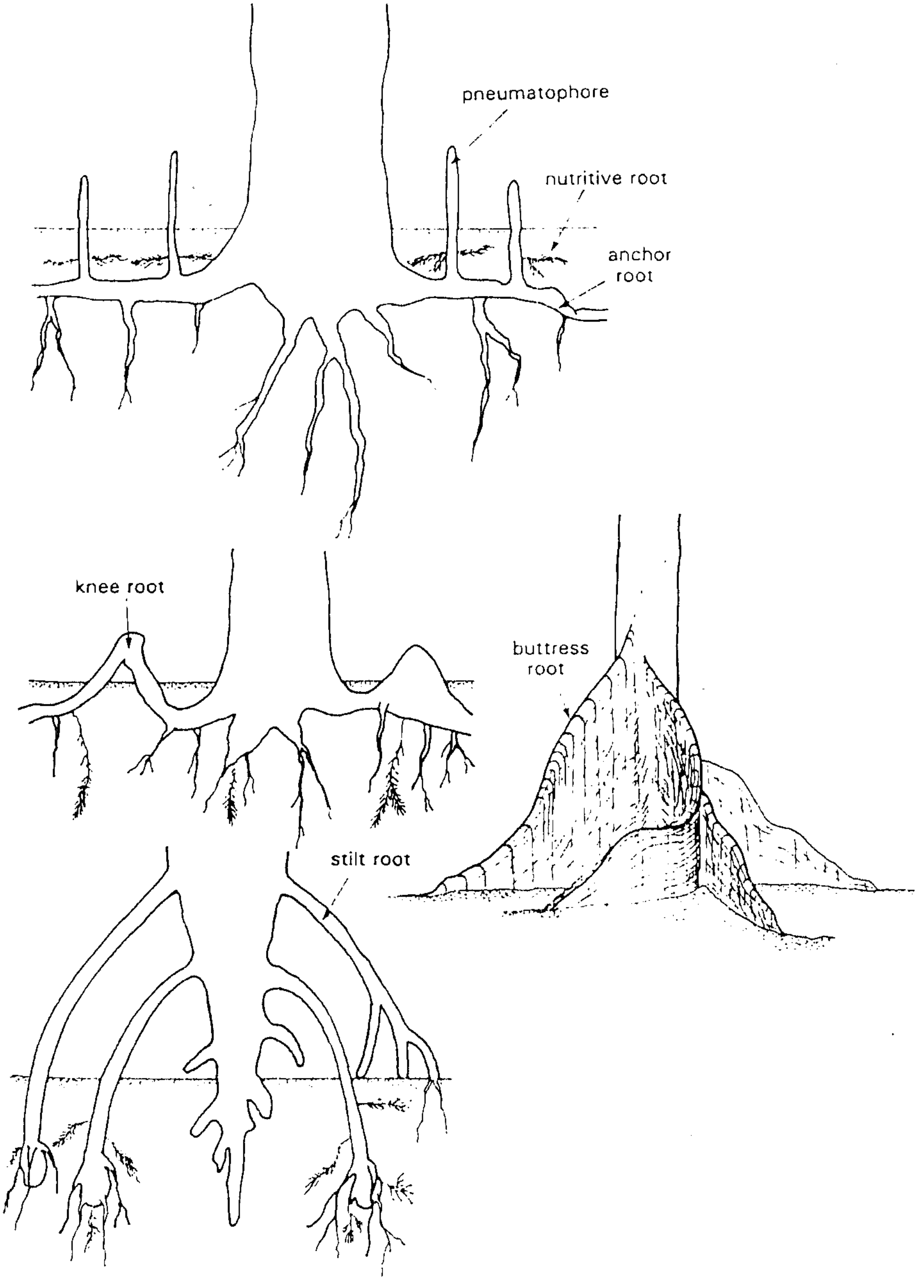


Figure 9 Major morphological root types found in mangroves.

Table 2 Occurrence of different root types in Australian mangroves (+ Present; + / - Present in some species; in monotypic genera sometimes present)

Genus	Surface cable roots	Pneumato-phores	Knee roots	Stilt roots	Buttress roots	Aerial roots
Acanthus	+			+		+
Aegialitis	+					
Aegiceras	+					
Avicennia		+	+ / -			+
Bruguiera		+ / -	+	+ / -	+ / -	+ / -
Camptostemon		+			+	
Ceriops			+	+	+	
Cynometra					+ / -	
Excoecaria	+					
Heritiera					+	
Lumnitzera		+ / -	+	+ / -		
Nypa	+ ?					
Osbornia	+	+ / -				
Rhizophora				+		+
Scyphiphora	+ ?					
Sonneratia	+ / -	+ / -			+ / -	
Xylocarpus	+ / -	+			+	

Rhizophora mangle and *Avicennia germinans*. Mangroves presumably rely on this mechanism only in situations where poor soil aeration occurs, for Gessner (1967) showed that for *Avicennia germinans* (as *A. nitida*) growing on coarse coral sand, presumably with reasonable drainage and aeration, the experimental removal of pneumatophores had no effect on the trees. On the other hand, in situations where soil aeration is poor, continued covering of the above-ground roots either by water or by flood-deposited sediments will cause widespread mortality (Breen and Hill 1969; Hegerl 1975) and a rapid degradation of root tissue (Albright 1976). Snedaker, Jimenez and Brown (1981) described the development of aerial roots in *Avicennia* in response to stresses which limit the normal functioning of pneumatophores — in this case an oil spill which coated the pneumatophores.

More direct evidence of the aerating function of stilt roots in *Rhizophora* was obtained by Canoy (1975), who noted an increase in the number of stilt roots produced per square metre with increased temperature (and consequently reduced dissolved oxygen concentrations) in a thermally polluted environment.

Under quiet sedimentary conditions, mud may accumulate at a rate of up to 1.5 cm per year (Bird 1971, 1973), and the root system must be able to respond in ways that continue to provide aeration for the roots. Pneumatophores that grow upwards into the air are an adaptation found in *Avicennia*, *Xylocarpus australasicus* and *Sonneratia*. Other species cope with sediment accumulation by forming extra arches of the stilt roots, additional knee roots or the upward secondary thickening of roots or buttresses.

In exposed situations where sediments are removed by erosion and do not accumulate, the problem is reversed and plants must remain firmly anchored in order to survive. Massive development of the various above-ground roots may serve to reduce water movement around the plant, and an extensive cable root system, as in *Avicennia* and *Osbornia* for example, may effectively anchor the plant despite its shallowness. Thom, Wright and Coleman (1975) described the successful colonization of tidal sand flats in the Joseph Bonaparte Gulf, Western Australia, by *Avicennia* despite rigorous conditions imposed by the passage of long-period waves.

The effect of water movement and inundation on above-ground root development in the Japanese mangrove, *Kandelia candel*, was described by Hosokawa, Tagawa and Chapman (1977). In this species of the Rhizophoraceae, the basal part of the stem is buttress-like on plants near creeks with flowing water, but in comparatively still water typical stilt roots are formed.

The anatomical changes occurring in the aerial and stilt roots of *Rhizophora* upon penetrating the substrate have been described by Bowman (1921), Gill and Tomlinson (1971, 1975, 1977) and Karsted and Parameswaran (1976); the external colour of the root changes from tan to white as the thin surface layers lose their chlorophyll, thickened walls are no longer formed and the ground parenchyma contains many gas-filled spaces. The aerial root has approximately 5 per cent gas space before penetration into the substrate compared with about 50 per cent after penetration.

Lenticels are common in the periderm of the stems and roots of most mangroves (Chapman 1947; Roth 1965; Lugo and Snedaker 1975). Outwardly, a lenticel often appears as a vertically or horizontally elongated mass of loose cells that protrudes above the surface through a fissure in the periderm. The dimensions and frequency of lenticels vary between species and with height above the water surface. Baker (1915) described the lenticels occurring on the pneumatophores and stems of *Avicennia marina* as "raised black spots scattered over the surface . . . a section showing these layers of cells to be raised over what is a vacant cavity or air space in direct communication with the ventilating system", and he concluded that they may be secondary organs of ventilation. On the stems, lenticels in this species were noted up to 3 metres above high-water mark.

Little information is available about the physiology and metabolism of mangrove roots (Clough, Andrews and Cowan 1982), and the following comments are highly speculative. The most important aspects requiring investigation are the metabolic adaptations of the root to waterlogging and oxygen deficiency on the one hand and to salt exclusion on the other.

Waterlogging and the accompanying anaerobic conditions in the soil are often associated with the development of aerenchyma (loose tissue containing many air spaces). Such tissue may serve either as an oxygen reservoir, or as a system which allows the maximum volume of root or rhizome per quantity of living tissue, thereby achieving an economy in oxygen consumption per unit volume. However, the facilitation of gaseous diffusion by morphological adaptation is not an entirely satisfactory explanation of waterlogging tolerance in mangroves, and the possible role of metabolic adaptations to anaerobic conditions must be considered.

Experiments with species other than mangroves during waterlogging have demonstrated a range of metabolic responses to anaerobic conditions. These studies suggest that under anaerobic conditions malic acid is more important than ethanol as an end product, that malic, shikimic and quinic acids accumulate in the roots and rhizomes and that succinic acid is a common product of anaerobic respiration. Crawford and Tyler (1969) examined organic acid accumulation in a selection of species ranging from tolerant to intolerant of waterlogging, and found that there was an immediate change in organic acid metabolism with the advent of flooding. Malic acid accumulated in those species tolerant of waterlogging but fell in those species that were intolerant. Species intolerant of waterlogging showed increases in succinic acid and to a lesser extent in lactic acid.

The significance of malic acid accumulation is threefold. First, malic acid, like other organic acids, can accumulate in plant cells in considerable quantities without injury to the plant, and in this respect differs considerably from ethanol. Second, malic acid is an alternative product to ethanol in anaerobic respiration in plants and it can subsequently be metabolized on the return of aerobic conditions. Third, in cation absorption, malic acid accumulates in greatest quantity and thus preserves the electrical neutrality of the cell.

Whether the malic acid respiratory pathway exists in mangroves as it does in other species tolerant to waterlogging is not presently known. If, however, respiration is involved in the salt-excluding mechanism, either directly in providing energy for the process or indirectly in the synthesis and maintenance of a salt-excluding membrane, the respiratory requirements of the roots of mangroves may be higher than those of non-mangrove plants (Clough, Andrews and Cowan 1982). Under such circumstances, the ability to switch to a non-damaging anaerobic respiratory pathway while waterlogged would clearly provide a significant benefit to the plant. If that pathway could, at the same time, assist in the maintenance of ionic neutrality in the root cells, it would seem to be a very important adaptation. Clearly, this is an aspect of the physiology of mangroves which may reward investigation.

Responses to Light

Light and Form

Wylie (1949) found that leaves developing in high light intensity show a higher degree of xeromorphy than those protected from it. Consequently, it is possible that some of the xeromorphic features discussed earlier may be responses to high light intensities rather than (or in addition to) water shortages. Isobilateral leaf anatomy is generally regarded as a xeromorphic character, but when it is combined with a mechanism for orientating the leaf towards the sun (as occurs for example in *Ceriops*) it seems reasonable to assume a light response also may be involved. Other leaf characteristics associated with high light intensities include such xeromorphic features as a high ratio of volume to surface area and a well-developed, highly differentiated, often isobilateral palisade mesophyll. These features are present in many mangrove species, and in conjunction with the leaf pattern of arrangement on the shoots (Tomlinson and Wheat 1979) may constitute an adaptation optimizing exposure to light under varying conditions of light and shade.

Since leaves developing in intense light show a greater degree of xeromorphy (Wylie 1949), one can distinguish between "sun" and "shade" leaves. Several mangrove species showed a marked morphological differentiation between sun and shade leaves, particularly *Lumnitzera*, *Ceriops* and *Aegiceras* (Saenger 1982). In a detailed examination of the leaves of *Ceriops tagal*, it was noted that shade leaves, when compared with sun leaves, are larger, thicker, have a higher volume-to-surface ratio, possess fewer stomata per square millimetre on the lower leaf surface and possess a proportionately thicker tannin-filled hypodermis on both upper and lower surface and a proportionately thinner upper palisade mesophyll, lower epidermis and lower cuticle (Saenger 1982). These characteristics are those associated with xeromorphy except that xeromorphic leaves generally possess a higher volume-to-surface-area ratio than shade leaves (Shields 1950).

Seedling leaves of *Avicennia marina* also can be subdivided into sun and shade leaves on a morphological basis; the shade leaves contained more chlorophyll on both a leaf-area and fresh-weight basis, were enriched in chlorophyll *b* relative to *a*, and had a lower specific weight and greater leaf area than sun leaves (Ball and

Critchley 1982). In terms of gas exchange and photosynthetic characteristics, however, distinction between sun and shade leaves could not be made; both leaf populations were typical of sun leaves. Unfortunately, no comparative photosynthetic data are available for other Australian mangrove seedlings.

The canopy shape of mangroves is determined largely by endogenous growth patterns which lend themselves to a plant architectural analysis (Halle, Oldeman and Tomlinson 1978). However, the canopy seems to assume certain shapes under specific environmental conditions. For example, an "umbrella-type" canopy has been recorded from *Avicennia marina* in certain situations (Macnae 1968; Wester 1967; Saenger and Hopkins 1975), and Baker (1915) has suggested that, since the pneumatophores of this species must be shaded, a flattened canopy may be an adaptation protecting pneumatophores of isolated trees from intense light.

Photosynthesis

Photosynthesis is necessary for production of food by plants, and many plants have adaptations or physiological responses that optimize this process.

In southern Australia, *A. marina* sun leaves have a rate of photosynthesis approximately 4.5 times that of shade leaves (Attiwill and Clough 1980), although at high light intensities both types of leaves can potentially reach the same maximum rate of photosynthesis per unit of leaf surface. In terms of the quantum efficiency of the canopy of *A. marina*, Attiwill and Clough (1980) found a value of 0.0135 mol CO_2 per mol of photosynthetically active radiation; this is low compared with non-mangrove plants (Bjorkman 1970). Furthermore, this quantum efficiency was obtained only at low light intensities; at full midday light intensities the quantum efficiency was reduced to approximately one-tenth of this level. While such a decline in efficiency is shared with many species, it appears to be of greater magnitude than in many non-mangrove species, and it suggests that although the photosynthetic mechanism of *Avicennia* is inefficient it is best adapted to shade conditions (Attiwill and Clough 1980).

Ball and Critchley (1982) investigated the photosynthetic responses of seedlings of *Avicennia marina* and suggested they are best adapted to growing in exposed conditions and appear to have a low capacity to acclimate to low light intensities. However, these seedlings appear to be able to use sunflecks highly efficiently, and consequently are able to survive in the understorey environment (Ball and Critchley 1982).

Joshi et al. (1974, 1975) investigated the photosynthetic carbon metabolism of two Indian species of mangroves and concluded that they were of the aspartate type. They suggested that this type of metabolism may be due to the inhibition of the enzyme malic dehydrogenase in the presence of high sodium chloride concentrations. To test this hypothesis, plants were labelled with radioactive carbon and the early products were identified; aspartate and alanine both had become heavily radioactive, and consequently it was concluded that the C_4 carbon fixation pathway operated in these species.

More recently, however, the occurrence of this biochemical adaptation of photosynthetic carbon fixation has been questioned for mangroves, and other evidence, drawn from leaf anatomy, the $^{13}C/^{12}C$ carbon isotope ratio and gas exchange properties (Moore et al. 1972; Cowan 1978; Clough, Andrews and Cowan 1982), seems to indicate that mangroves possess the more common C_3 photosynthetic carbon metabolism.

Light and Other Physical Factors

With high light intensity also come higher temperatures and increased water losses. Consequently, the adaptations of plants need to strike a balance between photosynthetic advantage and harmful effects of other physical conditions associated with intense radiation.

Different light and shade requirements have been noted in mangroves, and geographic variation among adults, seedlings and saplings are apparent (Saenger 1982). Two groups of mangroves seem to emerge (see table 8): (1) those which are shade tolerant both as seedlings and as adults (*Aegiceras*, *Ceriops*, *Bruguiera*, *Osbornia*, *Xylocarpus*, *Excoecaria*), and (2) those species which are shade intolerant (*Acrostichum*, *Acanthus*, *Aegialitis*, *Rhizophora*, *Lumnitzera*, *Scyphiphora*, *Sonneratia*). *Avicennia* may be shade intolerant in the seedling stage but shade tolerant as a tree.

Isobilateral leaves are found in both of the above groups. Three

Table 3 Early development of *Avicennia marina* seedlings grown under different salinities

Salinity (as % sea water)	Time (days) from planting until: Splitting of pericarp	Separation of cotyledons	Shoot emergence
0	2.2	12.8	18.8
10	3.6	14.1	25.1
25	4.1	16.6	21.4
50	4.6	18.6	20.8
75	7.9	25.1	33.1
100	7.0	37.8	53.0

Source: Downton (1982).

species, including *Ceriops* and *Osbornia* (shade tolerant) and *Lumnitzera* (shade intolerant), possess leaves that point upwards and are orientated towards the sun. By such leaf orientation, effective photosynthesis is increased along with the effective length of the photosynthetic day. At the same time, the heat input per unit leaf area is reduced. For example, measurements of leaf temperatures high in the canopy of *Rhizophora stylosa* in northern Queensland in full sunlight in summer showed that leaves at their natural inclination were often over 5°C cooler than leaves experimentally held horizontal; they also had correspondingly lower rates of water loss and higher photosynthetic rates than the horizontal leaves (Clough, Andrews and Cowan 1982).

Uphof (1941) suggested that as a water storage tissue is present between the epidemis and palisade mesophyll of most mangrove leaves, its function is to protect the mesophyll from excessive heat or from infra-red radiation. Tannin cells on the upper surface of the leaf of *Rhizophora* and *Ceriops*, for example, may protect the leaf from intense visible or ultraviolet radiation. However, the role of tannins is not clear. For example, the hypodermis is relatively reduced in sun leaves compared with the shade leaves; this finding does not support the theory that a tannin-filled hypodermis protects the palisade mesophyll from high levels of visible or ultraviolet radiation. It has been suggested also that tannins may be involved in preventing fungal infestations or in the removal of excess salt.

Lugo et al. (1975) were able to show that net daytime photosynthetic rates in two American species, *Rhizophora mangle* and *Avicennia germinans* (as *A. nitida*), were about twice as high in sun leaves as in shade leaves. At night, the shade leaves had respiration rates that were four times as high as those of sun leaves. The two species behaved differently in terms of transpiration. *Rhizophora* sun leaves had a higher transpiration rate than the shade leaves while in *Avicennia*, and also in *Laguncularia*, the sun leaves had lower transpiration rates when compared with shade leaves. For many Australian species, both leaf orientation and general leaf morphology vary according to the leaf's position in the canopy (Saenger 1982). Although comparable physiological data for Australian species is being collected only now, it is apparent that certain aspects of leaf physiology, such as responses to light and temperature, also vary with the leaf's position in the canopy (Clough, Andrews and Cowan 1982).

Living with Wind, Waves and Frosts

Mangroves have adapted in various ways to physical damage. When the factor causing damage is of low to moderate intensity, species differ in their degree of tolerance. At high to catastrophic intensities, most species are killed or damaged severely, but various recovery patterns can be observed.

Most mangroves are susceptible to frosts, although the degree of susceptibility varies with species and geographic location. McMillan (1975a) showed that both *Avicennia germinans* and *A. marina*, collected from a range of localities and subjected to frost under identical conditions, have populations selectively adapted to a latitudinal range of habitats, including ones with recurrent low winter temperatures. Leaf scorch seems to be the predominant symptom (Chapman and Ronaldson 1958), often followed by a reduction in the leaf area index (Lugo and Zucca 1977).

Tropical storms are of frequent occurrence in northern Australia. Stocker (1976) classified wind damage caused by cyclone "Tracy" into four types: (1) windthrow, where the tree is felled; (2) crown damage, where leaves and twigs are removed and/or branches are torn off; (3) bole damage, where the trunk is broken, severely fractured or leaning; and (4) death, where the tree remains standing. Because all these damage types also can be caused by wave action (which generally accompanies high winds), no distinction is made between wind and water damage in the following paragraphs.

Windthrow is the severest form of damage and Stocker (1976) found several mangroves to be particularly susceptible, including *Camptostemon schultzii*, *Ceriops tagal*, *Rhizophora stylosa*, *Bruguiera parviflora* and *Excoecaria agallocha*.

Other species such as *Xylocarpus australasicus*, *Aegiceras*, *Aegialitis* and *Lumnitzera racemosa* showed little or no windthrow, and they rapidly developed new crowns. It seems likely that windthrow-susceptible trees are those with weakly developed cable root systems, or whose root system is weakened by erosion or bank-slumping, or by some biological agency such as infestation by isopods or wood-boring molluscs. For most species, windthrow results in death, although for *Sonneratia* and *Avicennia* epicormic shoots will rapidly develop if some root connection remains.

Susceptibility to bole damage varies considerably among species. The anomalous wood structure of *Avicennia*, with its non-concentric, non-annual growth rings of alternating bands of xylem and phloem (Gill 1971), gives the wood unusual qualities: (1) it is extremely strong for its weight; (2) it is extremely difficult to spilt radially yet it is easy to do so tangentially (hence it was used to make shields by the Aborigines); and (3) the unusual ring structure ensures that, if any part of the trunk is damaged, sufficient intact conductive tissue remains to supply the crown and epicormic shoots — as a consequence of this distribution of xylem and phloem tissue, *Avicennia* cannot be killed by ringbarking, an apparently useful adaptation in minimizing damage from waterborne objects.

The secondary wood anatomy of other mangrove species has been studied slightly (Panshin 1932; Marco 1935; Venkatiswarlu and Rao 1964). In *Ceriops*, thick-walled bast fibres form a mechanical tissue cylinder giving strength and rigidity to the stem (Rao and Sharma 1968). In *Rhizophora*, abundance sclereids occur in non-functional phloem tissue (Karsted and Parameswaran 1976) and stone cells and fibres occur throughout the plant. The wood of *Bruguiera* has been described as extremely strong (Banerji 1958) as has that of *Heritiera*, *Rhizophora apiculata* and *Lumnitzera littorea* (Panshin 1932).

In the case of a broken bole, a few species are able to regrow from the stumps. *Avicennia*, *Sonneratia*, *Xylocarpus* and *Excoecaria* and the western hemisphere *Laguncularia* and *Conocarpus* coppice readily.

Crown damage is the most common type of damage, with the plant being defoliated in extreme cases. Leaves of most mangroves are leathery and strengthened by various sclerenchymatous cells, and in strong winds leaf-bearing twigs appear to be shed rather than individual leaves. Recovery from twig or leaf damage is usually rapid; *Avicennia*, *Excoecaria* and *Sonneratia* have abundant reserve buds in the stem. In *Rhizophora*, buds are present in the stems of saplings but become restricted to thin terminal branches as the tree matures (Gill and Tomlinson 1969). Conditions severe enough to remove or kill all branches possessing viable reserve buds will kill *Rhizophora*.

When the tree is dead but remains standing, a number of causative factors may be involved, including changes in the substrates, fatal root or bole damage caused by wind sway, or stress following the near-total loss of leaves.

Reproductive Adaptations

Flowering and Pollination

Flower primordia develop on young plants when little more than three or four years old. The initiation of flowering seems to be independent of size, but the actual factors involved are largely unknown. Most Australian species begin flowering in spring and continue through the summer months (Jones 1971; Saenger 1982; Duke, Bunt and Williams 1984); the predominance of summer flowering in central Queensland species is shown in figure 10.

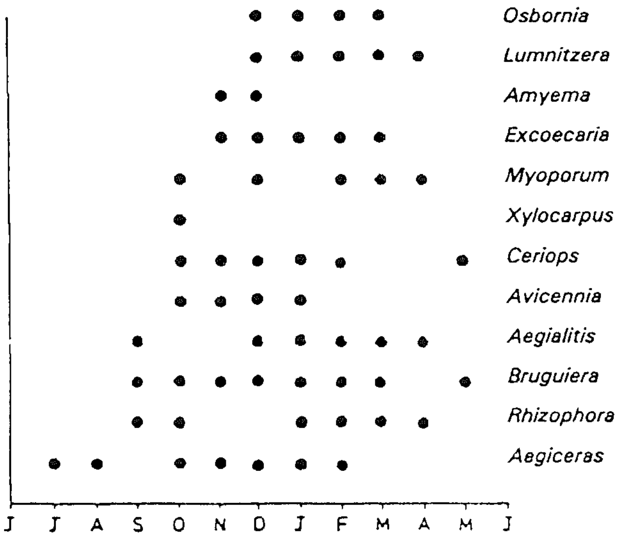


Figure 10 Flowering times of mangroves and mangrove associates in Port Curtis, Queensland, during 1975 to 1979.

Pollination in most mangroves occurs through the agency of wind, insects and birds (Clifford and Specht 1979; Saenger 1982), and most species possess small, non-sticky pollen grains (Wright 1977) which are distinctive for each species (Muller and Caratini 1977) and are even recognizable as fossils (Muller 1964; Churchill 1973). In *Nypa* the pollen is sticky and pollination probably occurs via the many insects that visit its inflorescences (Uhl 1972), particularly drosophilid flies (Essig 1973). The vasculature, histology and growth patterns of the flowers of *Nypa* appear to be directly related to insect pollination (Uhl and Moore 1977). *Aegiceras*, *Cynometra* and probably *Avicennia*, with their scented flowers, are predominantly bee-pollinated (Blake and Roff 1972; Chanda 1977; Clifford and Specht 1979); the western mangrove *Avicennia germinans* appears to be exclusively pollinated by the bee *Apis mellifera* (Percival 1974). *Excoecaria* is dioecious, bears flowers in catkins and possesses a two-celled pollen grain (Venkateswarlu and Rao 1975) and it can be presumed that it is wind-pollinated. *Sonneratia* releases copious amounts of dry or slightly sticky pollen at dusk when the flower opens (Muller 1969), and it is dispersed by bats (Faegri and van der Pijl 1971; Semeniuk, Kenneally and Wilson 1978) and moths (Primack, Duke and Tomlinson 1981). In South Africa, *Bruguiera gymnorhiza* is pollinated by insects and sunbirds, and the petals of this species are peculiarly adapted to this method of pollen dispersal (Davey 1975); *Bruguiera* petals possess a heavily cutinized epidermal region which, on the application of gentle pressure, causes the petal lobes to spring apart, thereby releasing the stamens together with a puff of pollen. Tomlinson, Primack and Bunt (1979) observed that large-flowered species of *Bruguiera* (such as *B. gymnorhiza*) are bird-pollinated whereas small-flowered species (such as *B. parviflora* and *B. cylindrica*) are pollinated by butterflies. They further reported that *Ceriops* is pollinated by moths whereas *Rhizophora* appears to be wind-pollinated, although Primack and Tomlinson (1978) noted that glands on the inner surface at the base of the stipules of the latter produce a sugary secretion which is attractive to birds. Tomlinson et al. (1978) found that whereas *Lumnitzera racemosa* was insect-pollinated, the red-flowered *L. littorea* was pollinated largely by honeyeaters, particularly *Meliphaga gracilis*. The flower structure of *Acanthus ilicifolius* requires a strong pollinator to separate the four stamens in order to reach the nectar at the base of the ovary; during field observations only the yellow-breasted sunbird *Nectarina jungularis* was noted to probe the flowers (Primack, Duke and Tomlinson 1981).

Propagule Production

Most mangroves on the eastern Australian coast bear mature propagules in the summer months (February to March) (Jones 1971; Graham et al. 1975; Saenger 1982; Duke, Bunt and Williams 1984); the occurrence of mature propagules in mangroves on the central Queensland coastline is shown in figure 11. Similarly, on the eastern coast of South Africa, *Avicennia marina* has its main fruiting period in March–April (Steinke 1975).

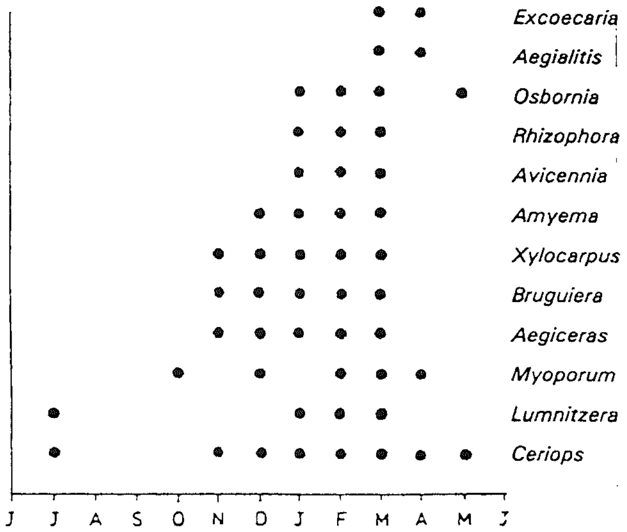


Figure 11 Fruiting times of mangroves and mangrove associates in Port Curtis, Queensland, during 1975 to 1979.

In some species, the time from flower primordium to mature propagule is considerable: 3 years in *Rhizophora apiculata* (Christensen and Wium-Anderson 1977); 1–1.5 years in *Bruguiera gymnorhiza*, *Ceriops tagal* and *Rhizophora stylosa* (Duke, Bunt and Williams 1984); 6 months from open flower to mature propagule in *Rhizophora mangle* (Guppy 1906); 12 months from flower buds to mature propagules in *Kandelia candel* (Nishihira and Urasaki 1976), *Rhizophora mangle* (Gill and Tomlinson 1971b) and *Aegiceras corniculatum* (Carey and Fraser 1932). In spite of this lag, both flowering and fruiting largely occur in the summer months, and it would seem that some common environmental parameter is involved in controlling both processes. Since leaf production in many species is also seasonal with the maxima for many species during summer (Saenger and Moverley 1985), it seems that fruiting, like flowering, is timed for the period most favourable for growth.

Considerable mortality has been reported for developing seedlings still attached to the tree. Gill and Tomlinson (1971b) showed that for *Rhizophora mangle* only between 0 and 7.2 per cent of flower buds produced mature seedlings, although the number of flowers produced may be increased markedly by an increase in nutrients (Onuf, Teal and Valiela 1977). Lugo and Snedaker (1975) followed the development of selected seedlings of *R. mangle* while still attached to the parent tree in Florida in the United States, and they found a mortality of 9 per cent, 13.4 per cent and 20.9 per cent for the months of January (winter), April and May (spring) respectively. Similar figures were noted in *Rhizophora apiculata*, for which Christensen and Wium-Andersen (1977) reported that only 7 per cent of flower buds formed flowers, and only 1–3 per cent formed fruits. In *Kandelia candel* less than 30 per cent of the flower buds ultimately developed into mature propagules (Nishihira and Urasaki 1976). For the Australian *Sonneratia alba*, young fruit developed from forty-one of forty-six flower buds (Primack, Duke and Tomlinson 1981). As in non-mangrove species, much of this pre-dispersal mortality can be attributed to fungal and insect attack on the fruit and to such inherent factors as albinism (Handler and Teas 1983) and other morphogenetic malfunctions.

Vivipary and Cryptovivipary

Various types of fruits are found among the mangroves and those of Australian genera are listed in table 4. In several genera, the fruits contain seeds which develop precociously; the seed germinates while still attached to the parent tree. In these species, the

Table 4 Reproductive units of Australian mangrove and associated genera, together with references to detailed descriptions of their embryology and/or seedling development

Genus	Fruit	Description of embryology and/or seedling development
Acanthus	Capsule with several flat seeds	
Acrostichum	Spore	Stokey and Atkinson 1952; Lloyd 1980
Aegialitis	Indehiscent nut	
Aegiceras	Fleshy capsule, shed with calyx attached	Haberlandt 1896; Carey and Fraser 1932; Collins 1921
Amyema	Baccate, with viscous seeds	
Avicennia	Fleshy capsule with single seed	Treub 1883; Collins 1921; Padmanabhan 1960, 1962a, 1962b; Butler and Steinke 1976
Bruguiera	Fleshy single-seeded berry, shed with calyx attached	
Camptostemon	Capsule with 2 to several woolly seeds	
Ceriops	Fleshy berry, usually single-seeded, shed with calyx attached	Carey 1934
Cynometra	Wrinkled one-seeded pod	
Excoecaria	Trilobed exploding capsule, each lobe one-seeded	Venkateswarlu and Rao 1975
Heritiera	Clusters of woody, keeled carpels	
Hibiscus	Hairy capsule splitting into 5 locules; many-seeded	
Lumnitzera	Indehiscent woody fruit with thin outer fleshy layer	Clifford and Specht 1979
Lysiana	Ovoid with single viscous seed	
Nypa	Aggregate head of one-seed fruits	Tomlinson 1971
Osbornia	Capsule	
Rhizophora	Ovoid fleshy berry, with single seed	Carey 1934; Cook 1907; Gill and Tomlinson 1969
Scyphiphora	Axillary clusters of ribbed fruits, surmounted by calyx	
Sonneratia	Many-celled, many-seeded capsule	Venkateswarlu 1935
Xylocarpus	Several-seeded capsule	Percival and Womersley 1975

embryo develops into a seedling without any dormant period (Gill and Tomlinson 1969), although a form of seedling dormancy may be induced by low water content (Sussex 1975). In *Bruguiera, Ceriops, Rhizophora, Kandelia* and *Nypa* the embryo ruptures the pericarp and grows beyond it, sometimes to considerable lengths, while still attached to the parent tree. This condition is known as vivipary. In *Aegialitis, Acanthus, Avicennia, Aegiceras, Laguncularia* and *Pelliciera*, the embryo, while developing within the

fruit, does not enlarge sufficiently to rupture the pericarp. This condition is termed cryptovivipary. In the remaining species, the seeds, like those of most plants, pass through a resting stage prior to germination, and do not germinate while still on the parent tree.

Vivipary and cryptovivipary frequently have been cited as an adaptation to some aspect of the mangrove environment. Its adaptive significance could include rapid rooting (Macnae 1968), salt regulation (Joshi 1933), ionic balance (Joshi et al. 1972), development of buoyancy (Gill 1975) and prolonged attainment of nutrients from the parent (nutritional parasitism) (Pannier and Pannier 1975; Bhosale and Shinde 1983). In the viviparous seagrasses, *Amphibolus* and *Thalassodendron*, vivipary appears to be an adaptation assisting rapid root attachment of the plant (Ducker and Knox 1976). However, the occurrence of apparently successful mangroves without viviparous fruits (such as *Osbornia, Sonneratia, Lumnitzera, Xylocarpus* and *Excoecaria*) makes it doubtful whether the possession of vivipary *per se* is of any real adaptive advantage. Tidal buffeting and waveborne objects pose a threat to establishing seedlings, and it would be expected that the smaller the seedling, the larger the threat. Because of this, vivipary in a mangrove may simply be a means of producing a large seedling which is less likely to be damaged by water movements (Saenger 1982). It is interesting to note in this respect that many of the non-viviparous genera also possess large seeds (such as *Xylocarpus, Heritiera, Cynometra*), which similarly may be a means of alleviating damage by water movement.

Propagule Dispersal and Establishment

The seeds of the mangrove mistletoes are dispersed by the mistletoe bird, *Dicaeum hirundinaceum*, and they are capable of withstanding passage through the alimentary canal of this species. The spores of the mangrove fern *Acrostichum* appear to be wind-dispersed since they do not float; the prothalli of this species, however, float in sea water but mostly sink in fresh water. The dispersal unit of mangroves may be a single seed (*Excoecaria*), a one-seeded fruit (*Cynometra iripa*), a several-seeded fruit (*Sonneratia, Xylocarpus*), a multiple fruit (*Heritiera*), an aggregated fruit (*Nypa*) or a precociously developed seedling (*Avicennia, Aegiceras, Rhizophora, Ceriops, Bruguiera*). The propagules of all mangroves trees are buoyant and are adapted to dispersal by water (Saenger 1982).

Few data are available on the periodicity of propagule dispersal but Clarke and Hannon (1971) found that dispersal of *Aegiceras* coincided with unusually high tides whereas that of *Avicennia* coincided with low tides.

Buoyancy of mangrove propagules may be due to the radicle as in *Rhizophora*, the pericarp and cotyledons as in *Avicennia* (Steinke 1975; Butler and Steinke 1976), the endoderm (for example, *Xylocarpus*) on the cotyledon as in the Panamanian *Pelliciera*. Changes in any of these features can alter the buoyancy. For example, Steinke (1975) showed that propagules of *Avicennia marina* sink after losing their pericarp, generally within four days. Subsequent investigation of the rate of pericarp shedding showed that high and low salinities decreased the rate at which they were shed when compared with the rate in water of intermediate salinity. Consequently, propagules in brackish water will disperse less than those in water of high or low salinity.

High temperatures also increase the rate of pericarp shedding and consequently shorten the potential dispersal distance (Steinke 1975). Using Australian material of *A. marina*, Downton (1982) showed that the time required for the splitting of the pericarp and the separation of the cotyledons increased with increasing salinity and, in this respect, appeared to differ from South African examples of the same species.

A buoyant propagule appears to be an efficient means of widespread, water-based dispersal. Among the seagrasses, however, only a few genera (*Posidonia*, *Thalassodendron* and *Enhalus*) have buoyant fruits and, paradoxically, these species have restricted distributions (Den Hartog 1970). It would appear from this that the role of buoyancy in effecting widespread dispersal needs experimental evaluation.

Rabinowitz (1978a) investigated the parameters affecting dispersal of six Panamanian mangroves, including longevity and vigour, period of floating, period required for establishment and the period of obligate dispersal. Two contrasting dispersal patterns were observed, one for small and another for large propagules.

In contrast to those of *Avicennia marina*, the propagules of *A. germinans* always float, and this species seems to have an absolute requirement for a period of stranding in order to establish itself. This species is restricted to higher ground where inundation is less frequent and where it is free of tidal disturbances. The time required for this species to root is approximately seven days whereas *A. marina*, whose propagules sink after approximately four days, becomes firmly rooted in five days (Clarke and Hannon 1970). *Laguncularia*, whose propagules sink after approximately twenty days, also requires a period of stranding of five days or more in order to become firmly rooted (Rabinowitz 1978a).

The two genera that have large propagules (*Rhizophora* and *Pelliciera*) tolerate tidal disturbance better than do either *Avicennia* and *Laguncularia*; the propagules of the former two are capable of taking root in water of various depths because their weight affords resistance to tidal buffeting, and growth continues under water. Longevity of propagules ranged from thirty-five days in *Laguncularia* to a year or more in *R. mangle* (Rabinowitz 1978a).

These findings led Rabinowitz (1978b) to suggest that the seedling populations of mangroves with smaller propagules turn over annually whereas those with larger ones are made up of overlapping cohorts. In other words, two reproductive strategies are involved: mangroves with small propagules pepper the swamp annually with short-lived seedlings which may establish in gaps that have arisen during the previous year; those with larger propagules form a persistent seedling bank which can maintain itself until a gap in the canopy occurs (if shade-intolerant), or grow in the shade to reach the canopy (if shade-tolerant).

It is doubtful, however, that such a simple scheme operates in Australian mangroves. The ability to utilize sunflecks efficiently, as can *Avicennia marina* seedlings (Ball and Critchley 1982), blurs the boundary between the shade-tolerant and shade-intolerant species with large propagules. Furthermore, newly arrived seedlings tagged in permanent study areas at Port Curtis, central Queensland, survived as two- to four-leaved seedlings for up to eight years whether from small (*Lumnitzera*), medium (*Avicennia*, *Aegiceras*, *Aegialitis*) or large (*Rhizophora*, *Ceriops*) propagules (Saenger, unpubl. data). Nevertheless, a persistent seedling bank appears to be an important colonization strategy in Australian mangroves.

The number of mangrove propagules establishing along 30 metres of intertidal shoreline in permanent study areas (Saenger and Robson 1977) at Port Curtis, a semi-enclosed bay in central coastal Queensland, is given in table 5 together with comparative data from Repulse Bay, near Proserpine. The number of propagules establishing per adult of the same species is also given. These figures are low in view of the apparently high numbers of propagules borne by most species. However, considerable mortality occurs prior to dispersal, and crabs (particularly species of *Sesarma*) and insects damage many propagules after they have fallen. Further mortality occurs during dispersal, including stranding on unfavourable substrates, injury by boring or decomposing marine organisms, and sinking as a result of the attachment of fouling organisms such as barnacles and tubeworms (serpulid polychaetes). Once the propagules are stranded, physical damage by waveborne objects frequently occurs. Among those that establish successfully — that is, become firmly rooted and possess at least one leaf — mortality rates are variable and site-dependent (see table 5). In Queensland, at Port Curtis, mortalities in the first year ranged from 72 per cent in *R. stylosa* to 0 per cent in *L. racemosa* and *A. annulata*. At Repulse Bay, mortality rates during the first year were much more equable. The main factors determin-

Table 5 Production, establishment and mortality rates for propagules of Queensland mangroves

Gladstone

Genus	No. of propagules establishing per 30 m of shoreline line during 4 years	No. of established propagules per adult of same species	% mortality of established propagules during first year	Mean mortality (%) of adults during one year
Rhizophora	276	1.64	71.7	2.98
Aegialitis	3	1.50	0	0
Avicennia	199	1.47	22.1	5.97
Lumnitzera	9	1.00	0	2.78
Aegiceras	27	0.18	14.8	1.51
Ceriops	52	0.13	36.5	1.01

Source: Data from permanent plots, 1975–1979 (after Saenger 1982).

Proserpine

Genus	No. of propagules establishing per 80 m of shoreline line in 1 year	No. of established propagules per adult of same species	% mortality of established propagules during first year	Seedling growth (% height increase/year)
Avicennia	28	1.58	38.1	18.7
Rhizophora	35	0.77	29.2	18.4
Excoecaria	9	0.21	25.0	41.6
Aegiceras	20	0.17	26.7	50.6
Ceriops	11	0.15	12.5	30.3
Lumnitzera	3	0.13	20.0	27.5

Source: Data from permanent plots, 1980–1982 (Saenger, unpubl. data).

ing post-establishment mortality are physical such as waveborne objects, biological such as crab damage, and physiological such as water stress, insufficient light and high soil salinities. The mortality rates from Queensland (table 5) show trends different from those reported by Rabinowitz (1978b), who found that mortality rate was inversely correlated with initial propagule weight.

3. *Mangroves and Their Environment*

If the broad ecological prerequisites outlined in the Introduction are fulfilled at a particular locality, a mangrove community is likely to develop. However, such communities are not uniform structurally, floristically or functionally when compared one with another, and even within any one community, considerable heterogeneity is apparent.

Differences in and among mangrove communities are due to a number of environmental factors — abiotic, biotic and fortuitous — which act differentially on individual mangrove species. These factors lead to three types of interactions: (1) those between the physico-chemical environment and the plants, (2) those among the plants themselves, and (3) those between plants and animals. The ultimate structure and function of a particular mangrove community is the outcome of all these interactions.

Physico-Chemical Environment–Plant Interactions

A number of physico-chemical factors, arising out of the broad mangrove environmental prerequisites, have been recognized as primary determinants of mangrove growth and development (figure 12). These can operate to modify one or more of the essential life processes within the mangrove community (table 6), and consequently determine whether a species is able to survive and grow at that particular locality.

In addition to these factors, there are others who are prerequisites for the normal growth of all plants such as gravity and the availability of carbon dioxide. However, as a specialized group of plants is under consideration, only those factors are discussed which either are specific to the mangrove environment, or to which mangroves show an interesting or unusual response.

Temperature

Temperature, because of its critical effect on both photosynthetic and respiratory processes, regulates a large number of internal energetic processes. Perhaps the most important of these are salt regulation and excretion, and root respiration.

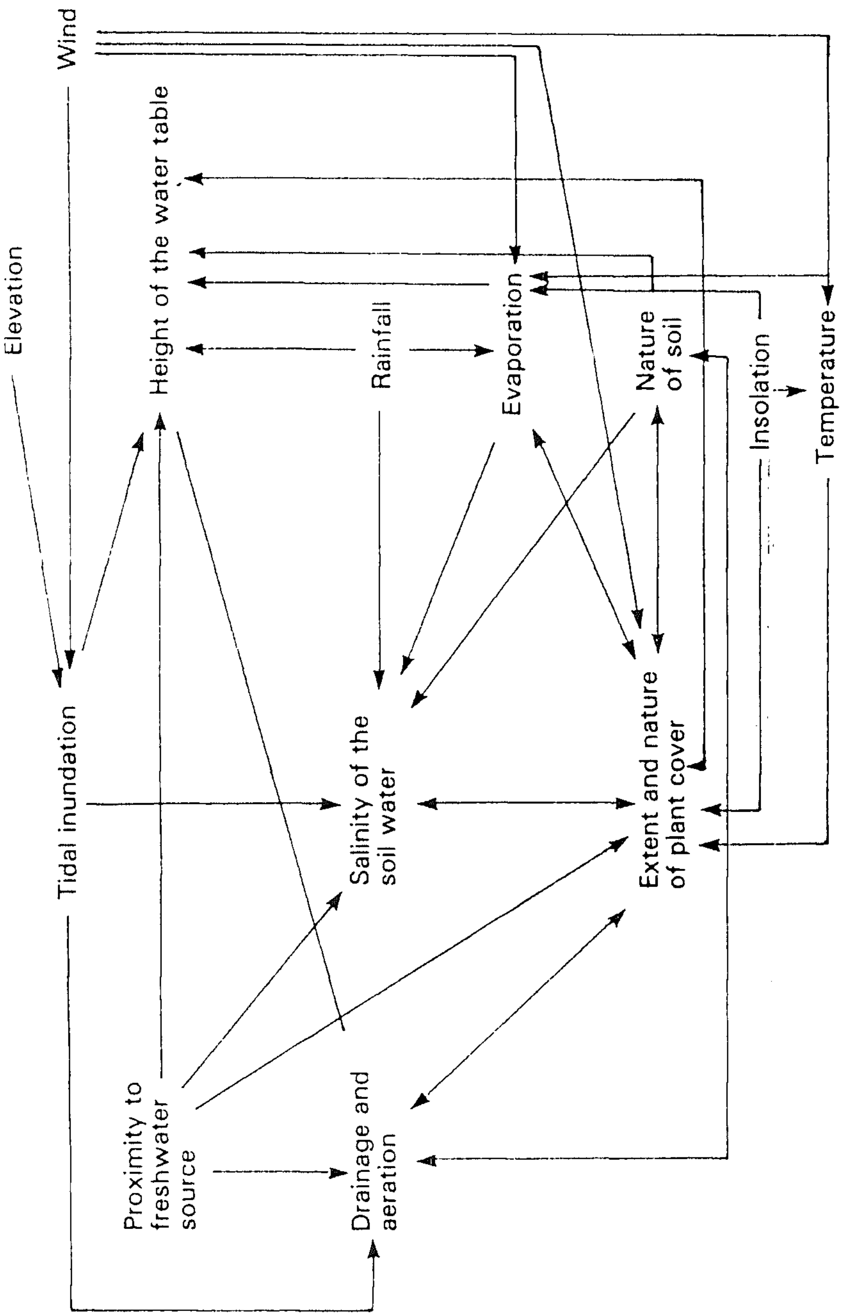
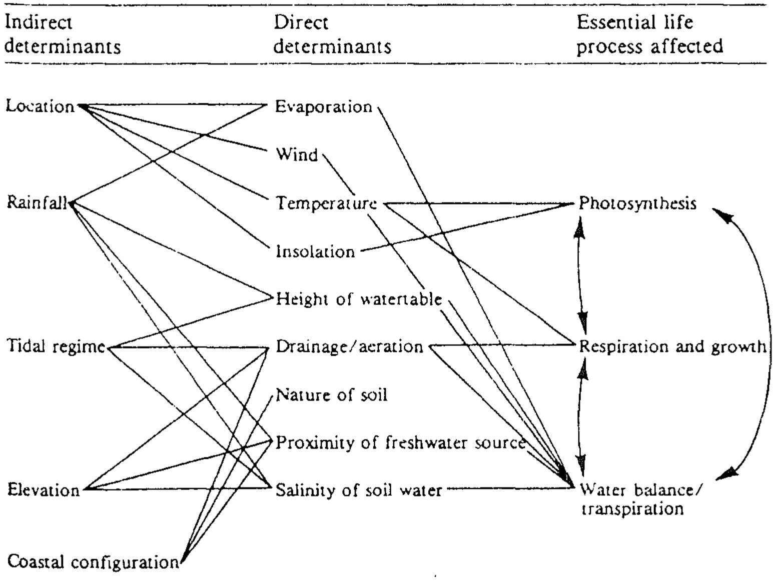


Figure 12 Interrelationships between major physico-chemical factors and the extent and nature of the mangrove plant cover.

Table 6 Relationship between physico-chemical factors and the essential life processes of mangroves



Specht (1981a) recognized three thermal groups in the Australian vegetation, based both on species distribution and on the threshold temperature at which shoot growth is initiated. In the tropical–subtropical group, shoot growth is initiated when the mean air temperature rises above 25°C; the warm-temperate group shows shoot growth between 15 and 25°C; and the cool-temperate group shows shoot growth when the mean air temperature rises above 10°C.

Based on species distributions, mangroves belong predominantly to the tropical–subtropical group (refer to figure 4, chapter 1), although some species extend considerably southwards of the subtropics.

Very few shoot-growth data are available for mangroves; consequently, leaf-growth data are used instead. The monthly production of new leaves (Saenger and Moverley 1985) for nine species of mangroves from Gladstone (lat. 24°S) are shown in relation to air temperature in figure 13. The data for *Avicennia* show an approximately linear increase in leaf production with increasing temperature up to 20°C, followed by a decline at higher temperatures. Extrapolating the line suggests that leaf production ceases at 12°C and that *Avicennia* belongs to the cool-temperate group.

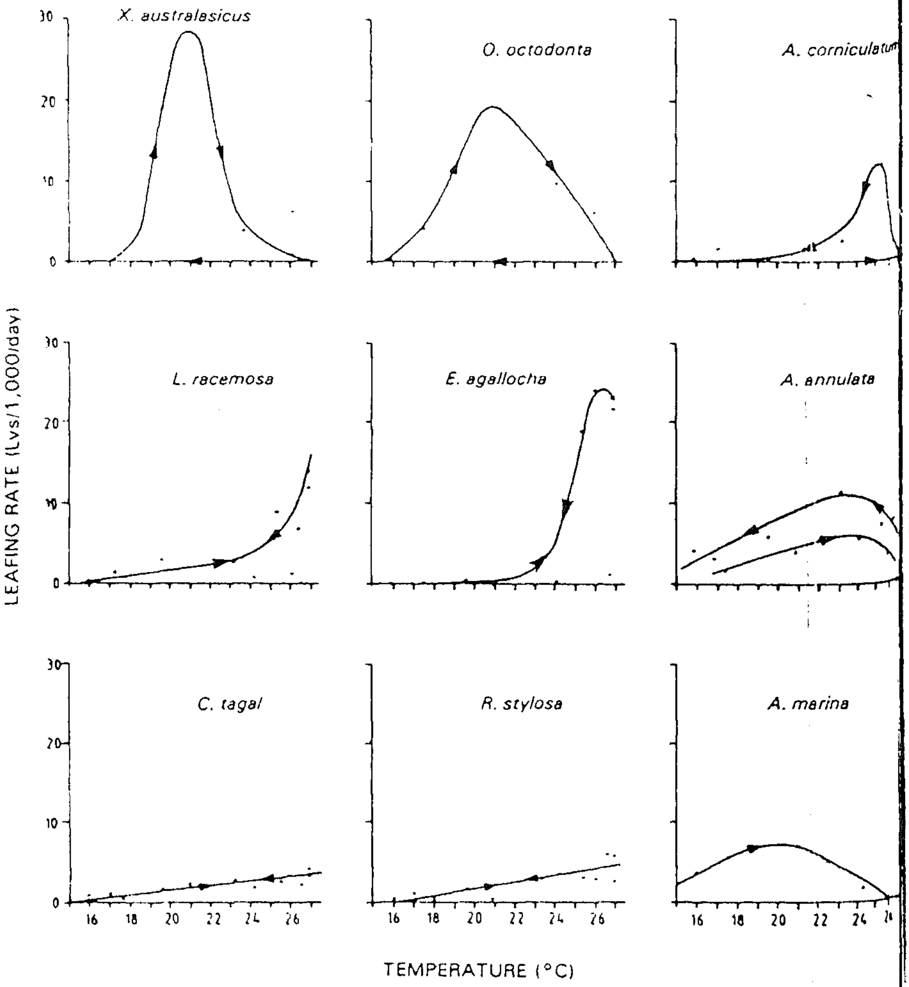


Figure 13 Rates of leaf formation in nine species of mangroves at different mean monthly temperatures at Gladstone, Queensland (after Saenger and Moverley 1985).

The data for *Rhizophora stylosa* suggest that leaf formation would cease below 16°C. Working with *R. mangle*, Miller (1975) demonstrated, by measuring leaf resistance, that the stomata of this species are only fully open above 18°C (figure 14), thereby restricting transpiration and photosynthetic gas exchange at low temperatures. Consequently, it appears that both *R. stylosa* and *R. mangle* fit well into the warm-temperate group.

Osbornia octodonta shows a slightly different pattern in that it

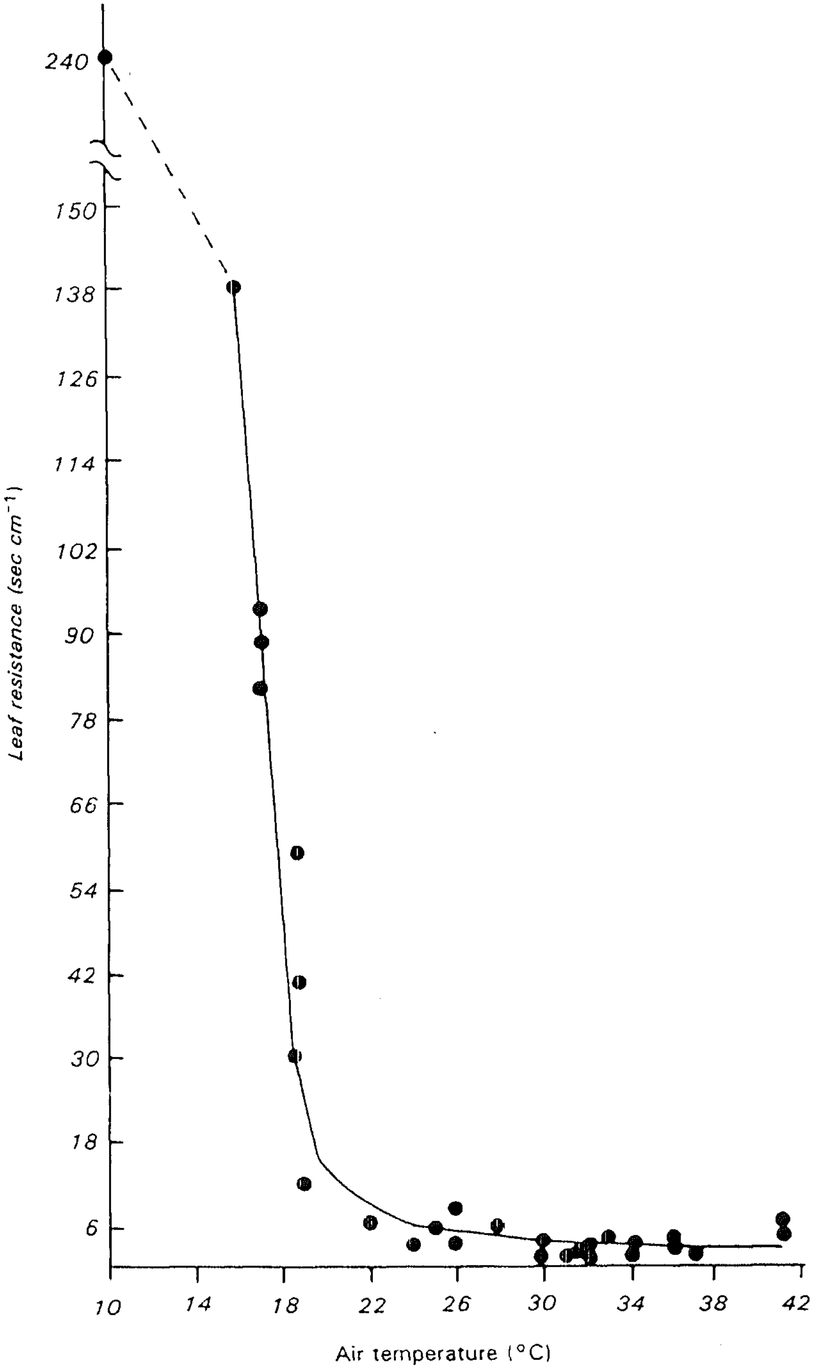


Figure 14 Stomatal opening (measured as decreasing leaf resistance) in *Rhizophora mangle* in response to various air temperatures (redrawn from Miller 1975).

produces nearly all of its new leaves from September to October and virtually no leaves during the remainder of the year regardless of temperature. Leaf production ceases below 16°C, whereas maximum leaf production occurs around 21°C in spring. In autumn, when the temperatures are again around 21°C, no leaf production occurs. There may be an hysteresis effect — that is, lagging behind of a normal level of response after the plant has been under a period of stress — similar to that observed in other terrestrial plant species (Specht 1981c), or there may be a diversion of photosynthates into reproductive channels rather than into leaf formation. Whatever its cause, the response of *O. octodonta* suggests that it falls into the warm-temperate group.

Aegiceras corniculatum shows a similar but inverted pattern to that of *O. octodonta*; it produces nearly all of its new leaves during February to April and virtually no leaves during the remainder of the year, regardless of temperature. Leaf production ceases below 16°C, whereas maximum leaf production occurs around 25°C in autumn. In spring, when temperature initially rises to 25°C, no leaf production occurs; it would seem that during the spring period, at around 25°C, leaf primordia are initiated at the shoot apex but that these do not develop until after maximum temperatures have been reached and the autumn thermal decline begins.

The data on leaf production for the nine species from Gladstone and for sixteen species from Proserpine (lat. 20° 30′S) have been used to provide a tentative allocation of these Australian mangroves into Specht's (1981a) three thermal groups (Saenger and Moverley 1985). The data in table 7 show that only *Avicennia marina* can be classified as cool-temperate and this is reflected in its geographical range. Most of the remaining species are classified as warm-temperate except *Xylocarpus granatum*, which shows tropical-subtropical thermal affinities. Clearly, however, those mangroves not occurring at these sites but further north — such as *Camptostemon* and *Scyphiphora* — must be classified as belonging to the tropical-subtropical group as well. *Cynometra* and *Sonneratia* both occur at Proserpine but in such low numbers that adequate data could not be obtained; they probably should be classified as tropical-subtropical.

The tolerance of mangroves to low temperatures, and its effect on geographical distribution, has been discussed already (chapter 1); *Avicennia marina* appears to be the most tolerant of low temperatures, extending outside tropical and subtropical latitudes in Australia, New Zealand and southern Africa. Chapman and Ronaldson (1958) and Farrell (1973) considered *Avicennia marina* to be limited by the occurrence of killing frosts. McMillan (1975a) and Markley, McMillan and Thompson (1982) showed latitudinal variation in response to chilling in a range of mangrove species from Australia and America.

Table 7 Classification of Australian mangroves into thermal groups (data from Port Curtis and Repulse Bay; where differences occur, the Repulse Bay data are given in parentheses)

Species	Temperature (°C) at which: Leaf production ceases	Leaf production is maximal
Cool-temperate		
Avicennia marina	12	20
Warm-temperate		
Aegialitis annulata	14(15)	23(27)
Ceriops tagal	15	27
Aegiceras corniculatum	16	25(27)
Rhizophora stylosa	16	28
Osbornia octodonta	16(17)	21
Xylocarpus australasicus	17(23)	21(26)
Lumnitzera racemosa	17(18)	28
Excoecaria agallocha	18(16)	26(28)
Bruguiera exaristata	17	27
Bruguiera parviflora	17	27
Bruguiera gymnorhiza	16	15
Heritiera littoralis	24	28
Acanthus ilicifolius	17	26
Hibiscus tiliaceus	22	27
Tropical-subtropical		
Xylocarpus granatum	26	>28

The response of Australian mangroves to high temperature is not well known. However, mangroves growing in the discharge areas of coastal power stations such as Torrens Island, Adelaide, and the Gladstone and Howard power stations, central Queensland, show no visible effect, although some thermal effects may be masked by related conditions associated with circulation and chlorination of cooling water, and the discharge of airborne pollutants (Saenger, unpubl. data).

Canoy (1975) showed that *Rhizophora mangle* in Puerto Rico developed more stilt roots per unit area where it was subjected to a 5°C temperature increase from a cooling water discharge point, and that in temperature-stressed areas this species formed more, but significantly smaller, leaves (Canoy 1975; Lugo and Snedaker 1974). McMillan (1971) reported that young seedlings of *Avicennia germinans* were killed by water temperatures of 39°C to 40°C, although established seedlings and trees were not damaged.

Based on modelling studies of the bioclimate, leaf temperatures and primary production of *R. mangle* in southern Florida, Miller (1972) suggested that production is decreased by increasing air temperature and increasing humidity above optimum levels. Moore et al. (1972, 1973) found that the optimum temperature for photosynthesis by Florida mangroves was subject to some seasonal variation, but for all species the optimum temperatures were below 35°C with little or no photosynthesis occurring at 40°C. These findings in American mangroves emphasize the need for studies of community metabolism in Australian species under the influence of elevated water and air temperatures. Preliminary data for the Australian *A. marina, R. apiculata* and *R. stylosa* indicate that they, too, show a sharp decline in photosynthesis above 35°C (Clough, Andrews and Cowan 1982).

Smillie (1984) investigated the cold and heat tolerances of Australian mangroves by measuring the decline in induced chlorophyll flourescence following application of a cold or heat stress to the leaf tissue, a technique initially developed for crop plants (Smillie and Hetherington 1983). Susceptibility to cold injury was assessed by the decrease in the rate of induced rise of chlorophyll flourescence in dark-adapted leaves kept at 0°C; heat tolerance was determined by the decrease in chlorophyll flourescence after heating in water to 49°C for ten minutes.

Cold tolerance was measured in twenty-seven species of mangroves. Certain species such as *Bruguiera exaristata* and *Ceriops decandra* were very intolerant, accounting for their confinement to the tropics and the warmer subtropics. Overall, a wide range of cold tolerances was found, but within genera the cold tolerances of species were correlated with their latitudinal distribution. In other words, the further south the species occurred, the greater its cold tolerance (Smillie 1984).

For *Avicennia marina*, the most southerly extending mangrove, there was considerable cold adaptation in the southern populations compared with the more northerly ones, a finding consistent with that described by McMillan (1975) from seedling growth studies.

Twenty mangrove species from tropical areas were assessed for their heat tolerance. It was concluded (Smillie 1984) that all the species showed a very high degree of heat tolerance compared with other plants tested by the same technique, and that mangroves appear to be at the extreme high end of the heat tolerance range for non-arid tropical plants. The most heat-sensitive species were the mangrove fern (*Acrostichum speciosum*), *Acanthus ilicifolius* and *Rhizophora stylosa*. Both *Acrostichum* and *Acanthus* grow in sunflecked shade and are subject to short periods only of solar heating. *Rhizophora stylosa*, on the other hand, most commonly grows in full sunlight, a situation difficult to reconcile with its apparent heat sensitivity.

In contrast to the finding of cold adaptation, there was no evidence for any latitudinal differentiation of heat tolerance in *Avicennia marina* and *Aegiceras corniculatum*, the only two species tested (Smillie 1984).

Insolation

The physiological and morphological adaptations of mangroves to high levels of incident solar radiation have been discussed in chapter 2, and it remains now to examine the ecological role of light.

Attiwill and Clough (1980) examined the relationship between light and photosynthesis in branches of *Avicennia marina*; for branches both within and at the top of the canopy, they found that photosynthesis became light saturated at a total short-wave radiation between 200 and 400 Wm^{-2} (figure 15). The photosynthetic efficiency of this species was low compared with non-mangrove plants. Moreover, at full midday light intensities (approximately 1,000 Wm^{-2}), this quantum efficiency was greatly reduced, and Attiwill and Clough (1980) suggested that the photosynthetic mechanism of *Avicennia marina* is relatively inefficient and best adapted to shade conditions.

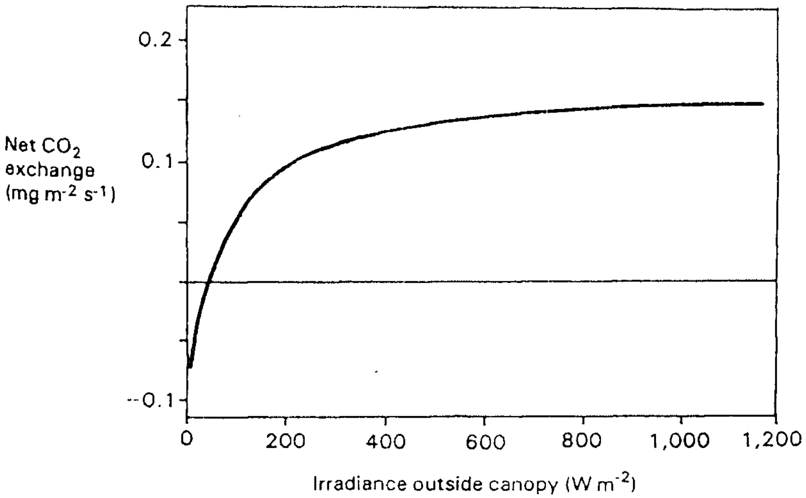


Figure 15 Light-saturation curve for *Avicennia marina* at Westernport Bay, Victoria (redrawn from Attiwill and Clough 1980).

Unfortunately, comparative data for other Australian mangroves are not available. However, based on observations in the field and from culture experiments, various authors have noted the light and shade requirements of different species (table 8). Two

Table 8 Shade tolerance of Australian mangroves

Genus	Shade tolerant	Shade intolerant
Acanthus		Macnae 1966, 1968
Acrostichum		Macnae 1966
Aegialitis		Macnae 1966, 1968
Aegiceras	Clarke and Hannon 1971; Thom, Wright and Coleman 1975	
Avicennia	Clarke and Hannon 1971; Attiwill and Clough 1980	Macnae 1963, 1966, 1968; Thom, Wright and Coleman 1975
Bruguiera	Macnae 1966; Macnae and Kalk 1962; Watson 1928	
Ceriops	Macnae and Kalk 1962; Thom, Wright and Coleman 1975	Macnae 1966, 1968
Excoecaria	Saenger 1982	
Lumnitzera		Macnae 1966, 1968
Osbornia	Saenger 1982	
Rhizophora	Macnae 1966	Macnae 1968
Sonneratia		Macnae 1968
Scyphiphora		Macnae 1966
Xylocarpus	Saenger 1982	

groups are apparent — those that are shade-tolerant both as seedlings and as adults, and those that are shade-intolerant — but until physiological confirmation is available, this classification must be treated as tentative.

Figure 16 shows the number of months each year that the mean radiation throughout the day falls below 350 Wm^{-2}, that is, below the saturation intensity. These data are based on the theoretical incident radiation falling on a horizontal surface (Paltridge and Proctor 1977) and are adjusted for local cloud cover and seasonally changing day lengths. For mangroves with a photosynthetic mechanism similar to that of *Avicennia marina*, light is unlikely to be a limiting factor because average daytime intensity exceeds saturation level. Even in Tasmania the mean daily light intensity exceeds the saturation level for five months of the year and, other conditions being suitable, *Avicennia marina* could enjoy a growing period of at least five months. Clearly, other factors are limiting, but the point is made that light *per se* is not limiting even in Tasmania. At increasingly lower latitudes, light is present above saturation levels for more and more of the time and has led to various morphological adaptations in the mangroves. Even so, Attiwill and Clough (1980) showed that at Westernport Bay in Victoria a decrease in photosynthesis of this species occurred on days of sustained high radiation levels, and they ascribed this to a photochemical inhibition of the photosynthetic mechanism.

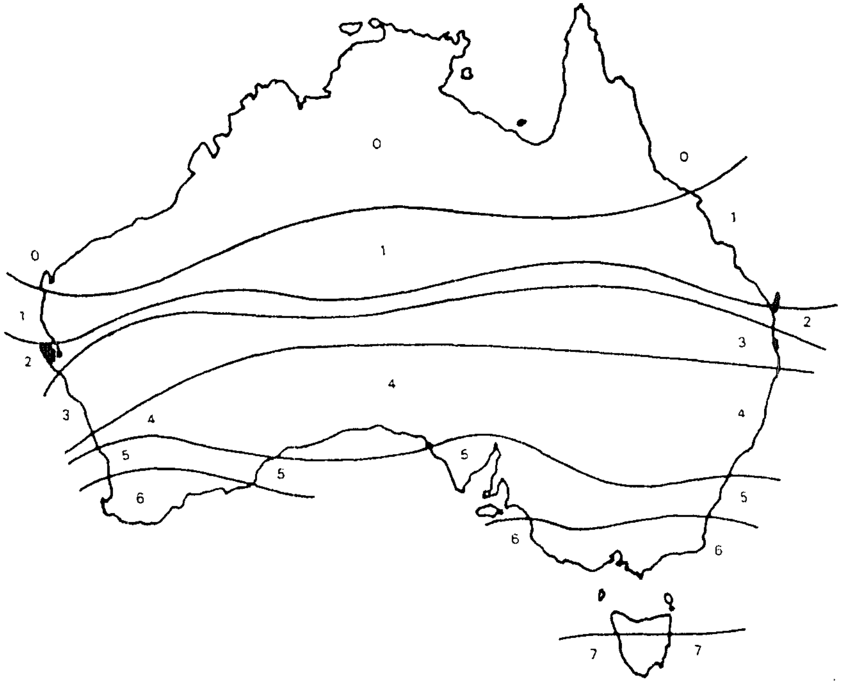


Figure 16 Number of months per year during which the mean radiation level between sunrise and sunset falls below 350 watts m^{-2}.

Wind and Evaporation

Wind affects mangroves in several separate ways. Coastal water drift and tidal currents are modified by wind direction and speed. Wave action is accentuated, especially at high tides, by stormy conditions. Both waves and water movement affect sediment transport. Wind has a major part to play in causing evaporation and in increasing salinity. In addition, it can cause physical damage to canopies and desiccate foliage. On the positive side, it facilitates pollination and the dispersal of propagules in a number of species.

There are, however, three aspects of wind that impinge directly on the physiological performance of mangroves: its evaporative capacity, its effect on sea-level and its role in regulating evapotranspiration from leaves.

Oliver (1982) pointed out that most of the standard wind data do not relate to the mangrove environment because wind recording is usually done close to the ground and some distance from the coast. The sea surface causes less mechanical and thermal obstruction to air flow and therefore wind speeds are greater over water than over land. As winds flow on to the shore, frictional drag of the land surface reduces wind speeds, but this is a progressive process and the mangrove zone tends to experience the speeds characteristic of winds over the sea. Recording stations are often on the landward side of the sharp decrease in wind speeds from sea to land.

Despite this shortcoming in wind data, it is established that climatic factors such as humidity, wind velocity and higher solar irradiance, together with the degree of plant cover, have a significant influence on evaporative losses from the mangrove environment, which, together with the frequency of inundation, largely determine soil salinity. The most severe conditions characterize the arid and semi-arid climates in the subtropics and tropical margins (Oliver 1982) where high seasonal rainfall combines with high all-year-round evaporation (figure 17). Usually, the areas along the coast with the highest rainfall also have the highest evaporation rates. However, some exceptions can be noted; for example, near Townsville and Gladstone on the eastern coast, around the southern shoreline of the Gulf of Carpentaria and in the vicinity of Wyndham and Derby on the western coast evaporation exceeds rainfall. Because rainfall is highly seasonal at these localities for six to eight months of the year, these areas are arid. These three areas correspond to the 2E, 2G and 2W biogeographic regions shown in figure 2 (chapter 1).

The inland margin of mangroves is particularly prone to high evaporative losses and drying out of the substrate. Often, an edge effect is noticeable where mangroves abut salt flats. The evaporative build-up of soil salinity results in mangrove dieback and gradual expansion of the salt flats. Similarly, where breaks occur in the canopy, especially in the mangroves towards the landward margin, evaporation may lead to increased soil salinities which, in turn, may prevent the regeneration of mangroves (Spenceley 1976). In the more humid tropics, on the other hand, rain wetting of leaf surfaces, cloud cover and high humidities reduce evaporative losses and the tendency towards salt flat formation is not so great.

Wind affects evapotranspiration from mangroves by the same mechanism as in other plants. However, because mangroves are at the land-sea interface, they tend to be more consistently exposed to windy conditions, and wind probably assumes a greater importance in relation to evapotranspiration in mangroves than in other plant communities.

As transpiration occurs, there is a tendency for a moist layer of air to form next to the leaf surface. This layer, termed the boundary layer, is variable in thickness, but in those mangroves with epidermal hairs or scales it is thicker than around those leaves with untextured surfaces. Wind conditions also affect the thickness of

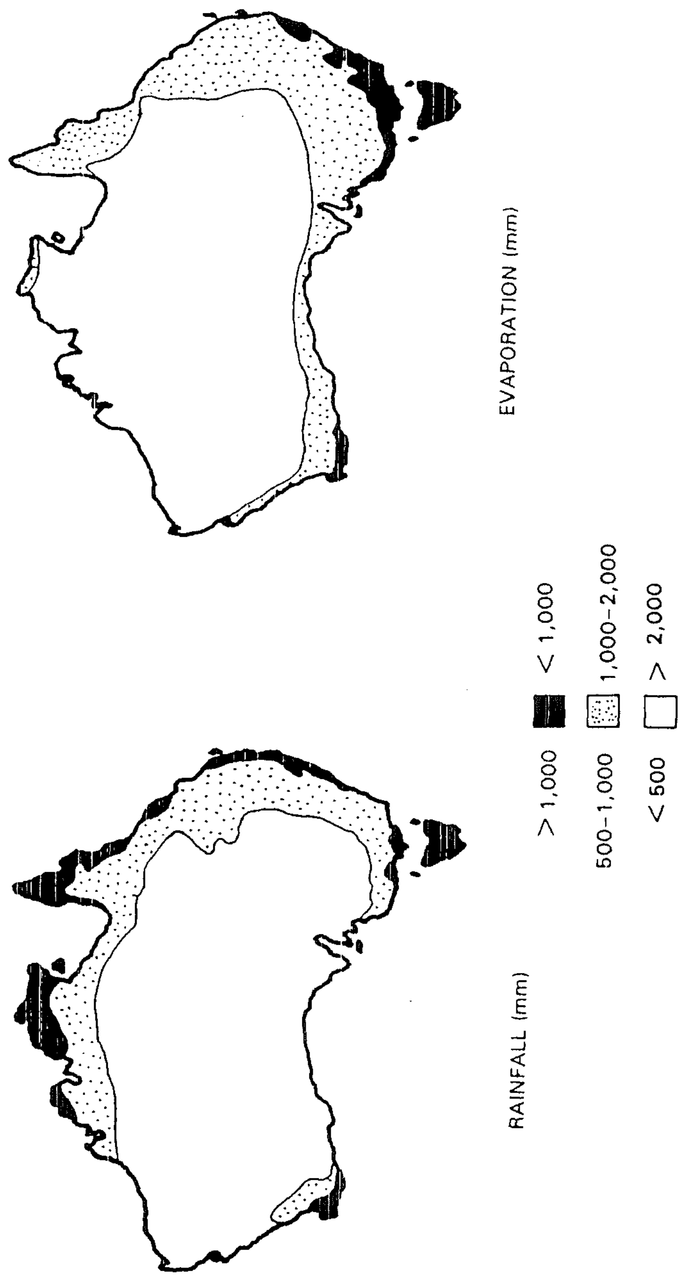


Figure 17 Annual rainfall and evaporation distribution in Australia.

this layer, with the greatest thickness in still air. The boundary layer decreases the diffusion gradient between the leaf and the atmosphere, and transpiration consequently decreases. On the other hand, air movement carries away this layer of humid air, replacing it with drier air, thereby causing an increase in transpiration. The more rapid the air movement, the faster the moist air will be carried away and the higher will be the rate of transpiration. If the wind is strong, stomata may close, possibly as a result of excessive water loss, and transpiration is then reduced. Temperature also affects the opening (Miller 1975) and closure (Steinke 1979) of stomata.

The implication to be drawn from the control of evapotranspiration by wind is that a plant within the general mangrove canopy will experience different growing conditions from one of the same species growing as an isolated individual at the front or the back of the stand. Indirect evidence of this was noted when *Phytophthora*-induced dieback became prevalent in the Port Curtis area on the central Queensland coastline. Pegg and Foresberg (1981) showed that *Phytophthora* killed its host (*Avicennia marina*) only when the host was also under some other sort of stress, especially water stress. The first trees to die were those growing as isolated specimens on mudbanks well away from the mangrove stands; these were followed by the very tall specimens which emerged well beyond the general level of the canopy, and it took approximately another year before the *Avicennia* within the mangrove canopy showed any signs of dieback.

The third aspect of wind relates to its effect on mean sea-level. Persistent onshore or offshore winds can raise or lower the effective mean sea-level to a considerable degree. Storm surges accompanying cyclones (table 9) are a dramatic illustration of this (although in this case there are pressure effects also). Wind patterns during normal conditions operate on a smaller scale, but nevertheless have physiological implications for the mangrove community.

Table 9 Storm surge heights recorded during cyclones in northern Australia

Date	Cyclone	Storm surge
1884	"Bowen"	3.0 m at Poole Island near Bowen
1899	"Mahina"	14.6 m at Barrow Point near Bathurst Bay
1918		3.7 m at Mackay
1918		3.0 m at Cairns to Ingham
1923	"Douglas Mawson"	7.0 m at Groote Eylandt in Gulf of Carpentaria
1931		0.8 m at Moreton Bay
1934		1.8 m at Port Douglas
1948		4.0 m at Sweers Island in the Gulf of Carpentaria
1958		1.6 m at Bowen
1964	Dora	4.6 m at Edward River Mission in Gulf of Carpentaria
1971	Althea	3.0 m at Townsville
1976	Ted	2.0 m at Karumba in the Gulf of Carpentaria

Munro (1973) described seasonal changes of mean sea-level of up to 1 metre in the southeastern part of the Gulf of Carpentaria owing to seasonally changing wind patterns (south to southeast in winter and mainly north to northeast in summer). Similar but less pronounced sea-level changes were detected from yearly tide recordings at Port Curtis on the central Queensland coastline (figure 18) where winter winds from the south to southwest are offshore and summer–autumn winds from the north to northeast are onshore.

Figure 18 Seasonal mean sea-level changes at Gladstone, Queensland, during 1975. Note that the long-term mean sea-level obtained from continuous tide records during 1970 to 1979 is also shown.

Even changes of 30 cm on a relatively flat coastline represent a significant increase in depth and frequency of tidal inundation and in terms of the area subject to tidal effects. The season during which such sea-level changes occur seems to be ecologically important. For example, in the Gulf of Carpentaria, mean sea-level is raised during the summer months when the river discharges are at their maximum. Consequently, flooding is frequent and freshwater inundation of the mangroves and salt flats aids in the leaching of salt from these communities. At Port Curtis, however, sea-level is raised during the dry autumn season and, rather than remove salt, may in fact contribute salt to those communities at or near high-water spring levels, particularly when winter evaporation is high. Occasional wetting of the salt flats during the dry autumn months at Port Curtis allows temporary development of filamentous algal mats which contribute to overall productivity. In contrast, the salt flats of the southeastern part of the Gulf of Carpentaria in the dry season are dried to the point of cracking, and are covered in salt crystals and are virtually lifeless (Saenger and Hopkins 1975).

Although it is too early to state categorically that seasonal changes in sea-level are important, the examples discussed above suggest that this is an area worthy of detailed investigation.

Drainage/Aeration

Soil aeration is important in mangrove environments in supplying oxygen for respiration. Aeration is directly related to soil drainage and is therefore highly variable. It depends upon elevation, steepness of the topography and the physical characteristics of the substrate, particularly texture. Experimental evidence is scant, but it does appear from field observations of distribution and growth that mangroves differ in their sensitivity to poorly drained and poorly aerated or anaerobic soils. As discussed in chapter 2, structures such as stilt roots, buttresses and pneumatophores are assumed to play a significant role in aerobic respiration of mangroves, although few data are available on their efficiency in terms of the plants' overall metabolic requirements.

Both aeration and drainage are relatively good in coarse-textured soils such as sand. However, there is a tendency for clays to accumulate even in coarse soils where these are frequently inundated. This accumulation results from the flocculant action of sea water on the one hand, and the physical reworking of sediments by tides and waves on the other. In consequence, drainage in the lower to middle regions of the intertidal zone may be reduced except in areas of turbulence owing to wave action or where there are high current velocities.

In those areas where the parent material of the catchment is predominantly argillaceous — that is, leading to the formation of clays during erosion — the entire estuarine system may consist of finely textured soils. Port Curtis on the Queensland coastline is an example (Jardine 1925; Conaghan 1966; Saenger and Robson 1977), with the major area of coastline consisting of clayey deposits, predominantly quartzite and albite. Even there, however, subsurface soil horizons of greater coarseness can sometimes provide good drainage and replenishment of oxygen through subsurface drainage. Finely textured sedimentary soils can act as plugs preventing drainage from higher elevations. Drainage problems at such sites may last for extended periods and impose stresses on the plants growing there.

Clays and sands are not the only soil types on which mangroves will grow. For example, Teas (1979) described mangroves growing on karst limestone formations with no sediment accumulation, and Macnae (1968), Thom (1975) and Stoddart (1980) reported them as growing on coral rubble on islands and cays in the northern Barrier Reef Province. However, in terms of aeration and drainage, sandy and clayey soils usually can be considered as the extremes in which mangroves will grow. The properties of these two kinds of soils are compared in table 10.

Table 10 Comparison of various soil characteristics between sand and clay

	Sand	Clay
Infiltration	High	Low
Porosity	High	Low
Permeability	High	Low
Seepage velocity	High	Low
Water-holding capacity	Low	High
Salt retention	Low	High
Leaching	Rapid	Slow
Capillarity	Low	High

Tidal inundation combined with specific drainage and aeration properties generally lead to mangrove soils characteristically having a high water content, low oxygen content, and often high levels of salinity, free hydrogen sulphide, Eh values between -100 and +400 mv and pH values ranging from 4.9 to 7.2. In addition, these soils are often semi-fluid and poorly consolidated.

The high water content (expressed on a wet-weight basis) of mangrove soils from Port Curtis ranges from 38 to 46 per cent in clay to 20 to 37 per cent in sand (figure 19). Clarke and Hannon (1967) reported higher values from Sydney mangrove soils, but their values were expressed on a dry-weight basis. When their values are converted to a wet-weight basis, the Sydney values for sandy mangrove soils range from 22.2 per cent to 58.9 per cent. These values are still significantly higher than those from Port Curtis, but the Sydney soils have a high content of roots and other organic material. Hesse (1961), working on West African mangroves, reported a moisture content (wet-weight basis) of 37.5 per cent in *Rhizophora* soils with 11.9 per cent fibrous organic matter, and only 33.9 per cent in soils with 5.5 per cent fibrous organic matter. Naidoo (1980), using South African mangrove soils, experimentally determined the moisture content at saturation using the methods of Bower and Wilcox (1965); saturation values ranged from 42.5 per cent in clay to 25.8 per cent in sand. In addition, a direct relationship was found between saturation water content and the organic content of the soil; the latter ranged from 2.5 to 6.3 per cent.

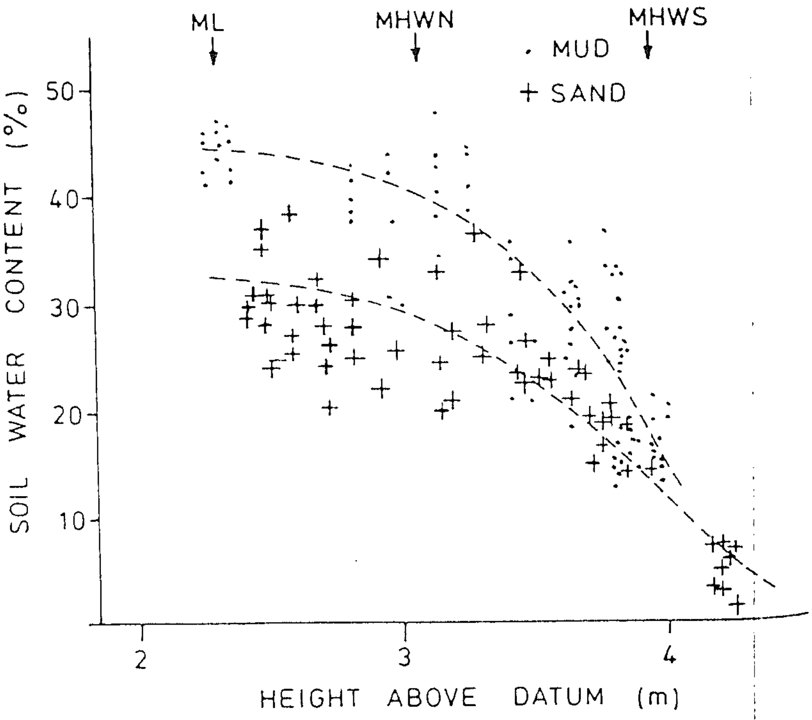


Figure 19 Soil water content (expressed as wet weight) from three study areas at Gladstone, Queensland, 1975–80.

Because many of the mangrove soils are nearly saturated most of the time, spaces in the soils are water-filled and consequently the penetration of oxygen, an essential requirement for active root growth and development, is reduced. Low soil oxygen levels generally lead to highly reducing conditions in the soil, a decrease in the soil pH, high soil Eh values and the formation of free sulphides or pyrites (FeS_2) from the anaerobic breakdown of organic matter.

Low rates of water infiltration into many mangrove soils can compound the already adverse soil conditions described above. Clarke and Hannon (1967) measured the infiltration rates into mangrove and saltmarsh soils in Sydney (table 11) and, with the exception of rates measured near crab holes, infiltration rates were low despite the sandy texture of these soils.

Table 11 Soil infiltration rates of mangrove soils in Sydney, NSW

Habitat	Replicate no.	Infiltration rate (cm/hour)	Mean
Mangrove	1	0	
	2	0.33*	
	3	0.08	
	4	0.02	
	5	0.36*	
	6	0.04	0.04
Salt marsh	1	0.30	
	2	0.67	
	3	0.25	
	4	0.02	
	5	0.42	
	6	0.06	0.29

* Near crab holes; values not included in means.
Source: Clarke and Hannon (1967).

With impeded drainage and little or no internal water movement, the interstitial water bathing the roots could quickly become exhausted of major plant nutrients. Low infiltration and the generally mediocre cation exchange capacity of the soils mean that little replacement of such nutrients occurs around the roots. Furthermore, in the immediate vicinity of the roots, the development of anaerobic conditions can lead to pH changes which, in turn, can change the availability of nutrients. For example, phosphorus becomes unavailable at low pH values.

The major effect of waterlogged soils, however, appears to be the induction of a root oxygen stress which, in turn, leads to decreased permeability of the root membranes, thereby inducing water stress on the plant. Two strategies have been adopted in terrestrial plants and it is likely that these are also of relevance to mangroves (Hook and Scholtens 1978).

In one strategy, auxin accumulates in the stem of the waterlogged plant, and the high levels of this growth hormone result in the formation of adventitious roots. For example, Snedaker, Jimenez and Brown (1981) reported intense aerial root formation in *Avicennia germinans* growing in areas subject to oil spills and prolonged waterlogging. It seems that by this strategy partial restoration of root function occurs, and water stress in the plant is reduced.

The second strategy also brings about a reduction in plant water stress by lowering the water loss through transpiration. Decreased cytokinin export from the waterlogged root system (Itai, Richmond and Vaadia 1968) and the accumulation of abscissic acid in the leaves lead to stomatal closure, rapid leaf senescence and shedding and a retardation of shoot development and elongation. All of these responses reduce the transpirational water loss. Growth rates of the shoots may also be reduced by the altered giberellin balance or the accumulation of ethylene in the plant; this may also contribute to a reduction of water losses through transpiration (Crawford 1978).

The root adaptations described in chapter 2 facilitate survival in the generally adverse soil environment of mangroves. Species vary, however, in their tolerance to soil conditions. For example, Hesse (1961) and Naidoo (1980) found that *Avicennia, Rhizophora* and *Bruguiera* grow on soils with different characteristics (table 12). Spenceley (1983) examined soil characteristics in various mangrove and saltmarsh zones at two Queensland localities; rather inconsistent patterns were found. Adequate characterization of Australian species of mangroves as far as tolerances to soil conditions are concerned awaits more complete data.

Table 12 Comparison of soils supporting stands of *Rhizophora, Avicennia* and *Bruguiera*

Soil parameter	Relative soil concentrations				
pH	Rhizophora	>	Avicennia	>	Bruguiera
S	Rhizophora	>	Avicennia	=	Bruguiera
N	Rhizophora	>	Avicennia		?
P	Rhizophora	>	Avicennia	>	Bruguiera
Organic carbon	Rhizophora	>	Avicennia	>	Bruguiera
Cation exchange capacity	?		Avicennia	>	Bruguiera
Exchangeable bases	?		Avicennia	>	Bruguiera
Exchangeable acidity	?		Avicennia	<	Bruguiera
Clay content	?		Avicennia	<	Bruguiera
Al^{+++}	?		Avicennia	<	Bruguiera

Source: After Hesse (1961) and Naidoo (1980).

The height of *Avicennia marina* appears to depend on drainage properties of the soil, with the tallest trees growing on well-drained banks close to streams (Chapman and Ronaldson 1958; Macnae 1966). Macnae (1966) maintained that *Ceriops tagal* in Australia is found only on well-drained soils, and he suggested that its virtual absence from areas of high rainfall may be as much due to drainage irregularities as to rainfall. Measurements of soil water content among *Ceriops tagal* stands along the Queensland coastline (Saenger and Robson 1977) do not support his suggestion but it is possible that considerable geographic variation occurs.

Macnae (1966) cited two examples of extreme variability in response to soil drainage: (1) *Rhizophora stylosa* grows on well-drained soils in Malaysia (Ding Hou 1958), whereas in Australia it grows on a range of substrates, but with the tallest trees occurring on soft, waterlogged muds; (2) in Australia, *Lumnitzera racemosa* is recorded from well-drained sandy soils on the landward fringe (Macnae 1966), but in southern Africa, however, Macnae (1966: 96) records it "as a true mangrove extending down to almost high water neaps".

Field data on the soil water content in which various species grow were collected from Proserpine from four sites over one-and-a-half years; the upper and lower limits are presented in table 13. Three groups, based on the water content of the soil on which they grow, can be recognized. *Osbornia octodonta* and *Bruguiera parviflora* grow on soils that have low water contents, either because of good drainage (*B. parviflora*) or because of their location on the landward margins of the mangroves where tidal inundation is infrequent (*O. octodonta*). The second group contains those species growing on soils with an intermediate water content and includes *Bruguiera gymnorhiza, B. exaristata, Clerodendron inerme* and the mangrove fern *Acrostichum*. The third group, containing eleven species, grows in soils that have high water contents, either because of frequent tidal inundation (such as *R. stylosa* and *A. marina*), or because high freshwater run-on occurs (such as *Heritiera littoralis* and *Cynometra iripa*).

Table 13 Soil water content at which various species occurred at Proserpine, Queensland, October 1980–May 1982 (water content is expressed as percentage of wet weight of soil)

Species	% soil water content
Osbornia octodonta	9–17
Bruguiera parviflora	17–21
Bruguiera gymnorhiza	21-27
Bruguiera exaristata	22–29
Clerodendron inerme	22–28
Acrostichum speciosum	22–28
Heritiera littoralis	26–28
Lumnitzera racemosa	27–30
Xylocarpus australasicus	28–33
Xylocarpus granatum	28–30
Cynometra iripa	28–38
Rhizophora stylosa	29–37
Ceriops tagal	29–32
Acanthus ilicifolius	30–32
Excoecaria agallocha	31–32
Avicennia marina	31–34
Aegiceras corniculatum	32–38

Although the above grouping is tentative, it provides some indication of the soil water regime under which the various species grow. It provides no information on the tolerances of these species under extreme conditions.

Salinity of the Soil Water

Salinity of the interstitial soil water has long been recognized as an important factor regulating growth, height, survival and zonation of mangroves (Bowman 1917; Macnae and Kalk 1962; Mogg 1963; Macnae 1968; Cintron et al. 1978; Teas 1979; Semeniuk 1983). The physiological importance of salinity has been investigated using culture experiments and these have provided many useful results (Connors 1969; Sidhu 1975a). However, in the field, the response to salinity is more variable, and mangroves have been found at salinity levels that exceed those suggested by laboratory experimentation. For example, Macnae (1968) showed that *Avicennia marina* and *Lumnitzera racemosa* can tolerate salinities of up to 90‰ in the soil whereas *Rhizophora mangle* is probably limited by soil salinities above 65‰ (Cintron et al. 1978; Teas 1979). *Avicennia germinans* was reported to become dwarfed and gnarled in Florida when soil salinities approached 60–80‰ . In culture, *Avicennia* and *Aegiceras* showed maximum growth at 25 per cent sea water (figures 20, 21).

Soil salinity is regulated by a number of factors, including tidal inundation, soil type and topography, depth of impervious subsoils, amount and seasonality of rainfall, freshwater discharge of rivers, run-on from adjacent terrestrial areas, run-off and evaporation. However, in tidally inundated situations, evaporative losses and the frequency of flooding are the major factors determining soil salinity (Oliver 1982). Other climatic factors, such as humidity, wind velocity and high solar radiation together with the extent of plant cover, have a significant influence on evaporative losses from the mangrove community.

Particularly where the clay content is high, soils have a high resistance to internal salt and water movement (Clarke and Hannon 1967; Blackmore 1976). As a result, tidal inundation, rainfall and evaporation principally affect the soil surface, although with time an equilibrium with the soil at considerable depths will be reached. However, as an approximation, an initial understanding of the regulation of soil salinities can be made considering only the surface processes. At any particular point in the intertidal gradient the soil salinity can be directly related to:

- salinity of the tidal water
- time interval between inundations
- rainfall
- evaporation rate
- retention properties of soil
- run-on minus run-off.

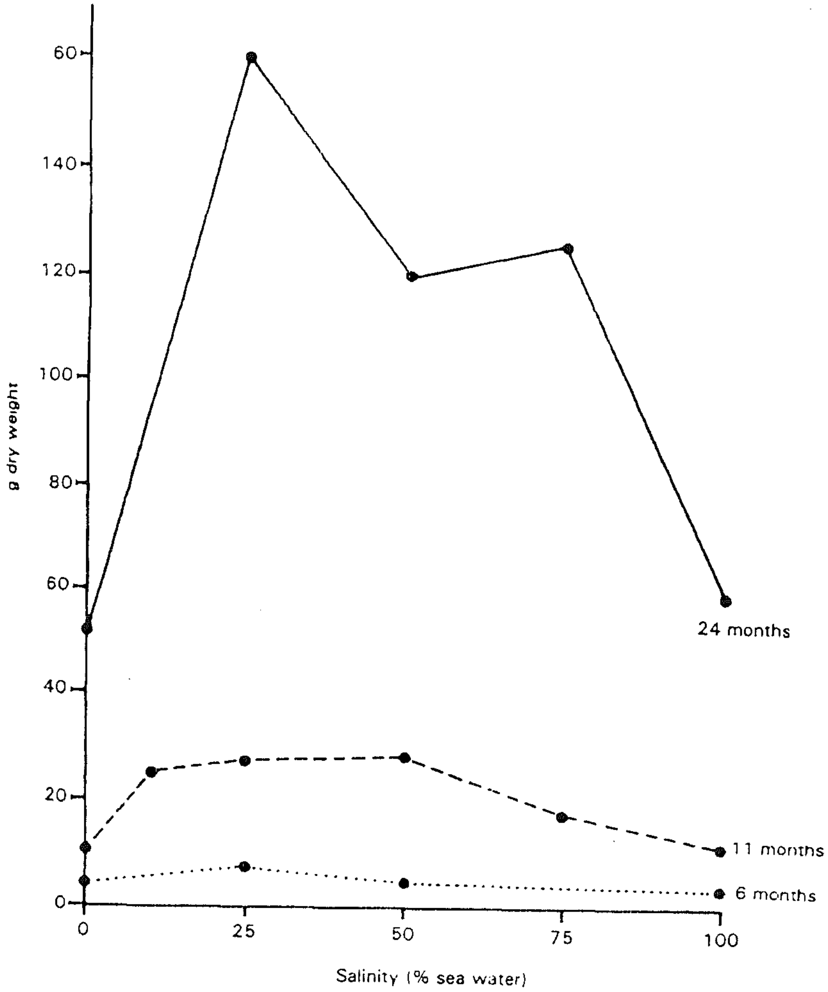


Figure 20 Growth (measured as grams of dry weight per plant) of *Avicennia marina* at various seawater concentrations over varying periods (24 months – B. Clough; 11 months – Downton 1982; 6 months – C.D. Field).

At any one locality, several of these processes are more or less constant, including evaporation, rainfall and run-on/run-off. Salinity of the tidal water and soil properties also can be relatively constant at a particular locality, and in this instance the soil salinity along the intertidal gradient is determined more or less by the time interval between inundations. For example, on the central Queensland coastline, where clayey soils predominate, where rainfall is low and

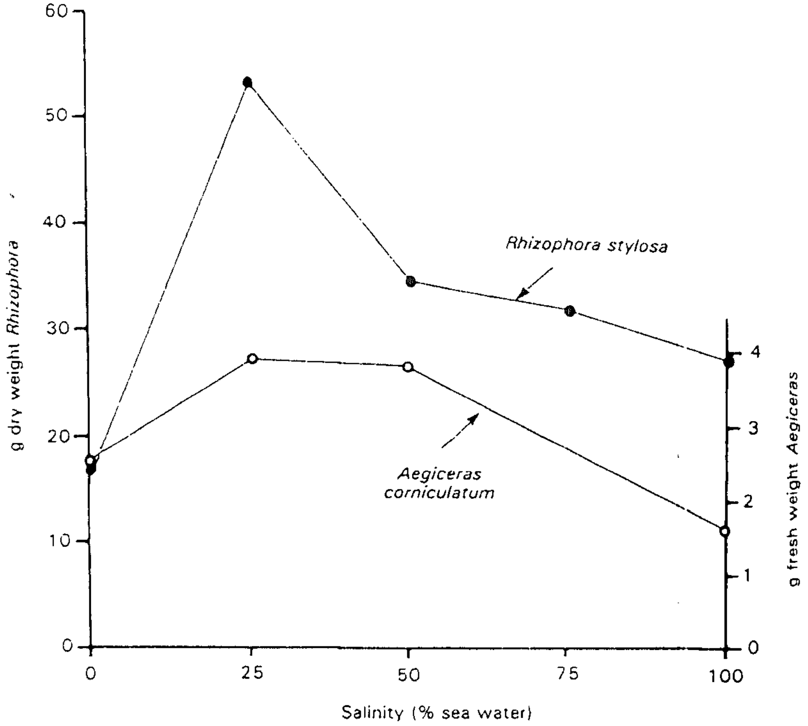


Figure 21 Growth of *Aegiceras corniculatum* (grams fresh weight per plant) and *Rhizophora stylosa* (grams dry weight per plant) at various seawater concentrations for 6 and 12 months respectively (*Aegiceras* – C.D. Field; *Rhizophora* – B. Clough).

evaporation high, and where run-off and run-on are negligible, the soil salinity shows a maximum at or just below mean high-water spring level where inundation occurs approximately four hundred times per year, but only 5 per cent of the total time (figure 22). It is clear, however, that at another locality with lower rainfall and higher evaporation, the soil salinity maximum may be broader and located lower down in the intertidal gradient. On the other hand, where rainfall greatly exceeds evaporation, no soil salinity build-up occurs, and the soil salinity will simply show an approximately linear decrease from seawards to landwards.

Baltzer and Lafond (1971) listed two extremes of coastal environment with respect to interstitial soil salinity: (1) areas of high rainfall that are permanently wet, where the soil salinity decreases progressively from the sea towards the inland and the vegetation ranges from mangroves to inland vegetation without discontinuity; and (2) areas of low rainfall where dry and wet seasons alternate, and where salt flats and/or saltmarshes appear between the mangrove community and the inland vegetation.

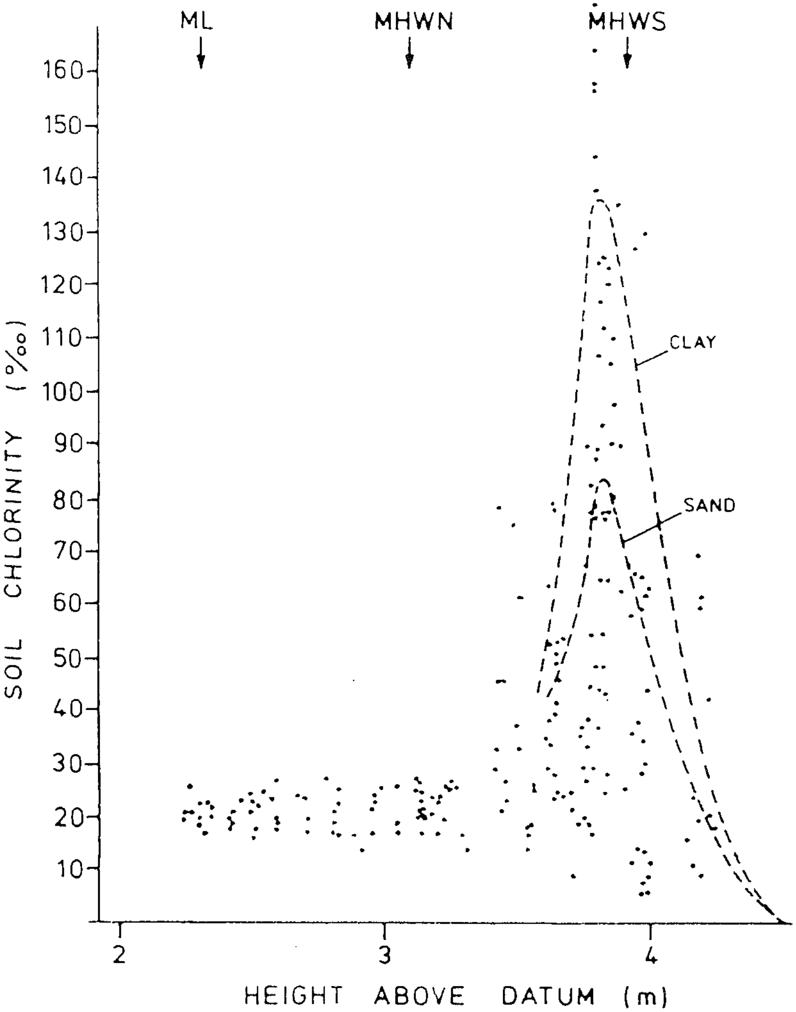


Figure 22 Relationship of soil chlorinity to tidal levels at four study areas at Gladstone, Queensland, 1975–80.

Both of these extremes are well represented in Australia: extensive mangrove communities with landward saltflats occur from Gladstone to Townsville and at Princess Charlotte Bay in Queensland (Fosberg 1961; Macnae 1966; Saenger and Robson 1977; Saenger et al. 1977; Elsol and Saenger 1983), in the southeastern Gulf of Carpentaria (Saenger and Hopkins 1975) and around Cambridge Gulf in Western Australia (Thom, Wright and Coleman 1975). These have been identified as biogeographic zones 2E, 2G and 2W/2Wa in figure 2 (Saenger et al. 1977; Semeniuk, Kenneally and Wilson 1978). On the other hand, mangroves abutting directly on to landward vegetation occur in the high-rainfall areas of Papua New Guinea (Taylor 1959) and northern Australia, and on the eastern coastline south of Brisbane where rainfall is rather uniformly distributed throughout the year.

The tolerance of Australian mangroves to various levels of soil salinities is poorly known, and until more laboratory and field data are available conclusions must remain tentative.

From the limited data available (table 14), it can be appreciated that salinity tolerances of Australian mangroves are not clear-cut. Ranking the species for the various salinity parameters does not show any consistent sequence of species either in the field or in culture. However, the following points are worth noting. *Avicennia marina* appears to grow over the largest salinity range whereas *Cynometra iripa* and *Heritiera littoralis* seem to have the narrowest ranges and do not grow where salinity is high. *Rhizophora stylosa*, *Aegialitis annulata*, *Bruguiera gymnorhiza* and *Ceriops tagal* grow at salinities up to three to four times the concentration of sea water. *Aegiceras corniculatum* will tolerate extremes of salinity both at high and low concentrations, although its overall range is less than that of *Avicennia marina*.

Where data are available for pairs of species, generally one is found at high-salinity levels and the other at lower levels: high — *A. marina*, *B. gymnorhiza*, *C. tagal*, *L. racemosa*, *R. stylosa*, *S. alba*, *X. australasicus*; low — *A. officinalis*, *B. sexangula*, *C. decandra*, *L. littorea*, *R. apiculata*, *S. caseolaris*, *X. granatum*. Bunt, Williams and Clay (1982) examined upriver distributions of mangroves and related these to the upriver salinity gradients in order to determine the extent to which salinity explains the observed pattern of distribution. Five rivers were examined in north-eastern Queensland and, although some variation was found among river systems, nine species showed significant correlation with upriver salinity gradients. Of these nine species, four showed positive correlations, that is, they occurred at the high-salinity areas and were absent at lower salinities. These were *Rhizophora stylosa*, *R. apiculata*, *Sonneratia alba* and *Ceriops tagal*. Five species (*Heritiera littoralis*, *Excoecaria agallocha*, *Acrostichum* sp., *Aegiceras corniculatum* and *Rhizophora mucronata*) showed negative correlations in the above ranking, indicating their presence in the upstream, low-salinity areas. Three further species (*Avicennia*, *Bruguiera gymnorhiza* and *Xylocarpus granatum*) showed no significant correlations suggesting that they can grow over almost the complete salinity range from fresh water to sea water, and that their upriver distributions are determined by factors other than salinity.

Table 14 Salinity data for Australian mangroves

Species	Salinity Parameters (‰)			
	Max. salinity of tidal water (Wells 1982)	Soil salinity range over 1.5 years, Repulse Bay, Qld	Mean soil salinity and range over 7 years, Port Curtis, Qld	Salinity for optimal growth in culture
Acanthus ilicifolius	65	40–44		8[c]
Acrostichum speciosum		61–90		
Aegialitis annulata	85		33–83–114	
Aegiceras corniculatum	67	34–36	16–85–148	8–15[g]
Avicennia marina	85	24–34	11–126–300	8–15[a, c, d, e, f]
Avicennia officinalis	63			
Bruguiera exaristata	72	53–69		8[c]
Bruguiera gymnorhiza	37	59–62	33–79–85	8[c]–34[b]
Bruguiera parviflora	66	61–90		8[c]–17[b]
Bruguiera sexangula	33			
Camptostemon schultzii	75			
Ceriops decandra	67			17[b]
Ceriops tagal	72	35–39	49–110–300	34[b]
Clerodendron inerme		60–63		
Cynometra iripa		8–15		
Excoecaria agallocha	85	33–44		
Heritiera littoralis		9–16		
Lumnitzera littorea	35			
Lumnitzera racemosa	78	36–41	11–47–110	
Osbornia octodonta	56	92–99		
Rhizophora apiculata	65			8[c]
Rhizophora stylosa	74	33–35	43–92–148	8[c]
Scyphiphora hydrophyllacea	63			
Sonneratia alba	44			
Sonneratia caseolaris	35			
Xylocarpus australasicus	76	30–34		8[c]
Xylocarpus granatum	34	25–29		8[c]

[a] Connors (1969)
[b] Sidhu (1975)
[c] Clarke and Hannon (1970)
[d] Farrell (1973)
[e] Clough (unpubl. data)
[f] Downton (1982)
[g] Field (unpubl. data)

Bunt, Williams and Clay (1982) concluded that, to the extent generalizations are possible from their analysis, the species can be ranked in order of decreasing tolerance of or adaptation to sea water: *Rhizophora stylosa*; *R. apiculata*; Sonneratia alba; *Ceriops tagal* > *Aegiceras corniculatum*; *Bruguiera parviflora* > *Excoecaria agallocha*; *R. mucronata*; *Acrostichum* sp.; *Heritiera littoralis*; *Nypa fruticans* > *Barringtonia* sp.; *B. sexangula*; *Sonneratia caseolaris*; *Hibiscus tiliaceus*. Although this ranking shows some similarities to those in table 14, particularly that of Wells (1982), it must be remembered that salinity of the tidal water is only one of the variables determining soil salinities and that the salinities immediately adjacent to the roots of mangroves — be they maxima, minima, means or ranges — will ultimately determine growth and success of mangroves in that particular situation. As Bunt, Williams and Clay (1982) have emphasized, tidal water salinity is only one of the factors affecting the distributions of even those species with significant correlations. In the case of those species not showing significant correlations, factors other than salinity appear to be more important.

Interaction of soil texture with salinity tolerance of mangroves was suggested by experimental studies on the effects of hypersalinity (McMillan 1975b). Two American mangroves — *Avicennia germinans* and *Laguncularia racemosa* — were experimentally subjected to hypersaline conditions while growing in a range of soils with differing clay contents (McMillan 1975). Seedlings of various ages up to three-and-a-half years were subjected to salinities up to five times that of sea water for forty-eight hours, and their responses noted. In soils with a high sand content, whether coarse- or fine-grained, the plants failed to survive this treatment. In soils with a clay content of 7–10 per cent, the hypersaline exposure was tolerated. *Avicennia* seedlings tested over a broad range of salinity survived forty-eight-hour exposure to 60‰ in sand and water culture but failed to survive at higher salinities (McMillan 1975b).

It was suggested by McMillan (1975b) that, although the actual mechanisms underlying interaction of soil texture and salinity tolerance is not understood, depression of the pH in all the experimental soils indicated the involvement of cation exchange. It was suggested that in clay soils the exchange of Na^+ and H^+ ions may reduce the salinity of the interstitial water immediately around the roots, and that the adsorption of Na^+ ions would cause the clay particles to deflocculate. In turn, this would reduce the contact of roots and hypersaline water, thereby facilitating the uptake of water and simultaneously reducing the uptake of salt; wilting and salt excretion by the experimental plants suggested that this took place (McMillan 1975b).

Whether such a mechanism operates in the field has not been investigated, but some supportive evidence suggests that it does. Core samples of clayey soils from salt flats on the seasonally arid coastline of Queensland were compared with clayey soils from adjacent monospecific stands of *Ceriops tagal*. The results obtained (figure 23) indicate a higher water content in the soils of the salt flats, particularly at depth, than in those under *Ceriops*. The soil salinity is also higher on the salt flats than among the *Ceriops*, but it should be noted that in the *Ceriops* soil only surface salinities are high and there is a decrease with depth. X-ray fluorescence analyses of these soils showed that concentrations of two major soil components — calcium and iron — were twice as high in the *Ceriops* soils as in those of the salt flats.

Blackmore (1976) has shown that calcium is involved in reversing the "salt-sieving" ability of clay soil aggregates, a process whereby salt is constrained within the pores of clay particles by anion exclusion. He also found that when sodium ions are present but salt is at relatively low concentrations, salt is trapped and held within the microfabric of the clay. In the presence of calcium ions and when salt was at high concentrations this retention could be reversed, so that salt moved out of the clay much more easily.

In other words, in highly saline situations, the tendency for salt retention by clays appears to be reduced by high calcium ion concentrations, or by the addition of gypsum (Blackmore 1976). Consequently, the concentration of exchangeable calcium in the clay will modify the salinity of the pore spaces with which the roots are in direct contact. The possibility thus exists, that the often sharp boundary between salt flats and *Ceriops* stands is influenced not only by water content and salinity *per se*, but also by the levels of exchangeable calcium.

Height of the Watertable

The subsurface height of the watertable is one of the complex of factors determining the water status of the soil. At the outset, however, it should be emphasized that a "watertable" — the upper surface of free-moving interstitial ground water — is expressed only in those soils whose texture allows such a water surface to develop. In clays, with their low infiltration, low lateral and vertical seepage velocities, low porosity, low permeability, high water-holding capacity and high capillarity, such an internal water surface rarely develops. Clays may be saturated beyond a certain depth, above which they might be below their water-holding capacity. Nevertheless, a hole drilled to the saturated clay level will not fill with water. This is in sharp contrast to sandy or loamy soils in which an actual internal water surface may exist (Ericksen 1970; Lanyon, Eliot and Clarke 1982), and where a hole drilled to an adequate depth will fill with water at a rate depending on permeability and on the lateral seepage velocity.

Despite this reservation, the concept of a watertable, even in

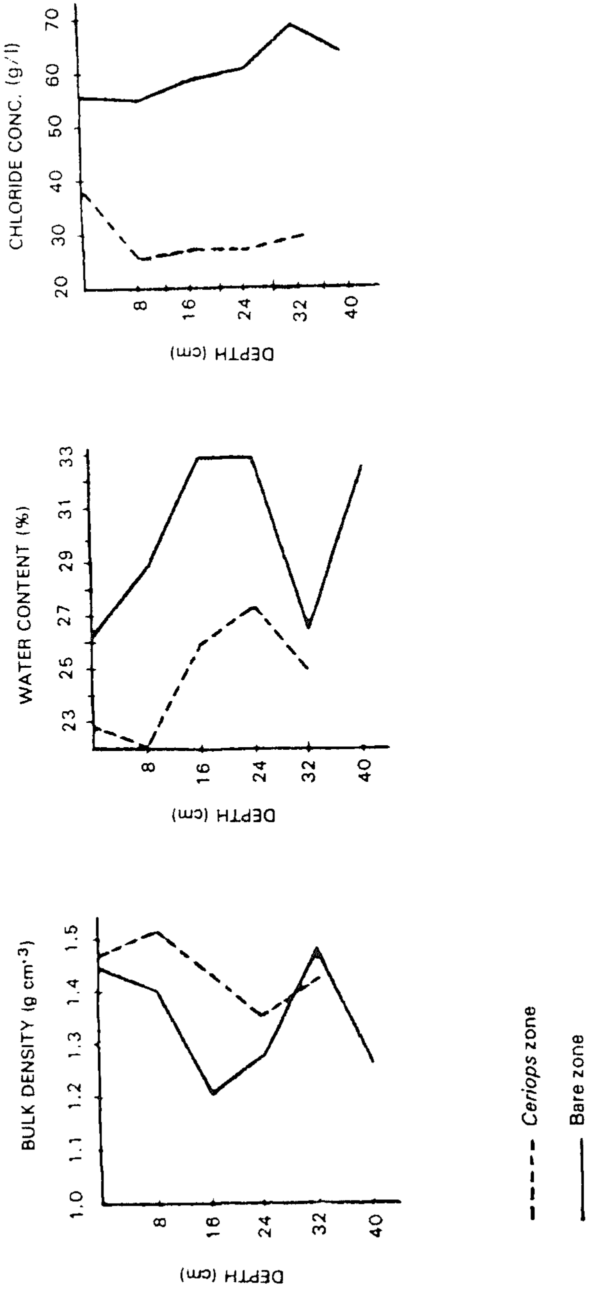


Figure 23 Characteristics of the soils from the vegetation-free salt flats and adjacent mangrove (*Ceriops*) communities at Gladstone, Queensland.

clays, is a useful one, and in the field, plugs or layers of coarser materials or crab burrows can facilitate subsurface flows in clay and result in considerable groundwater movement.

The importance of the subsurface height of the watertable to mangrove and saltmarsh communities has received little attention except by Chapman (1938) and more recently by Clarke and Hannon (1969) and by Semeniuk (1983).

Chapman (1938) found an almost linear relationship between tide and watertable level for non-flooding tides, whereas during flooding tides, even when the surface was inundated, the watertable rarely rose to the surface. This was considered to be due to an aerated layer in the mud immediately below the surface.

Clarke and Hannon (1969) studied the movement of the watertable in Woolooware Bay, Sydney, by inserting perforated plastic tubes into the ground and measuring the level of water that accumulated in them. They found that tides were the most important factor in determining watertable height, and that watertable fluctuations were greatest in the mangroves, followed in descending order by the saltmarsh and *Casuarina glauca* zones. They also found that heavy rainfall caused a rise in watertable level, but this effect was diminished by the fact that water may lie on the soil surface without infiltrating.

The physical properties of the soils in Woolooware Bay suggest that rapid drainage should occur, but the infiltration rates showed such not to be the case (table 11). Clarke and Hannon (1969) observed that both rainwater and sea water may lie on the soil surface for some days when the watertable is several centimetres below the soil surface. This appears to support Chapman's (1938, 1960) hypothesis that even when the soil is covered by a flooding tide, air is available to plant roots because it is trapped just below the soil surface in small pockets. On the other hand, Clarke and Hannon (1969) found that the water level did rise to the surface especially during spring tides, and they did not substantiate Chapman's (1938) hypothesis in its entirety. They concluded that an aerated layer may be present in poorly drained areas, but in their study area such a layer did not exist throughout.

The fact that the amount of water lying on the surface is not necessarily an accurate indication of watertable depth (Clarke and Hannon 1969) has certain implications of relevance to clayey soils. The relationship between tidal and watertable movement may be the result of lateral seepage owing to saturated flow rather than to actual inundation. This could be due to the permeability of the subsurface soil being greater than that of the surface soil, or possibly because the forces behind tidal movement are more effective in causing lateral seepage than in causing vertical seepage. As pointed out earlier, in clayey soils, layers of shell material and crab burrows are important in facilitating lateral flows (Wolanski and Gardiner 1981).

Additional implications are that (1) heavy rainfall is relatively ineffective in leaching salt down into the soil, (2) evaporation of water lying on the soil surface is important in overall salt balance, and (3) if an area can be flooded by sea water without infiltration, tidal inundation may not always add fresh salt but may, in fact, dissolve salt crystallized on the soil surface. These points have been discussed under the section on soil salinity, and at least for clayey soils the assumption has been made that soil salinity is largely determined by surface processes.

The ecological role of watertable heights and fluctuations is poorly understood. Clarke and Hannon (1969: 232) suggested:

> The various components of the physiographic factors are closely interrelated, but that the overall governing element is that of the tide-elevation complex which control plant distribution through the frequency of inundation and exposure, mechanical action of tidal water and salinity. The movement of the watertable and drainage and aeration in the soil are less important components of the tide-elevation complex in explaining plant distribution.

By following salinity changes in a small mangrove creek on Hinchinbrook Island, Queensland, Wolanski and Gardiner (1981) were able to postulate that considerable salt was removed from the mangroves bordering the creek by groundwater flow during periods of non-inundation, and that once back in the creek, tidal flushing removed salt from the creek. This finding is at odds with that of Clarke and Hannon (1969), who suggested that even heavy rainfall is ineffective in leaching salt through the soil. At Hinchinbrook Island, however, Wolanski and Gardiner (1981) observed that rainwater percolated directly into the mud with no surface run-off; in other words, the Hinchinbrook muds have extremely high infiltration rates. In this system, groundwater flows were observed to be the dominant water-transport process, at least when inundation was minimal, and it was greatly accelerated near the surface of such biological disturbances as crab holes (Wolanski and Gardiner 1981).

Another potential role of watertable movement was postulated by Hicks and Burns (1975) from their study of the effects of drainage canals which intercept the overland sheet flow in the mangroves of southwestern Florida. They suggested that nutrients regenerated by the breakdown of detritus may be transported into the root zone of the mangroves by the vertical motion of the watertable; unfortunately, no evidence to affirm or negate this suggestion is presently available.

It thus seems that, although the ecological role of watertable levels (or groundwater flows) is not clear, fluctuations in watertables are relatively unimportant in explaining plant distributions within the mangroves and littoral complex (Clarke and Hannon 1969); they may be important in salt flushing (Wolanski and Gardiner 1981) and nutrient recycling (Hicks and Burns 1975). However, in view of the apparent array of adaptations to growing in waterlogged and oxygen-deficient conditions displayed by mangroves as a group, it seems that, along with drainage and waterlogging, watertables close to the surface give mangroves a competitive edge over other plants lacking such adaptations which might otherwise invade this environment.

Nature of the Soil

The nature of the soil in a mangrove community is largely determined by a range of geological and geomorphological processes. Some of these (such as sea-level change or erosion) may affect the mangroves directly, but more often they change certain characteristics of the sediment which, in turn, renders it more (or less) suitable for mangrove growth and development.

Mangrove communities develop best in sheltered depositional environments where, in the absence of drastic resculpturing of the coastline, there is a steady accretion of sediments. A gradual elevation of the sediment surface in relation to sea-level results, and with it a gradual change in soil water characteristics. However, such gradual and directed changes rarely occur, for the coastal environment is a dynamic one where erosion occasioned by storms or flooding can rapidly reverse the biologically mediated depositional phase (Bird 1971, 1972; Spenceley 1982). The likelihood of such disruptive change depends on the geography of the coast and on its geomorphological history.

Two major types of intertidal landforms can be recognized: those which contain a veneer of transported or trapped sediment over a consolidated parent material, and those which are the result of sedimentary accretion, producing prograding shorelines (Thom 1982). The latter is the more common and includes many fringing substrates and deltas. The former type may be important regionally, for example, where sediments accumulate over fossil coral platforms. This type also includes the comparatively narrow terrigenous beaches which occur along sunken river valleys.

Stability of the landform is strongly influenced by differing geomorphological origins. Accretion or erosion may be a continuing, seasonal or periodic process in depositional substrates. Modification of the landforms of more consolidated shores may be intermittent and arise from catastrophic events such as severe storms.

Thom (1967, 1975) and Thom, Wright and Coleman (1975) studied the ecology of mangroves in terms of the response of the plants to habitat change induced primarily by geomorphic processes. They considered that given the climatic-tidal environment and a pool of mangrove species, each of which possesses a certain physiological response to habitat conditions, the history of the land surface and contemporary geomorphic processes jointly determine the nature of the soil surface on which mangroves grow (Thom 1982). Such attributes of the substrate as moisture content, texture, salinity, redox potential and chemical composition are, to a large extent, a function of past and present geomorphic processes. The mangroves reflect each of these geomorphic situations by responding to the environmental gradients of elevation, drainage, stability, soil characteristics and nutrient input, which each of these situations produces. According to the physiological response of species to moisture and/or salinity stress, for example, there will be more, or less, favourable plant growth in a particular habitat. Thus, landform properties and geomorphic processes find expression in the variation in growth, morphology and metabolism of mangroves along environmental gradients.

Although mangrove development is bound historically to the geomorphic processes of a region, it is an expression of the resultant properties of the soils that occur there. From an ecological viewpoint, a study of the soil relationships of the mangroves will provide more direct information on mangrove growth and development than will historical (geomorphological) analysis. This is not to deny the importance of geomorphological studies, for these place mangrove soil characteristics into broader, more causally related contexts. For example, Spenceley (1983) showed that there are differences in elemental concentrations between open accreting shores and estuarine coastlines, and that the temporal and spatial behaviour of the elements also differ.

Understanding mangrove-soil relationships is complicated by the ability of most mangrove species to grow on a variety of substrates and because they often alter the substrate through peat formation or by changing the pattern of sedimentation. Mangrove trees are found on a wide variety of substrates including muds, silts, peat, sand, and even rock and coral shingle, provided there are sufficient crevices for root attachment. Mangrove ecosystems, on the other hand, appear to be best developed only on muds and fine-grained sand (Butler et al. 1977a; Galloway 1982); these muds are often highly saline and gypseous, with soft loose surfaces showing neither seasonal cracking nor change in texture with depth. These physical characteristics are important in terms of the drainage and aeration of the soils.

The composition and texture of the soil also can affect its salinity on the one hand, and the response by mangroves to that salinity on the other.

Nutrient availability in mangrove soils is another important consideration of mangrove-soil relationships. Although the level of nutrients in a particular mangrove soil will reflect the chemistry of its parent material and of the surrounding waters, the availability of nutrients will depend largely on the type of soil and its microbial characteristics.

For the two major plant nutrients — nitrogen and phosphorus (N and P) — microbiological processes are the main determinants of their release in a form available for plant growth. In the mangrove environment, nitrogen becomes available through microbial fixation of atmospheric N_2 and through the biological decomposition of organic matter in the soil. Nitrogen bound up in proteins is converted to ammonia by numerous proteolytic bacteria and fungi; this process is termed "ammonification". Ammonia can serve directly as a source of nitrogen but, more importantly, it provides energy for nitrite bacteria which, in the presence of oxygen, oxidize the ammonia to nitrite. As a rule, the nitrite is further oxidized to nitrate by another group of nitrifying bacteria; this whole process is termed "nitrification". These various pathways are summarized in table 15.

Table 15 Microbial reactions involved in the availability of nitrogen for plant growth

Process	Facilitating organisms	Reaction
1. N_2 fixation	N_2 fixers e.g. bacteria and blue-green algae	$8\ H^+ + N_2 \rightarrow 2\ NH_4^+ - \text{Organic N}$
2. Ammonification	Most proteolytic bacteria and fungi	$\text{Organic N} - NH_4^+$
3. Nitrification		
(a) Nitrition	Nitrite bacteria	$NH_4^+ + 1\tfrac{1}{2}\ O_2 - NO_2^- + H_2O + 2\ H^+$
(b) Nitration	Nitrifying bacteria	$NO_2^- + \tfrac{1}{2}\ O_2 - NO_3^-$

Studies of nitrogen fixation in mangroves have been limited (Zuberer and Silver 1975, 1978; Kimball and Teas 1975; Potts 1979; van der Valk and Attiwill 1984). In the mangroves of Florida, Zuberer and Silver (1978) found that the order of nitrogen-fixing activity was: plant-free muds < plant-associated muds < root tissue of *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*. Most of the nitrogen fixation appeared to be carried out by photosynthetic bacteria.

Zuberer and Silver (1975) suggested that the establishment of a nitrogen-fixing bacterial population around the roots may be a critical factor in mangrove establishment during early stages of stand development when trapped detritus is minimal and nitrogen is limiting. Furthermore, once such microbial populations are established, the rates of nitrogen fixation are sufficient to supply much of the nitrogen requirements for these Floridian mangrove communities (Zuberer and Silver 1978).

The importance of nitrogen fixation to Australian mangrove communities is questionable; preliminary studies of northern Queensland mangroves have not revealed any potential areas of high nitrogen-fixing activity (Boto 1982), and van der Valk and Attiwill (1984) found low rates of nitrogen fixation associated with the root zone and sediments of the mangroves in Westernport Bay, Victoria. Consequently, the process of ammonification and nitrification may be more important for maintaining nitrogen levels in Australian mangrove soils.

With the seasonal discharge of fresh water, a short-term increase in phosphate occurs in Australian estuaries (Rochford 1951; Spencer 1956). This phosphate does not remain in the water column but becomes adsorbed on the sediments and suspended particulate matter as insoluble ferric phosphate (Rochford 1951). Under reducing conditions resulting from an oxygen deficiency in the overlying water or through bacterial activity, ferric phosphate is reduced to ferrous phosphate and may subsequently be leached into the water column. Evidence in support of the bacterial mediation of such phosphate adsorption and release (Mee 1978) comes from two studies which demonstrated that (1) this process was temperature dependent and (2) poisoning the sediments with formalin impeded phosphorus exchange between the sediments and the water column. Thus, the sediments from mangrove areas are able to remove dissolved phosphates from the overlying water and bind them. In the reduced mangrove sediments, they would then be available for uptake by mangrove rootlets, and the generally clayey nature of the soils, with their low porosity, would prevent leaching and loss of these soluble phosphates to the overlying waters. As phosphate retention is more efficient in fine sediments than in coarse ones, fine sediments generally possess a greater store of available phosphates; this may partly explain the better development of mangrove communities on fine sediments such as alluvial muds in deltaic environments.

Work on Hawaiian mangroves by Walsh (1967) demonstrated that there is considerable removal of nitrate and phosphate from the tidal water entering the mangrove community. Carter et al. (1973) and Lugo, Sell and Snedaker (1976) confirmed these observations for mangrove communities in Florida. Comparative data from Australian mangrove communities are presently not available (Boto 1982), but it seems likely that the removal of nutrients from overlying tidal waters (sea water and land drainage) together with the release of NO_3 from organic material in the soil are the major mechanisms for maintaining nutrient availability in Australian mangrove soils.

The response of an entire mangrove community to nutrient input and cycling was studied by means of a mathematical model (Lugo, Sell and Snedaker 1976) based on a mangrove forest in southern Florida. In this model, the incoming radiation interacts with nutrients and the mangrove plants to form organic matter through the process of photosynthesis. Some of this gross production is respired by the forest, some is stored as a net increase in forest biomass, and some is deposited on the forest floor as detritus. The detritus may be exported from the forest to the estuary by tidal action. Some of it is grazed *in situ* by mangrove consumers, and some decomposes or accumulates as peat. Decomposition may occur under the influence of oxygen-saturated waters of incoming tides, or of atmospheric oxygen when the forest floor is exposed to the air. Decomposition of detritus within the mangrove system represents a source of nutrients for photosynthesis. Other nutrient sources are from terrestrial drainage, tidal waters, rainfall and sediment storage. Of these, terrestrial drainage is the most significant. In the model, they are all grouped as a single source. Some nutrients are not used and are lost from the system; the rest are sequestered through plant photosynthesis, thus completing the cyclic loop in the model. This model was validated using field data for the various forcing functions, state variables and for the flows within the system, including nutrient input, nutrient uptake and nutrients either not used or exported in the detritus.

The model was highly sensitive to nutrient availability, and when nutrient input to the system was set at zero, mangrove biomass decreased steadily. The decrease in mangrove biomass, gross photosynthesis and nutrient storage with three levels of nutrient input are shown in figure 24. These simulations indicate the dependency of mangrove communities on nutrient inputs derived from the land. Decomposition within the forest and inputs from sea water do not seem to be enough to maintain the observed rates of metabolism because of losses via detrital export. Lugo, Sell and Snedaker (1976) found that the contribution of nutrients from land drainage was ten to twenty times that from sea water during the dry and wet seasons respectively.

Lugo, Sell and Snedaker (1976) concluded that gross photosynthesis appears to be sensitive to terrestrial nutrient input and that the development of mangrove biomass is dependent on the quantity of nutrients and the efficiency of nutrient uptake. In addition, they concluded that during succession, mangroves exert significant control over the amount of nutrients in adjacent water but, if terrestrial nutrient input is reduced, they do not have the capacity to maintain themselves at the same level of production. This is due to

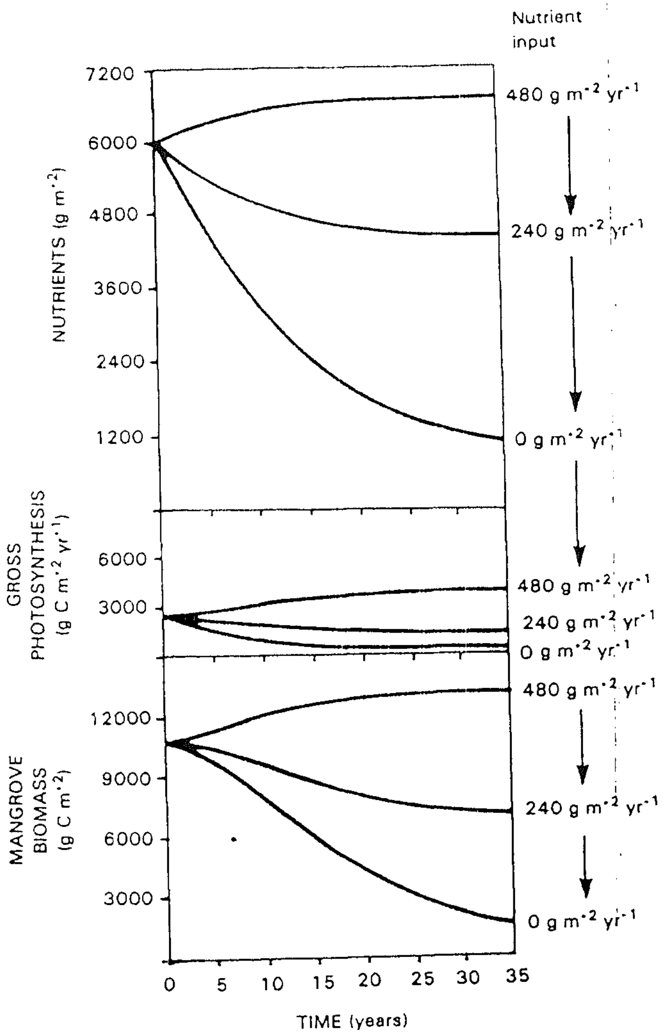


Figure 24 Results of model simulation of Florida mangrove ecosystem. Rates of gross photosynthesis and level of nutrients in system with initial conditions of high nutrient level, mean rates of metabolism and three rates of nutrient input. The response in the mangrove biomass of the system is shown for the same conditions (after Lugo, Sell and Snedaker 1976).

a loss of nutrients via export from the mangrove community, which suggests that there must be selective pressure for mechanisms of recycling.

Onuf, Teal and Valiela (1977) studied the effects of nutrient enrichment of *Rhizophora mangle* islands in Florida. Two islands were compared: one (high-nutrient) with, and one (low-nutrient) without a breeding colony of pelicans and egrets. Their data indicate higher growth rates at the high-nutrient site; trees at the high-nutrient site showed greater additions of leaves, reproductive parts and new lateral branches and larger increases to existing stems. Growth in the fertilized stand began earlier in the year and had a second peak of growth not shared by mangroves at the low-nutrient site.

The nutrient response found in the field by Onuf, Teal and Valiela (1977) appears to verify the more theoretical predictions regarding the effect of nutrients on a mangrove community made by Lugo, Sell and Snedaker (1976).

Comparable data for Australian mangroves are not available; however, the luxuriance of mangroves along the Queensland coastline correlates with those areas where high rainfall results from the proximity of coastal mountain ranges in excess of 700 metres elevation (figure 5). While this may be ascribed in broad terms to high rainfall, these areas are also areas of high-nutrient run-off owing to the erosion of the ranges, and therefore are rich sources of nutrient input for the mangrove communities on the coast. On the other hand, Boto's (1982) preliminary data from selected rivers in northeastern Queensland show that just prior to the onset of the wet season, fresh water flowing into mangrove communities is not a major supplier of dissolved nutrients.

In more detailed studies at Hinchinbrook Island, however, Boto (1983) reported that mangrove standing crop biomass was significantly correlated with (1) extractable phosphorus, (2) soil salinity (negative correlation) and (3) the redox potential or reducing conditions of the soil. Mean ranges of phosphate and ammonium concentrations were 5–20 μg P/g dry soil and 4.6–7.3 μg N/g dry soil respectively.

Experimental fertilization, conducted over a year, showed a significant growth response to soil ammonium enrichment, suggesting that nitrogen limitation was common to all sites (Boto 1983; Boto and Wellington 1983). On the other hand, phosphate limitation was indicated only in those areas where phosphates were less than 5 μg P/g dry soil — the areas where higher elevations occurred in proximity to the coast.

Preliminary data from six Cape York river systems indicate that all sites had low to extremely low phosphate concentrations (0.1–5 μg P/g dry soil), whereas ammonium levels were similar to those at Hinchinbrook Island (Boto 1983). These preliminary findings strongly suggest that phosphorus status is a dominant influence on mangrove primary productivity, at least in northern

Australia, and is consistent with the generally low phosphorus level of Australian soils and its influence on terrestrial plant communities (Beadle 1954).

Proximity of Freshwater Source

There is little doubt that the availability and proximity of fresh water affects mangrove development. For example, along the Queensland coastline the more luxuriant mangroves occur in high rainfall areas (figure 5). Similarly, the biogeographic regions, based in part on floristic data, correlate to a large extent with rainfall. Bunt, Williams and Duke (1982) refined these analyses by examining species assemblages within fifty-six coastal systems between Rockhampton and Cape York and relating these to prevailing hydrological conditions. Analysis of their data included classification of species and sites into species-groups and site-groups respectively and an examination of the relationship between these categories. Nine species-groups and nine site-groups were recognized (tables 16, 17), each of which could be characterized by their ecological tolerances or hydrological characteristics. One site-group comprised members whose shared characteristic was that they were unlike any other members of the system, including one another. These members were allocated to their closest other group (table 17).

The data suggest that species distribution is strongly influenced by the extent of freshwater influence either from rainfall or from "wet" rivers, that is, rivers that flow reliably for most of the year (Bunt, Williams and Duke 1982). In contrast, Macnae (1966) was convinced that rainfall was the more important factor, stating that run-off from most Australian rivers is too variable.

Table 16 Species groups and their characteristics as derived from classification of floristic data from northeastern Australian coastal systems

Species group	Species	Groups characteristics	Common in site groups
1.	*Aegiceras corniculatum* *Avicennia marina* *Bruguiera gymnorhiza* *Excoecaria agallocha* *Osbornia octodonta* *Rhizophora stylosa*	Species of wide ecological amplitude, i.e., tolerant of wide range of salinity and temperature; ubiquitous and often dominant	1, 2, 3, 4, 5, 7 and 8
2.	*Acanthus ilicifolius* *Acrostichum speciosum* *Heritiera littoralis* *Xylocarpus granatum*	Species associated with freshwater influence and characteristics of the middle and upper reaches of rivers	1, 2, 3, 4, 5 and 6
3.	*Rhizophora apiculata* *Rhizophora lamarckii* *Xylocarpus australasicus*	Species often growing together behind frontal stands of *R. stylosa*	1, 2 and 3

Table 16 (cont'd)

Species group	Species	Groups characteristics	Common in site groups
4.	*Aegialitis annulata* *Bruguiera exaristata* *Ceriops tagal* var. *tagal* *Lumnitzera racemosa*	Species associated with mid to inner mangrove zones	3 and 5
5.	*Bruguiera parviflora* *Ceriops decandra* *Sonneratia alba* (apetalous)	A degree of freshwater influence seems to be important and limits the distribution of this group	4 and 5
6.	*Cynometra iripa* *Lumnitzera littorea* *Rhizophora mucronata* *Scyphiphora hydrophyllacea*	Species rarely or never found near river mouths or close to seawater influence	1
7.	*Barringtonia racemosa* *Bruguiera sexangula* (daintree) *Sonneratia caseolaris* (johnstone) *S. caseolaris* (tully)	Species associated with freshwater influence and characteristic of middle and upper reaches of in restricted area	4
8.	*Bruguiera cylindrica* *Bruguiera sexangula* (Jacky Jacky) *Camptostemon schultzii* *Ceriops tagal* var. australis *Diospyros ferrea* *Nypa fruticans* *S. alba* (semipetalous)	Mostly species of limited distributions or rare or uncommon within their distribution; no unifying ecological features	
9.	*Barringtonia acutangula* *Dolichandrone spathacea* *Pemphis acidula* *S. alba* (petalous) *S. caseolaris* (claudie) *S. caseolaris* (olive) *S. caseolaris* (mcivor/morgan)		

Source: After Bunt, Williams and Duke (1982).

Table 17 Site groups and their group characteristics as derived from classification of floristic data from northeastern Australian coastal systems

Site group	Drainage basin	Coastal system	Group characteristics	Common species groups
1.	Jardine	Jardine River	Far northern sites, extensive in areas and covering wide environmental range; all are subject to freshwater influence	1, 2, 3 and 6
	Olive/Pascoe	Olive River		
	Olive/Pascoe	Pascoe River		
	Jardine	Cowal Creek		
2.	Tully	Hull River	Either rivers receiving limited or only sporadic fresh water from the land and/or medium to large inlets strongly influenced by the sea; intermediate between high- and low-saline areas	1, 2, 3, 4 and 6
	Olive/Pascoe	Kangaroo River		
	Jacky Jacky	Barnia Creek		
	Daintree	Coopers Creek		
	Jacky Jacky	Harmer Creek		
	Murray	Deluge Inlet		
	Barron	Trinity Inlet		
	* Jacky Jacky	Capt. Billy Creek		
	* Proserpine	Saltwater Creek		
3.	Lockhart	Claudie River	Except for the Claudie River, all are extensive estuaries under well-sustained marine influence; the Claudie River is a low-salinity river but, floristically, it appears to resemble the geographically closer but more saline Lockhart River	1, 2, 3, 4, 5 and 6
	Jacky Jacky	Escape River		
	Lockhart	Lockhart River		
	Hinchinbrook	Missionary Bay		
	Jacky Jacky	Jacky Jacky Creek		
4.	Daintree	Daintree River	Large rivers with strong freshwater influence	1, 2, 3, 5, 6 and 7
	Endeavour	Endeavour River		
	Jeannie	McIvor/Morgan Rivers		
	Mulgrave/Russel	Mulgrave River		
	Murray	Murray River		
	Tully	Tully River		
	* Daintree	Bloomfield River		
	* Johnstone	Moresby River		
5.	Endeavour	Annan River	Relatively dry environments with extensive salt flats and only a narrow mangrove fringe	1, 2, 4 and 5
	Normanby	Annie River		
	Lockhart	Nesbit River		
	* Jacky Jacky	Mew River		
	* Ross	Alligator Creek		
	* Hinchinbrook	Fisherman's Point		
6.		Bloomfield River	Non-conformist group; members respectively reallocated to site-groups 4, 5, 4, 5, 2, 8, 5 and 2	
		Mew River		
		Moresby River		
		Alligator Creek		
		Captain Billy Creek		
		Haydock Island		
		Fisherman's Point		
		Saltwater Creek		
7.	Jacky Jacky	Macmillan River	Locations under a balance of salt and freshwater influence with neither extreme saline or freshwater conditions developing	1, 3 and 4
	Stewart	Rocky River		
	Stewart	Steward River		
	Lockhart	Lloyd Island		
	Haughton	Chunda Bay		
	Hinchinbrook	Zoe Bay		
	Ross	Crocodile Creek		
	Jacky Jacky	Round Point Creek		
	Shoalwater	Port Clinton		
	Hinchinbrook	Scraggy Point		
8.	Jeannie	Jeannie River	Under predominantly marine influence but with parts under sustained freshwater supply	1 and 4
	Stewart	Cliff Island		
	Herbert	Sunday Creek		
	* Hinchinbrook	Haydock Island		
9.	Jeannie	Flinders Island	Islands which, apart from rain, have little or no freshwater influence; mangrove development restricted to sheltered bays regularly influenced by tides	1
	Jacky Jacky	Haggerstone Island		
	Jacky Jacky	Halfway Island		
	Jardine	Horn Island		
	Jardine	Prince of Wales Islands		
	Jacky Jacky	Sir Charles Hardy Is.		
	Jeannie	Stanley Island		
	Jardine	Tuesday Island		
	Jardine	Wednesday Island		

* Reallocated from site-group 6.
Source: After Bunt, Williams and Duke (1982).

Bunt, Williams and Duke (1982) doubted that rainfall adequately explained the observed distributions, since the islands, dependent entirely on rainfall, have relatively depauperate mangrove floras.

After dismissing the suggestion that catchment size might be involved, they suggested that the mangrove communities of northeastern Australia had been floristically richer in the past, but with increasing aridity of Australia in recent geological time, the less adaptable species began dying out (Mepham 1983). However, a reasonable number of species survived, even though the long-term future of the rarities may be doubtful (Bunt, Williams and Duke 1982).

This approach raises the question as to what aspect of "increasing aridity" is reduced in certain river systems. Bunt, Williams and Clay (1982) and Bunt, Williams and Duke (1982) examined rainfall, catchment size and the effects of upriver salinity gradients, and although these go far in explaining mangrove floristics, there appears to be some inadequacy. Whereas temperatures and evaporation do not vary sufficiently over the study area to allow for such differential floristic development, catchment characteristics appear to do so, but these have not been examined in detail. Rainfall and flow reliability also may be involved as may their seasonality. However, insufficient data are available, particularly for areas in northern and northeastern Australia, to make an adequate assessment.

Catchment characteristics are sufficiently well known, at least at the level of drainage basins, for some comments to be made. Given identical rainfalls, two catchments may, through their characteristics of geology, topography, soils and vegetation cover, effectively absorb and utilize different proportions of that rainfall, with the residual proportion remaining after evaporation becoming part of the surface run-off from that catchment. For example, the continental islands examined by Bunt, Williams and Duke (1982) and shown to be depauperate have small catchments largely of rock, steep slopes, skeletal soils and sparse vegetative cover. Their run-off coefficients, primarily the ratio of run-off to rainfall, are high because little of the rain is able to infiltrate into the soil where it can be retained and utilized. Those catchments, on the other hand, with extensive swamps, overflow basins, dense vegetation or sandy landscapes, have low run-off coefficients and allow considerable retention of water with more regulated and sustained release to their drainage river systems. However, some catchments without these characteristics may also have low run-off coefficients because of low rainfall and high evaporation or transpiration over the catchment.

Insufficient data are available on rainfall, run-off and catchment characteristics to examine in detail each of the coastal systems treated by Bunt, Williams and Duke (1982). However, a broad picture can be obtained using data (Australian Water Resources Council 1976) on the respective drainage basins to which they belong.

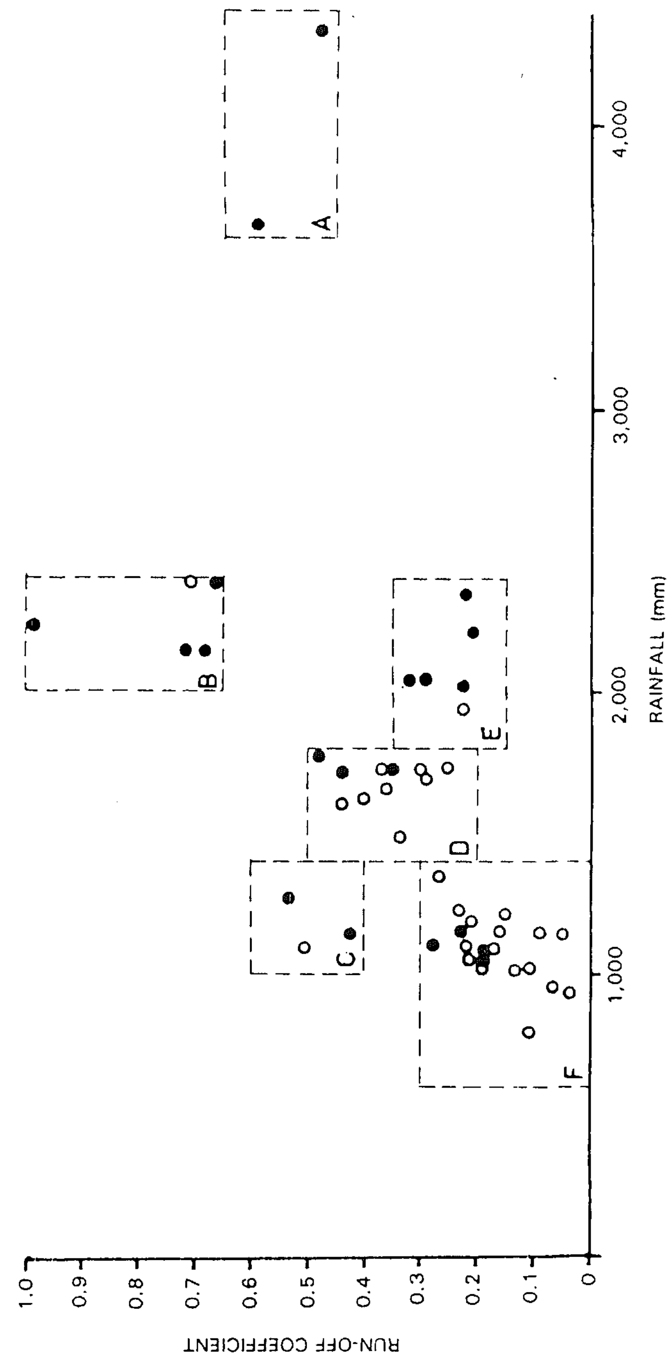


Figure 25 Classification of Queensland drainage basins into six groups on the basis of their run-off coefficients and mean rainfall.

Run-off coefficients for all Queensland east-coast drainage basins in relation to their mean annual rainfall are shown in figure 25. Six discrete groups of drainage basins can be recognized on the basis of their rainfall and run-off coefficients respectively. Group A comprises drainage basins with high rainfall and intermediate run-off coefficients; it includes catchments with a more or less sustained release of fresh water throughout the year. Groups B and E represent drainage basins of intermediate rainfall with high and low run-off coefficients respectively; the river systems of group B show large and sudden freshwater inflows with proportionately little sustained flow. Groups C, D and F are in the low-rainfall range with intermediate to low run-off coefficients. Consequently, the river systems in these groups generally have either very low flows or low but sustained flows. These groups can thus be broadly arranged in some order on two hydrological gradients — increasing freshwater inputs and increasing catchment retention of flows (figure 25). A third dimension should be added to this arrangement, namely the reliability of the freshwater input. Reliability data are available for a restricted number of drainage basins, and the ratio of minimum annual discharge to maximum annual discharge (both as a percentage of average) over the entire time period of the records was used. The more reliable and the less variable the annual flow, the more closely this ratio approaches unity. Using these data, the drainage basins can be subdivided tentatively into those of high or low reliability (figure 26).

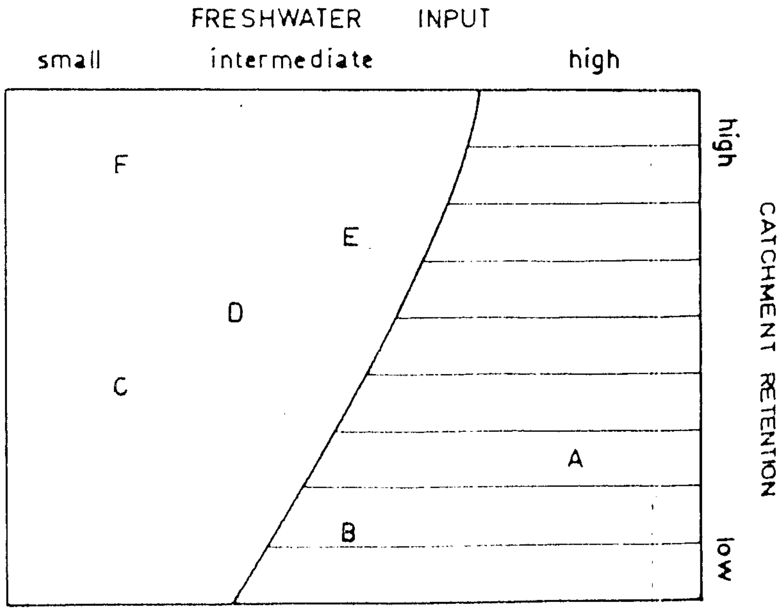


Figure 26 Queensland drainage basin groups showing those that can be considered as having reliable rainfall (striped area). Note the absence of any drainage basins with high and reliable rainfall and high catchment retention.

Using the above data, a classification of the east-coast drainage systems can be attained based only on hydrological data (table 18). These groupings show some similarity to the detailed classification based on floristic data (Bunt, Williams and Duke 1982) and suggest that catchment characteristics and, to a lesser extent, flow reliabili-

Table 18 Hydrological classification of the Queensland east-coast drainage basins

Group A.	High freshwater input; intermediate catchment retention; high flow reliability:		
	+ Johnstone River	+ Tully River•	
Group B.	Intermediate freshwater input; low catchment retention; high flow reliability:		
	Mossman River	+ Mulgrave–Russell Rivers	Murray River
	+ Hinchinbrook Island	+ Daintree River	
Group C.	Low freshwater input; intermediate catchment retention; low flow reliability:		
	Black River	+ Jeannie River	+ Stewart River
Group D.	Intermediate freshwater input; intermediate catchment retention; low flow reliability:		
	+ Jardine River	+ Jacky Jacky Creek	+ Endeavour River
	O'Connell River	Pioneer River	Plane Creek
	Fraser Island	Noosa River	Maroochy River
	Stradbroke Island	South Coast Rivers	
Group E.	Intermediate freshwater input; high catchment retention; low flow reliability:		
	+ Olive–Pascoe Rivers	+ Lockhart River	+ Barron Rivers•
	+ Herbert River	+ Proserpine River	Whitsunday Islands
Group F.	Low freshwater input; high catchment retention; low flow reliability:		
	+ Normanby River	+ Ross River	+ Haughton River
	+ Shoalwater Creek	Burdekin River•	Fitzroy River•
	Water Park Creek	Burnett River•	Baffle Creek
	Burrum River	Curtis Island	Calliope River
	Boyne River	Styx River	Mary River•
	Kolan River•	Don River	Pine River
	Logan–Albert Rivers		

+ Rivers from these drainage basins were examined by Bunt, Williams and Duke (1982).

• More than 100 m^3 x 10^6 diverted for irrigation purposes.

ty are about equal in importance to average rainfall of the catchment area in shaping the floristic composition of the mangroves in the various coastal regions.

The additional comment should be made that northeastern Australia does not have any drainage basins which show both high and reliable rainfall and high catchment retention (figure 26, table 18). Although this probably reflects the general aridity and low relief of the continent, it results in the absence of such river basins as the New Guinean Fly River or Purari River deltas with their extensive mangrove development and vast *Nypa* forests in the reduced-salinity reaches (Womersley 1975; Percival and Womersley 1975).

Plant-Plant Interactions

As in any other plant community, the constituent plants of the mangrove community interact with one another, often in specific or defined ways. Many of these interactions are subtle, and most are poorly studied and little understood. There is, however, a gradually increasing awareness that plant-plant interactions within the mangrove community must be important because the distribution and success of the mangroves cannot be adequately explained solely in terms of their interaction with the physico-chemical environment.

Several categories of plant-plant interactions can be recognized as important in determining the structure and/or function of the mangrove community. They are: parasitic, antagonistic, mutualistic and competitive interactions.

Parasitism

Parasitic relationships are those in which the parasite obtains food from its host, which may or may not suffer harm as a result. Many such relationships occur in the mangrove community, but two of them suffice as examples.

Mistletoes (family Loranthaceae) are parasitic plants which, although capable of photosynthesis, tap into the host's vascular system to obtain water and mineral nutrients (see chapter 4). They are relatively benign parasites and rarely kill the host plant. Nevertheless, they deprive the host of desalinated water and nutrients, both of which may be scarce resources for mangroves, as well as causing growth modification and shading of the affected branches.

Being relatively benign and uncommon, the mistletoes exert little influence on the mangrove community as a whole, although individual host plants may suffer considerable stress.

Parasitic fungi, on the other hand, can have devastating effects. Many parasitic fungi occur in the mangroves from the canopy to the root (see chapter 4). Usually some equilibrium is established with the host, but sometimes equilibrium is disturbed and considerable mortality results. For example, on the central Queensland coastline, a species of *Phytophthora* has caused considerable mortality in *Avicennia marina* (Pegg, Gillespie and Foresberg 1980). This fungus is normally a leaf litter decomposer and, as such, it occurs throughout Australian mangrove communities. However, it does have the capacity to become pathogenic, attacking the roots of its mangrove host. As a result, the roots cease to function, or function inefficiently, and severe water stress is induced, leading ultimately to death of the mangrove.

So far, wherever outbreaks of *Phytophthora* and high mortality have been recorded, only one host — *Avicennia marina* — has been involved, and it appears that its susceptibility to this parasite is considerably higher than that of other mangrove species (figure 27).

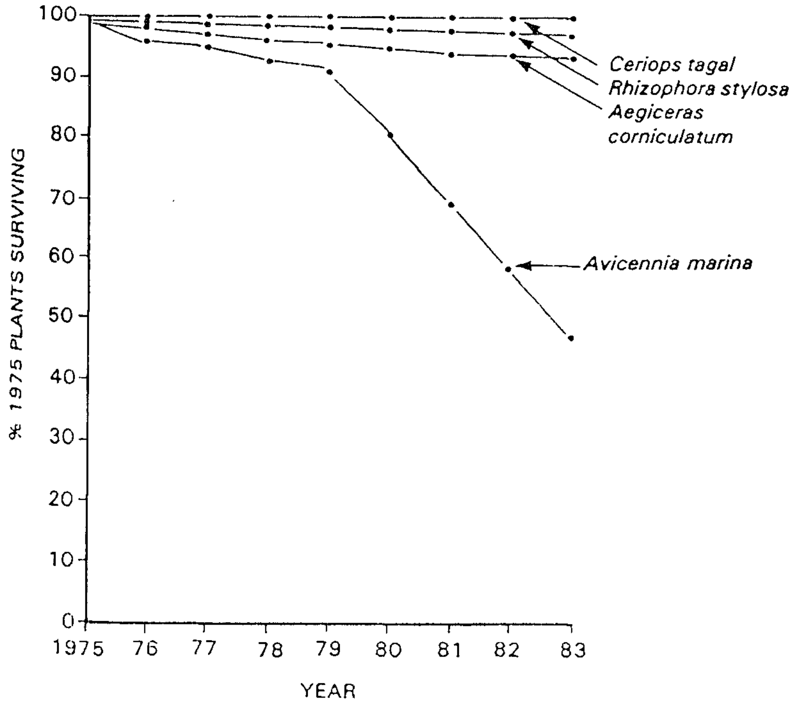


Figure 27 Depletion curves for mangroves at Gladstone, Queensland, showing the high *Phytophthora*-induced mortality in *Avicennia marina*, and the unaffected mortality of the other mangrove species present in the area.

The resultant selective mortality has led to a dramatic change in the species composition at particular localities. For example, in Port Curtis, where almost pure stands of *Avicennia* once occurred, the mangrove community contains virtually no mature *Avicennia marina* at present, and *Rhizophora stylosa* appears to be rapidly filling the gap. Hence, the change from an *Avicennia marina* community to one dominated by *Rhizophora stylosa* has occurred as a result of a fungus over a relatively short period — less than four years.

Antagonism (Ammensalism)

Antagonistic relationships are those in which the growth of a particular plant is inhibited or interfered with through the creation of adverse conditions by another plant, generally through the production and secretion of toxic or inhibitory substances (Garb 1961; Woods 1960; Muller 1966).

Numerous examples have been reported in which vegetational composition and species distributions have been attributed to the action of chemical inhibitors of both shoot and root origin. Clarke and Hannon (1971) investigated the potential importance of such compounds in the mangrove communities around Sydney.

Examination of the physico-chemical environment of the Sydney mangrove and saltmarsh species indicated the importance of salinity and waterlogging in determining species' distributional patterns (Clarke and Hannon 1969, 1970), but suggested that additional factors also must be operative in maintaining the sharply defined vegetation zones. For example, species that overlap in their tolerance of salinity and waterlogging form mixed stands unless interaction between them favours only one. In New South Wales, *Sarcocornia quinqueflora* rarely grows beneath mangroves, although it is not limited by salinity or in many situations by waterlogging, nor by light where the canopy is open. Similarly, seedlings of *Casuarina glauca* have not been observed beneath mature trees in the *Casuarina* zone (Clarke and Hannon 1971).

Clarke and Hannon (1971) used leachate and macerate extracts of both bark and leaves from *Avicennia* and cladodes and litter from *Casuarina* to detect any growth-inhibiting substances that might be derived from rain falling through the tree canopy. Leaf detritus from the soil surface of the *Avicennia* and *Casuarina* zones was also tested for the accumulation of any toxins.

No inhibition of *Sarcocornia* seedlings or of mature plants of any of the associated species (*Suaeda*, *Triglochin* and *Sporobolus*) by mangrove extracts was found. *Juncus* plants were healthy only in the control treatment (tap water), and yellowing of the shoots was common where leachates and macerates were included. Survival and growth of seedlings of both *C. glauca* and *J. maritimus* were inhibited by the presence of a layer of *Casuarina* litter on the soil surface, but no significant differences in growth were found using *Casuarina* extracts.

Clarke and Hannon (1971) concluded that in these Sydney communities it appears highly unlikely that phytotoxic exudates influence the establishment and maintenance of zonation patterns but that *Casuarina* litter creates physical difficulties for germination and seedling growth.

It seems likely, however, that in the more tropical and species-rich mangroves, toxic and inhibitory exudates are potentially of greater significance. Catechol-type tannins, as well as a range of more exotic compounds, are abundant in the bark, wood and leaves of many Queensland mangroves (Brunnich and Smith 1911; Hogg and Gillan 1984). For example, brugine has been recorded from stem and bark extracts of *Bruguiera sexangula*, *B. exarista* and *B. cylindrica* (Loder and Russell 1969; Kato 1975) and a triterpenoidal saponin has been recorded from the roots of *Acanthus ilicifolius* (Minocha and Tiwari 1981). The fish-poisoning properties of the bark and stems of *Barringtonia*, *Thespesia* and *Derris*, three common associates of northern mangroves, were well known and exploited by the Aborigines (Everist 1974). All of these are physiologically active compounds, capable of regulating or inhibiting growth; however, at present, no evidence is available that they do so under field conditions although this would seem to be an aspect worthy of detailed investigation.

Mutualism

Mutualism is the association of individuals of different species such that their ability to survive and reproduce is greater when together than when apart (Roughgarden 1975; Margulis 1981; Lewin 1982).

Numerous mutualistic associations have been documented (Boucher, James and Keeler 1982; Henry 1966, 1967; Trench 1979; Law and Lewis 1983), but the few that are known from mangroves mostly involve interactions of plants and micro-organisms.

Some of the epiphytes occurring in mangroves (see chapter 4) may have a mutualistic association, but whereas the benefit to the epiphyte is easily discernible, the benefit, if any, to the mangrove partner remains questionable.

Four types of mutualistic interactions between mangroves and micro-organisms can be identified, although details of their frequency of occurrence are not available.

Probably the most widespread interaction occurs in the rhizosphere, that zone immediately surrounding the fine roots which is characterized by an enhanced microbial activity (Smith and

Delaune 1984). Although generally not intimately connected with root cells, the fungi and bacteria modify the micro-environment around each root through their metabolic activity, releasing nutrients and altering the pH of the soil. In turn, this microbial flora probably depends on the leakage of organic material from the roots, which can be utilized by the micro-organisms as a source of energy. A number of soil fungi are characteristically associated with mangrove roots (see chapter 4) and form part of this rhizosphere flora.

The second type of interaction is more intimate and involves fungi which form a direct association with roots. These fungal associations are termed mycorrhizae (Harley 1969). In some cases, the fungi are unicellular and live within individual root cells ("endomycorrhizae"), but in many cases the fungi cover the root tips in a thick mat and penetrate the intercellular spaces of the cortex ("ectomycorrhizae"). Although no mycorrhizae have been reported specifically from mangroves so far, they are frequently found in forest and swamp soils that are rich in organic matter. Mycorrhizae also have been reported from sand-dunes with low organic matter, where they appear to facilitate the availability of phosphorus from the mineralized coating on sand grains (Jehne and Thompson 1981). In view of their habitat diversity, it would seem likely that some mangrove mycorrhizae do occur. Like the rhizosphere flora, mycorrhizae facilitate the movement of phosphorus, potassium and calcium into the roots and the movement of metabolites from the roots to the fungus.

Root nodules comprise a third type of mutualistic interaction. The bacterial genus *Rhizobium* forms nitrogen-fixing nodules almost exclusively on the roots of the angiosperm family Leguminosae (Allen and Allen 1981). Nodulated legumes grow more vigorously than do non-nodulated ones in nitrogen-deficient soils. In view of the low nitrogen status of most mangrove soils (Boto 1983), root nodules may be important to the two legumes commonly found in mangroves — that is, the mangrove *Cynometra iripa* and the climbing associate *Derris trifoliata*; critical investigation of these two species is desirable.

Another kind of micro-organism that forms nitrogen-fixing root nodules with higher plants is the actinobacterial genus *Frankia*. A number of unrelated genera of flowering plants form nodules with *Frankia*, including *Casuarina* (Bond 1956, 1963); plants with nodules grow much better in nitrogen-deficient media than those without nodules (Bond 1963). For *Casuarina glauca*, a common inhabitant of the landward margins of mangroves where they abut freshwater swamps, these nodules may be of considerable ecological significance.

The fourth type of mutualistic interaction involves bacterial leaf nodules, and is common in over four hundred species of the angiosperm families Rubiaceae and Myrsinaceae (Lersten and Horner 1976). The bacteria are maintained as a colony in the closed shoot tips of the plant and enter developing leaves through the stomatal pores, ultimately forming chambers along the leaf margin (Miller, Gardner and Scott 1983). These bacterial leaf nodules have been shown to be capable of nitrogen fixation (Van Hove 1976), and they may be involved in synthesis of cytokinin (Miller, Gardner and Scott 1983).

Bacterial leaf nodules are present in the American mangrove *Laguncularia racemosa* (Humm 1944). The Australian mangroves *Lumnitzera racemosa* and *L. littorea* (Combretaceae) possess a small "gland" or domatium at the apex of the leaf, with occasionally smaller glands in the axils of the lesser veins (Jones 1971). These glands are elliptical chambers immediately below the epidermis and are similar in appearance to the leaf nodules of genera that have received detailed study. The species of *Lumnitzera* undoubtedly would repay detailed investigation; similarly, *Aegiceras corniculatum* and *Scyphiphora hydrophyllacea* (which belong respectively to the Myrsinaceae and Rubiaceae), in which bacterial leaf nodule formation is extremely common (Lersten and Horner 1976), would be worthy of detailed study.

Although the information available on mutualistic interactions in the Australian mangrove flora is extremely limited, there is sufficient to suggest that the study of mutualism may be a potentially productive line of investigation. The fact that most of the interactions involve the availability of nitrogen, which is otherwise in short supply in Australian mangroves, suggests that considerable ecological significance may attach to an understanding of the relationships between mangroves and micro-organisms.

Competition

Competition between plants has been defined as the tendency of neighbouring plants to utilize the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space (Grime 1973). According to this definition, competition refers exclusively to the capture of resources and is only one of the mechanisms whereby a plant may inhibit the growth of a neighbour by adversely modifying its environment. In this sense, competition is strongly contrasted with antagonism, two interactions which are often lumped together in the more traditional usage of the term "competition" (Milne 1961; Harper 1961).

The competitive ability of a plant is a function of the area, activity and distribution in space and time of the plant surfaces through which resources are absorbed and, as such, it depends upon a combination of plant characteristics including storage organs, height, lateral spread, phenology, growth rate, response to stress and response to damage (Grime 1979). Several of these characteristics have been discussed already (chapter 2) under the heading of adaptation — the selective change of a particular set of characteristics in a way suited to a particular environment.

Stated in another way, plants will tend to disperse as widely as possible. This may take them into habitats where their physiological optima are exceeded. If they encounter other individuals better suited to the prevailing environment, differences in growth potential, either above or below ground, will result in the suppression of the less-suited individual.

Within the mangrove environment, most plant species are widely dispersed. However, large differences in the environmental conditions also occur, particularly in relation to water, salt, nutrients and light. It seems clear from the experimental work of Clarke and Hannon (1971) that the sharp boundaries between communities dominated by different species are often the direct result of competition.

Even within communities, species composition may be determined, or at least influenced, by competitive interactions between component species. For example, in a detailed transect of the mangroves of the open shoreline at Princess Charlotte Bay, it was found that the distributions of *Ceriops* and *Avicennia* overlapped to a large extent (Elsol and Saenger 1983). Their relative importance values (figure 28) indicate that two broad bands are recognizable: (1) the landward 55 metres in which the importance values of the two species lie on a negatively sloping line, that is, one varies inversely with the other, and (2) from 60 metres seawards with a positive slope, where both species vary in proportion to each other. This suggests that from 0 to 55 metres in the transect the environmental conditions are favourable for both species and they compete with each other. From 60 metres onwards, the conditions are no longer so favourable, and both species together decline in importance (Elsol and Saenger 1983). The similarity of these species, in terms of their salinity (see table 14) and waterlogging (see table 13) tolerances, supports the notion of such a competitive interaction. Undoubtedly, other examples of competition between various mangrove species occur, although little work has been done on this aspect.

Grime (1973, 1979) argued that competition must be viewed in the context of major adaptive strategies which have evolved in plants, and it is important to relate these strategies to the processes which determine the structure and species composition of vegetation.

Two categories of external factors limit the amount of living and

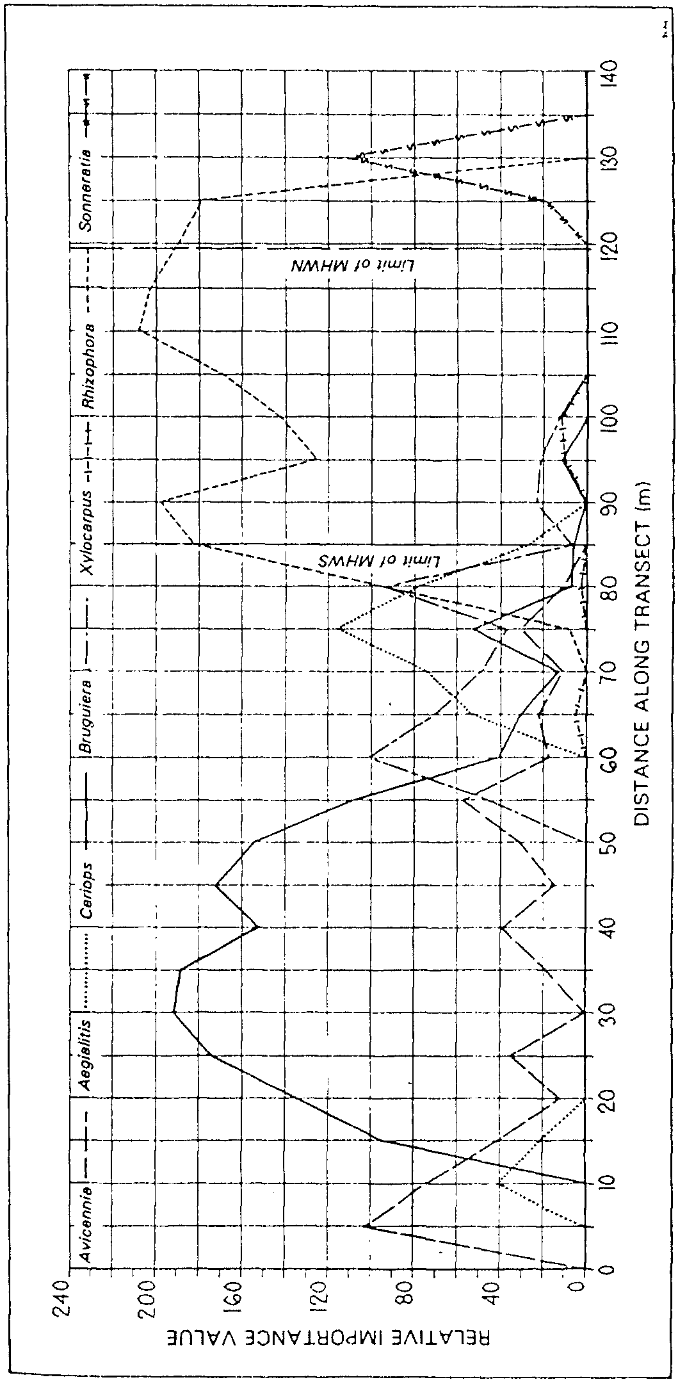


Figure 28 Open shoreline zonation at Princess Charlotte Bay using the distribution of relative importance values of the various species across a transect at right angles to the shoreline (from Elsol and Saenger 1983).

dead plant material in any habitat. The first is stress, which includes those factors restricting photosynthetic production, such as shortages of water, light and nutrients or unfavourable temperatures. The second category is disturbance, which includes those factors involved with the destruction of plant tissue, such as the activities of herbivores, pathogens, humans and such phenomena as wind, frost, fire and erosion.

Grime (1973, 1979) suggested that three strategies have evolved among established plants which relate to these categories of factors limiting the amount of plant material. These are the "competitors", which exploit conditions of low stress and low disturbance, the "stress-tolerators" (high stress, low disturbance) and the "disturbance-tolerators" or "opportunists" (low stress, high disturbance). These three strategies are extremes of evolutionary specialization, and many plants have adopted various combinations which adapt them to habitats with intermediate intensities of stress and disturbance.

A triangular ordination technique was developed (Grimes 1977) which provides a basis for classifying plants and vegetation types. Species are classified with respect to (1) potential maximum rate of dry-matter production and (2) a morphology index, reflecting the maximum size obtained by the plant under favourable conditions. This approach assumes that the three primary strategies correspond to the three permutations of primary production rates and morphology, that is, rapidly growing and large ("competitors"), rapidly growing and small ("disturbance-tolerators") and slow growing and small ("stress-tolerators").

Much of the required data are not available for assessing mangroves in this context. However, some equivalent data are available from permanent study sites at Proserpine (table 19) and these have been adapted as follows: the maximum monthly rate of leaf production was used as a measure of potential maximum dry-matter production; a dominance index consisting of the product of the maximum height and mean density of each species in the area was used. The results of this strategic ordination are shown in figure 29. Clearly, the spread of the species is a relative one in that the scales have been suited to mangroves and, as such, cannot be compared with similar ordinations of other plant communities. As has been discussed earlier, mangroves as a group are difficult to compare with non-mangroves for a variety of reasons, which apply here. Nevertheless, the ordination gives a relative indication of the tendency towards the three strategies adopted by the various species of mangroves at Proserpine.

The ordinations (figure 29) suggest that, even on a relative scale, none of the mangroves has adopted the strategies of extreme "competitors" or "disturbance-tolerators", but there is a general

Table 19 Data used to derive growth and dominance indices for the strategic analysis of Proserpine mangroves

Species	Maximum monthly leafing rate (lvs./1000 day^{-1})	Maximum height (m) *H*	Density (No./1,000 m^2) *D*	Dominance index *H* x *D*
Cynometra iripa	0.5	3.5	4	14
Bruguiera parviflora	2.9	10.	2	20
Bruguiera gymnorhiza	3.4	12	2	24
Heritiera littoralis	3.5	15	6	90
Bruguiera exaristata	4.3	10	18	180
Ceriops tagal	6.1	10	102	1020
Avicennia marina	6.2	15	62	930
Rhizophora stylosa	6.7	15	208	3120
Aegiceras corniculatum	7.2	3.5	183	640
Acanthus ilicifolius	7.9	1.5	582	873
Osbornia octodonta	16.4	5	2	10
Xylocarpus granatum	28.4	12	8	96
Xylocarpus australasicus	46.6	12	14	168
Lumnitzera racemosa	48.1	8	44	352
Excoecaria agallocha	131.6	10	136	1360

Source: Saenger (unpubl. data).

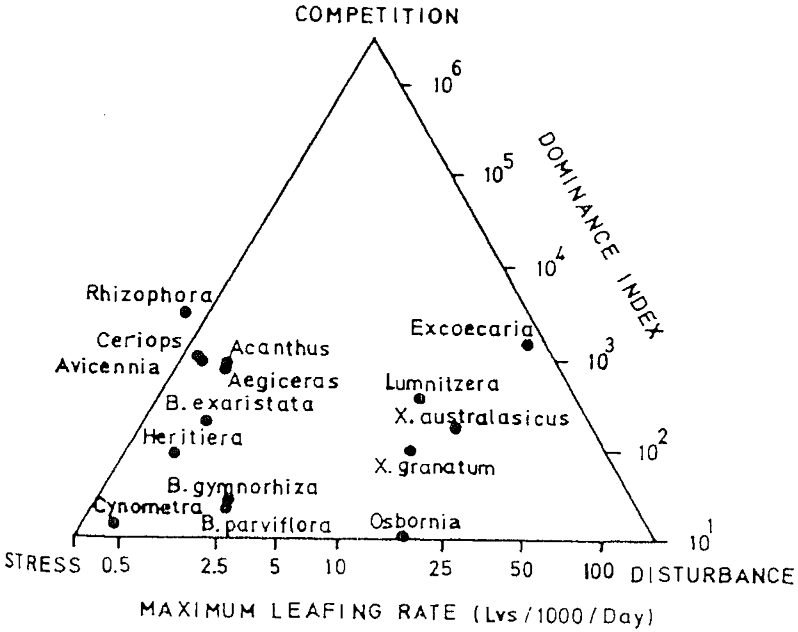


Figure 29 Strategic ordination of mangrove species at Repulse Bay, Queensland. Note that the dominance index was calculated using the maximum height of each species in the study area multiplied by that species' density in number m^{-2}.

distribution of these species towards the "stress-tolerator" strategy. The numerically most abundant and widespread species — *Avicennia marina*, *Rhizophora stylosa*, *Aegiceras corniculatum* and *Ceriops tagal* — appear to have a combined "competitor/stress-tolerator" strategy which would enable them to persist during unfavourable periods on the one hand and to exploit favourable periods reasonably efficiently on the other. *Avicennia* is probably the most-studied member of this group; its ability to grow in a wide range of habitats appears to be due to its response to increasing stress by reducing its growth rate and adjusting its growth habit. It is also worth noting, in relation to the previous comments concerning the competitive interactions between *Avicennia* and *Ceriops*, that these two species appear to be almost identical in their adopted strategy which, together with their similar tolerances to certain environmental conditions, suggests that they are indeed competing with each other. *Acanthus* and *Aegiceras* is another possible competitive pair that should be investigated where their distributions overlap.

It may seem surprising to find species such as *Excoecaria agallocha*, *Xylocarpus* spp., *Lumnitzera racemosa* and *Osbornia octodonta* tending towards the "opportunist" strategy. As slow-growing members of the landward fringes, they do not give the impression of being opportunistic species. However, all of these species are deciduous or near-deciduous (Saenger and Moverley 1985), and they produce a new canopy of leaves over a very short time at the most favourable period of the year. The number of leaves in their canopy varies greatly from year to year, and presumably reflects the degree to which conditions are favourable during their leafing period. In this sense, these species respond very rapidly to favourable or unfavourable conditions during their leafing period and, at least during this restricted time, can be viewed as "opportunists".

Some of the adaptations that have been discussed earlier (chapter 2) can now be placed in the context of this strategic analysis, and may assist in deciding which of those adaptations enhance or are part of the varying strategies. Selected adaptations are superimposed on this ordination in figure 30.

The tolerance of high salinity does not appear to be associated with any particular strategy, although all those species approaching the "competition" strategy show a medium tolerance of salinity stress (figure 30a). Similarly, the possession of salt glands does not appear to be associated with any particular strategy, although the "competition-stress" strategy group (*Rhizophora*, *Acanthus*, *Avicennia*, *Ceriops*, *B. exaristata* and *Aegiceras*) includes all the species with salt glands. Figure 30 also shows that there is little relationship between the ability to tolerate high soil salinities and the

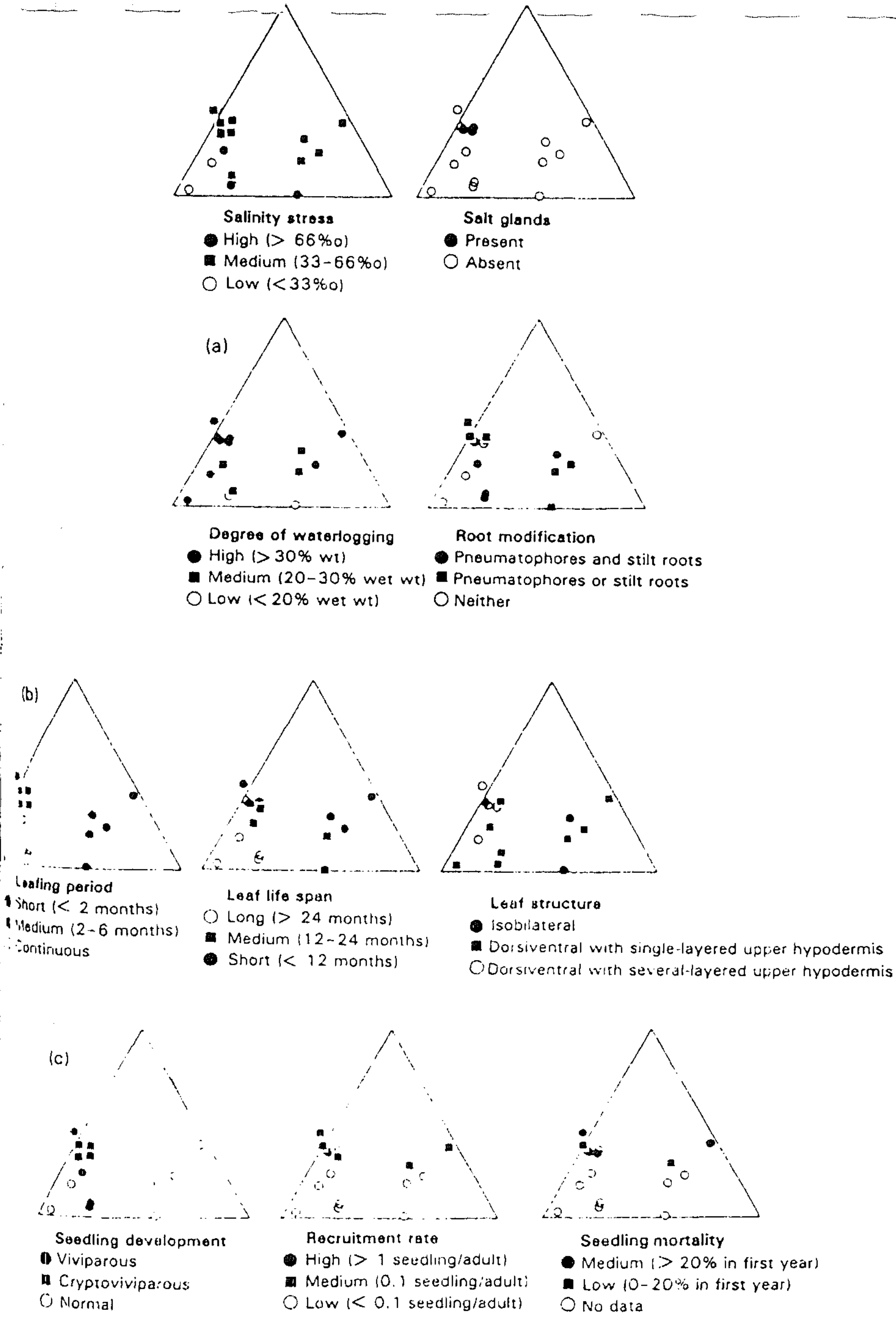


Figure 30 Superimposition of various characteristics on the ordination shown in figure 29: (a) salinity of their environment, presence of salt glands, degree of waterlogging and root modifications; (b) length of leafing period, leaf life span and leaf structure; and (c) type of seedling development, recruitment rate and seedling survival.

possession of salt glands. Nevertheless, such a relationship cannot be ruled out, for the competitive value of salt glands may become apparent only under extreme conditions, when excessive soil salinities develop over a relatively short period.

Neither tolerance to waterlogging nor the possession of certain root modifications can be linked with any one of the strategies (figure 30b). However, a slight relationship is apparent between tolerance to waterlogging and the possession of root modifications; this may be due to the continuous nature of waterlogging and anaerobic soils.

Various leaf characteristics are shown in figure 30b. Clearly, the length of the season when leaves are produced shows a relationship to the strategies. "Stress-tolerators" have continuous leafing periods, those species approaching the "disturbance-tolerator" strategy have short leafing periods, whereas those with "competition-stress" strategies possess medium leafing periods. The life span of the leaves shows a similar relationship, with the "stress-tolerators" retaining their leaves for two years or more, and those species in the centre of the ordination showing short to medium leaf retention. Most interestingly, leaf structure appears to have no special relationship with any of the strategies.

Various reproductive characteristics are shown in figure 30 and they indicate that precocious seedling development may be associated with the "competitor-stress" strategy. The remaining two characteristics are not associated with any particular strategy, but there is a tendency towards medium to high seedling recruitment and survival rates in those species closest to the "competitor" strategy.

Although this strategic analysis has not provided any distinct indications of which of the morphological or reproductive features are adaptations contributing to the success of any particular species, it has indicated that certain features of growth, particularly leafing period and leaf life span, may be of significance. In turn, this suggests that intrinsic physiological processes may be of prime importance in the struggle of a species against the environment and against those other species that would occupy it.

Plant–Animal Interactions

In later chapters (chapters 4 and 5), some of the more specific plant–animal interactions are described and discussed. The intimate link between certain animals and mangrove pollination is examined; the mutualistic cohabitation of mangroves with such

animals as ants and butterflies is discussed; the occurrence of various termite species and their effects on mangroves are noted; and the various species of boring organisms and their roles in living and decomposing wood are summarized.

The plant–animal interactions discussed in this chapter are those that are of widespread significance or which directly or indirectly affect the physical environment in which mangroves grow.

Sediment Turnover

Probably the best example of this kind of interaction is the activities of crabs and mud lobsters in reworking the sediments among the mangroves (Macnae 1966; Bennett 1968). Mud lobsters (*Thalassina anomala*) build large tunnelling burrows which are generally recognized by the mound of fresh mud up to 75 centimetres high around their entrances. The burrows are U-shaped and extend up to 1.5 metres below the surface. Their entrances generally are blocked by a mud plug during the day, but at night they are opened when the mud lobster emerges to feed on surface muds. These burrowing activities have various effects, but the enormous amounts of mud these animals bring to the surface help to mix the soils and to change their surface characteristics. Often, the soil brought to the surface is rich in organic matter and pyrite and may be characterized by strong sulphate reduction and the presence of FeS (Andriesse, van Breeman and Blokhills 1973). This fresh mud oxidizes on the surface and often forms localized patches of highly acidic muds (acid-sulphate soils). Gradually, however, as the mud mounds age, the sulphur content decreases as a result of leaching, and these slightly raised areas then are suitable for mangrove colonization. In *Rhizophora* or *Bruguiera* forests, such elevations are colonized by the mangrove fern (*Acrostichum speciosum*) in small discrete patches.

The mud lobster provides an example of a species which can markedly alter the mangrove environment: the burrows allow drainage of and interchange between surface water and subsoil water; the mud is turned over, with subsurface muds placed on the surface where they can be oxidized which, in turn, leads to their acidification. Once the sulphides are oxidized to sulphates, they can be leached from the mounds, allowing the mounds to be colonized by the mangrove fern which is not able to grow at the general level of the surrounding mud surface.

Other burrowing organisms have similar effects, although generally on a smaller scale. The burrows of fiddler crabs, mudskippers and even the mud crab (*Scylla serrata*) allow drainage, mixing and a degree of aeration of subsurface waters in the mangroves, and in this way enhance the growth of mangroves.

Grazing and Trampling

Another important example of plant–animal interaction in the mangroves is that of grazing and trampling. The importance of grazing in the mangrove ecosystem is not well documented, but probably has the effect of maintaining the mangrove community at a lower level of plant biomass that would occur in its absence. In this sense, grazing and trampling are not unlike other regularly continuing disturbances.

Mangrove foliage contains significant quantities of minerals, vitamins, amino acids, proteins, fat and crude fibre, and is thus a nutritious food source for herbivores (Kehar and Negi 1953; Sokoloff, Redd and Dutcher 1950; Sundararaj 1954). In fact, Morton (1965) found that when used as cattle feed the leaves of *Rhizophora mangle* increased the yield of milk. Consequently, it is not surprising that mangrove foliage is grazed by cattle, sheep, goats and camels.

In Australia, grazing of mangroves by coastal species of wallabies and kangaroos is important locally, and in the Northern Territory the naturalized buffalo (*Bubalus bubalis*) grazes mangroves in substantial numbers. Probably of far greater significance, however, is the widespread grazing by insects (Johnstone 1981). Leaves of *Avicennia*, *Bruguiera*, *Rhizophora*, *Ceriops* and *Heritiera* often are found with serrated edges owing to damage by insects (particularly tettigonids) and by crabs of the family Grapsidae. Heald (1969) estimated a mean grazing effect on Florida mangrove leaves of 5.1 per cent of the total leaf area, ranging from 0 per cent to 18 per cent on a leaf-by-leaf basis. Beever, Simberloff and King (1979) found grazing by an arboreal grapsid crab (*Aratus pisonii*) on *Rhizophora mangle* leaves to range from 0.4 per cent to 7.1 per cent of total leaf area. The significance of these activities in litter breakdown (Malley 1978) and in the export and recycling of organic matter is being investigated currently; Johnstone (1981) has suggested that approximately one-fifth of all mangrove leaf material is diverted to herbivorous rather than detrital food chains.

Wilson and Simberloff (1969) and Simberloff and Wilson (1969, 1970) found over one hundred insect species on small mangrove islands in Florida Bay. They also found that the insect population re-established quickly after fumigating these islands with methyl bromide, and that it reached pre-fumigation levels within one year. After that, total species numbers remained more or less constant although there was considerable species turnover from year to year.

The size and diversity of the insect populations suggest that insect grazing is a significant factor in the structure and function of mangrove communities. Onuf, Teal and Valiela (1977) tested this experimentally by comparing two mangrove islands in Florida (see page 83): one island (high-nutrient area) had breeding colonies of pelicans and egrets, and the other (low-nutrient area) did not. The effect of the input of nutrients by birds on plant growth and reproduction has been noted already. More striking, however, was the significant stimulation of herbivory by insects in response to nutrient enrichment. Larvae of five lepidopteran species that fed on leaves and/or buds were either more abundant or present in the high-nutrient area only, as was the mangrove borer (*Poecilips rhizophorae*) that infested propagules before they dropped from the parent tree. This resulted in a fourfold greater loss to herbivores (26 per cent of total leaf area lost to grazing) and more than offset the increased leaf production owing to high nutrient input.

The observed difference in grazing in the two areas disappeared when the birds seasonally migrated from their nesting area at the high-nutrient island. This relationship between birds, nutrient enrichment and insect damage illustrates the complex interactions that occur in mangroves, as in other vegetation types. However, the effects of large nesting or roosting aggregations in mangroves such as those of white ibis (*Threskiornis molucca*) in northern Australia, lesser noddies (*Anous tenuirostris*) on the Albrolhos Islands in Western Australia and fruit bats (*Pteropus alecto* and *P. conspicillatus*) in eastern Australia undoubtedly enhance the local nutrient status, and may simultaneously be increasing the general level of herbivory.

At present, it is not known whether any of the mangrove species have developed specialized defence mechanisms against grazing. Many mangrove leaves are extremely tough and high in tannins (chapter 2); this feature may reduce their palatability. *Acanthus ilicifolius* has leaves with spinous margins which may discourage grazing, and it contains saponins (Minocha and Tiwari 1981) which may render it unpalatable. Several species of *Melaleuca* occurring near swampy margins of mangroves contain various oils (Jones and Harvey 1936), of which nerolidol recently has been demonstrated to have anti-feeding properties effective against larvae of the gypsy moth, *Lymantia dispar* (Doskotch et al. 1980). The mangrove *Excoecaria agallocha*, which contains a milky sap, rarely shows evidence of grazing, and it seems likely that the latex discourages grazing either by its taste or by its toxic properties.

Other animal–plant interactions include the damage done to the foliage by nesting birds and leaf-weaver ants. Leaf-weaver ants (*Oecophylla smaragdina*) weave leaves into nests within the mangrove canopy and, in turn, provide some protection to the mangroves by preying on herbivorous insects. Nevertheless, for mangroves of the family Rhizophoraceae which have strictly terminal growing points, these ant nests effectively inhibit the further development of the affected shoot, and thus can impair the full development of the tree. Similar results have been noted where large aggregations of nesting birds occur. Nesting birds may use twigs pruned from the top of the mangrove canopy to build massive nests (for example white ibis), and they commonly peck at and damage the young growing tips within reach while attending their young.

Interactions Expressed as Structure

All of the interactions discussed in the previous sections produce a range of physico-chemical settings and of mangrove communities, which differ in their function and structure.

These various attributes can be used to classify mangrove communities (see page 119), a process which through its data reduction can provide some overview of the types of mangrove communities and how dominant interactions shape them.

There are, however, a number of situations where the mangroves are zoned, and these provide a particularly good opportunity to investigate and perhaps answer many ecological questions, for these zoned communities can be treated as the outcome of a natural experiment (Pielou 1977). Especially where uniformly sloping environmental gradients are involved, the zonation pattern can be interpreted and used to study the plant–environment interactions of the constituent species.

Two types of zonation are discussed below: the parallel zonation along open shorelines and the longitudinal zonation along rivers. As pointed out by Elsol and Saenger (1983), both types are superimposed in the lower reaches of rivers and their deltas and may produce diverse floristic assemblages with highly complex patterns that cannot be interpreted even with sophisticated techniques of pattern analysis (Bunt and Williams 1980, 1981). Consequently, both types of zonation are discussed separately, although a preliminary attempt at their integration is then made.

Parallel Shoreline Zonation

The phenomenon of rather predictable, often monospecific zones of mangroves parallel to shorelines is well documented (table 20), and there is general agreement on the sequence of zones (Macnae 1966, 1967; Saenger et al. 1977). However, the underlying causes as to why mangroves so frequently appear in zones are far from clear. Snedaker (1982) critically reviewed suggested causes and found that they fell into the following general categories: plant succession, geomorphology, physiological ecology and population dynamics.

Table 20 References dealing with zonation of mangrove communities in Australasia

AUSTRALIA

General
Macnae 1966; Saenger et al. 1977; Lear and Turner 1977

Queensland
Macnae (1966, 1967, Townsville and Cairns); Spenceley (1983, Townsville); Saenger and Hopkins (1975, Gulf of Carpentaria); Saenger and Robson (1977, Port Curtis); Graham et al. (1975, Trinity Inlet); Elsol and Saenger (1983, Princess Charlotte Bay); Shanco and Timmins (1975, Bustard Bay); Thom (1975, low wooded islands on Great Barrier Reef)

Northern Territory
Specht (1958, Arnhem Land); Hegerl et al. (1979, Alligator Rivers region)

Western Australia
Semeniuk, Kenneally and Wilson (1978, general); Thom, Wright and Coleman (1975, Cambridge Gulf); Sauer (1965, Port Hedland); Semeniuk (1980, King Sound); Congdon (1981, Blackwood River salt marshes)

South Australia
Osborn and Wood (1923, Port Wakefield)

Victoria
Bird (1971, Westernport Bay); Bridgewater (1975, Westernport Bay)

Tasmania
Kirkpatrick and Glasby (1981, general salt marshes); Curtis and Sommerville (1947, Boomer Marsh); Guiler (1951, Pipe Clay Lagoon)

New South Wales
Kratochvil, Hannon and Clarke (1973, Sydney); Hutchings and Recher (1974, Careel Bay)

New Zealand
Chapman (1977, general); Chapman and Ronaldson (1958, Auckland Isthmus)

Papua New Guinea
Chapman (1977, general); Womersley (1983, general); Percival and Womersley (1975, general); Johnstone (1983, Hood lagoon)

Oceania
Baltzer (1969, Dumbea River, New Caledonia); Chapman (1977, general)

Zonation as the spatial expression of plant succession was the earliest view, going back to Curtiss (1888). This view interprets zoned mangrove communities as a sequence of seral communities from seawards to landwards. It hinges on the apparent ability of *Rhizophora* to build and colonize new land (primary succession) by trapping sediments among its root system into which fall the viviparous propagules that colonize the newly won land (Davis 1940; Richards 1964). Further build-up of the substrate allows other mangrove species to invade and eventually replace the *Rhizophora* (secondary succession), until build-up exceeds the level of tidal inundation. At this point, terrestrial species that are not salt-tolerant invade and replace (out-compete) the mangroves.

The view that plant succession is the basis for mangrove zonation is logical and appealing (Snedaker 1982). However, with more detailed study of succession in ecosystems, it is becoming increasingly clear that mangrove zonation does not conform to the general characteristics of secondary succession (Snedaker 1982; Johnstone 1983).

Because of the undoubted ability of mangroves to trap sediment and thus build land, mangrove zonation has been interpreted as a response to geomorphic change. Snedaker (1982) and Woodroffe (1983) summarized the evidence of geomorphic control over vegetational patterns and species assemblages, particularly landform patterns and vegetation. Thom (1967, 1975) and Thom, Wright and Coleman (1975) investigated vegetation in Mexico and Australia. They were able to relate species assemblages, distributions and overall spatial organization to the depositional and erosional histories and to subsidence, compaction, freshwater discharge and sea-level rise.

As discussed earlier, mangrove development and zonation are historically bound to the geomorphic process of a region through the particular soils and soil conditions that these processes have produced. Consequently, more direct information on mangrove growth, development and zonation clearly can be obtained from more direct (physiological and ecological) studies of the soil–mangrove relationship.

Zonation as a physiological response to tidally maintained gradients has received considerable attention since the classical work of Watson (1928). The interactions between surface hydrology and salinity on the one hand and mangrove zonation on the other has been reviewed extensively (Macnae 1967, 1968; Clarke and Hannon 1967, 1969, 1970, 1971; Walsh 1974; Lugo and Snedaker 1974; Chapman 1976). However, as Snedaker (1982) pointed out, although good correlations may exist between salinity, tidal inundation and mangrove zonation, the physiological response of the mangroves to many of these features is so poorly known for most species that it is premature to conclude such correlations imply causality.

Clarke and Hannon (1967, 1969, 1970, 1971) have shown experimentally and in the field that species of salt-tolerant plants near Sydney do have definable tolerances and optima under specific conditions, and that these can be used to explain landward and seaward boundaries for each species (Clarke and Hannon 1971).

Other authors also have established experimental optima for several mangroves, especially in relation to salinity (McMillan 1971, 1974; Connor 1969; Kylin and Gee 1970; Cintron et al. 1978; Teas 1979; Downton 1982); some long-term field data on the soil salinities and degrees of waterlogging under which different species occur are given in tables 13 and 14.

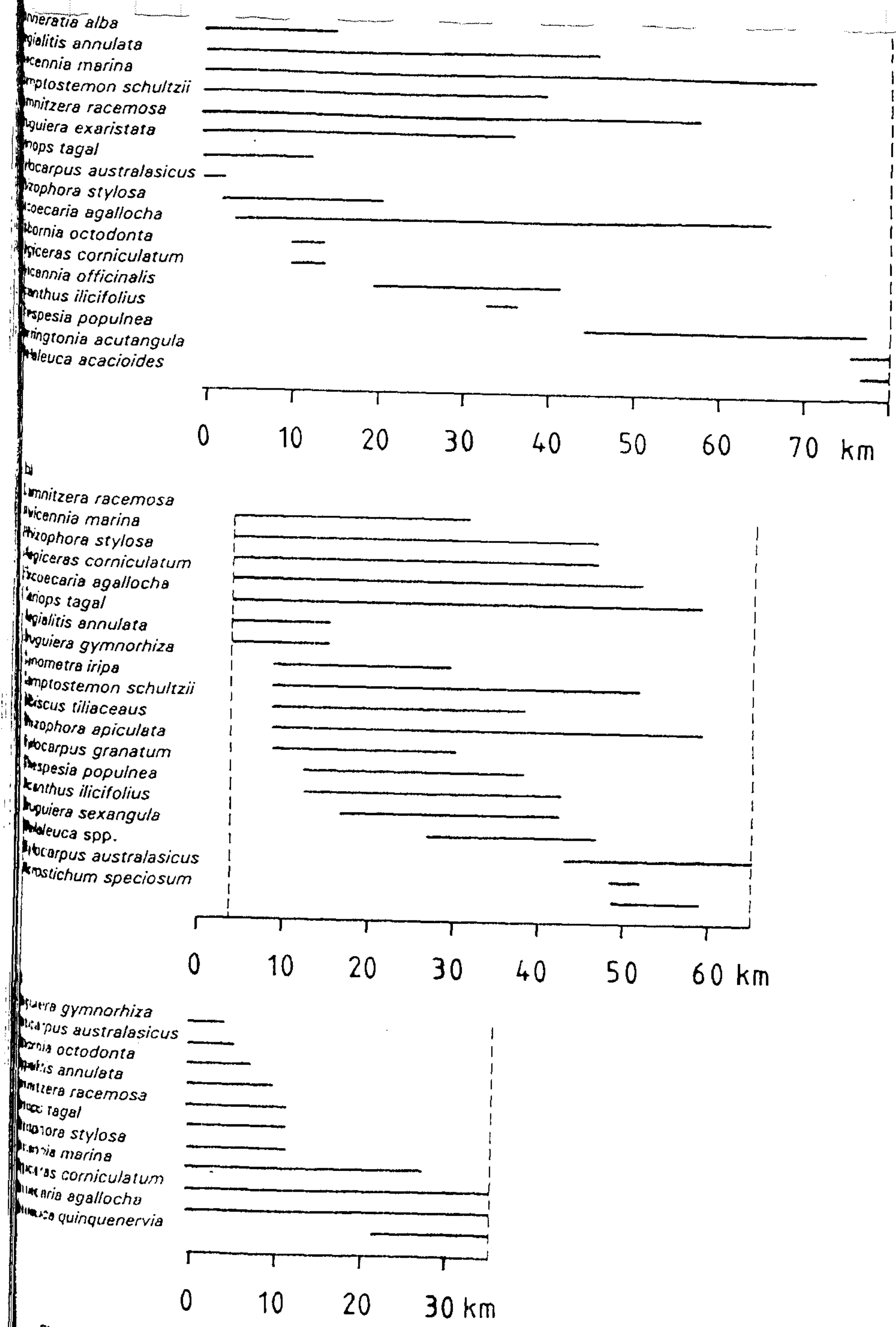


Figure 31 Upriver distribution patterns of mangroves in (a) East Alligator River, Northern Territory (after Hegerl et al. 1979, and from Wells and Saenger, unpubl. data); (b) Watson River, Cape York (Saenger, unpubl. data); and (c) Calliope River, central Queensland (Saenger, unpubl. data).

The metabolic basis of responses of species and communities to salinity, for example, has been examined, and rests on the decrease in transpiration rates with increasing salinity (Bowman 1917; Teas 1979), the increase in respiration with increasing salinity (Carter et al. 1973; Hicks and Burns 1975), and the maximization of photosynthesis at particular salinity levels in each mangrove species (Lugo et al. 1975).

On this basis, it becomes apparent that if a salinity gradient is present then a gradational sequence of species can result. Thus, although the relationship between soil salinity and mangrove metabolism and zonation has been described (Carter et al. 1973; Lugo et al. 1975; Cintron et al. 1978), the extreme variability in soil salinity makes the concept difficult to apply to specific field conditions. Snedaker (1982) argued that short-term measurements do not necessarily reveal the long-term mean to which mangroves must adapt; however, he indicated this to be an error in technique, not in concept.

Recently, the view has been put forward that zonation is a consequence of differential dispersal of propagules and their survival. In a series of studies based on field work in Panama, Rabinowitz (1975, 1978a, 1978b, 1978c) found that (1) mangrove genera which dominate lower tidal levels have large propagules whereas those that dominate at high elevations further inland have small propagule requiring a period of stranding prior to becoming established, (2) seedling mortality rates were inversely correlated to propagule weight, and (3) seedlings did not exhibit better growth under the canopies of their respective adults.

Based on these findings, Rabinowitz (1978c) concluded that zonation was probably the result of differential tidal sorting and dispersion according to propagule size and the frequency of tidal inundation of potential sites. She postulated further that, following establishment, the competitive interaction between seedlings and adults dominates subsequent survival.

In the species-rich mangroves of northeastern Australia, the three underlying conditions for tidal sorting are not present. For example, on the basis of long-term data from Port Curtis, Queensland, Saenger (1982) showed that the largest propagules (those of *Rhizophora stylosa*) were the most widely dispersed throughout the intertidal zone, and also had the highest first-year mortality rate. In addition, propagule survival in nearly all species was enhanced when they occurred close to (within 2 metres) their respective adults (Saenger 1982). Similar findings for the species-poor mangroves of Florida were reported by Snedaker (1982).

From this discussion, it is apparent that tidal sorting cannot be invoked as a universal mechanism, and that in at least some mangrove communities it has a minor role, if any at all.

Snedaker (1982) concluded that of the four views mentioned above, those advocating geomorphology and environmental physiology appeared to be most relevant in furthering an understanding of zonation and plant succession in the intertidal zone. He argued that there is a temporal tendency for each species to assume competitive dominance in its preferred zone. Whether this occupation is guided by physical forces or results from interspecific competition, the species which can maximize its photosynthetic output with greatest metabolic efficiency dominates in competition with other species. The concept of a zone or environmental preference implies that each mangrove species does have a preferred optimum and a limit of tolerance related to the metabolic cost of existence along an environmental gradient. Variations in that gradient may either last long enough to result in competitive exclusion or domination by a previously subordinate competitor or fluctuate around a long-term mean which enhances the likelihood of survival of the existing dominant and, thus, the zone.

Longitudinal Upriver Zonation

Although sharing some features with the parallel zonation of shorelines, upriver zonation has been recognized as a distinct phenomenon since the descriptive accounts of Myers (1935) on the riverine vegetation of South America.

Myers defined upriver zonation as the definite sequence of plant communities along the course of a stream, determined not by edaphic factors of the area through which the river flows, but by factors dependent on the stream itself (for example, its width in a given place or the distance from the sea) and thus recurring in an essentially similar sequence in all the streams of the region where modification by humans has not obscured it.

As shown by the species distributions in figure 31, sequences of mangrove communities also occur in Australian river systems, and show some similarities despite the great geographical and geological differences among the three river systems considered. For example, both *Avicennia marina* and *Excoecaria agallocha* have wide upriver distributions, whereas *Ceriops tagal* and *Lumnitzera racemosa* have limited, downriver distributions. On the other hand, *Aegiceras corniculatum* and *Xylocarpus australasicus* show very different upriver distributional patterns in the three river systems (Bunt, Williams and Clay 1982; Elsol and Saenger 1983; Hegerl et al. 1979).

Bunt, Williams and Clay (1982) related upriver distributions of mangroves to upriver distance and salinity gradients (see fuller discussion on p. 70) in rivers of northeastern Australia. They found that *Rhizophora stylosa*, *R. apiculata*, *Sonneratia alba* and *Ceriops* *tagal* were mainly from downstream, high-salinity areas, whereas *Heritiera littoralis*, *Excoecaria agallocha*, *Acrostichum* sp., *Aegiceras corniculatum* and *Rhizophora mucronata* occurred principally in upstream, low-salinity areas. Three other species, including *Avicennia marina*, showed no correlations with site and were found over almost the entire salinity range of the river systems.

Correlations with distance from river mouth were always better than those with salinity, and in the Lockhart River, where virtually no salinity gradient was found, Bunt, Williams and Clay (1982) concluded that certain of the mangroves were responding to some aspect of distance other than salinity. Furthermore, their study indicated that distance does not simply act as an integrated measure of salinity, or at least not universally.

Myers (1935) tentatively identified three factors which influence the upriver zonation, including (1) width of the river, (2) character of the water and (3) distance from the sea. According to him, the width of the river was of importance because it determined whether the waterway acted as a light gap, exposing the vegetation on the bank to full sunlight. The character of the water largely depends on catchment characteristics, whereas the distance from the sea is important because salinity is a function of that distance and of the size of the river.

Two additional factors can be suggested which appear to correlate with upriver distance: upstream gradients of decreasing salinity fluctuation (or range) and increasing turbulent flow. Clearly, the salinity range to which a mangrove species is exposed may be just as important as the absolute levels of salinity, and may influence upriver distributions of individual species. Leaf thickness in *Rhizophora mangle*, for example, is related more to salinity fluctuations than to absolute levels of salinity (Camilleri and Ribi 1983).

There is little evidence to support any direct effects of turbulent flow on mangroves, although flow characteristics can affect the meanders in a river, which in turn may affect species absence or presence. Erosion of concave banks and accretion on convex lobes are largely associated with the intermittent seasonal flow of floodwaters. The species composition of actively accreting convex lobes are generally strikingly different from nearby, non-accreting river banks (Elsol and Saenger 1983).

Clearly, the phenomenon of upriver zonation is still poorly understood. Gradients of absolute salinity or of degree of salinity fluctuation are clearly involved (Bunt, Williams and Clay 1982), but other factors such as the width of the stream and its geomorphological characteristics may also have an effect. As has been discussed already under parallel shoreline zonation, if a salinity gradient is present, then a gradational species sequence can result, although in river systems the sequence may be secondarily modified by river width and sedimentary characteristics. The fact that Bunt, Williams and Clay (1982) found better correlations with distance than with salinity may be referable to shortcomings of measuring salinity. As previously discussed, short-term measurements in a river system are unlikely to reveal long-term means or ranges to which mangroves must adapt. As in the case of soil salinities in shoreline zonation, this can be viewed as an error in technique rather than concept (Snedaker 1982). Consequently, it seems appropriate that, until detailed long-term salinity studies can be related to upriver mangrove distributions, the view that salinity gradients are important should not be discarded despite some of its presently known imperfections.

Unifying Both Zonation Types

In figures 19 and 22, the gradients of soil salinity and waterlogging are shown for four permanent studies sites at Gladstone, Queensland, monitored over nine years. To these tidally maintained gradients, those for percentage submergence and tidal frequency can be added. In this way, four intertidal gradients are established, each of which is related to tidal levels in a way specific for this particular locality.

Figure 32 shows these gradients together with the topographic distributions of the intertidal communities in the study areas. Two approaches can now be adopted to describe the upper and lower limits of these communities and to compare these with other localities.

The traditional approach has been to relate the limits of communities to the various tidal levels, and because these are well established for most coastal sites, comparisons can be made easily. This approach assumes that the various communities have a constant relationship to specific tide levels, an assumption that is difficult to justify on the one hand, and tautological on the other.

The alternative approach is to relate the upper and lower limits to each of the four gradients, and to use these to define boundary conditions for each of the plant communities. This provides ecologically meaningful conditions which may limit the distributions of the plant communities. To compare the distributions at different localities, the level at which the boundary conditions are identical must be determined. In other words, although the gradients are all tidally maintained, tide levels as such are not used but rather certain cut-off points along each of the four gradients.

The relationships of these cut-off points to tidal levels will vary

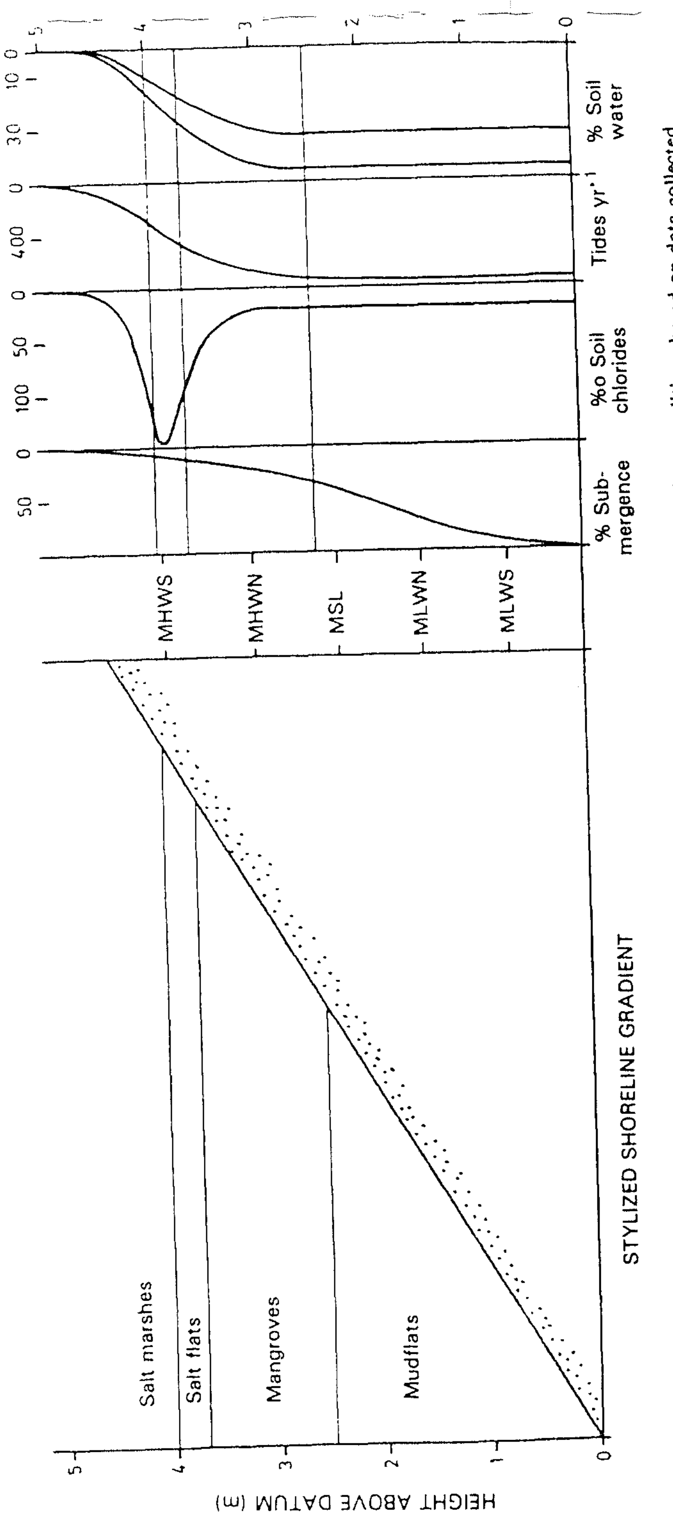


Figure 32 —Integration of vegetational boundaries with gradient-related and tidally induced boundary conditions based on data collected from study areas in Gladstone, Queensland, 1975–1983.

from one locality to another, but the ecologically significant cut-off points can be expected to have a constant relationship with each of the plant communities under consideration. By a detailed comparison of boundary conditions at several sites, the more important boundary conditions can be identified as these will remain relatively constant in relation to each plant community from site to site.

Agreement is apparent in the boundary conditions for Port Curtis and Repulse Bay (table 21) with the exception of the number of tides per year for the saltflat and saltmarsh boundaries. This is significant in that the three boundaries involved are clearly at different tidal levels at the two localities, yet, ecologically, there is little to separate them. For example, critical per cent submergence time is 1 and 10 at Repulse Bay and Port Curtis respectively, and both soil salinity and soil water levels are similar at the two sites. The same conditions in terms of soil salinity and waterlogging obviously can be attained at different tidal levels at the two localities.

Table 21 Boundary conditions for the various intertidal plant communities at Port Curtis and Repulse Bay (Saenger, unpubl. data).

Community	Boundary	% Submergence	Tides/ year	% Soil water	‰ Soil chlorinity
Mudflats	upper	< 30	< 720	> 40	~ 20
Mangroves	lower	> 30		> 40	
	upper			< 5	> 70
Salt flats	lower	> 15	> 5/> 420*		< 70
	upper	< 1 < 10*	< 2/< 360*		< 70
Salt marshes	lower	> 1 > 10*	> 2/> 360*	> 15-20	> 70
	upper				
Fringing vegetation	lower		> 0		> 5

* Given for Repulse Bay and Port Curtis respectively.
Source: Saenger (unpubl. data).

For each of the plant communities, several boundary conditions are given. This has been done because, on the present data, no single critical boundary condition can be identified. On the other hand, no tidally related boundary condition is provided for the upper limit of saltmarshes and this is consistent with their extensive non-coastal occurrence. The lower boundary conditions for saltmarshes are given, and when these are compared with those determined in other areas (table 22), good agreement is found, particularly with soil water and soil salinity levels. In turn, this suggests that soil salinity and the degree of waterlogging are the major factors in determining the lower limits of these plant communities.

A similar approach could be used to determine boundary conditions for each species individually. At present, the available data

Table 22 Comparative boundary conditions for the lower limit of salt marshes

Location	% Submergence	Tides/ year	% Soil water	‰ Soil chlorinity
Port Curtis	10	360	15-20	< 70
Repulse Bay	1	2	15-20	< 70
NSW[1]		420		< 55
South Aust.[2]			21.8	
Tasmania[3]	0-30			

[1] Clarke and Hannon (1971)
[2] Osborn and Wood (1923)
[3] Guiler (1951)

are insufficient to do this, although the parallel zonation along open shorelines provides a hint of which species are most tolerant of waterlogging and high salinities.

Mangroves, saltmarsh plants and other vegetation can be broadly grouped by their tolerance with respect to salinity and waterlogging. This has been attempted in table 23, and the results may be interpreted as follows. On the open shoreline where salinities range from medium to high, the plant sequence is likely to follow the waterlogging gradient, that is, high at the seaward margin and low at the landward margin. On the other hand, in the upriver situation where waterlogging ranges from medium to high, the plant sequence is likely to follow the salinity gradient, that is, high salinities at the mouth and low salinities in the upper reaches. Both of these likely sequences are indicated by arrows in table 23.

Table 23 Tolerance of mangrove, saltmarsh and fringing plants to soil salinity and waterlogging

SALT TOLERANCE

WATERLOGGING TOLERANCE	High	Medium	Low
High	Most mangroves	*Heritiera, Pemphis, Hibiscus, Cynometra, Aegiceras, Xylocarpus granatum, Acrostichum*	*Melaleuca* spp. *Casuarina glauca* Most freshwater aquatics
Medium	*Clerodendron inerme* *Lumnitzera racemosa* *Sporobolus virginicus*	*Camptostemon* *Excoecaria* Most strand plants	Some swamp margin plants
Low	Most saltmarsh species	*Triglochin procera*	Most upland plants

OPEN SHORELINE SEQUENCE

On two identically shaped coastlines where one is fully open shoreline and the other is a river mouth discharging water of reduced salinity, the vegetation sequence is likely to be as shown in figure 33. Salt flats are absent upstream because very high salinity levels do not occur there. In addition, the tidal influence decreases upstream with the result that the tidal zone becomes narrower and the terrestrial fringing vegetation approaches the river bank. Those plants adapted to medium-low salinities become increasingly common and are able to out-compete most of the species tolerant of high salinities. This, in turn, would result in the loss of the most seaward mangrove zones somewhere in the lower reaches of the river at the same time that the driest landward zones (salt flats and saltmarshes) are lost. The middle and landward mangrove zones, because of their medium tolerance of both salinity and waterlogging, would extend furthest upriver. Gradually, the mangrove zone would become dominated by those species able to optimize growth in medium to low salinity conditions (such as *Aegiceras*, *Heritiera*, *Hibiscus*, *Cynometra*, *X. granatum* and *Acrostichum*).

Irregular coastlines would tend to disrupt the idealized pattern shown in figure 33, and may introduce various site-specific anomalies. Nevertheless, the general patterns described can be recognized with sufficient frequency to suggest that gradients of salinity and waterlogging are the interconnecting features of upriver and shoreline zonation.

Classification of Mangrove Communities

Any of the various attributes (physico-chemical, functional, structural) of mangrove communities may be useful in classifying them, and the appropriate selection of attributes depends upon the purpose of the classification. However, three classificatory schemes appear to be of some universal value in comparing mangrove communities, two at the medium to local scale and the other at the medium to regional scale. Brief summaries and discussions of these schemes are given below.

Classification Using Structural Attributes

Specht (1970) developed a structural classification of evergreen plant communities which uses those properties reflecting the amount of photosynthetic tissue (contributing to energy input) and the biomass of respiring aerial plant tissue (involved in energy output). The properties used are (1) the height and life form of the tallest stratum (which provides an estimate of the biomass) and (2) the "foliage projective cover" (FPC) of the tallest stratum. The FPC is the proportion of photosynthetic tissue vertically above the landscape. Ideally, it should be measured using some crosswire

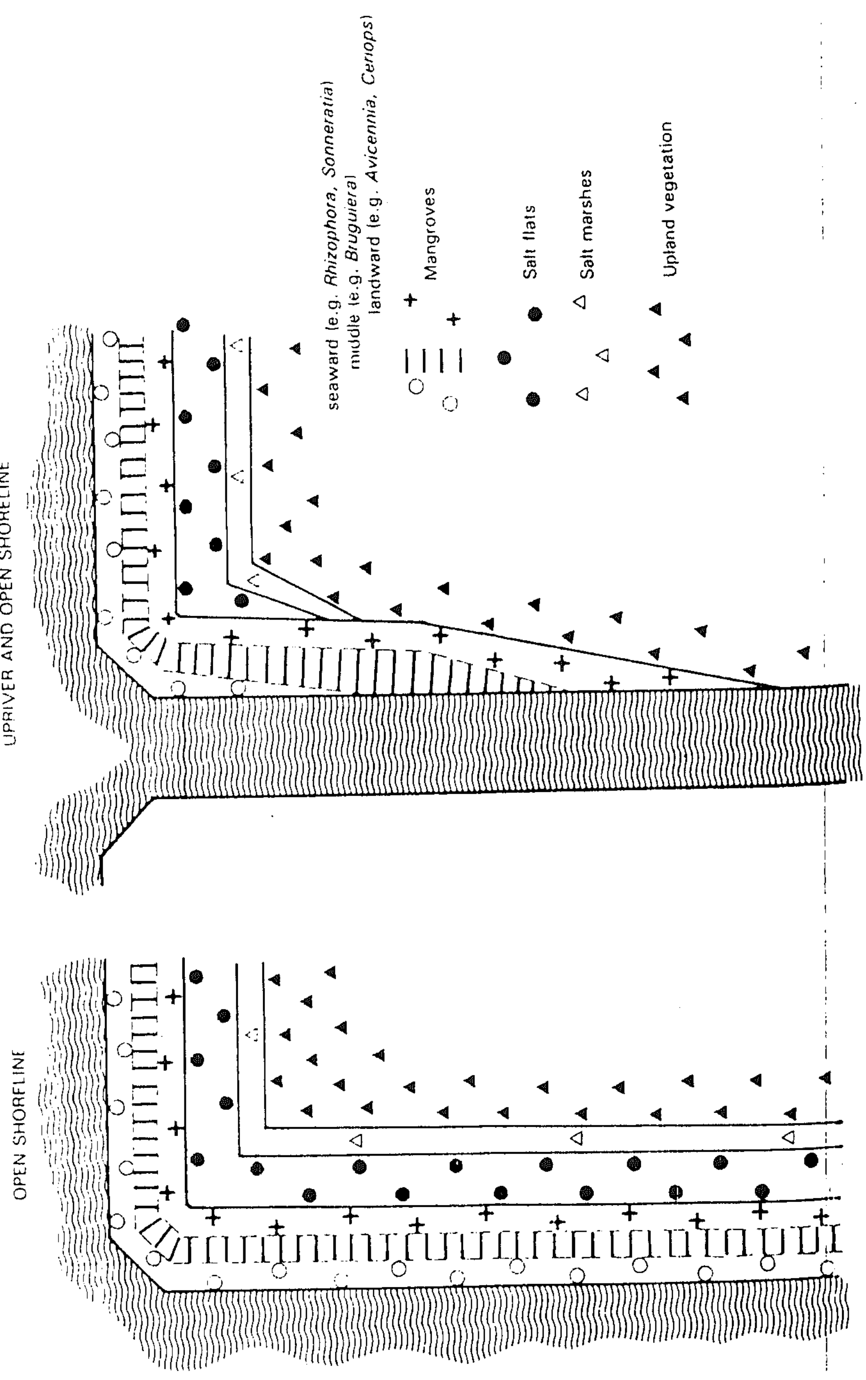


Figure 33 Stylized zonational sequences along open shorelines and into adjacent river mouths.

device to determine the presence or absence of foliage vertically above a large number of randomly selected points in the community.

Using these two properties, the identification of structural formations can be achieved. These formations (such as forest or woodland) can be defined further by including the name of the dominant genus or species (such as *Avicennia* woodland). The general absence of well-developed understorey and shrub strata in mangrove communities and their marked tendency towards dominance by one species of canopy tree mean that it is rarely necessary to seek further precision. Using this classification, the range of mangrove structural formations that have been encountered are shown in table 24. The most common of these are closed communities. Only rarely do trees exceed 30 metres in height. Open canopies are associated with high salinity sites, often at or near high-water spring levels, where rainfall or run-off are low or moderately seasonal. Open canopies also may occur where persistent waterlogging is a feature of the environment and, in some other instances, in dwarfed communities whose structure is not readily explained as yet.

Table 24 Structural formations of Australian mangrove communities

Life form and height of tallest stratum		Foliage projective cover of tallest stratum		
		Dense 70–100%	Mid dense 30–70%	Sparse 10–30%
Trees*	30 m	Tall closed forest	—	—
Trees	10–30 m	Closed forest	—	—
Trees	5–10 m	Low closed forest	Low open forest	Low woodland
Shrubs**	2–8 m	Closed scrub	Open scrub	Tall shrublands

* A tree is defined as a woody plant more than 5 m tall usually with a single stem.

** A shrub is defined as a woody plant less than 8 m tall, usually with many stems at or near the base.

The assumption is made in this classification that the communities are mature, that is, fully reflecting the constraining effects of water balance, soil fertility, temperature and light. In practice, this assumption is not difficult to meet as successional response by FPC is rapid (Specht and Morgan 1981), minimizing any error arising from this parameter; the age/size structure of the population in relation to neighbouring sites permits a reasonable assessment of the developmental (successional) phase of the ecosystem. This scheme can be used validly also where the community is not mature because of disturbance if that disturbance is regular. In this instance, regular disturbance can be viewed as an integral part of the environment.

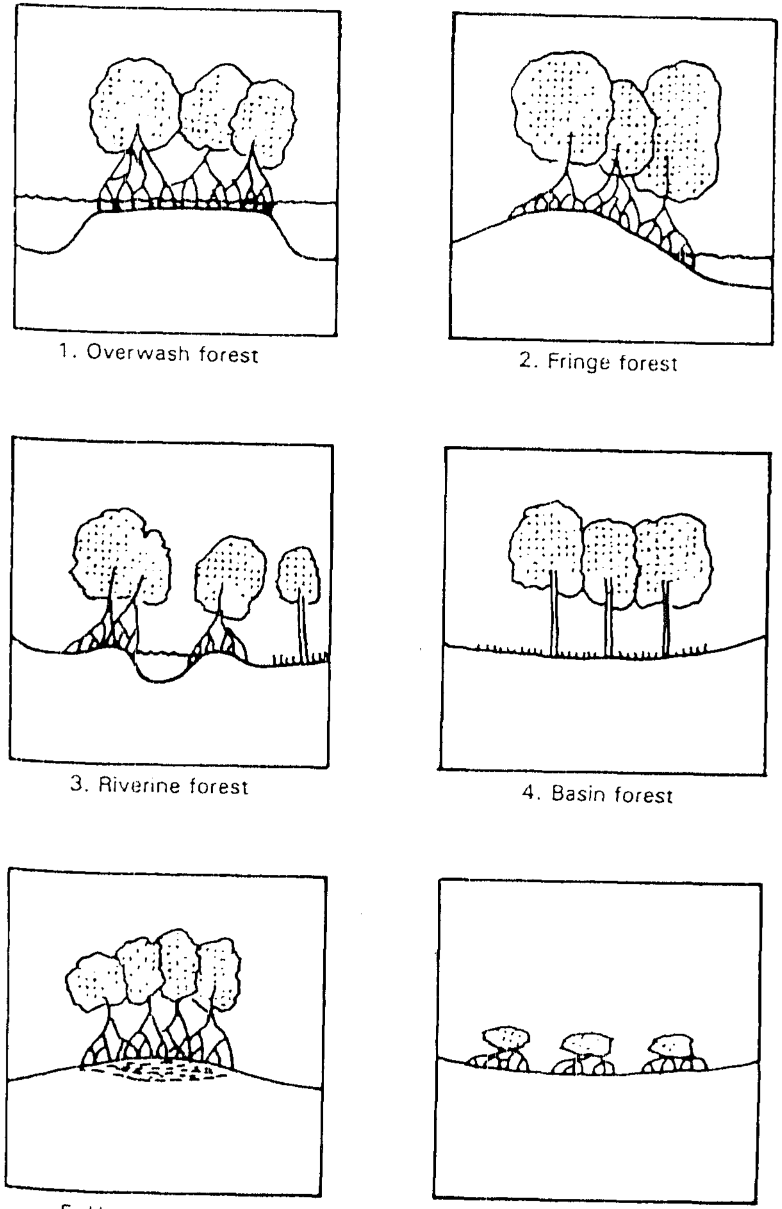
In terms of understanding the ecological biogeography of mangrove plant communities, this classification is extremely useful. The selected parameters (FPC and height) relate to community growth and, consequently, allow some functional interpretations of structural variation to be made. An assessment of mangrove plant communities in these terms conveys clues about the environment and will enable some approximate predictions to be made about the direction of any change in the community following environmental manipulations.

Classification Using Physiographic and Structural Attributes

Lugo and Snedaker (1974) suggested that, as mangrove communities exhibit a tremendous range of form, a convenient system of classification can be based on the geomorphic and hydrological processes that induce that form. From their work in Florida, they subsequently identified six major community types based largely on their physiographic setting. Correlation between community physiography and community structure was found to be high, and led Lugo and Snedaker (1974) to recognize, on structure alone, one community type whose physiography was extremely variable and poorly understood.

Each of the six community types (figure 34) has its own characteristic set of environmental variables, such as soil type and depth, soil salinity range and tidal flushing rates. In addition, each community type has characteristic ranges of primary production, litter decomposition and carbon export along with differences in nutrient recycling rates and community components. The types are:

1. *Overwash mangrove forests*: These occur on the smaller, low islands and finger-like projections of large land masses in shallow bays and estuaries. Their positions and alignments obstruct tidal flow, and thus they are overwashed frequently by tides and much of the organic matter is washed away. In Florida, all local mangrove species may be present but *Rhizophora mangle* usually dominates. Maximum height is about 7 metres.
2. *Fringe mangrove forests*: These form thin fringes along protected shorelines and islands, being best developed along shorelines whose elevations are higher than mean high tide. This community type generally shows characteristic zonation. The low velocities of the incoming and retreating tides and the dense, well-developed stilt root systems entrap all but the smallest organic debris. Because of the relatively open exposure along shorelines, the fringe forest is occasionally affected by strong winds, causing breakage and resulting in the accumulation of relatively large amounts of debris among the stilt roots.



1. Overwash forest

2. Fringe forest

3. Riverine forest

4. Basin forest

5. Hammock forest

6. Scrub forest

Figure 34 Classification of mangrove environments using physiographic characteristics (adapted from Lugo and Snedaker 1974).

3. *Riverine mangrove forests*: These include the tall (up to 20 metres) floodplain forests along flowing waters such as tidal rivers and creeks. Although a shallow berm often exists along such creeks, the entire forest is usually flushed by daily tides. This forest type is often fronted by a fringe forest occupying the slope on the creek side of the berm. During the wet season, water levels rise and salinity drops because of upland terrestrial drainage. Low flow velocities over the surface preclude scouring and redistribution of ground litter.
4. *Basin mangrove forests*: These occur in inland areas along drainage depressions channelling terrestrial run-off towards the coast. Close to the coast, they are influenced by daily tides and, in Florida, are dominated by *R. mangle*. Moving inland, the tidal influence lessens and the dominance is increasingly shared with *Avicennia germinans* and *Laguncularia racemosa*. Tree may reach 15 metres in height.
5. *Hummock forests*: These are similar to the basin type except that they occur on ground that is slightly elevated (about 5–10 centimetres) relative to surrounding areas, often by underlying peat deposits.
6. *Scrub or dwarf forests*: In Florida, this community type is limited to the flat coastal fringe of southern Florida and the Keys. Individual plants rarely exceed 1.5 metres in height, except where they grow over depressions filled with mangrove peat, and many trees (shrubs) are forty or more years old. Nutrients appear to be limiting although highly calcareous substrates also may play a role. All three species of Floridian mangroves may occur in this situation.

While this classifactory scheme is based on Floridian mangrove communities, Lugo and Snedaker (1974) report comparable forest types in similar environments in Mexico, Puerto Rico, Costa Rica, Panama and Ecuador. The apparent success of this scheme strengthens the idea that physiographic control, via surface hydrology and tidal dynamics, is important in the distribution of mangrove species and structural units (Lugo and Snedaker 1974).

Although this scheme can be applied usefully to the physiographic classification of Australian mangrove communities, it remains untested in terms of how well these physiographic features correlate with floristic and structural attributes; this is particularly relevant because, in contrast to Florida with its three species, the number of species to be considered is ten to fifteen times larger.

Classification Using Geomorphological Settings

Comparisons of thirty-four major river systems by Wright, Coleman and Erickson (1974) in terms of particular sets of physico-

chemical variables (such as river discharge, wave energy regimes, river-mouth morphology and delta-plain landform suites) revealed that deltas tend to cluster together into a relatively few categories. Further generalization (Coleman and Wright 1975; Wright 1978) resulted in the classification of a number of general delta types, with each reflecting a particular combination of processes and physico-chemical controls.

Thom (1982) used this classification as the basis for a broader classification of coastal settings in which mangroves grow, and has described five types of terrigenous sedimentary coasts (figure 35). Although relatively unimportant on a global scale, the carbonate (coral coast) setting, where sediment accumulation is either from *in situ* growth of coral reefs or from deposition of carbonate particulates, should be added to this broad scheme; consequently six classes of settings now are recognized.

Galloway (1982) used this scheme to interpret patterns in aerial photographs of mangroves around the Australian coastline, recognizing twenty-six regional patterns within the six classes of settings. The six classes are described below together with some of the variations described by Galloway (1982).

Alluvial Plains

This setting is characteristic of coasts with a low tidal range and where the discharge of fresh water and sediment leads to rapid deposition of terrigenous sands, silts and clays to form deltas. These deltas build seawards over flat offshore slopes composed of fine-grained sediments. Such slopes help dampen wave energy and any tendency for longshore drift. The delta consists of multiple branching distributaries forming elongate, finger-like protrusions, resulting in a highly crenulate coastline with shallow bays and lagoons between and adjacent to the distributaries.

The active distributary region is predominantly an area of high freshwater discharge, so that salt-tolerant plants are not common. However, where abandoned distributaries occur into which saline waters penetrate seasonally or more frequently, salt-tolerant vegetation will develop. The area around these distributaries is also relevant to this setting as longshore drift of muds and reworking of sands and shells by waves influence plant establishment and regeneration, a phenomenon particularly striking on chenier plains. Thus, parts of the alluvial plain may contain an array of habitats where mangroves can establish or be maintained. Such plains are subject to rapid rates of subsidence and changes in freshwater discharge point and deposition, and are consequently characterized by a high degree of physico-chemical diversity and rapid habitat change.

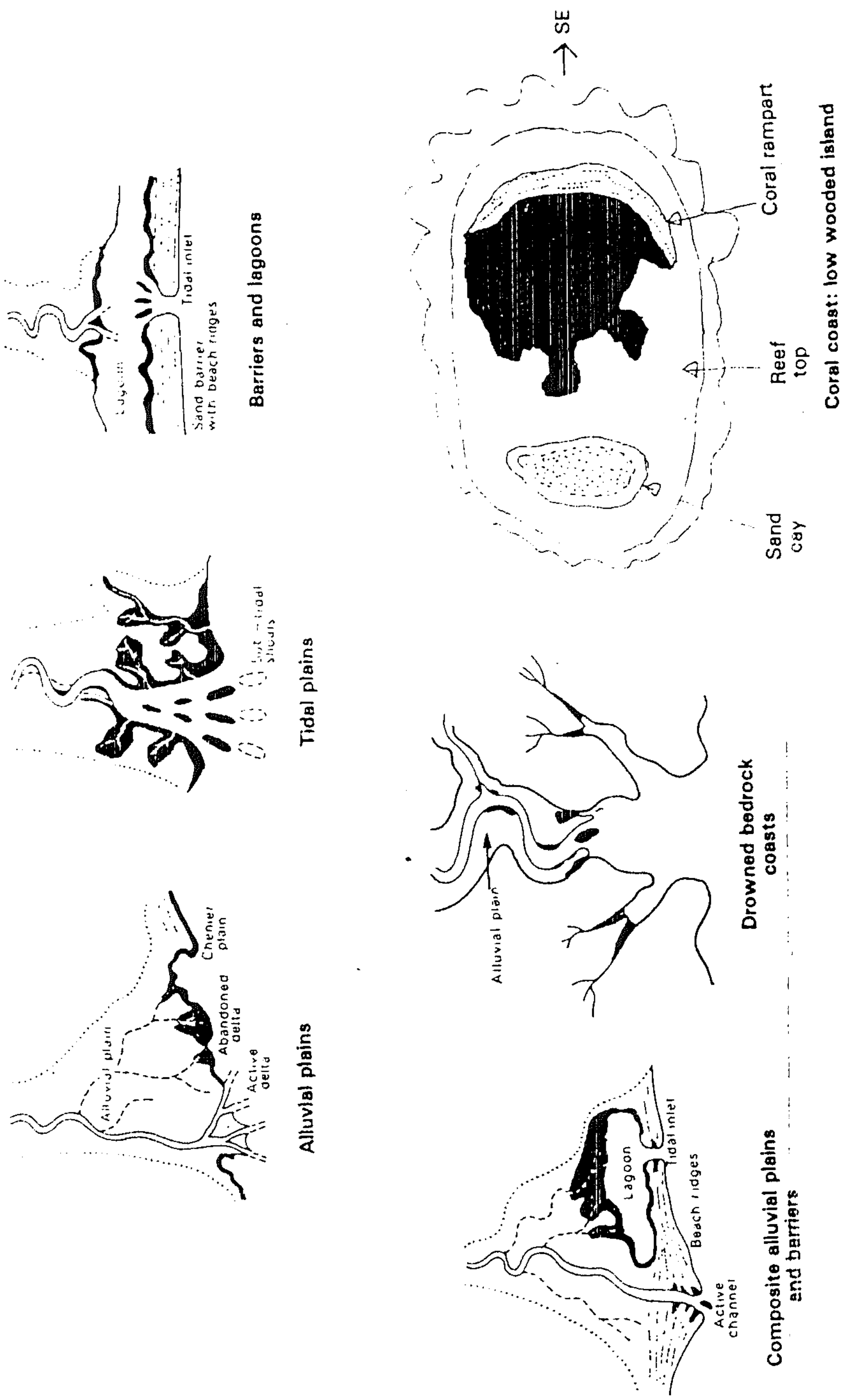


Figure 35 Classification of mangrove environments using geomorphological characteristics (after Thom 1982).

Examples of this setting include the eastern side of Exmouth Gulf, Western Australia; the southern shores of Van Diemens Gulf in the Northern Territory; the southeastern Gulf of Carpentaria (Rhodes 1982; Saenger and Hopkins 1975) and Princess Charlotte Bay in Queensland (Elsol and Saenger 1983); and the shores of the South Australian gulfs (Butler et al. 1977a).

Tidal Plains

This setting occurs on coasts where high tidal ranges and associated strong bidirectional tidal currents predominate. These currents are responsible for the dispersion of sediments brought to the coast by rivers, and in the offshore zone they form elongate sand bodies. Wave power is often low because of frictional damping over broad intertidal shoals. The main river channels are typically funnel-shaped and are fed by numerous tidal creeks; these creeks are often separated by extensive tidal flats.

Examples include the Ord River (Thom, Wright and Coleman 1975), Fitzroy River (Jennings and Coventry 1973) and King Sound (Semeniuk 1980) in Western Australia; Fitzroy River and the mud islands and shores of Moreton Bay, Queensland (Flood 1980); and the shores of Westernport Bay, Victoria (Enright 1973).

Barriers and Lagoons

This setting is characterized by much higher wave energy than previous ones, and by relatively low amounts of river discharge. Offshore barrier islands, barrier spits and bay barriers are typical of this setting. Small finger-like deltas prograde into these water bodies without significant opposition from marine forces. Considerable tidal modification may occur within the barrier system. Where the barriers project from the coast or link islands to the mainland, sheltered water in their lee provides sites for extensive mangroves if a sediment supply is available. Salt-tolerant plants occur around the margins of the lagoon in a variety of habitats.

Examples include the western shores of the Gulf of Carpentaria, in the Northern Territory; Eyre Peninsula, South Australia; and Port Curtis and Cape Bowling Green, Queensland.

Composite Alluvial Plains and Barriers

This setting represents a combination of high wave energy and high river discharge. Sand carried to the sea by the river is rapidly redistributed by waves along shore to form extensive sand sheets. Much of the sand deposited on the inner continental shelf during lower sea-levels is reworked landward during periods of rising or stable sea-levels. The result is a coastal plain dominated by sand beach ridges and narrow discontinuous lagoons with an alluvial plain to landward.

Salt-tolerant plants such as mangroves are concentrated along abandoned distributaries and in areas near river mouths and adjacent lagoons. Where the tidal range is large and the climate dry, as in the case of the Burdekin delta, there is a spread of saline habitats to interdistributary areas which are periodically inundated by high spring tides.

Examples include the Burdekin Delta and Repulse Bay, Queensland; and the Purari Delta of Papua New Guinea.

Drowned Bedrock Coasts

This setting can be described as a drowned river valley complex. The depth of deposition is confined by a bedrock valley system which has been drowned by rising sea-levels. Neither marine nor river deposition has been sufficient to infill what is an open estuarine system. However, the heads of the valleys may contain relatively small river deltas which are little modified by waves, and often maintained by self-scouring (Bunt and Wolanski 1980). At the mouth of the drowned valley bordering the open sea, a tidal delta may occur, composed of marine mud and sand reworked landward during rising sea-levels.

Mangroves flourish in the fine sediments at the heads of the drowned tributary valleys, and in lagoons behind bay barriers near the mouth of the estuary.

Examples include Broken Bay, New South Wales; Port Darwin, Northern Territory; Kimberley Coast, Western Australia; Hinchinbrook Channel, Newcastle Bay, Shoalwater Bay, and Trinity Inlet, Queensland (Bird 1970).

Coral Coasts

Two expressions of this setting occur: mangroves may grow on terrestrial sediments which have accumulated behind fringing reefs, or they may occur on coral sediments (sand) on platform reefs. Stoddart (1980) provided a detailed account of the mangrove communities occurring on the coral islands of the northern Great Barrier Reef, while Thom (1975) described their general response to varying substrate and energy conditions.

As Galloway (1982) has shown, this scheme has considerable practical value when used on a regional scale, as it is based on both structural and dynamic characteristics of a particular section of coastline. For these reasons, this scheme also may have considerable value when applied on a more local scale, although to date it has not been used in such a context.

4. *Associated Flora*

Apart from the mangroves themselves, a number of characteristic species of other plants occur in the mangrove communities throughout Australia. Many of these species occur in other communities also, but there are some which are confined to mangroves. The association of these species with mangroves may be an intimate one; conversely, the association may be strictly casual or fortuitous, but these associated species increase the diversity of the mangrove communities.

In this chapter, a basic taxonomic and ecological outline is given for the various associated plant groups including bacteria, fungi, algae, lichens, epiphytes, mistletoes and saltmarsh plants, as well as other species of vascular plants which occur at the margins of mangroves.

Bacteria

As discussed elsewhere (chapter 8), bacteria, together with the fungi, form an important component of the mangrove community, and as decomposers play a central role in the functioning of the ecosystem.

Bacterial numbers in mangroves and related communities are high (table 25); sediments carry populations of heterotrophic bacteria two or three orders of magnitude higher than the waters above them, and the populations on clays and muds are usually several orders of magnitude greater than those on sandy substrates (Millis 1981).

The estuarine marine environment contains bacteria belonging to the same range of genera as found in fresh water, although an absolute requirement for sodium ions has been shown in most marine species. Marine bacteria are generally smaller than non-marine forms, and a large proportion consists of gram-negative rods; most of these are actively motile, flagellated forms. Cocci (spherical bacteria) are less common than the rod forms. Many marine bacteria are sedentary, attaching themselves to solid surfaces by means of a mucilaginous holdfast. In this way, bacteria may form a surface film on muds and make them more susceptible to subse-

Proteolytic. Relating to the metabolic breakdown of proteins.

Prothallus/i. The sexually reproducing form (in ferns) that alternates with the sporophyte, spore bearing, form (which is the familiar fern plant).

Proximal. Regarding position — closest to (cf distal).

Pseudofaeces. End product of digestion not passed through but rather regurgitated.

Radicle. The rudimentary root in the embryo of a plant.

Resistance — of leaf. The degree of inhibition of water loss through stomata by transpiration.

Saponin. Steroid vegetable glycosides that act as emulsifiers of oils. They dissolve red corpuscles, irritate the eyes and organs of taste and are toxic to lower animals.

Saprophyte. A plant which obtains nutrients from dead or decaying material.

Sclereids. Type of cells within plant sclerenchyma tissue (thick walled supporting tissue). Sclereids (or stone cells) are usually not much longer than wide. Common in fruits and seed coats.

Setae. Bristles of invertebrates — produced by epidermis.

Sublingual. Beneath the tongue.

Sympatric. Describes overlapping species distributions; (cf allopatric, i.e. species with different distributions — not overlapping).

Terrigenous. Derived from the land.

Thallus. A simple plant body which is not differentiated into stem, branches and roots, e.g. as in ferns and algae.

Trophic levels. The sequence of steps in a food chain or pyramid from producer to primary, secondary or tertiary consumer.

Turgor potential. The pressure within the cell resulting from the absorption of water into the vacuole and the imbibition of water by the protoplasm.

Upwelling. An upward movement within an ocean of cold water bringing nutrients to the surface.

Xeromorphic. Regarding plants — bearing characters which apparently enable it to survive dry conditions (adaptation).

Zooflagellate. Protozoans possessing flagella as adult locomotor organelles — not containing chromoplasts (cf phytoflagellate).

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