

3.4. Biology of Mangroves

Prof. K. Kathiresan

Centre of Advanced Study in Marine Biology
Annamalai University

Taxonomy

Mangroves are not a single genetic group but representing a large variety of plant families that are adapted to tropical intertidal environment. Tomlinson (1986) recognized three groups of mangroves: (i) major mangrove species; (ii) minor mangrove species; and, (iii) mangrove associates. The minor mangrove species are less conspicuous elements of the vegetation and rarely form pure stands. The major species are the strict or true mangroves, recognized by most or all of the following features:

1. They occur exclusively in mangal.
2. They play a major role in the structure of the community and have the ability to form pure stands.
3. They have morphological specializations – especially aerial roots and specialized mechanisms of gas exchange.
4. They have physiological mechanisms for salt exclusion and/or excretion.
5. They have viviparous reproduction.
6. They are taxonomically isolated from terrestrial relatives. The strict mangroves are separated from their nearest relatives at least at the generic level, and often at the sub-family or family level.

According to Tomlinson (1986), the major mangroves include 34 species in 9 genera and 5 families. The minor species contribute 20 species in 11 genera and 11 families. Thus a total of 54 mangrove species in 20 genera and 16 families are present globally. Duke (1992), on the other hand, identified 69 mangrove species belonging to 26 genera in 20 families. One family falls in the fern division (Polypodiophyta); the remainders are in the Magnoliophyta (angiosperms). Families containing only mangroves are the *Aegialitidaceae*, *Avicenniaceae*, *Nypaceae* and *Pellicieraceae*. Two orders (Myrtales and Rhizophorales) contain 25% of all mangrove families and 50% of all species. By reconciling common features from Tomlinson (1986) and Duke (1992), we recognize 65 mangrove species in 22 genera and 16 families (Table 1; Kathiresan and Bingham, 2001).

Table 1. Mangrove species, their taxonomic authorities, and global distributions (*e.g.* Kathiresan & Bingham, 2001)

Family	Species	South-east USA	Central / South America	Africa	South Asia	South-east Asia	Malay Archipelago	East Asia	Australia	South-west Pacific	West Pacific
Avicenniaceae	<i>Avicennia alba</i> Blume				•	•	•	•			
	<i>Avicennia balanophora</i> Stapf and Moldenke ex Moldenke								•		
	<i>Avicennia bicolor</i> Standley		•								
	<i>Avicennia eucalyptifolia</i> (Zipp. ex Miq.) Moldenke								•		
	<i>Avicennia germinans</i> (L.) Stearn	•	•								
	<i>Avicennia lanata</i> Ridley						•				
	<i>Avicennia marina</i> (Forsk.) Vierh.			•	•	•	•	•	•	•	
	<i>Avicennia officinalis</i> L.						•	•	•		
	<i>Avicennia schaueriana</i> Stapf and Leechman ex Moldenke		•								
	<i>Avicennia africana</i> Palisot de Beauvois			•							
Bignoniaceae	<i>Dolichandrone spathacea</i> (L.f.) K.Schumann					•	•	•			
Bombacaceae	<i>Camptostemon philippinensis</i> (Vidal) Becc.						•	•			
	<i>Camptostemon schultzei</i> Masters						•				
Caesalpinaceae	<i>Cynometra iripa</i> Kostel				•	•	•		•		
	<i>Cynometra ramiflora</i> L.				•	•	•				
Combretaceae	<i>Conocarpus erectus</i> L.	•	•								
	<i>Laguncularia racemosa</i> (L.) Gaertn. f.	•	•		•	•					
	<i>Lumnitzera littorea</i> (Jack) Voigt.				•	•	•				
	<i>Lumnitzera racemosa</i> Willd.			•	•	•	•	•			
	<i>Lumnitzera x rosea</i> (Gaud.) Presl. (hybrid of <i>L. racemosa</i> and <i>L. littorea</i>)								•		

Euphorbiaceae	<i>Excoecaria agallocha</i> L.	•	•	•	•	•	•	•
	<i>Excoecaria indica</i> (Willd.) Muell. – Arg.	•	•	•				
	<i>Excoecaria dallachyana</i> (Baill.) Benth.						•	
Lythraceae	<i>Pemphis acidula</i> Forst.	•	•	•	•	•	•	
	<i>Pemphis madagascariensis</i> (Baker) Koehne	•						
Meliaceae	<i>Aglaiia cucullata</i> (Pellegrin) Roxb.		•					
	<i>Xylocarpus granatum</i> Koen.		•	•	•	•	•	•
	<i>Xylocarpus mekongensis</i> Pierre		•	•	•		•	
	<i>Xylocarpus moluccensis</i> (Lamk.) Roem.		•	•	•			
Myrsinaceae	<i>Aegiceras corniculatum</i> (L.) Balanco		•	•	•	•	•	
	<i>Aegiceras floridum</i> Roemer and Schultes			•	•	•		
Myrtaceae	<i>Osbornia octodonta</i> F. Muell. loc. cit.				•	•		
Pellicieraceae	<i>Pelliciera rhizophoreae</i> Triana and Planchon			•				
Plumbaginaceae	<i>Aegialitis annulata</i> R. Brown				•			
	<i>Aegialitis rotundifolia</i> Roxburgh		•	•				
Rhizophoraceae	<i>Bruguiera cylindrica</i> (L.) Bl.		•	•	•	•		
	<i>Bruguiera exaristata</i> Ding Hou				•			
	<i>Bruguiera gymnorrhiza</i> (L.) Lamk.	•	•	•	•	•	•	•
	<i>Bruguiera hainesii</i> C.G. Rogers				•	•		
	<i>Bruguiera parviflora</i> Wight and Arnold ex Griffith		•	•	•	•	•	
	<i>Bruguiera sexangula</i> (Lour.) Poir.	•	•	•	•	•		
	<i>Ceriops decandra</i> (Griff.) Ding Hou		•	•	•	•		
	<i>Ceriops tagal</i> (Perr.) C.B. Robinson	•	•	•	•	•	•	•
	<i>Kandelia candel</i> (L.) Druce.		•	•	•	•	•	•
	<i>Rhizophora apiculata</i> Bl.		•	•	•	•	•	•
<i>Rhizophora mangle</i> L.	•	•						
<i>Rhizophora mucronata</i> Poir.		•	•	•	•	•	•	

	<i>Rhizophora racemosa</i> Meyer								
	<i>Rhizophora samoensis</i> (Hochr.) Salvoza								•
	<i>Rhizophora stylosa</i> Griff.	•	•	•	•	•	•	•	•
	<i>Rhizophora x lamarckii</i> Montr. (hybrid of <i>R. apiculata</i> and <i>R. stylosa</i>)	•		•			•		
	<i>Rhizophora x annamalayana</i> Kathir. (hybrid of <i>R. apiculata</i> and <i>R. mucronata</i>)	•							
	<i>Rhizophora x selala</i> (Salvoza)								
	Tomlinson (hybrid of <i>R. stylosa</i> and <i>R. samoensis</i>)								•
	<i>Rhizophora x harrisonii</i> Leechman (hybrid of <i>R. mangal</i> and <i>R. stylosa</i>)	•	•						
Rubiaceae	<i>Scyphiphora hydrophyllacea</i> Gaetrn. f.	•	•	•	•				
Sonneratiaceae	<i>Sonneratia alba</i> J. Smith	•	•	•	•	•		•	•
	<i>Sonneratia apetala</i> Buch. Ham.	•							
	<i>Sonneratia caseolaris</i> (L.) Engler	•	•	•	•				
	<i>Sonneratia griffithii</i> Kurz	•	•	•					
	<i>Sonneratia lanceolata</i> Blume				•				
	<i>Sonneratia ovata</i> Backer		•	•					
	<i>Sonneratia x gulngai</i> Duke (hybrid of <i>S. alba</i> and <i>S. caseolaris</i>)				•				
Sterculiaceae	<i>Heritiera fomes</i> Buch. Ham.	•	•	•					
	<i>Heritiera globosa</i> Kostermans			•					
	<i>Heritiera littoralis</i> Dryand. In Aiton	•	•	•	•				

Diversity of mangroves is extremely low as compared to that of tropical rainforests. About 40 species exist in Southeast Asia, 15 in Africa and 10 occur in the Americas. There are 65 species of mangroves globally, whereas the rainforests of the Malay Peninsula alone have about 8000 floral species of vascular plants that include 2500 tree species (ITTO/ISME, 1993).

Mangrove taxonomy needs much attention (Duke, 1992). For example, *Acrostichum* species are still poorly identified. *Sonneratia lanceolata* and *S. caseolaris* in Australia lack clear distinction in descriptions from Indonesia and Southeast Asia (Duke & Jackes, 1987). *Rhizophora apiculata* has under-leaf spots from Indo-Malaysia, but not in northern Australia (Duke & Bunt, 1979). *Rhizophora mucronata* from east Africa and Southeast Asia is not distinct from *R. stylosa*. *Acanthus ilicifolius* is not clearly identified from *A. ebracteatus*. For some species like *Avicennia marina* and *Ceriops tagal*, ecological varieties need to be recognized (Dodd *et al.*, 1999). In addition, there are several natural hybrids, but their parental species are not clearly understood, especially for species of *Rhizophora*. *Rhizophora x annamalayana*, found in a south Indian mangrove forest, was first identified as *R. lamarckii*, but has been reidentified as a new hybrid species between *R. mucronata* and *R. apiculata* (Kathiresan, 1995, 1999a). Some other hybrids like *Rhizophora x harissoni*, could not be confirmed. Molecular analyses may eventually help resolve the taxonomic problems. For example, DNA sequence data from the chloroplast gene **rbcl** indicate that the Rhizophoraceae belongs not to the order-Myrtales, but to a rosid clade that includes the families Euphorbiaceae, Humiriaceae and Malpighiaceae (Conti *et al.*, 1996).

Another problem in the taxonomy of mangroves is the confusion between the species of true mangroves and mangrove associates. Besides, often the same species is named differently at different sites, as in the case of *Avicennia rumphiana* and *A. lanata* and hence the total number of species is not constant (Duke, 1991).

There are mangrove species endemic to certain places. Only one species – *Rhizophora annamalayana* Kathir., is restricted to Pichavaram, in India (Kathiresan, 2003). *Aegiceras floridum* and *Camptostemon philippensis* are found only in Indonesia. *Avicennia integra* and *Ceriops australis* are confined to Australia. Other species with restricted distribution to only two countries - Malaysia and Indonesia, are *Aegiceras annulata*, *Avicennia*

lanata, *Bruguiera exaristata*, *Camptostemon schultzei*, *Cynometra iripa*, *Sonneratia lanceolata*, *S. gulngai* and *S. urama*.

Besides endemism, discontinuous distribution is also of interest. *Sonneratia alba* has populations located on East Africa, India, Sri Lanka and Australia. *Sonneratia ovata* occurs only between Thailand and Indonesia. *Ceriops tagal* and *Bruguiera gymnorrhiza* show major discontinuities between eastern Africa and southwest Asia. *Aegialities rotundifolia* is restricted to shorelines of the Bay of Bengal and the Andaman Sea (Saenger, 1998). Similarly *Camptostemon schultzei* occurs in Indonesia and northern Australia (Duke, 1992).

Genetic Variation

There is significant inter- and intraspecific variability among mangroves. For example, physiological differences have been identified between West African and Western Atlantic populations of *Avicennia germinans* (Saenger and Bellan, 1995). Variability may result from genotype differences, or from phenotypic responses to local environments. Mean leaf area of *Rhizophora mangle* in Mexico, for example is positively correlated with annual precipitation and negatively correlated with latitude. This morphological response to local conditions may allow the trees to maximize their photosynthetic efficiency. Similarly, leaf area indices can be used to differentiate *Rhizophora mangle* from basin and dwarf forest types in southeast Florida, USA.

Genetic variability has been clearly demonstrated through biochemical markers like iridioid glycosides (Fauvel *et al.*, 1995), foliar leaf waxes (Dodd *et al.*, 1995; Rafii *et al.*, 1996) and isoenzymes (Duke, 1991). It is also evident in differences in length and volume of chromosomes (Das *et al.*, 1994). Lakshmi *et al.* (1997) measured intraspecific genetic variability in *Acanthus ilicifolius* through DNA-based molecular markers that are insensitive to environmental influences (*i.e.* random amplified polymorphic DNAs and restriction fragment length polymorphisms). They found 48 genotypes in eight distinct populations and there were no differences in chromosome number ($2n = 48$). Genetic polymorphism is even higher in *Excoecaria agallocha* and the polymorphism is independent of morphological and sexual differences (Parani *et al.*, 1997).

Morphology and Anatomy

Mangroves are highly adapted to the coastal environment, with exposed breathing roots, extensive support roots, buttress roots, salt-excreting

leaves, and viviparous water-dispersed propagules (Fig.1). These adaptations vary among taxa and with the physico-chemical nature of the habitat (Duke, 1992). Perhaps the most remarkable adaptations of the mangroves are the stilt (= support) roots of *Rhizophora*, the pneumatophores of *Avicennia*, *Sonneratia* and *Lumnitzera*, the knee roots of *Bruguiera*, *Ceriops* and the buttress roots of *Xylocarpus* and *Heritiera*. The roots of many mangroves do not penetrate far into the anaerobic substrata. Instead, the trees produce profuse lateral roots for support.

The specialized roots are important sites of gas exchange for mangroves living in anaerobic substrata. The exposed surfaces of roots may have numerous lenticels (loose, air-breathing aggregations of cells; Tamlinson, 1986). *Avicennia* possesses lenticel – equipped pneumatophores (upward directed roots) through which oxygen passively diffuses. The lenticels may be closed, partially opened or fully opened, depending on environmental conditions. The spongy pneumatophores are generally short (<30cm), but grow much larger and become more numerous in *Avicennia marina* living in anaerobic and oil-polluted conditions. This phenotypic response apparently increases surface area for gas exchange. In *Sonneratia*, the pneumatophores may be 3 m long and stout with heavy secondary thickening (Tomlinson, 1986). Pneumatophores are normally unbranched. However, following the 1991 Gulf War, mangroves in the Arabian Gulf began developing branched pneumatophores and adventitious roots (Boer, 1993).

Sonneratia, *Avicennia*, *Xylocarpus*, *Bruguiera*, and *Ceriops* exhibit a system of air-filled cable roots. These are horizontal roots, lying 20-50 cm below soil surface. These cable roots give off anchoring roots downwards for nutrients absorption and, negatively geotropic aerial roots upwards that may be human-knee shaped roots or lengthy pneumatophores (Fig.1).

Root anatomy

The general structure of mangrove roots is similar to that of most other vascular plants. There are two important differences – 1) great development of aerenchyma in pneumatophores, and 2) high content of lignin in buttress roots and plank roots. They typically have a root cap, lateral roots arising endogenously, exarch protoxylem, and alternating strands of primary phloem and xylem. Many also have an enlarged polyarch stele with a wide parenchymatous medulla. Aerial roots are modified for life above - ground. Compared to the underground roots,

they have an exaggerated zone of elongation behind the apical meristem. They also have significant secondary thickening (similar to the stems). When the aerial roots reach the ground, they shift to having a short elongation zone. They also become thinner and form “capillary rootlets” with a simple diarch stele and a narrow cortex. Like aquatic plants, true mangroves lack root hairs. Hence, the endodermis is an effective absorbing layer (Tomlinson, 1986).

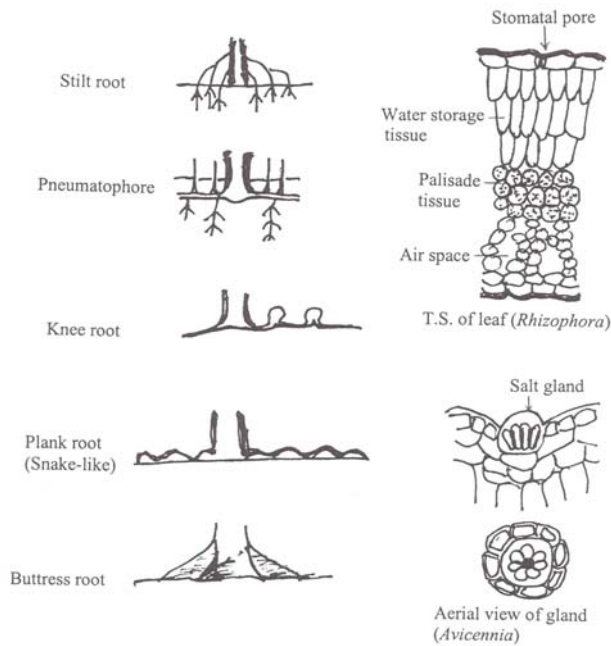


Fig. 1. Aerial roots and anatomy of leaves in mangroves

Wood anatomy

Water conduction through wood is strongly influenced by size and distributions of the vessels, present in the wood. Water moves most quickly through ring-porous woods in which the largest vessels are in the outermost growth layer. Conduction is much slower in diffuse-porous woods where vessels are more uniform in size and distribution. The wood of most mangroves is diffuse-porous, but *Aegialitis rotundifolia* has ring-porous wood (Das and Ghose, 1998).

Leaf anatomy

Mangroves have xerophytic adaptations to live in physiologically dry (or) saline environment. Water storage tissue is, in general, present in the leaves and this tissue helps in filtering off heat rays (Fig. 1).

The leaves are of moderate size and are arranged in a modified decussate (bijugate) pattern with each pair at an angle less than 180° to the preceding pair. This arrangement reduces self-shading and produces branch systems that fill space in the most photosynthetically efficient way (Tomlinson, 1986).

Mangrove leaves are leathery with obscure leaf veins. The cuticle is thick and smooth with small hairs, giving the plant a glossy appearance.

In general, sunken stomata are present in mangrove leaves. In most species, a horn or beak-like cuticular outgrowth covers the stomatal pores. These structures reduce stomatal transpiration, which is important, given the high solute concentration of the water.

Aerenchyma is often well developed. In *Nypa*, there is neither erect stem nor pneumatophores, but the lower portion of each leaf is largely swollen due to the presence of well developed aerenchyma tissue.

Seed and seedling anatomy

The seedlings have special anatomical features that allow them to tolerate flooding. Lacunae in the ground tissue conserve oxygen that enables the mangrove seedlings to maintain aerobic metabolism during periods of flooding. Tannin cells are present in the aerenchymatous tissues. Stone cells are present in the outer cortex and trichosclereids appear in the cortex and medulla. Since epidermis lacks stomata, numerous lenticels facilitate gas exchange.

Physiology

Salt regulation

Mangroves are physiologically tolerant of high salt levels (Ball, 1996). They do require salt in their tissue, because of water to flow from the roots to the shoots. Water tends to flow from a region of low concentration of salt to a region of higher concentration. Because of this,

the concentration of salt in the plant tissue has to be higher than that around the roots, for water to flow from soil to roots. The mangroves regulate salt concentration in the plant tissue through a combination of salt exclusion, salt excretion and salt accumulation. For example, *Rhizophora*, *Bruguiera*, and *Ceriops* may possess ultra filters in their root systems. The ultra filters exclude excessive salts while extracting water from the soil. Other genera (e.g. *Avicennia*, *Acanthus*, *Aegiceras*) take salt up, but excrete through specialized salt glands in the leaves. Salt excretion is an active process, as evidenced by ATPase activity in the plasmalemma of the excretory cells.

A plant cell is a balloon-like structure containing cytoplasm with a central cavity filled with fluid, known as the vacuole. In mangroves the vacuole is the main site for salt accumulation. This high concentration of salt in the vacuole must have a balance in chemical concentration in the cytoplasm. If the balance does not exist, the water will flow from the cytoplasm to the vacuole and damage the cell. In order to achieve this balance, low molecular organic compounds are synthesized in the cytoplasm to balance the build-up of salt in the vacuole. Mangrove cell vacuole represents about 80% of the cell volume and the remaining 20% by cytoplasm. Maintaining an osmotic balance between the two components is a remarkable adaptation of mangroves to cope up with their saline environment. Species of *Lumnitzera* and *Excoecaria* accumulate salts in leaf vacuoles and become succulent. Salt concentrations in the sap may also be reduced by transferring the salts into senescent leaves or by storing them in the bark or the wood (Tomlinson, 1986).

Mangroves are very conservative in using water. They can regulate the loss of water vapour from the leaf or transpiration stream. In the wet season, the fine root biomass increases in response to decreased salinity of the surface waters, directly enhancing the uptake of low-salinity water (Lin and Sternberg, 1994). Water use becomes increasingly conservative with increasing salinity in the environment and with increasing salt tolerance of mangrove species. The restriction of transpiration of water vapours through stomatal leaf openings may reduce entry of CO₂, photosynthesis and growth.

Photosynthesis

Mangroves show characteristic C₃ photosynthesis. Chloroplasts of mangroves function just like chloroplasts in other terrestrial plants. They are in fact sensitive to high salts. Hence, excessive salts are

excluded from the chloroplasts. The chloroplast otherwise, do not have any special metabolic process.

Photosynthetic rates of some species are strongly affected by environmental conditions. In general, mangroves do not exhibit maximum growth under conditions of high salinity. In fact, many mangroves show maximum growth when there is a plentiful supply of fresh water into their saline environment. The growth differs with a range of salinity. For example, low salinity conditions reduce carbon losses in *Avicennia germinans* and *Aegialitis annulata* and lead to greater CO₂ assimilation (Naidoo and Von-Willert, 1995). Fluctuating soil salinities lead to significantly lower intercellular CO₂ concentration and reduced photosynthesis in scrub forests of South Florida (Lin and Sternberg, 1992). The stunted mangroves in these habitats have much lower canopies and smaller leaves than mangroves in fringe forests that experience less salinity variability.

Strong sunlight can also reduce mangrove photosynthesis through inhibition of Photosystem II (Cheeseman *et al.*, 1991). The photosynthetic rates of mangroves saturate at relatively low light levels despite their presence in high sunlight tropical environments. To prevent damage to the photosystems, the mangroves dissipate excess light energy *via* the xanthophyll cycle (Gilmore and Bjorkman, 1994) and through the conversion of O₂ to phenolics and peroxidases (Cheeseman *et al.*, 1997).

Application of aliphatic alcohols can have a major stimulatory effect on mangrove photosynthesis by reducing photo-respiration. Treatment with triacontanol (a long-chain aliphatic alcohol) increased the photosynthetic rate of *Rhizophora apiculata* by 225%. A similar treatment with methanol (a short-chain aliphatic alcohol) increased photosynthesis in *R. mucronata* by 612% (Kathiresan and Moorthy, 1994a; Kathiresan *et al.*, 1996c).

Biochemistry

Mangroves are biochemically unique, producing a wide array of novel natural products. *Excoecaria agallocha*, for example, exudes acrid latex that is injurious to the human eye, hence its designation as “the blinding tree”. The latex is toxic to a variety of marine organisms (Kathiresan and Thangam, 1987; Kathiresan *et al.*, 1990b). Soil bacteria and yeasts

degrade the toxic latex, preventing its accumulation in the mangal (Reddy *et al.*, 1991).

Mangroves are rich in polyphenols and tannins (Kathiresan and Ravi, 1990; Ravi and Kathiresan, 1990). The levels of these substances may vary seasonally. Phenols and flavonoids in mangrove leaves serve as UV-screen compounds. Hence, mangroves tolerate solar-UV radiation and create a UV-free, under-canopy environment (Moorthy, 1995). Researchers have isolated a variety of other mangrove compounds including taraxerol careaborin and taraxeryl cis-p-hydroxycinnamate from leaves of *Rhizophora apiculata* (Kokpol *et al.*, 1990); 2-nitro-4 (2'-nitroethenyl phenol) from leaves of *Sonneratia acida* (Bose *et al.*, 1992); alkanes (46.7-97.9% wax) and triterpenoids (53.3% wax) from leaves of *Rhizophora* species (Dodd *et al.*, 1995); and, iridoid glycosides from leaves of *Avicennia officinalis* and *A. germinans* (Fauvel *et al.*, 1995; Sharma and Garg, 1996).

Pigment concentrations may vary with species, environmental conditions and seasons. For example, Oswin and Kathiresan (1994) found that mangrove chlorophyll and carotenoid levels, in general, are high during the summer but anthocyanin levels are highest in the monsoon months. Flavonoids increase during the premonsoon period.

Pollination Biology

Pollination in most mangrove species is by wind, insects, and birds and in some instances bats. Pollination proceeds after flowering. Flowering begins in spring and continues throughout the summer in Australia, whereas in Malaysia most species flower and fruit continuously throughout the year.

Mangroves have both self-pollinating and cross-pollinating mechanisms that vary with species. For example, *Aegiceras corniculatum* and *Lumnitzera racemosa* are self-pollinated. *Avicennia officinalis* is self-fertile, but can also cross-fertilize (Aluri, 1990). In *Avicennia marina*, protandry makes self-pollination of an individual flower unlikely. However, some fruits are set even when flowers are experimentally bagged to prevent cross-pollination (between 4 and 41% of cross-pollinated flowers set fruit). Fruit abortion is significantly higher in self-fertilized treatments, indicating some inbreeding depression (Clarke and Myerscough, 1991a).

Mangroves are pollinated by a diverse group of animals including bats, birds and insects. Pollen is deposited on the animals as

they deeply probe the flowers looking for nectar; they subsequently transfer the pollen grains to the stigma of another flower. The identity of the pollinators differs from species to species. *Lumnitzera littorea*, for example, is pollinated primarily by birds, while *L. racemosa* and small-flowered *Bruguiera* species are pollinated by insects (Tomlinson, 1986). Sunbirds visit and pollinate *Acanthus ilicifolius* (Aluri, 1990) and large-flowered *Bruguiera hainesii* (Noske, 1993, 1995). Birds are particularly important pollinators in the dry season.

Bats are the major pollinators for *Sonneratia*, which opens its flowers to expose the powdery stamens in the late night/early morning hours. If there are no bats, hawk moths become the primary night-time pollinators (Hockey and de Baar, 1991). Two lycaenid butterflies may be important in the pollination of mangroves in Brisbane, Australia where their abundance is directly correlated with the abundance of mangrove flowers (Hill, 1992). Bees regularly visit and pollinate species of *Avicennia*, *Acanthus*, *Excoecaria*, *Rhizophora*, *Scyphiphora* and *Xylocarpus*. Some wasps and flies are highly dependent on mangroves for nesting and are particularly important pollinators of *Ceriops decandra*, *Kandelia candel* and *Lumnitzera racemosa* (Tomlinson, 1986). *Rhizophora* species produce prolific amounts of pollens and are mainly wind-pollinated, though the stigma has no special modifications to capture the wind-borne pollen (Tomlinson, 1986).

Reproduction, Dispersal and Establishment

Mangroves reproduce sexually by means of flowers. These flowers generally are small. There are four methods of mangrove reproduction; vivipary, cryptovivipary, normal germination on soil, and vegetative propagation (Bhosale and Mulik, 1991). Vivipary, the continuous growth of offspring while still attached to the mother plant, is a unique adaptation to shallow marine habitats. True viviparous species remain attached to the mother plant for a full year, while cryptoviviparous offsprings are only attached for 1-2 months (Bhosale and Mulik, 1991). The viviparous reproduction allows seedlings to develop some salinity tolerance before being released from the parent tree (Smith and Snedaker, 1995). The vivipary provides a store of nutrients before the seedling falls from the plant and it assists quick rooting in the muddy environment. It also helps to develop buoyancy for distribution of the seedling and structural stability to protect the seedling from damage. In

the case of non-viviparous mangroves, seeds or fruits are larger which assist flotation.

The timing of mangrove reproduction depends on local environmental conditions and may differ broadly over the range of a species. For example, Duke (1990) found that flowering in *Avicennia marina* occurred 6 months earlier in Papua New Guinea than in Southern Australia and New Zealand. The period from flowering to fruiting was 2-3 months in the northern tropical site, but stretched to 10 months in the southern temperate locations. Flowering appeared to be controlled by day length, while air temperature sets the period for fruit maturation.

Phytohormones are important in development, growth, and dispersal of mangrove seeds, (Farrant *et al.*, 1992, 1993). Phytohormones, like cytokinin (particularly zeatin riboside) accumulate in both axes and cotyledons during reserve accumulation. The level of abscissic acid (ABA) in the embryo stays low during this period, making them sensitive to desiccation, but it increases with development (Farrent *et al.*, 1993). ABA levels in the pericarp increase throughout seed development; the ABA in the pericarp may prevent precocious germination. Mature propagules of *Rhizophora* species exhibit high chlorophyll levels in the hypocotyl and high polyphenol content in the radicle regions (Kulkarni and Bhosale, 1991).

Smith *et al.* (1995) investigated the role of hormones in controlling flotation and the development of roots and shoots in *Rhizophora mangle* propagules. Application of gibberallic acid [GA₃] caused the propagules to float horizontally, but painting with naphthalene acetic acid [NAA] produced vertically floating propagules. The NAA promoted root elongation while the GA₃ enhanced stem elongation and leaf expansion (Smith *et al.*, 1996). A variety of hormones and chemicals (*e.g.* NAA, IBA, IAA, GA₃, phenolics, methanol, boric acids, triacontanol) promoted root growth in propagules of *Rhizophora* and *Avicennia* species (Kathiresan and Thangam, 1990b; Kathiresan *et al.*, 1990a, 1990b, 1996b; Kathiresan and Moorthy, 1992, 1994a, b, c, d).

Mangrove propagules have an obligate dispersal phase of several weeks before the radicle extends for root development. If however, the propagules do not contact the sediment, they remain viable in seawater for several months (Clarke, 1993). Dispersal of propagules depends on the buoyancy and longevity and on the activity of tides and currents. The propagules of *Kandelia candel* are sensitive to light; high levels inhibit rooting. Fan and Chen (1993) suggest that this is an adaptation as it keeps the floating propagules alive during potentially long

dispersal periods. It is unclear, however, how common it is for mangrove propagules to travel great distances. It has been experimentally shown that most *Avicennia marina* propagules become stranded and established close to their parents; it is uncommon for them to move very far (Clarke and Myerscough, 1991b; Kathiresan and Ramesh, 1991; Kathiresan, 1999).

Mangrove propagules may suffer high mortality during their dispersal. In field studies, propagules of *Ceriops tagal* in northern Australia dispersed very short distances (only 9% moved more than 3 m from the parent tree). Within that short distance, however, a high percentage of them were damaged or eaten by animals (McGuinness, 1997). Farnsworth and Ellison (1997) measured attack on mangrove propagules in 42 mangrove swamps in 16 countries and found rates ranging from 0 to 93% with a global average of 28.3%. The major consumers were grapsid crabs, insects in the Coleoptera and Lepidoptera. In Kenya, grapsid crabs cleared nearly 100% of the seeds from landward mangrove plantation (Dahdouh-Guebas *et al.*, 1998). Such high levels of seed loss undoubtedly have significant effects on population dynamics and stand regeneration.

Mortality is not restricted to propagules. Mangroves are also vulnerable during establishment and early growth. In Belize, mortality of *Rhizophora mangle* and *Avicennia germinans* is highest during establishment. The mortality can be attributed to (1) a failure to establish before seed viability is lost, (2) predation, and (3) desiccation (Farnsworth & Ellison, 1991).

After establishment, survival and growth are strongly influenced by physiochemical stresses. For example, shading, orientation of the seedling axis (*e.g.* upright *vs.* horizontal), soil fertility, and flooding can all have significant impacts on survival (McKee, 1995; McGuinness, 1997). Experimental work with *Rhizophora* species demonstrates that propagule length, planting depth, soil type, salinity concentration of leachates, pH and light intensity are important determinants of growth (Kathiresan and Thangam, 1989, 1990a; Kathiresan and Ramesh, 1991; Kathiresan and Moorthy, 1993; Kathiresan *et al.*, 1993, 1994, 1995, 1996a; Kathiresan, 1999).

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