

Biology of Mangroves and Mangrove Ecosystems

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Mangroves are woody plants that grow at the interface between land and sea in tropical and sub-tropical latitudes where they exist in conditions of high salinity, extreme tides, strong winds, high temperatures and muddy, anaerobic soils. There may be no other group of plants with such highly developed morphological and physiological adaptations to extreme conditions.

Because of their environment, mangroves are necessarily tolerant of high salt levels and have mechanisms to take up water despite strong osmotic potentials. Some also take up salts, but excrete them through specialized glands in the leaves. Others transfer salts into senescent leaves or store them in the bark or the wood. Still others simply become increasingly conservative in their water use as water salinity increases. Morphological specializations include profuse lateral roots that anchor the trees in the loose sediments, exposed aerial roots for gas exchange and viviparous water-dispersed propagules.

Mangroves create unique ecological environments that host rich assemblages of species. The muddy or sandy sediments of the mangal are home to a variety of epibenthic, infaunal, and meiofaunal invertebrates. Channels within the mangal support communities of phytoplankton, zooplankton, and fish. The mangal may play a special role as nursery habitat for juveniles of fish whose adults occupy other habitats (e.g., coral reefs and seagrass beds)

Because they are surrounded by loose sediments, the submerged mangroves roots, trunks, and branches are islands of habitat that may attract rich epifaunal communities including bacteria, fungi, macroalgae, and invertebrates. The aerial roots, trunks, leaves

and branches host other groups of organisms. A number of crab species live among the roots, on the trunks or even forage in the canopy. Insects, reptiles, amphibians, birds and mammals thrive in the habitat and contribute to its unique character.

Living at the interface between land and sea, mangroves are well adapted to deal with natural stressors (e.g., temperature, salinity, anoxia, UV). However, because they live close to their tolerance limits, they may be particularly sensitive to disturbances like those created by human activities. Because of their proximity to population centers, mangals have historically been favored sites for sewage disposal. Industrial effluents have contributed to heavy metal contamination in the sediments. Oil from spills and from petroleum production has flowed into many mangals. These insults have had significant negative effects on the mangroves.

Habitat destruction through human encroachment has been the primary cause of mangrove loss. Diversion of freshwater for irrigation and land reclamation has destroyed extensive mangrove forests. In the past several decades, numerous tracts of mangrove have been converted for aquaculture, fundamentally altering the nature of the habitat. Measurements reveal alarming levels of mangrove destruction. Some estimates put global loss rates at one million ha y⁻¹, with mangroves in some regions in danger of complete collapse. Heavy historical exploitation of mangroves has left many remaining habitats severely damaged.

These impacts are likely to continue, and worsen, as human populations expand further into the mangals. In regions where mangrove removal has produced significant environmental problems, efforts are underway to launch mangrove agroforestry and agriculture projects. Mangrove systems require intensive care to save threatened areas. So far, conservation and management efforts lag behind the destruction; there is still much to learn about proper management and sustainable harvesting of mangrove forests.

Mangroves have enormous ecological value. They protect and stabilize coastlines, enrich coastal waters, yield commercial forest products and support coastal fisheries. Mangrove forests are among the world's most productive ecosystems, producing organic carbon well in excess of the ecosystem requirements and contributing significantly to the global carbon cycle. Extracts from mangroves and mangrove-dependent species have proven activity against human, animal and plant pathogens. Mangroves may be further developed as sources of high-value commercial products and fishery resources and as sites for a burgeoning ecotourism industry. Their unique features also make them ideal sites for experimental studies of biodiversity and ecosystem function. Where degraded areas are being revegetated, continued monitoring and thorough assessment must be done to help understand the recovery process. This knowledge will help develop strategies to promote better rehabilitation of degraded mangrove habitats the world over and ensure that these unique ecosystems survive and flourish.

1. INTRODUCTION

1.1. Preface

Mangrove forests are among the world's most productive ecosystems. They enrich coastal waters, yield commercial forest products, protect coastlines, and support coastal fisheries (Figures 1 and 2). However, mangroves exist under conditions of high salinity, extreme tides, strong winds, high temperatures and muddy, anaerobic soils. There may be no other group of plants with such highly developed morphological, biological, ecological and physiological adaptations to extreme conditions.

Mangroves and mangrove ecosystems have been studied extensively but remain poorly understood. With continuing degradation and destruction of mangroves, there is a critical need to understand them better. Aspects of mangrove biology have been treated in several recent reviews. Tomlinson

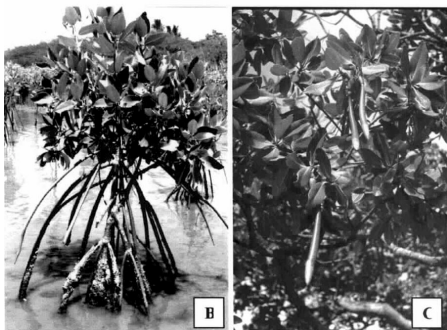


Figure 1. A) The seaward edge of a mangrove forest, showing red mangroves, *Rhizophora*. B) A young plant of *Rhizophora*, showing prop roots carrying epifauna, including barnacles and oysters. C) The propagules of *Rhizophora*, developed from the fruit, before release (photos: A, A.J. Southward; B, K. Kathiresan; C, B.L. Bingham)



Figure 2. A) General view of coastal edge of a mangrove forest. B) A black mangrove thicket, *Avicennia*, showing aerial roots (pneumatophores). C) Closer view of the pneumatophores of

(1986) described the basic botany of mangroves. Snedaker and Snedaker (1984) reviewed earlier mangrove research and made recommendations for further research. An overview of tropical mangrove community ecology, based primarily on Australian work, can be found in Robertson and Alongi (1992). Li and Lee (1997) reviewed much of the Chinese mangrove literature published between 1950 and 1995. Ellison and Farnsworth (2000) have recently published a general review of mangrove ecology.

As researchers continue to discover important facts about mangroves and the role they play in the global ecosystem, the volume of published information has grown enormously and increasing numbers of workers are drawn to these unique environments. Thus, there is a need for periodic reviews of the rapidly expanding literature. In this review, we emphasize work on mangrove ecosystems completed between 1990 and 2000, though for space reasons we can list only a fraction of the studies. Our intent is to make information more readily available to

researchers around the world in hopes of facilitating and stimulating further study of the mangrove environment.

1.2. Definition

Mangroves are woody plants that grow at the interface between land and sea in tropical and sub-tropical latitudes (Figures 1 and 2). These plants, and the associated microbes, fungi, plants, and animals, constitute the **mangrove forest community** or **mangal**. The mangal and its associated abiotic factors constitute the **mangrove ecosystem** (Figure 3). The term “*mangrove*” often refers to both the plants and the forest community. To avoid confusion, Macnae (1968) proposed that “*mangal*” should refer to the forest community while “*mangroves*” should refer to the individual plant species. Duke (1992) defined a mangrove as, “...a tree, shrub, palm or ground fern, generally exceeding one half metre in height, and which normally grows above mean sea level in the intertidal zone of marine coastal environments, or estuarine margins.” This definition is acceptable except that ground ferns should probably be considered mangrove associates rather than true mangroves. The term “*mangrove*” is also used as an adjective, as in “mangrove tree” or “mangrove fauna.” Mangrove forests are sometimes called “tidal forests”, “coastal woodlands”, or “oceanic rain forests.”

The word “*mangrove*” is usually considered a compound of the Portuguese word “*mangue*” and the English word “*grove*.” The corresponding French words are “*manglier*” and “*paletuvier*” (Macnae, 1968) while the Spanish term is “*manglar*”. The Dutch use “*vloedbosschen*” for the mangrove community and “*mangrove*” for the individual trees. German use follows the English. The word “*mangro*” is a common name for *Rhizophora* in Surinam (Chapman, 1976). It is believed that all these words originated from the Malaysian word, “*manggi-manggi*” meaning “above the soil.” This word is no longer used in Malaysia, but is used in eastern Indonesia to refer to *Avicennia* species.

1.3. Global distribution

Mangroves are distributed circumtropically, occurring in 112 countries and territories. Global coverage has been variously estimated at 10 million hectares (Bunt, 1992), 14-15 million hectares (Schwamborn and Saint-Paul, 1996), and 24 million hectares (Twilley *et al.*, 1992). Spalding (1997) gave a recent estimate of over 18 million hectares, with 41.4% in south and southeast Asia and an additional 23.5% in Indonesia (Figure 4). Mangroves are largely restricted to latitudes between 30° north and 30° south. Northern extensions of this limit occur in Japan (31°22'N) and Bermuda (32°20'N); southern extensions are in New Zealand (38°03'S), Australia (38°45'S) and on the east coast of

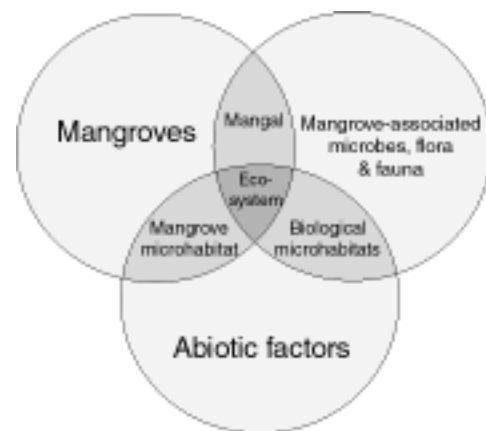


Figure 3. Physical and biological components of mangrove ecosystems.

South Africa (32°59'S; Spalding, 1997, Yang *et al.*, 1997). Mangroves are not native to the Hawaiian Islands, but since the early 1900's, at least 6 species have been introduced there.

Mangrove distributions within their ranges are strongly affected by temperature (Duke, 1992) and moisture (Saenger and Snedaker, 1993). Large-scale currents may also influence distributions by preventing propagules from reaching some areas (De Lange and De Lange, 1994). Individual mangrove species differ in the length of time their propagules remain viable, their establishment success, their growth rate, and their tolerance limits. These factors, which appear quite consistent around the world, interact to produce characteristic distributional ranges for most species (Duke *et al.*, 1998a; Table 1).

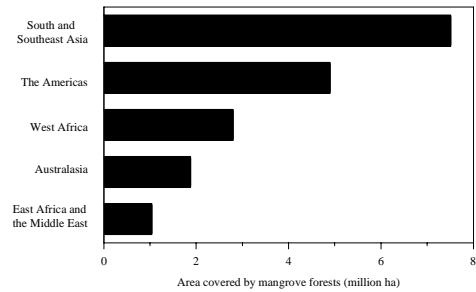


Figure 4. Global coverage of mangrove forests (modified from Spalding, 1997).

Table 1. Mangrove species, their taxonomic authorities, and global distributions.

Family	Species	Southeast USA	Central/South America	Africa	South Asia	Southeast Asia	Malay Archipelago	East Asia	Australia	Southwest 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						•				
Caesalpiniaceae	<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>)							•			

	<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.mangle</i> and <i>R. stylosa</i>)	●	●					
Rubiaceae	<i>Scyphiphora hydrophyllacea</i> Gaetn. 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		●	●	●	●		

Mangroves have broader ranges along the warmer eastern coastlines of the Americas and Africa than along the cooler western coastlines. Mangroves prefer a humid climate and freshwater inflow that brings in abundant nutrients and silt. Mangroves grow luxuriantly in alluvial soils (loose, fine-textured mud or silt, rich in humus). They are abundant in broad, sheltered, low-lying coastal plains where topographic gradients are small and tidal amplitudes are large. Repeatedly flooded but well-drained soils support good mangrove growth and high species diversity (e.g., Azariah *et al.*, 1992). Mangroves do poorly in stagnant water (Gopal and Krishnamurthy, 1993).

2. HISTORY AND EVOLUTION

2.1. Historical background

Mangroves have been known and studied since ancient times. Descriptions by Nearchus (325 B.C.) and Theophrastus (305 B.C) of *Rhizophora* trees in the Red Sea and the Persian Gulf are the earliest known records. Plutarch (70 A.D.) and Abou'l Abass (1230) wrote about *Rhizophora* and its seedlings (Macnae, 1968; Chapman, 1976). The bibliography of mangrove research compiled by Rollet (1981), however, shows only 14 references before 1600, 25 references from the 17th century, 48 references in the 18th century, and 427 in the 19th century. In contrast, there were 4500 mangrove references between 1900 and 1975 and approximately 3000 between 1978 and 1997, illustrating the explosion of interest in mangroves.

Mangroves have a long historical link with human culture and civilization. In the Solomon Islands, the bodies of the dead are disposed of and special rites are performed in the mangrove waters (Vannucci, 1997). In the third century, a Hindu temple to the mangrove *Excoecaria agallocha* was erected in south India. Rock carvings show the plant being worshipped anciently as a “sacred grove” and even today it is believed that a dip in the holy pond of the temple cures leprosy. The city where this temple is found bears the name of the mangrove. In Kenya, shrines built in the mangrove forests are worshipped by the local people, who believe spirits of the shrine will bring death to those who cut the surrounding trees.

The Portuguese, probably the first Europeans to visit the mangrove forests of the Indian Ocean (around the 14th century), learned the traditional Indian technique of rice-fish-mangrove farming, as demonstrated by letters from the Viceroys to the King of Portugal. Some six centuries ago, this Indian technology was also transferred by Jesuit and Franciscan Fathers to the African countries of Angola and Mozambique (Vannucci, 1997). In the 19th century, the British used the practical knowledge gained over centuries by the Indians to manage mangroves at Sunderbans for commercial timber production (Vannucci, 1997). An unusually creative use of mangroves is described in a traditional story from India about two countries at war. The larger country planned to invade their small neighbors during the night. The smaller nation, which had mangrove forests on its coastline, plotted to discourage their enemies by placing lighted lamps on the aerial roots of mangroves. What appeared to be a large flotilla of ships discouraged the invaders and ended the hostilities.

2.2. Evolution

The evolutionary history of mangroves remains problematic with a number of competing theories. Mangroves evolved from terrestrial rather than marine plants. Mangrove pollen fossils have been found below marine foraminiferan assemblages (*i.e.*, in the lower deposits of estuarine environments) suggesting the evolution of these plants from a non-marine habitat to an estuarine habitat (Srivastava and Binda, 1991). In the distant past, these land plants adapted to brackish water and became the “core” mangrove flora. The diversity of mangroves is much higher in the Indo-West Pacific than in the Western Atlantic and Caribbean. Two competing hypotheses have been presented to explain this pattern. The center-of-origin hypothesis suggests that all mangrove taxa first appeared in the Indo-West Pacific and subsequently dispersed to other regions. The vicariance hypothesis, on the other hand, states that all mangroves originated around the Tethys Sea. Continental drift then isolated the flora in different regions of the earth where diversification created distinct faunas.

Ellison *et al.* (1999) evaluated these two hypotheses using 1) a review of the mangrove fossil record, 2) a comparison of modern and fossil distributions of mangroves and mangrove-associated gastropods, 3) an analysis of species-area relationships of mangroves and gastropods, 4) an analysis of nestedness patterns of individual plants and gastropod communities, and 5) an analysis of nestedness patterns of individual plants and individual gastropod species. The evidence from all 5 analyses supported the vicariance hypothesis, suggesting a Tethyan origin of mangroves. This argues that the much higher diversity of mangroves in the Indo-West Pacific relates to conditions there that favored diversification. For example, the continual presence of extensive wet habitat may have allowed more species to make the transition from terrestrial to brackish-water habitats. The Atlantic, Caribbean or and East Pacific all saw periods of drying which could have prevented such adaptation. Ricklefs and Latham (1993) suggest that limited dispersal, combined with the closure of the Tethys connection to the Atlantic Ocean in the mid-Tertiary, restricted most mangrove taxa to the Indo-Pacific.

Studies of mangrove biochemistry and genetics should provide further evidence concerning mangrove evolution and dispersal. For example, Dodd *et al.* (1998) found significant genetic differentiation between mangroves in eastern and western Atlantic provinces. Three species from western Africa showed significantly greater lipid diversity and longer carbon chains than conspecifics from eastern South America, suggesting that the western Atlantic mangroves show derived characteristics. The authors concluded that this evidence suggests it is unlikely that Atlantic mangroves dispersed from the Tethys via the Pacific.

Mangroves are quite old, possibly arising just after the first angiosperms, around 114 million years ago (Duke, 1992). *Avicennia* and *Rhizophora* were probably the first genera to evolve, appearing near the end of the Cretaceous period (Chapman, 1976). Pollen records provide important information about subsequent radiation. Fossil pollen from sediments in the Leizhou Peninsula, China suggest that mangroves expanded from south to north, reaching their northern limit on the Changjiang Delta by the mid-Holocene (Y. Zhang *et al.*, 1997). A similar study of pollen from late Holocene samples in Bermuda suggests that mangroves were established there in the last 3000 years, when sea level rise decreased from 26 to 7 cm per century (J.C. Ellison, 1996).

A detailed study of pollen records from Mexico, the Antilles, Central America and northern South America (Graham, 1995) show that neotropical environments were first occupied by *Acrostichum*, *Brevitricolpites variabilis*, *Nypa* and *Pelliceria* in the early Eocene, about 50 million years ago. *Avicennia* appeared in this region in the late Miocene (about 10 million years ago). Six mangrove species and three associated genera were present by the middle Pliocene (3.5 million years ago), and fifteen plant genera were present by the Quaternary period. Twelve additional species were added during the Cenozoic to produce the present-day assemblage of about 27 genera of mangroves and associated plants (Rico-Gray, 1993; Graham, 1995).

Continental drift produced massive mixing and dispersal of genes in geologically recent times, greatly enhancing evolutionary processes. Though mangroves evolved in the tropics, one species, *Avicennia marina*, is found in temperate latitudes, particularly in the southern hemisphere (Saenger, 1998). This genus is of a western Gondwanan origin with the subsequent radiation of several taxa facilitated by tectonic dispersal of southern continental fragments (Duke, 1995). Mangrove fossils have clearly provided valuable information about prehistorical mangrove evolution and dispersal. However, Burnham (1990) cautions that reconstructions based on organic remains can differ substantially depending on the mangrove parts studied (e.g., fruits and seeds vs. leaf litter).

Mangrove ecosystems, in general, are dynamic, undergoing changes on time scales of $10^2 - 10^4$ y (Woodroffe, 1992). Indeed fossil mangroves are often found in regions where they no longer exist: in Texas, USA (Westgate and Gee, 1990; Westgate 1994), west Africa (Marius and Lucas, 1991), Hungary (Nagy and Kokay, 1991), India (Bonde, 1991; Barni and Chanda, 1992), the Chao-Shan Plain of China (Z. Zheng, 1991), and Western Australia (Kendrick and Morse, 1990), for example.

Historical changes in mangrove distributions can reveal details about paleoclimates and sea-level changes (Somboon, 1990; Khandelwal and Gupta, 1993; Y. Zhang and Wang, 1994; Plaziat, 1995; Saito *et al.*, 1995; Lezine, 1996; W. Zhang and Huang 1996; Y. Zhang *et al.*, 1997). For example, in the equatorial Pacific Ocean, there are alternating reef and mangrove fossils in upper Miocene and lower Pliocene deposits (Cronin *et al.*, 1991). Similarly, Holocene sediments from the Maya Wetland of Belize indicate that mangrove peat filled the lagoon by 4800 y ago (Alcala-Herrera *et al.*, 1994). These patterns may reflect fluctuating sea levels or large-scale climatic shifts. In Poverty Bay, New Zealand, the presence of *Avicennia marina* var. *resinifera* during the early to mid-Holocene suggests that the area then had a frost-free climate (Mildenhall, 1994). The mangrove fossil record is clearly an area where continued research has the potential for providing significant information, not only about the history of these unique plants, but also about the recent history of the earth.

3. BIOLOGY OF MANGROVES

3.1. Taxonomy and genetics

3.1.1. Taxonomy

Tomlinson (1986) recognized three groups of mangroves: major mangrove species, minor mangrove species and mangrove associates. 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, and 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.

The minor mangrove species are less conspicuous elements of the vegetation and rarely form pure stands. According to Tomlinson (1986), the major mangroves include 34 species in 9 genera and 5 families. The minor species contribute 20 additional species in 11 genera and 11 families for a total of 54 mangrove species in 20 genera and 16 families. 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 remainder are in the Magnoliophyta (angiosperms). Families containing only mangroves are the Aegialitiaceae, Avicenniaceae, Nypaceae and Pellicieraceae. Two orders (Myrtales and Rhizophorales) contain 25% of all mangrove families. By reconciling common features from Tomlinson (1986) and Duke (1992), we recognize 65 mangrove species in 22 genera and 16 families (Table I).

There are a number of problems with mangrove taxonomy (Duke, 1992) and many of these are based on hybridization between described species. For instance, the systematic distinction between *Rhizophora mucronata* in eastern Africa, *R. stylosa* in Australia, and their putative hybrids is unclear. *Rhizophora lamarckii*, which occurs in New Caledonia, Papua New Guinea and Queensland, Australia, is a sterile F1 hybrid between *R. apiculata* and *R. stylosa*. *Rhizophora x annamalayana*, found in a south Indian mangrove forest, was first identified as *R. lamarckii* but has since been reidentified as a new species hybrid between *R. mucronata* and *R. apiculata* (Kathiresan, 1995a). Some hybrids, like *Rhizophora x harrissoni*, can not be confirmed with wax chemistry (Dodd *et al.*, 1995). Molecular analyses may help eventually resolve the taxonomic problems. For example, DNA sequence data from the chloroplast gene **rbcL** indicate that the Rhizophoraceae belongs not to the Myrtales, but to a rosid clade that includes the families Euphorbiaceae, Humiriaceae and Malpighiaceae (Conti *et al.*, 1996).

3.1.2. Genetic variation

There is significant inter- and intraspecific variability among mangroves. For example, physiological differences have been identified between West African and Western Atlantic *Avicennia germinans* (Saenger and Bellan, 1995) and distinct chemotypes have been described for *A. germinans* and *Rhizophora* (Corredor *et al.*, 1995; Dodd *et al.*, 1995; Rafii *et al.*, 1996). Variability may result from genotypic 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 (Rico-Gray and Palacios-Rios, 1996a). Similarly, leaf area indices can be used to differentiate *Rhizophora mangle* from basin and dwarf forest types in southeast Florida, USA (Araujo *et al.*, 1997). In contrast, variation in *Rhizophora mangle* flower morphology appears to have a genetic basis. Dominguez *et al.* (1998) found significant differences between populations on the Pacific and Atlantic coasts of Mexico, among populations on each coast, and within individual populations. They

hypothesized that frequent extinctions, followed by recolonization of a few individuals, has produced genetic differentiation.

Genetic variability has been clearly demonstrated through biochemical markers like iridoid glycosides (Fauvel *et al.*, 1995), foliar leaf waxes (Dodd *et al.*, 1995, 1998; 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. There were no differences in chromosome number ($2n = 48$). Genetic polymorphism is even higher in *Excoecaria agallocha*. The *E. agallocha* polymorphism is independent of morphological and sexual differences (Parani *et al.*, 1997).

Changes in gene frequency, such as those produced by inbreeding, can lead to genetic differentiation. Inbreeding may result if pollen are shed before the flower opens (Lowenfeld and Klekowski, 1992). If inbreeding is prevalent, a mangrove forest may be a virtually monospecific stand with little genetic diversity. Pollination by bees produces geitonogamous selfing in *Kandelia candel*. However, there is little genetic differentiation among 13 populations along the coastlines of Hong Kong, indicating that dispersion of propagules is sufficient to maintain high levels of gene flow in this species (Sun *et al.*, 1998). In contrast, genetic differentiation, has led to subspeciation in *Avicennia marina* (Duke, 1991, 1995). It has been assumed that *Avicennia* propagules commonly move long distances. However, allozyme studies suggest that *Avicennia* species in the Indo-West Pacific and eastern North America have limited gene flow. This may indicate that true dispersal distances are much shorter than has been commonly believed (Duke *et al.*, 1998b).

Gene mutations can also cause species divergence. One or 2 gene mutations are needed for biochemical differences, 5-10 for physiological changes, >10 for morphological variations and >100 for taxonomic changes (Saenger, 1998). A single recessive gene causes albinism in *Rhizophora* seedlings. This albino mutation is in the nuclear genome but has a profound effect on ultrastructure of the chloroplasts (Klekowski *et al.*, 1994a). Pigment fingerprint studies of chlorophyll-deficient mutants show that most albino genotypes are deficient in chlorophylls, xanthophylls, and carotenes (Corredor *et al.*, 1995). Recent studies of post-zygotic mutations reveal that fewer than 0.1% of the *Rhizophora* in Puerto Rico exhibit somatic mutations. These mutations are often manifest in shoot apices as complete or partial periclinal chimeras (Klekowski *et al.*, 1996). Rates of both mutation and outcrossing vary among mangrove populations. For instance, the Puerto Rican *Rhizophora* are more outcrossed and have lower mutation rates for chlorophyll-deficiency than Florida *Rhizophora*.

3.13. Tissue Culture

There have been few studies of tissue culture in mangroves. This is because explants frequently turn brown or black shortly after isolation, with tissue death usually following (Kathiresan, 1990, 1994). The high tannin and phenol content of mangroves may be responsible for the browning problem (Kathiresan and Ravi, 1990; Ravi and Kathiresan, 1990). Antioxidants can prevent phenolic browning in explants collected during the monsoon season (Kathiresan and Ravikumar, 1997).

Callus induction has been achieved in *Sonneratia apetala* and *Xylocarpus granatum* by supplementing the medium with double strength vitamins (Kathiresan and Ravikumar, 1997). Baba and Onizuka (1997) have improved techniques for callus induction and initiation of redifferentiation in the callus of *Bruguiera gymnorrhiza*, *Kandelia candel*, *Pemphis acidula* and *Rhizophora stylosa*. Adventitious roots were produced in *P. acidula*, but neither adventitious buds nor roots could be induced in the remaining species.

Researchers are currently working to identify and micropropagate unique plant genotypes for commercial purposes. Mangals may provide good raw material for such work. For instance, *in vitro* multiplication of the salt-marsh *Sesuvium portulacastrum*, associated with Indian mangroves, has been achieved by axillary bud culture (Kathiresan, 1994; Kathiresan *et al.*, 1997). *In vitro* cell cultures of this plant synthesize antibacterial substances in higher quantities than do the intact plants, demonstrating the potential of these systems for production of valuable metabolites (Kathiresan and Ravikumar, 1997).

Cell protoplast fusion techniques may allow us to transfer salinity tolerance from mangrove plants to non-salt-tolerant species (Swaminathan, 1991). Methods for extracting and preparing protoplasts from tissue cultures of *Bruguiera gymnorrhiza* have been developed by Eguchi *et al.* (1995). Sasamota *et al.* (1997) have done similar work with the cotyledons of *Avicennia marina* and *A. lanata*. Such creative tissue culture work may allow researchers to better understand, and make use of, the unique characteristics of mangroves.

3.2. Morphology and anatomy

3.2.1. Root anatomy

Mangroves are highly adapted to the coastal environment, with exposed breathing roots, extensive support roots and buttresses, salt-excreting leaves, and viviparous water-dispersed propagules. These adaptations vary among taxa and with the physico-chemical nature of the habitat (Duke, 1992). Perhaps the most remarkable adaptations of the mangroves, however are the stilt roots of *Rhizophora*, the pneumatophores of *Avicennia*, *Sonneratia* and *Lumnitzera*, the root knees of *Bruguiera*, *Ceriops* and *Xylocarpus* 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. Their effectiveness is well illustrated by the tallest mangrove trees, found in Ecuador, which attain heights of more than 60 m and may be 100 yold (Emilio, 1997).

The specialized roots are important sites of gas exchange for mangroves living in anaerobic substrata. The exposed surfaces may have numerous lenticels (loose, air-breathing aggregations of cells; Tomlinson, 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 (Ish-Shalom-Gordon and Dubinsky, 1992). The spongy pneumatophores are generally short (< 30 cm), 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 (Saifullah and Elahi, 1992). In

Sonneratia, the pneumatophores may be 3 m long and stout from heavy secondary thickening (Tomlinson, 1986).

Oxygen may also pass through non-lenticellular portions of the pneumatophores. Horizontal structures (subrisules) may be important in air exchange, particularly in rapidly growing pneumatophores where the newly formed tip lacks lenticels (Hovenden and Allaway, 1994). Pneumatophores are normally unbranched. However, following the 1991 Gulf War, mangroves in the Arabian Gulf began developing branched pneumatophores and adventitious roots (Boer, 1993).

The general structure of mangrove roots is similar to that of most other vascular plants. 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 (Tomlinson, 1986). 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 and little to no secondary growth. They also become spongy to adapt to sub-soil existence. In *Rhizophora*, the roots 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).

3.2.2. Wood anatomy

Tomlinson (1986) has summarized the unique anatomical features of mangrove woods. Growth rings are conspicuously anomalous (as in *Avicennia*; Das and Ghose, 1998) or completely absent. Hence, aging trees is difficult. Duke and Pinzon (1992) suggest that leaf scar nodal number is a better way to estimate the age of *Rhizophora* seedlings.

Mangrove wood has special features that enable the trees to overcome the high osmotic potential of seawater and the transpiration caused by high temperatures. There are numerous narrow vessels running through the wood. These range in density from $32 \cdot \text{mm}^{-2}$ in *Excoecaria* to $270 \cdot \text{mm}^{-2}$ in *Aegiceras* (Das and Ghose, 1998). The vessels help create high tensions in the xylem since a slight decrease in vessel diameter produces a disproportionally large increase in flow resistance (Scholander *et al.*, 1964, 1965; Tomlinson, 1986). The vessel elements, which form the vessels, normally have simple perforation plates (Tomlinson, 1986). However, mangroves in the family Rhizophoraceae (except *Kandelia candel*) have scalariform perforation plates.

Water conduction through wood is strongly influenced by size and distribution of the vessels. 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).

Wier *et al.* (1996) studied wound repair in *Rhizophora mangle*. A closing layer isolates necrotic tissue within 17 d, and the wound is completely enclosed by periderm by 52 d. Isolation of the damage site and development of wound periderm may prevent spread of pathogens to undamaged tissues.

3.2.3. Leaf anatomy

Mangrove leaves are almost leathery with obscure leaf veins (there are no vein sheaths). The cuticle is thick and smooth with small hairs, giving the plant a glossy appearance. 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). The leaves generally show dorsiventral symmetry though isolateral leaves are also found in *Kandelia candel*, *Sonneratia apetala* and *Phoenix paludosa* (Das *et al.*, 1996).

Six types of stomata are known from mangrove leaves. These differ in their arrangement of guard cells and subsidiary cells. In most species, a horn or beak-like cuticular outgrowth covers either the outer side of the stomatal pore or both the inner and outer sides. These structures reduce stomatal transpiration (Das and Ghose, 1993), which is important given the high solute concentration of the water and the “physiological drought” the trees experience. *Heritiera fomes* has deeply sunken stomata covered by trichomes. The leaves in this species also have a palisade-spongy ratio that is small compared to other halophytes (Das *et al.*, 1995).

Mangrove leaves have specialized idioblast cells including tannin cells (Rhizophoraceae), mucous cells (*Rhizophora*, *Sonneratia*), crystalliferous cells (Rhizophoraceae), oil cells (*Osbornia*) and laticifers (*Excoecaria*; Tomlinson, 1986). In general, the leaves lack bundle sheath fibres and bundle sheath extensions, but possess enlarged tracheids terminating in vein endings. Branched sclereids are abundant and well developed in *Aegiceras*, *Rhizophora*, *Sonneratia* and *Aegialitis*. The sclereids may give mechanical support to leaves or discourage herbivores. Both sclereids and tracheids may also be involved in water storage (Tomlinson, 1986). Water is also stored in colourless, non-assimilatory water-storage tissue that is hypodermal in dorsiventral leaves, but is deep-seated in the extensive mesophyll region of isolateral leaves. In some species, the thick layer of non-assimilatory tissue occurs in front of the assimilatory cells. This back scatters incoming light, creating a gradient that may help the plant capture weak light, increasing photosynthetic efficiency (Koizumi *et al.*, 1998).

Yoshihira *et al.* (1992) studied the distribution of pigments in mangrove leaves. They found that different species concentrated the pigments in different parts of the leaves. In *Aegiceras corniculatum*, the highest concentration of carotenoids and chlorophylls was in the light-harvesting complex. In *Rhizophora apiculata*, however, chlorophyll was concentrated in the chloroplast reaction center. The chlorophyll-binding proteins (including the functional cytochrome B 6/f complex and the protein kinases) were found in the thylakoid membranes in *Bruguiera gymnorrhiza* and *Kandelia candel*

3.2.4. Seed and seedling anatomy

Avicennia marina forms endosperm haustoria during early embryonic histodifferentiation. Once the growth phase is initiated, subsequent embryonic development is extra-ovular. The mature seed, therefore, is enclosed by a pericarp that originates entirely from the ovary wall. From the end of histodifferentiation until the mature seeds are abscised, cotyledon cells become highly vacuolated and contain large amounts of soluble sugars, which constitute the major nutrient reserves of the mature seed (Farrant *et al.*, 1992).

Incipient phellogen usually develops toward the radicle end of mangrove seedlings and masks the chlorophyllous tissue. Tannin cells are present in the aerenchymatous tissue, stone cells are present in the outer cortex, and trichosclereids appear in the cortex and medulla. Since the epidermis lacks stomata, numerous lenticels facilitate gas exchange.

In experiments with six mangrove species, Youssef and Saenger (1996) demonstrated that the seedlings have special features that allow them to tolerate flooding and facilitate rhizosphere oxidation. Lacunae in the ground tissue constrict air flow passages, conserving oxygen and enabling the mangrove to maintain aerobic metabolism during periods of flooding. Variations in this anatomical feature are responsible for species differences in tolerance to flood stress.

3.3. Physiology

3.3.1. Salt regulation

Mangroves are physiologically tolerant of high salt levels and have mechanisms to obtain fresh water despite the strong osmotic potential of the sediments (Ball, 1996). They avoid heavy salt loads through a combination of salt exclusion, salt excretion, and salt accumulation. For example, *Rhizophora*, *Bruguiera*, and *Ceriops* all possess ultrafilters in their root systems. These filters exclude salts while extracting water from the soil. Other genera (e.g., *Avicennia*, *Acanthus*, *Aegiceras*) take some salt up, but excrete it through specialized salt glands in the leaves (Dschida *et al.*, 1992; Fitzgerald *et al.*, 1992). The salt-excreting species allow more salt into the xylem than do the non-excretors, but still exclude about 90% of the salts (Scholander *et al.*, 1962, Azocar *et al.*, 1992). Salt excretion is an active process, as evidenced by ATPase activity in the plasmalemma of the excretory cells (Drennan *et al.*, 1992). The process is probably regulated by leaf hypodermal cells, which may store salt as well as water (Balsamo and Thomson, 1995).

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). As water salinity increases, some species simply become increasingly conservative in their water use, thus achieving greater tolerance (Ball and Passioura, 1993). In south Florida, *Rhizophora mangle* decreases its salt stress by using surface water as its sole water source. 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).

Most mangrove species directly regulate salts. However, they may also accumulate or synthesize other solutes to regulate and maintain osmotic balance (Werner and Stelzer, 1990; Popp *et al.*, 1993). For example, *Aegiceras corniculatum*, *Aegialitis annulata* and *Laguncularia racemosa* accumulate mannitol and proline (Polania, 1990). *Avicennia marina* accumulates glycine betaine, asparagine and stachyose (Ashihara *et al.*, 1997). *Sonneratia alba* synthesizes purine nucleotides that help it adapt to salt loads of 100 mM NaCl (Akatsu *et al.*, 1996). To facilitate the flow of water from root to leaves, the water potential at the leaves is held lower (-2.5 to -6 MPa) than in the roots (-2.5 MPa; Scholander *et al.*, 1964).

Because mangrove roots exclude salts when they extract water from soil, soil salts could become very concentrated, creating strong osmotic gradients (Passioura *et al.*, 1992).

However, viscous, polymeric substances in the sap limit flow rate and decrease transpiration (Zimmermann *et al.*, 1994). This, combined with high water-use efficiency, slows the rate of water uptake and prevents salts from accumulating in the soil surrounding the roots. This helps the mangroves conserve water and regulate internal salt concentrations (Ball and Passioura, 1993; Ball, 1996). Low transpiration and slow water uptake, however, are not characteristic of all mangrove species. Becker *et al.* (1997) measured relatively high transpiration rates in both *Avicennia alba* and *Rhizophora apiculata*.

Transpiration rates vary with season, being higher in the dry season than in the wet season in *Bruguiera cylindrica* (Herppich and Von Willert, 1995; Hirano *et al.*, 1996). This corresponds to changes in stomatal movement. The oscillatory behaviour of *Avicennia germinans* stomata is affected by any factor that changes hydraulic flow through the plant. This includes increases in vapour pressure deficit and osmotic potential of the substrata (Naidoo and Von-Willert, 1994).

Fukushima *et al.* (1997) studied the effects of salt on sugar catabolism in leaves and roots of *Avicennia marina*. They showed that sugar catabolic pathways are different in roots and leaves. Over 50% of the ¹⁴C-labeled sucrose the gave the plants was incorporated into an unidentified sugar in the leaves. The remainder appeared in the roots as glucose, fructose and sucrose. Neither pathway was significantly affected by salt levels.

3.3.2. Photosynthesis

Mangroves show characteristic C₃ photosynthesis. Basak *et al.* (1996) found significant intra- and interspecific variation in photosynthetic activity of 14 mangrove species, suggesting that the rates of photosynthesis may have an underlying genetic basis. This possibility is supported by observations that the photosynthetic rate of *Bruguiera* is under direct internal control and is not influenced by stomatal activity induced by changes in salinity or light (Cheeseman *et al.*, 1991; Cheeseman, 1994).

In contrast, other researchers have shown that photosynthetic rates of some species are strongly affected by environmental conditions. 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, more main stems and smaller leaves than mangroves in fringe forests that experience less salinity variability. Steinke and Naidoo (1991) also demonstrated experimentally that temperature affects the photosynthetic rate of *Avicennia marina*. Temperature-induced changes in the relative rates of photosynthesis and respiration, in turn, influence overall growth rates.

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. The fairly low photosynthetic efficiency may be related to the concentration of zeaxanthin pigments in the leaves (Lovell and Clough, 1992). 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).

Kathiresan and Moorthy (1994a) and Kathiresan *et al.* (1996c) demonstrated that application of aliphatic alcohols can have a major stimulatory effect on mangrove photosynthesis. 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%.

3.4. Biochemistry

Mangroves are biochemically unique, producing a wide array of novel natural products. *Excoecaria agallocha*, for example, exudes an 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) and has sublethal effects on the rice-field crab *Oziotephusa senex senex*, in which exposure decreases whole-animal oxygen consumption and inhibits the ATPase system in gill and hepatopancreas tissues (R. Ramamurthi *et al.*, 1991). Soil bacteria and yeasts degrade the toxic latex, preventing its accumulation in the mangal (Reddy *et al.*, 1991).

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). C.K.Rao *et al.* (1991) found arsenic in mangroves from the Goa Coast.

Mangroves are also rich in polyphenols and tannins (Kathiresan and Ravi, 1990; Ravi and Kathiresan, 1990; Achmadi *et al.*, 1994). The levels of these substances may vary seasonally (Basak *et al.*, 1998), but older data should be interpreted cautiously since standard methods for measuring tannins are very inaccurate for mangrove leaves (Benner *et al.*, 1990a).

Substances in mangroves have long been used in folk medicine to treat disease (Bandaranayake, 1998). Extracts have proven activity against human, animal and plant pathogenic viruses including human immuno-deficiency virus (Premanathan *et al.*, 1996), Semliki forest virus (Premanathan *et al.*, 1995), Tobacco Mosaic virus (Padmakumar and Ayyakannu, 1997), *Vaccinia* virus (Premanathan *et al.*, 1994a), Encephalomyocarditis virus (Premanathan *et al.*, 1994b), New castle disease virus (Premanathan *et al.*, 1993), and Hepatitis-B viruses (Premanathan *et al.*, 1992). A few mangrove species, particularly those belonging to the family Rhizophoraceae, show particularly strong antiviral activity (Premanathan *et al.*, 1992; Kathiresan *et al.*, 1995a). Purified active fractions like acid polysaccharides (galactose, galactosamine, glucose and arabinose) show potent anti-HIV activity (Premanathan *et al.*, 1999).

Other unique mangrove biochemicals have potential commercial applications (reviewed by Kathiresan, 2000). For example, mangrove extracts kill larvae of the mosquitoes *Anopheles stephensi* (Thangam and Kathiresan, 1988), *Culex tritaeniorhynchus* (Thangam and Kathiresan, 1989), *Aedes aegypti* (Thangam and Kathiresan, 1991, 1992a, 1994), and *Culex quinquefasciatus* (Thangam and Kathiresan, 1997). A pyrethrin-like compound in stilt roots of *Rhizophora apiculata* shows strong mosquito larvicidal activity

(Thangam, 1990). Smoke from burned extracts repels and kills both *Aedes aegypti* (Thangam *et al.*, 1992) and *Culex quinquefasciatus* (Thangam and Kathiresan, 1992b) and extracts applied directly to human skin repel adult *Aedes aegypti* (Thangam and Kathiresan, 1993a).

Phenols and flavonoids in mangrove leaves serve as UV-screening compounds. Hence, mangroves tolerate solar-UV radiation and create a UV-free, under-canopy environment (Moorthy, 1995). These substances also contribute to a black tea that can be extracted from mangrove leaves (Kathiresan, 1995b). The “mangrove tea” is rich in theaflavin, the substance responsible for the briskness and colour of tea. The tea, which shows no mammalian toxicity, can be improved by UV irradiation (Kathiresan and Pandian, 1991, 1993, Kathiresan, 1995b).

Moorthy and Kathiresan, (1997a) proposed a physiological grouping of mangrove species based on pigments, which may differ significantly among species (Basak *et al.*, 1996). Pigments concentrations may also vary with environmental conditions and season. For example, Menon and Neelakantan (1992) found that total chlorophyll content was positively related to light levels. 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.

3.5. Pollination biology

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). There is a similar distinct trend for self-incompatibility in *Rhizophora*, *Ceriops* and *Sonneratia*. This pattern is less clear in *Bruguiera* and *Kandelia* (Ananda Rao, 1998).

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 may pollinate *Acanthus ilicifolius* (Aluri, 1990) and large-flowered *Bruguiera hainesii* (Noske, 1993, 1995). Birds are particularly important pollinators in the dry season when absence of terrestrial plant flowers causes them to turn to mangroves as a food source.

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 nighttime 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*, *Scyphipora*, 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 pollen and are mainly wind-pollinated, though the stigma has no special modifications to capture the wind-borne pollen (Tomlinson, 1986).

3.6. Reproduction, dispersal and establishment

Bhosale and Mulik (1991) described four methods of mangrove reproduction: viviparity, cryptoviviparity, normal germination on soil, and vegetative propagation. Vivipary, the precocious and continuous growth of offspring while still attached to the maternal plant, is a unique adaptation to shallow marine habitats (Thomas and Paul, 1996). True viviparous species remain attached to the maternal plant for a full year while cryptoviviparous offspring are only attached for 1-2 months (Bhosale and Mulik, 1991). S.M. Smith and Snedaker (1995a) suggest that viviparous reproductive patterns allow seedlings to develop some salinity tolerance before being released from the parent tree. Figure 2c illustrates propagules of *Rhizophora* still attached to the parent.

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 daylength while air temperature set the period for fruit maturation.

Phytohormones are important in development, growth, and dispersal of mangrove seeds, which may undergo no maturation drying, and remain metabolically active throughout development (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 (though their dehydration tolerance increases with development; Farrant *et al.*, 1993). ABA levels in the pericarp increase throughout seed development; the ABA in the pericarp may prevent precocious germination. Farnsworth and Farrant (1998) suggest that ABA concentrations represent a trade-off between salinity adjustment by the parental plant and developmental demands of the embryo. Other biochemicals may be compartmentalized in the seeds. Mature propagules of *Rhizophora* species exhibit high chlorophyll levels in the hypocotyl and high polyphenol content in the radicle regions (Kulkarni and Bhosale, 1991).

S.M. 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 gibberellic acid (GA₃) caused the propagules to float horizontally, but painting with naphthalene acetic acid (NAA) produced vertically floating propagules. NAA promoted root elongation while GA₃ enhanced stem elongation and leaf expansion (S.M. Smith *et al.*, 1996). A variety of hormones and chemicals (*e.g.*, NAA, IBA, IAA, GA₃, phenolics, methanol, boric acids, triacontanol) promote root growth in propagules of other

Rhizophora and *Avicennia* species (Kathiresan and Thangam, 1990b; Kathiresan and Moorthy, 1992, 1994a,b,c,d; Kathiresan *et al.*, 1990a, 1994b, 1996b).

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 their 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 adaptive 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 strand and establish close to their parents; it is uncommon for them to move very far (Clarke and Myerscough, 1991b; Kathiresan and Ramesh, 1991; Kathiresan, 1999). This conclusion is supported by the observation of Saifullah *et al.* (1994) that dispersal only determines small-scale distributional patterns of mangroves in Karachi, Pakistan. Larger-scale patterns are created by environmental heterogeneity.

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 predators (McGuinness, 1997a; Figure 5). Farnsworth and Ellison (1997a) measured predation on mangrove propagules in 42 mangrove swamps in 16 countries and found rates ranging from 0 - 93% with a global average of 28.3%. The major predators were grapsid crabs and insects in the Coleoptera, and Lepidoptera. In Kenya, grapsid crabs cleared nearly 100% of the seeds from landward

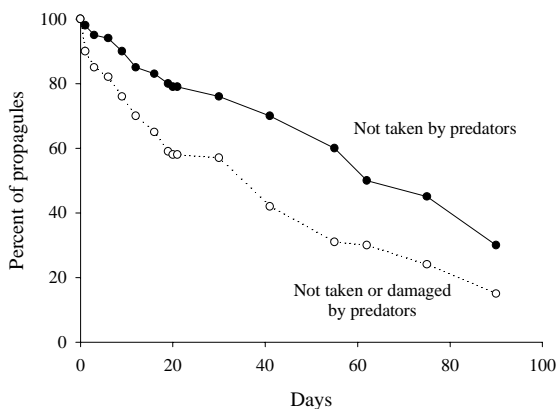


Figure 5. Loss of *Ceriops tagal* propagules to predators in a northern Australia mangal. Propagules were marked and tethered then monitored for disappearance and damage. Crab predators removed or damaged 83% of the propagules within the first 90 days (after McGuinness 1997a).

mangrove plantations (Dahdouh-Guebas *et al.*, 1998). Such high levels of seed predation 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 *R. mangle* and *A. 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 (Ellison and Farnsworth, 1993).

After establishment, survival is strongly influenced by physicochemical 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 (Hovendon *et al.*, 1995; McKee, 1995a; Koch, 1997; McGuinness, 1997a). Post-establishment growth is also affected by a suite of physical and chemical factors. 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; Kathiresan *et al.*, 1995b, 1996a; Kathiresan, 1999). Seedling growth can be artificially stimulated by application of triacantanol and methanol. Both of these substances increase the photosynthetic rate of the seedlings, the *in vivo* nitrate reductase activity, the growth of roots and shoots, the protein and energy contents of leaves and roots, the chlorophyll and carotenoid content in leaves, and the amount of chlorophyll in photosystems I and II and in the light harvesting complex of the chloroplasts (Moorthy and Kathiresan, 1993; Kathiresan and Moorthy, 1994a; Kathiresan *et al.*, 1996a).

New mangrove growth comes primarily from seeds and density of newly established individuals can be very high (seedling densities reach 27,750 individuals \cdot ha⁻¹ in the Sunderbans of Bangladesh; Siddiqi, 1997). Vegetative regrowth from stump sprouts (“copicing”) also occurs in some species (e.g., *Excoecaria*, *Avicennia*, *Laguncularia*, *Sonneratia*; Tomlinson, 1986). Recently an air-layering technique has been used to successfully induce vegetative propagation in *Avicennia alba*, *A. officinalis*, *Sonneratia apetala*, *Xylocarpus granatum* and *Rhizophora mangle*. The technique was not successful for *A. marina* or *Kandelia* (Kathiresan and Ravikumar, 1995a; Calderon and Echeverri, 1997; Ananda Rao, 1998). External application of auxins can stimulate growth of newly planted mangrove cuttings. The auxins produce metabolic changes during initiation and development of roots, enhancing levels of reducing sugars and increasing the mobilization of nitrogen to the rooting zone (Basak *et al.*, 1995; Das *et al.*, 1997).

3.7. Biomass and litter production

Mangroves and mangrove habitats contribute significantly to the global carbon cycle. Mangrove forest biomass may reach 700 t ha⁻¹ (Clough, 1992, Table 2) and Twilley *et al.* (1992) estimate the total global mangrove biomass to be approximately 8.7 gigatons dry weight (*i.e.*, 4.0 gigatons of carbon). Accurate biomass estimates require measuring volumes of individual trees. Da Silva *et al.* (1993) have developed equations for making such measurements on living mangroves.

Mangroves generally grow better in wet equatorial climates than they do in seasonally monsoonal or arid climates (Clough, 1992) and the amount of litter they produce is negatively correlated with latitude. Estimates of the annual global litterfall from mangroves range from 130 to 1870 g m⁻². In general, the litterfall is heaviest 1) in dry summer months when thinning of the canopy reduces transpiration, and 2) in the wet rainy season when fresh water input increases the nutrient supply (Roy, 1997; Wafar *et al.*, 1997). However, individual species may differ in the conditions that produce heavy litter. For instance, Australian *Rhizophora stylosa* and *Avicennia marina* show heaviest litterfall in hot climates with short dry seasons, but *Ceriops tagal* litterfall is heaviest in hot climates

Table 2. Mangrove standing biomass measurements.

Location	Species	Biomass measured	Amount (t • ha ⁻¹)	Reference
Cuba (North America)	<i>R. mangle</i>	Roots	31.3	Fiala and Hernandez, 1993
	<i>A. germinans</i>	Roots	24.4	
French Guiana (S. America)	Mixed forest	Total	31 – 315	Fromard <i>et al.</i> , 1998
Mgeni Estuary (S. Africa)	Mixed forest	Above-ground	94.4	Steinke <i>et al.</i> , 1995
	<i>A. germinans</i>	Below-ground	9.6	
Sunderbans (India) (6 yr old trees)	<i>Avicennia</i> sp.	Total	147.7	Choudhuri, 1991
	<i>B. gymnorrhiza</i>		11.2	
	<i>S. apetala</i>		34.5	
	<i>C. tagal</i>		4.8	
Tritih, Java (Indonesia)	<i>R. mucronata</i>	Above-ground	93.7	Sukardjo and Yamada, 1992
Matang mangal (Malaysia)	Mixed forest	Total	202.4	Gong and Ong, 1990
Hainan Island, (China)	Mixed forest <i>S. caseolaris</i>	Total	9.6-14.2	Liao <i>et al.</i> , 1993
		Total	47.2	Liao <i>et al.</i> , 1990
Near Brisbane (Australia)	<i>A. marina</i>	Above-ground Below-ground+ pneumatophores	110-340 109-126	Mackey, 1993
Mary River (Australia)	<i>A. corniculatum</i>	Above-ground/ below ground	40/50	Saintilan, 1997
	<i>A. marina</i>	Above-ground/ below ground	150/80	
	<i>E. agallocha</i>	Above-ground/ below ground	140/40	
	<i>R. stylosa</i>	Above-ground/ below ground	70/100	
	<i>C. australis</i>	Above-ground/ below ground	110/50	

with a long dry winter (Bunt, 1995). In India, *Avicennia marina* litter production is high in the post-monsoon period and low in the pre-monsoon season (Ghosh *et al.*, 1990). Deviations from these general patterns of litterfall may result from habitat-specific stresses (e.g., aridity, poor soils; Saenger and Snedaker, 1993; Imbert and Ménard, 1997).

A number of researchers have measured mangrove litterfall. Results show a broad range of litter volumes with production varying significantly from habitat to habitat. The production appears to depend largely on local conditions, species composition, and

productivity of the individual mangal. Litter production has been variously measured at $0.011 \text{ t ha}^{-1} \text{ y}^{-1}$ in the mangroves of Kenya, $9.4 \text{ t ha}^{-1} \text{ y}^{-1}$ in Bermuda, and $23.69 \text{ t ha}^{-1} \text{ y}^{-1}$ in Australia (Table 3).

Table 3. Litter production in mangrove forests.

Location	Species	Litter production ($\text{t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$)	Reference
Guyana (South America)	<i>A. germinans</i>	17.71	Chale, 1996
Teacapan-Ague Brava Lagoon (Mexico)	Mixed forest	14.17	Flores-Verdugo <i>et al</i> , 1990
Bermuda (North America)	Mixed forest	9.40	Ellison, 1997
Bonny estuary (Nigeria)	<i>R. racemosa</i>	8.46	Abbey-Kalio, 1992
	<i>A. africana</i>	6.41	
	<i>Laguncularia</i> sp.	8.18	
South Africa	Mixed forest	4.50	Steinke and Ward, 1990
Gazi Bay (Kenya)	<i>R. mucronata</i>	0.02	Slim <i>et al</i> , 1996
	<i>C. tagal</i>	0.01	
Andaman Islands (India)	Mixed forest	7.10 - 8.50	Mall <i>et al</i> , 1991 Dagar and Sharma, 1993 Dagar and Sharma, 1991
	<i>B. gymnorrhiza</i>	5.11 - 7.09	
	<i>R. apiculata</i>	8.08 - 10.30	
Mandovi-Zuari Estuary (India)	<i>R. apiculata</i>	11.70	Wafer <i>et al</i> , 1997
	<i>R. mucronata</i>	11.10	
	<i>S. alba</i>	17.00	
	<i>A. officinalis</i>	10.20	
Fly River Estuary (New Guinea)	Mixed forest	8.00 - 14.00	Twilley <i>et al</i> , 1992
Matang mangal (Malaysia)	Mixed forest	3.90	Gong and Ong, 1990
Jervis Bay, NSW (Australia)	<i>A. marina</i>	3.10	Clarke, 1994
	<i>A. corniculatum</i>	2.10	
Embley River (Australia)	<i>R. stylosa</i>	12.23	Conacher <i>et al.</i> , 1996
	<i>C. tagal</i>	5.39	
	<i>A. marina</i>	6.28	
Australia	<i>A. marina</i>	15.98	Bunt, 1995
	<i>R. stylosa</i>	23.69	
	<i>C. tagal</i>	12.90	

Litter from the mangroves is composed of leaves, twigs, branches, and seeds. Seeds alone accounted for 25% of the total litterfall for *Avicennia germinans* and *Rhizophora*

mangle in a mangrove habitat in Martinique (Imbert and Ménard, 1997). In a temperate mangal, the reproductive material was approximately 9% of the total for *Avicennia marina* and 32% of the total for *Aegiceras corniculatum*. Clarke (1994) suggested that such relatively high reproductive output may contribute to the low productivity and stunting of mangroves at high latitude.

Accumulated mangrove litter may wash into rivers and streams when rain or tides inundate the forest. Consequently, mangrove litter may decompose either in the source forest or in the river, with nutrients being retained or exported (Conacher *et al.*, 1996). Whether the litter (and its nutrients) remain in the habitat or are exported by water flow may depend largely on the local animal community. On the east coast of Queensland, the litter accumulation in a *Ceriops* forest was 6 g m^{-2} (0.06 t ha^{-1}) while in an *Avicennia* forest, it was closer to 84 g m^{-2} (0.84 t ha^{-1} ; Robertson *et al.*, 1992). This enormous difference in accumulation was attributed to the feeding activities of crabs.

4. MANGROVE-ASSOCIATED FLORA

4.1. Bacteria

Mangroves provide a unique ecological environment for diverse bacterial communities. The bacteria fill a number of niches and are fundamental to the functioning of these habitats. They are particularly important in controlling the chemical environment of the mangal. For example, sulfate-reducing bacteria (e.g., *Desulfovibrio*, *Desulfotomaculu*, *Desulfosarcina*, and *Desulfococcus*; Chandrika *et al.*, 1990; Loka-Bharathi *et al.*, 1991) are the primary decomposers in anoxic mangrove sediments. These bacteria largely control iron, phosphorus, and sulfur dynamics and contribute to soil and vegetation patterns (Sherman *et al.*, 1998). Methanogenic bacteria are seasonally abundant in sediments where *Avicennia* species dominate (T. Ramamurthy *et al.*, 1990; Mohanraju and Natarajan, 1992). Subsurface bacterial communities (along with epibenthic microalgae) may sequester nutrients and hold them within nutrient-limited mangrove muds (Alongi *et al.*, 1993; Rivera-Monroy and Twilley, 1996).

Bacteria are critical to the cycling of nitrogen in mangrove environments. Marine cyanobacteria are a particularly important component of the microbiota, constituting a source of nitrogen in every mangrove system (Sheridan, 1991, 1992; Hussain and Khoja, 1993; Krishnamurthy *et al.*, 1995a; Palaniselvam, 1998). N_2 -fixing cyanobacteria isolated from *Avicennia* pneumatophores in the Beachwood Mangrove Reserve, South Africa supply 24.3% of the annual nitrogen requirements of that swamp. The N_2 -fixation rates are controlled by light and temperature and show seasonal trends (low in the winter and high in the summer; Mann and Steinke, 1993). Fixation rates are higher when the cyanobacteria are on the mangrove than when they are held on an artificial growth medium (Toledo *et al.*, 1995b).

N_2 -fixing bacteria are efficient at using a variety of mangrove substrates despite differences in carbon content and phenol concentrations (Pelegri and Twilley, 1998). However, their abundance may be dependent on physical conditions and mangrove community composition. N_2 -fixing *Azotobacter*, which show potential as biofertilizers, are abundant in the mangrove habitats of Pichavaram, south India. Their abundance in the mangal exceeds that in marine backwaters and estuarine systems (S. Ravikumar, 1995). Sengupta and Choudhuri (1991) studied N_2 -fixing bacteria in a Ganges River mangrove

community. They found high numbers in the rhizospheres of plants in inundated areas but plants on occasionally inundated ridges and in degraded areas had fewer rhizosphere bacteria. Ogan (1990) found similar distinct differences in nodulation and nitrogenase activity among sites and among species in a Nigerian mangal.

Two halotolerant N_2 -fixing *Rhizobium* strains have been isolated from root nodules of *Derris scandens* and *Sesbania* species growing in the mangrove swamps of Sunderbans (Sengupta and Choudhuri, 1990). If the non- N_2 -fixing bacteria are removed from the rhizosphere, N_2 -fixing activity drops, indicating that other rhizosphere bacteria contribute to the fixation process (Holguin *et al.*, 1992). The non- N_2 fixer, *Staphylococcus* sp., isolated from mangrove roots, promotes N_2 -fixation by *Azospirillum brasilense*. This can be achieved by growing the two species in mixed culture or simply by adding a cell-free dialysate of the *Staphylococcus* sp. to the *A. brasilense* culture. Aspartic acid is the compound responsible for the effect (Holguin and Bashan, 1996).

In addition to processing nutrients, mangrove bacteria may also help process industrial wastes. Iron-reducing bacteria are common in mangrove habitats in some mining areas (Panchanadikar, 1993). Eighteen bacterial isolates that metabolize waste drilling fluid have been collected from a mangrove swamp in Nigeria (Benka-Coker and Olumagin, 1995). Interestingly, four additional bacterial strains isolated from the same swamp depress growth rates of *Staphylococcus* and *Pseudomonas* species and could, therefore, decrease normal rates of organic decomposition (Benka-Coker and Olumagin, 1996).

Bacteria play a number of other roles in the mangal. Some live symbiotically with other organisms. For example, rod bacteria can be commonly found in the hindguts of mangrove detritivores (Harris, 1993) and deeply branched sulfur-oxidizing bacteria occur as endosymbionts within members of the bivalve family Lucinacea in sulfide-rich, muddy mangrove areas. Bauer-Nebelsick *et al.* (1996) and Ott *et al.* (1998) have described sulfur-oxidizing bacteria that live as obligate ectosymbionts on colonial sessile ciliates (*Zoothamnium niveum*) in a Belizian mangal.

Other mangrove bacteria are parasitic or pathogenic. Bdellovibrios capable of parasitizing *Vibrio* spp. are common in an Australian mangrove habitat. Their abundance there (36.6 ml^{-1}) is much higher than in nearby Great Barrier Reef habitats (9.5 ml^{-1} ; Sutton and Besant, 1994). Also in Australia, *Bacillus thuringiensis*, which shows insecticidal activity against mosquito larvae of *Anopheles maculatus*, *Aedes aegypti* and *Culex quinquefasciatus*, has been isolated from mangrove sediments (Lee *et al.*, 1990a; Lee and Seleena, 1990). Actinomycetes (fungi-like bacteria) that occur in many mangrove habitats (Kala and Chandrika, 1993; Vikineswary *et al.*, 1997) may show antifungal activity (Vikineswary *et al.*, 1997).

Bacterial populations show distinct spatial distribution patterns. Many live epiphytically on the surfaces of mangroves, but different species appear to prefer different parts of the tree. Leaves of *Avicennia marina* and *Sesuvium portulacastrum* harbour large numbers of *Flavobacterium* while roots and stems have large populations of *Vibrio* spp. (Abhaykumar and Dube, 1991). In many species, the aerial roots, especially pneumatophores, harbour particularly dense bacterial cyanopopulations that may show sharp vertical zonation. Coccoid forms occur in the upper zone of the pneumatophores. Filamentous non-heterocystous forms predominate in the middle zone, and filamentous heterocystous forms are largely restricted to the lower zones (Toledo *et al.*, 1995a; Palaniselvam, 1998). In the forests of Aldabra Lagoon, heterocystous forms like

Scytonema sp. also form conspicuous growths on pneumatophores, but non-heterocystous species are restricted to the sediment surface (e.g., Alongi and Sasekumar, 1992).

Cyanobacteria in the mangal colonize any submerged surface including sediments, roots, aerial roots, branches and trunks (Sheridan, 1991). Microbial mats in mangrove tidal channels often have an outer layer of cyanobacteria and a reddish inner layer of anoxygenic phototrophic bacteria (Lopez-Cortes, 1990). A cyanobacterium (*Calothrix viguieri*) isolated from the surface of mangrove roots show a peculiar morphological response to salinity variation. In low salinity, it develops hairs (Figure 6). The hairs are shed if salinity is increased. The hairs may be an adaptation to hydrolyze pulses of organic phosphorus that occur in the habitat after heavy rains (Mahasneh *et al.*, 1990).

Bacterial counts are generally higher on attached mangrove vegetation than they are on fresh leaf litter. This is probably because attached, undamaged leaves leak amino acids and sugars but do not release much tannin (Kathiresan and Ravikumar, 1995b). Shome *et al.* (1995) isolated thirty-eight distinct bacteria from mangrove leaf litter and sediments in south Andaman and characterized the bacterial community. The bacteria were generally gram-positive (76.3%), motile (87%), fermentative (6.9-82.1%), pigmented (31%), and antibiotic resistant (100% against polymixin B and 50% against chloramphenicol). Photosynthetic bacteria, including purple sulfur bacteria (*Chromatium* spp.) and purple non-sulfur bacteria (*Rhodospseudomonas* spp.), have been isolated from mangroves in Pichavaram, south India (Vethanayagam, 1991; Vethanayagam and Krishnamurthy, 1995). Nine species of purple non-sulfur bacteria have also been found in mangroves of Egypt (Shoreit *et al.*, 1994). Growth of the purple sulfur bacteria in these habitats is limited by low light and sulfide. In contrast, high light and sulfide limit growth of green sulfur bacteria (Chandrika *et al.*, 1990).

4.2. Fungi and fungus-like protists

Mangals are home to a group of fungi called “manglicolous fungi.” These organisms are vitally important to nutrient cycling in these habitats (Hyde and Lee, 1995; Kohlmeyer *et al.*, 1995). Kohlmeyer and Kohlmeyer (1979) were the first to review this group. They recognized 43 species of higher fungi, including 23 Ascomycetes, 17 Deuteromycetes, and 3 Basidiomycetes. Hyde (1990a) listed 120 species from 29 mangrove forests around the world. These included 87 Ascomycetes, 31 Deuteromycetes, and 2 Basidiomycetes.

Work in individual habitats has revealed surprisingly diverse fungal communities (e.g., Hyde, 1990b; Hyde, 1996). Chinnaraj (1993a) identified 63 species of higher fungi in

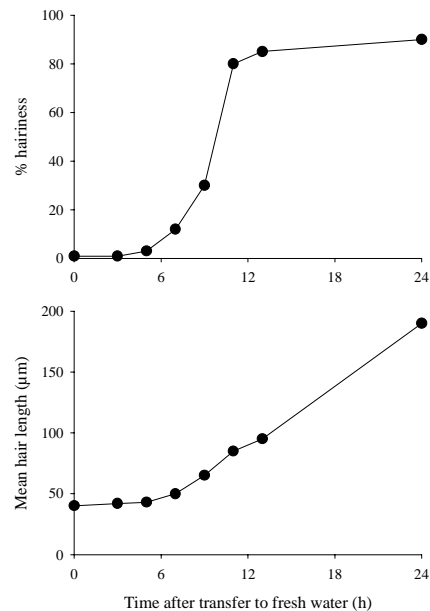


Figure 6. Effects of salinity on hair formation in the mangrove bacterium

mangrove samples from Andaman and Nicobar Islands alone. Similar samples from Lakshadweep Island yielded 32 species (Chinnaraj, 1992) and 39 species were found in mangrove samples from the Maldives (Chinnaraj, 1993b). D.R. Ravikumar and Vittal (1996) found 48 fungal species in decomposing *Rhizophora* debris in Pichavaram, south India. On the Indian Ocean coast of South Africa, Steinke and Jones, (1993) identified 93 species of marine fungi, including 55 from mangrove wood (particularly *Avicennia marina*). Table 4 lists some of the fungal species identified in these studies.

Table 4. Some fungal species isolated from mangrove habitats.

Species	Author
<i>Aigialus striatipora</i>	Hyde (1992c)
<i>Aniptodera longispora</i>	Hyde (1990b)
<i>Aniptodera salsuginosa</i>	Nakagiri and Ito (1994)
<i>Calathella mangrovei</i>	Jones and Agerer (1992)
<i>Cryptovalsa halosarceicola</i>	Hyde (1993)
<i>Eutypa bathurstensis</i>	Hyde and Rappaz (1993)
<i>Falciformispora lignatilis</i>	Hyde (1992d)
<i>Halophytophthora kandeliae</i>	Ho <i>et al</i> (1991)
<i>Halophytophthora kandeliae</i>	Newell and Fell (1992b)
<i>Halophytophthora vesicula</i>	Newell and Fell (1992b)
<i>Halophytophthora spinosa</i>	Newell and Fell (1992b)
<i>Halosarpheia minuta</i>	Leong <i>et al</i> (1991)
<i>Hapsidascus hadrus</i>	Kohlmeyer and Kohlmeyer (1991)
<i>Hypoxylon oceanicum</i>	Whalley <i>et al</i> (1994)
<i>Julella avicenniae</i>	Hyde (1992a)
<i>Khuskia oryzae</i>	Pal and Purkayastha (1992a)
<i>Lophiostoma asiana</i>	Hyde (1995)
<i>M. ramunculicola</i>	Hyde (1991b)
<i>Massarina armatispora</i>	Hyde <i>et al</i> (1992)
<i>Massarina velatospora</i>	Hyde (1991b)
<i>Payosphaeria minuta</i>	Leong <i>et al</i> (1990)
<i>Pedumispora</i>	Hyde and Jones (1992)
<i>Phomopsis mangrovei</i>	Hyde (1991a)
<i>Saccardoella</i>	Hyde (1992b)
<i>Trematosphaeria lineolatispora</i>	Hyde (1992d)

Surveys are revealing a number of range extensions, new species, and even new genera. Collections of mangrove fungi in Macau and Hong Kong, for instance, yielded 45 species. Twenty-eight of these were new records for Macau and 21 were new records for Hong Kong (Vrijmoed *et al.*, 1994). These discoveries are leading to significant taxonomic revision of these groups (Jones *et al.*, 1994, 1996; Alias *et al.*, 1996; Goh and Yipp 1996; Ho and Hyde, 1996; Vrijmoed *et al.*, 1996; Honda *et al.*, 1998).

The fungus-like thraustochytrids are important endobionts in dead or living plants and in calcareous shells (S. Raghukumar, 1990). A number of these occur in mangrove swamps where they help decompose mangrove leaf litter (S. Raghukumar *et al.*, 1994; Bremer, 1995). Both thraustochytrids and chytridiomycetes (including *Schizochytrium*,

Thraustochytrium and *Ulkenia*) have been isolated from Costa Rican mangrove swamps (Ulken *et al.*, 1990). Two thraustochytrids, *Thraustochytrium striatum* and *Schizochytrium mangrovei*, have been isolated from an Indian mangal at Goa. Both produce amoebae-like structures, move using pseudopodia, and phagocytose bacterial cells (S. Raghukumar, 1992).

Marine oomycetes (fungus-like protists) also occur in mangrove communities. T.K. Tan and Pek (1997) found five *Halophytophthora* species in Singapore mangroves. This is the first time three of them have been seen in tropical mangroves and the first time one has been reported outside Australia. Oomycetes in the genus *Halophytophthora* have special importance in mangrove habitats (Newell and Fell, 1992a). They greatly facilitate the decomposition of mangrove material. Newly fallen *Rhizophora mangle* leaves are quickly infested with mycelial growths of *Halophytophthora vesicula* and *H. spinosa*. Rapid lateral extension of the mycelia within the leaves apparently follows establishment of a single zoospore (Newell and Fell, 1995). In laboratory cultures, the established *Holophytophthora* are subsequently colonized by bacteria and labyrinthulas (Newell and Fell, 1994). *Holophytophthora* species are generally good competitors against true fungi but have difficulty colonizing leaves that already have bacterial films (Newell and Fell, 1997).

Newell and Fell (1996) speculate that *Halophytophthora* completes its colonization of submerged leaves, from attachment of zoospore cysts to release of new zoospores, in the early stages of leaf decomposition, before there is substantial entry into the leaves themselves. Mild drying, low salinity and low temperatures may enhance zoospore release. The release rates are low in older, decaying leaves and high in newer, less-decayed leaves (Newell and Fell, 1996). Leñaño *et al.* (1998) showed that the zoospores of other mangrove fungi are chemically attracted to plant material and extracts. This undoubtedly aids in the colonization of new substrata.

A few researchers have studied the physiology and biochemistry of manglicolous fungi. Many of the species produce interesting compounds. For example, most of the soil fungi produce lignocellulose-modifying exoenzymes like laccase (C. Raghukumar *et al.*, 1994). *Preussia aurantiaca* synthesizes two new depsidones (Auranticins A and B) that display antimicrobial activity (Poch and Gloer, 1991). *Cirrenalia pygmaea* produces melanin pigments that appear to protect the hyphae from sudden changes in osmotic pressure; when melanin synthesis in cultures is inhibited with tricyclazole, the fungus becomes sensitive to osmotic shock (Ravishanker *et al.*, 1995). High salinities also increase the number and types of amino acids this species produces (Ravishankar *et al.*, 1996).

Ascus and ascospore ultrastructure have been studied in the fungi *Swampomyces armeniacus* and *Marinosphaera mangrovei* (Read *et al.*, 1995) and in *Dactylospora haliotrepha* (Au *et al.*, 1996). Ascocarp formation has been tested in single and mixed cultures of *Aigialus parvus*, *Lignincola laevis* and *Verruculina enalia* growing on the wood of *Avicennia alba*, *Bruguiera cylindrica* and *Rhizophora apiculata*. Sporulation was delayed and fewer ascocarps were formed in mixed cultures, suggesting competition among the fungi (T.K. Tan *et al.*, 1995).

A number of fungal species live directly on living mangroves but, in general, they are not well known. Sivakumar and Kathiresan (1990) isolated ten fungal species from leaf surfaces of seven mangrove species. The dominant phylloplane fungi were *Alternaria alternata*, *Rhizopus nigricans*, *Aspergillus* and *Penicillium* spp. Abundances of these fungi

were negatively correlated with tannin content of the leaves. The fungi appear to prefer leaf litter (which contain more amino acids) to fresh leaves (which contain more tannins and sugars; S. Ravikumar and Kathiresan, 1993). Other fungi are harmful to the living mangroves. Two new parasitic species (*Pestalotiopsis agallochae* and *Cladosporium marinum*) have been isolated from the leaves of *Excoecaria agallocha* and *Avicennia marina* (Pal and Purkayastha, 1992b). Pathogenic fungi may have contribute to diebacks of *Rhizophora mangle* stands in Costa Rica (Tattar *et al.*, 1994).

A number of fungal species colonize subsurface mangrove roots. Nair *et al.* (1991) found 25 fungal species from 15 genera in the rhizosphere of *Avicennia officinalis*; adjacent non-rhizosphere soil held only 16 species from 10 genera. Sengupta and Choudhuri (1994) found *Rhizoctonia* and VA-mycorrhiza-like fungi in the mangrove community at Sunderbans. When *Cajanas* seedlings in nutrient-poor conditions were inoculated with the VA-mycorrhizal isolates, there was a significant increase in growth. This was due, in part, to mobilization of insoluble phosphate by the fungus.

Distributions of fungal species within the mangrove habitat may reflect physical conditions and/or habitat preference. It may also reflect age of the stand. Working in Belize (Central America), Kohlmeyer and Kohlmeyer (1993) found that fungal diversity depends on age of the mangrove stand. They discovered 43 species in established *Rhizophora* stands but only 7 in recently introduced *Rhizophora*. Some species may be quite specific in their habitat preferences. For example, of the 48 fungal species Ravikumar and Vittal (1996) found in a south Indian mangal, 44 were on prop root while seedling and wood samples only held 18 and 16 species respectively. The fungal species appeared to partition the mangrove habitat. *Verruculina enalia* was most abundant on prop roots and seedlings while *Lophiostoma mangrovei* was most common on wood. Physical conditions, or genetic differentiation created by isolation, may lead to differences in fungal morphology and physiology. *Pestalotiopsis versicolor* strains, isolated from *Ceriops decandra* growing in different regions of the Sunderbans, vary in mycelial mat texture, growth rate and sporulation intensity (Bera and Purkayastha, 1992).

Differences in physical requirements may lead to vertical zonation of the fungi. Hyde (1990b) found 57 intertidal fungal species on *Rhizophora apiculata* at Brunei mangal. Most of these occurred above the mean tidal level. A similar study of senescent *Acanthus ilicifolius* at Mai Po, Hong Kong revealed that the apical portions of the trees are colonized by typical terrestrial fungi but the basal portions are colonized by marine species (Sadaba *et al.*, 1995). The authors attributed this to the nature of the substratum and the frequency of tidal inundation. Other fungal species live directly on the sediment surface but are still entirely restricted to mangrove habitats (Soares *et al.*, 1997).

Wood degrading fungi are well-known in mangrove habitats. Thirty species of such lignicolous fungi have been recorded in Malaysian mangals. The most abundant are *Halosarpheia marina*, *Lulworthia* sp., *Lignincola laevis*, *Halosarpheia retorquens*, *Eutypa* sp., *Kallichroma tethys*, *Marinosphaera mangrovei*, *Phoma* sp. and *Julelia avicenniae*. Diversity and abundance are greatest on *Avicennia* wood (T.K. Tan and Leong, 1992; Alias *et al.*, 1995). Test panels of different woods placed in mangrove waters along the Goa coast of India showed four common lignicolous fungi (*Periconia prolifica*, *Lignincola laevis*, *Aniptoder* sp. and *Lulworthia* sp.). Panels treated with copper chrome arsenic were more resistant to fungal infestation than those treated with chrome boric (Santhakumaran *et al.*, 1994).

Nakagiri and Ito (1994) found a new lignicolous fungus (*Aniptodera salsuginosa*) with unique ascospore appendages and an unusual ascus apical apparatus on decomposing mangrove wood. The ascospore appendages are functional only when they are submerged in brackish water. The ascospores are discharged through a fissure in the ascus wall at the margin of the apical disc; the ascus pore in this disc does not function in ascospore release.

4.3. Microalgae

Phytoplankton and benthic microalgal communities make important contributions to the functioning of mangrove environments. However, their contribution to total estuarine production is relatively small in most regions of southeast Asia, Australia, Central America and tropical South America. Robertson and Blaber (1992) suggested that the contribution of plankton to total net production in mangrove habitats ranges from 20-50%. Careful measurements are verifying that predication for large systems. Phytoplankton are responsible for 20% of the total production in mangrove estuaries in the Fly River Delta in Papua New Guinea (Robertson *et al.*, 1991, 1992) and 20-22% of the total production in the Pichavaram mangroves of south India (Kawabata *et al.*, 1993).

Phytoplankton contributions to productivity in localized mangrove areas may be much smaller. Lee (1990) found that phytoplankton and benthic macroalgae together contribute less than 10% of the net primary production in Hong Kong mangals and Boto and Robertson (1990), using nitrogen measurements, estimated that benthic cyanobacteria, microalgae and macroalgae together contribute only 6% of the gross primary production in mangrove ecosystem of northeastern Australia. Robertson and Blaber (1992) state that phytoplankton productivity is significantly lower in estuarine mangrove areas than it is in lagoons or open embayments fringed by mangroves.

High turbidity, large salinity fluctuations and a generally small ratio of open waterway to mangrove forest area contribute to the low light levels and shading that limit productivity of the microalgae, especially the benthic forms (Alongi, 1994; Harrison *et al.*, 1994). High summer temperatures may also limit production (Lee, 1990). Rates of primary production, which are generally low in the dry season, increase on ebb tides and decrease on flood tides (Kitheka, 1996).

In the Fly River delta of Papua New Guinea, Robertson *et al.*, (1992) measured very low production rates of only 0.022 to 0.0693 g C m⁻³ d⁻¹. However, localized conditions may lead to much higher rates. For example, daily production in the coastal lagoons of Mexico may reach 2.4 g C m⁻³ d⁻¹ (Robertson *et al.*, 1992). Increased productivity may relate to elevated nutrient levels. Production in lagoons of the Ivory Coast reach 5 g C m⁻³ d⁻¹. However, the effect is largely a result of nitrogen and phosphorus input from nearby human population centers.

Naturally occurring substances may also regulate phytoplankton growth. Selvam *et al.* (1992) found phytoplankton productivity to be four times higher in mangrove waters than in adjacent marine waters in south India. Refractive materials like humic acid, which are abundant in the mangroves, stimulate phytoplankton growth there (Schwamborn and Saint-Paul, 1996). In the Celestun Lagoon (northern Yucatan Peninsula, Mexico) low

concentrations of natural phenolics stimulate phytoplankton growth, but higher wintertime levels depress the growth rates (Herrera Silveira and Ramirez Ramirez, 1996).

While microalgae may make only small contributions to total productivity in estuarine mangrove systems, they may be critical to supporting higher trophic levels (Robertson and Blaber, 1992). This may be particularly true because of the high nutritional quality of phytoplankton relative to mangrove detritus. Phytoplankton biomass, productivity, and size are closely tied to diversity and abundance of higher trophic levels. Teixeira and Gaeta (1991) determined the composition of the phytoplankton community in a Brazilian mangal. Nanoplankton (cells from 2 - 20 μm) constituted over 80% of the total phytoplankton. Laboratory testing showed that the smaller cells were responsible for a significant part of the total productivity. Picoplankton (cells < 2 μm) accounted for 3-29% of the total ^{14}C uptake. The effects of this skewed phytoplankton size distribution on the zooplankton community composition has not been studied.

Despite relatively low productivity, mangrove phytoplankton communities can be quite diverse. However, composition and density of the plankton community are strongly affected by local environmental conditions (Lee, 1990). For example, low phytoplankton diversity in *Rhizophora* habitats is related to the release of tannins by roots, decomposing wood, and leaves (Robertson and Blaber, 1992). Phytoplankton populations also respond to temperature and salinity variation. Thus, communities may show marked seasonal variation (Mani, 1994). Phytoplankton studies at West Bengal, India revealed 46 species of Bacillariophyceae, Dinophyceae and Cyanophyceae (Santra *et al.*, 1991). *Coscinodiscus*, *Rhizosolenia*, *Chaetoceros*, *Biddulphia*, *Pleurosigma*, *Ceratium* and *Protopteridinium* were the dominant genera, existing almost year round. At least 82 phytoplankton species (72% diatoms, 15% dinoflagellates) occur in the Pichavaram mangroves of south India (Kannan and Vasantha, 1992). The diatoms *Nitzschia closterium*, *Pleurosigma* spp., *Thalassionema nitzschioides* and *Thalassiothrix frauenfeldii* are most abundant. Thirty-one of those species may form seasonal blooms (Mani, 1992). Chaghtai and Saifullah (1992) reported such a bloom of the diatom *Navicula* in the Karachi mangroves of Pakistan.

Dinoflagellate assemblages have been particularly well studied in Belizean mangrove habitats where a diverse collection of benthic and epiphytic species exists (Faust, 1993a,b,c,d; Faust and Balech, 1993). Many are new species (e.g., *Prorocentrum maculosum*, *P. foraminosum*, *P. formosum*, *Plagiodinium belizeanum*, *Sinophysis microcephalus*). Faust and Gullede (1996) found many microalgal species associated with floating mangrove detritus. Dinoflagellates constituted the greatest proportion (50-90%), followed by diatoms (5-15%), cyanobacteria (3-25%) and dinoflagellate cysts (1-7%). Ciliates and nematodes were the major dinoflagellate consumers in the detritus.

4.4. Macroalgae

The macroalgal flora is rich in mangrove habitats where it contributes to production while also providing habitat and food for a number of invertebrate and fish species. Red algae, especially in the genera *Bostrychia*, *Caloglossa* and *Catenella*, are most commonly associated with mangroves and may be quite abundant. For instance, the total annual biomass of *Bostrychia tenella* in a south Nigerian estuary reaches $1.84 \text{ mg} \cdot \text{cm}^{-2}$, which is 38% of the total algal production there (Ewa-Oboho and Abby-Kalio, 1993). The biomass of algae in the mangrove lagoons of Puerto Rico is similar to the total annual leaf litterfall

from the *Rhizophora* fringe, leading to an algal-dominated foodweb (Rodriguez and Stoner, 1990).

Algal diversity can also be quite high in mangrove environments. Recent surveys have revealed diverse macroalgal communities in Papua New Guinea (25 species; King, 1990), the Nicobar Islands in the Andaman Sea (61 species; Jagtap, 1992), and the coast of Mauritius (127 species; Jagtap, 1993). King and Puttock (1994) and King (1995) provide exhaustive reviews of the very diverse Australian mangrove macroalgal flora. Algal assemblages tend to be richest in shallow areas with a mixture of hard and soft substrates. Lowest diversity occurs where there is low light, soupy muds, or homogeneous, large-grain sands (as in the Netherlands Antilles, Kuenen and Debrot, 1995).

Algal surveys have produced new records for a number of species including *Stictosiphonia kelanensis* from Atlantic mangroves (Fujii *et al.*, 1990); *Bostrychia pinnata*, *Bostrychia simpliciuscula*, *Caloglossa angustalata* (Rhodophyta) and *Boodleopsis carolinensis* (Chlorophyta) from Singapore (West, 1991a); *Bostrychia pinnata*, *Caloglossa ogasawaraensis*, *C. stipitata* and *Halochlorococcum operculatum* from Peru (West, 1991b); *Bostrychia pinnata* and *Caloglossa ogasawaraensis* from the Atlantic coast, USA (West and Zuccarello, 1995); *Bostrychia calliptera* from the Central Gulf of Mexico (Collado-Vides and West, 1996) and *C. ogasawaraensis*, *C. stipitata*, *C. lepricuriil*, *B. moritziana*, *B. pinnata*, *B. radicans* and *Catenella caespitosa* in Southern Mexico and Guatemala (Pedroche *et al.*, 1995).

Recent work has investigated genetic differentiation of some of the widely distributed red algae. Male *Caloglossa ogasawaraensis* from a Peruvian mangle readily hybridize with female *C. ogasawaraensis* from Brazil, producing viable tetrasporophytes (West, 1991b). Similar studies with *Bostrychia radicans* from the Pacific and Atlantic coasts of North America have been done. Almost all isolates from the northern Pacific coast of Mexico are compatible and produce cystocarps that release viable carpospores. However, isolates from the Atlantic coast of the United States show greater incompatibility (Zuccarello and West, 1995).

Algal abundance and diversity are largely determined by the physico-chemical characteristics of the mangal (Mazda *et al.*, 1990a) and these may be extremely variable. As with the mangroves themselves, the most successful macroalgae have special adaptations that help them tolerate extreme conditions. Work on the physiology of algae associated with mangroves includes a study of salinity and the polyol (D-dulcitol, D-sorbitol) content of *Bostrychia* (West *et al.*, 1992). The success of *B. simpliciuscula* in the mangrove swamps of Singapore may be attributed to its physiological adaptations to salinity extremes. The polyols serve as osmoprotectors that *B. simpliciuscula* synthesizes and sequesters as salinity increases (Karsten *et al.*, 1994, 1996). Floridoside compounds, which may be essential for survival of the algae, also change with salinity (Karsten *et al.*, 1995). *Caloglossa lepricuriil*, which is also common in mangrove environments, has a novel metabolic pathway that may be a similar biochemical adaptation to environmental extremes (Karsten *et al.*, 1997). Salinity gradients create distinct ecotypes of *Caloglossa lepricuriil* in mangals along the Brisbane River, Australia (Mosisch, 1993).

Salinity, temperature, desiccation, tidal inundation, wave action, wetting frequency and light intensity are all environmental factors likely to produce patterns of horizontal and vertical distribution seen in many mangrove algae (e.g., Phillips *et al.*, 1994; Farnsworth and Ellison, 1996b). In the Gazi Bay of Kenya, there is distinct macroalgal zonation. The

upper intertidal is covered by *Boodleopsis pusilla* while the mid-intertidal is dominated by *Halimeda opuntia*, *Gracilaria salicornia* and *G. corticata*. The low water mark has primarily *Halimeda macroloba* and *Avrainvillea obscura* (Coppejans *et al.*, 1992). A distinct zonation has also been described for algae growing on the pneumatophores of *Avicennia marina* (Steinke and Naidoo, 1990). There are generally three zones: an upper *Rhizoclonium* zone; a middle *Bostrychia* zone, and a lower *Caloglossa* zone (Phillips *et al.*, 1996).

The composition of the mangrove algal community may depend largely on the nature of the early colonizers. Eston *et al.* (1992) monitored colonization of artificial substrata by mangrove macroalgae and found that *Bostrychia radicans* and several other species settled early. There was no evidence that later species could displace the early colonists. This macroalgal community showed no succession; the pioneer community was also the final community. Established macroalgae can also affect distribution of the mangroves directly. For example, in southeastern Australia, the alga *Hormosira banksii* inhibits intertidal establishment of grey mangrove (*Avicennia marina*) seedlings (Clarke and Myerscough, 1993).

A number of algae from mangrove habitats have potential commercial value. For example, the red alga *Gracilaria changii* from Malaysian mangrove habitats is an excellent source of agar; the agar content is between 12 and 25% of its dry weight (Phang *et al.*, 1996). *Monostroma oxyspermum*, *Catenella impudica* and *Caloglossa leprieurii* are all edible food resources. The latter two species are also potential sources of dyes. *Caulerpa* sp. has yielded bioactive substances that may hold promise as pharmaceutical agents (*e.g.*, Ananda Rao *et al.*, 1998).

4.5. Seagrasses

Seagrasses are closely associated with mangrove habitats in many parts of the world. In the Andaman Sea, there are three mangrove-associated sea-grasses, *Thalassia hemprichii*, *Enhalus acoroides* and *Halophila ovalis* (Poovachiranon and Chansang, 1994). Intertidal mangrove areas in the Gazi Bay, Kenya are colonized by *Thalassia hemprichii*, *Halophila ovalis* and *Halodule wrightii* (Coppejans *et al.*, 1992) while *Halophila baccarii* occurs on intertidal mudflats of Indian mangals (Jagtap, 1991).

The seagrass biomass in mangrove areas may be quite high. In an Andaman Sea mangal, Poovachiranon and Chansang (1994) measured seagrass biomass ranging from 55-1941 g wet wt \cdot m⁻², corresponding to 32-297 g dry wt \cdot m⁻². As with the macroalgal communities, seagrass diversity and abundance are largely regulated by a combination of light level and substrate type. In the Spaanse waters of the Netherland Antilles, the richest assemblages of seagrasses occur in shallow areas with high light and a mix of hard and soft substrates. Diversity is much lower where light is low and the substrates are loose muds or homogeneous, coarse-grained sands (Kuenen and Debrot, 1995).

Seagrasses generally require high light levels to grow and survive. Planktonic primary producers require only about 1% of the surface irradiance to maintain a net positive carbon balance. In contrast, seagrasses may require 10-20% of the daily average surface irradiance to survive (Fourqurean and Zieman, 1991). Growth rate may decrease naturally in the winter months as a result of low temperatures and shortened daylengths. However, in recent years, there have been precipitous declines of seagrass beds in

mangrove environments. Seagrass mortality has often been linked to reduced water quality and increased turbidity that decrease light penetration (Giesen *et al.*, 1990; Larkum and West, 1990). In turbid waters, flocs from the mangroves themselves contribute to shading of the seagrass (Wolanski *et al.*, 1997).

Though seagrass beds often occur in close proximity to mangroves, the two habitats may not be closely coupled. Tussenbroek (1995) found that seagrass growth, biomass and primary production were all higher in the vicinity of mangrove discharges than they were in other habitats. Respiratory CO₂ derived from mangrove particulate organic matter (POM) could be a carbon source for seagrass and could promote faster growth. Ebb flows are generally stronger than flood flows in mangrove creeks, which should promote a net export of nutrients and POM. In general, however, fluxes from mangrove forests seem to have little effect on adjacent seagrass beds (Fleming *et al.*, 1990). For example, Hemminga *et al.* (1994) failed to detect any input of mangrove POM in a seagrass bed only 3 km away. POM was exported from the mangrove forest, but deposition was rapid and little material reached the seagrass bed. Similarly, in the Gazi Bay of Kenya, leaf production and nitrogen:phosphorus ratios of *Thalassodendron ciliatum* were unrelated to the input of mangrove carbon and ¹³C studies confirmed that the mangroves contribute little reduced carbon to adjacent seagrass beds (Lin *et al.*, 1991). Nor does it appear that dissolved nutrients move from the mangal to nearby grassbeds. The few dissolved nutrients generated by the mangroves are likely to be used for primary production within the mangrove zone itself (Kitheka *et al.*, 1996).

Mangroves and seagrasses serve parallel functions in the habitats they share. Both trap sediments and help capture chemical elements, including trace metals (Costa and Davy, 1992; Lacerda, 1998). Both also help support fish population by serving as food for fish, as critical habitat for fish, and as growth surfaces for epizonts that fish eat. A number of fish species may use seagrass/mangrove habitat as a nursery area. In Guadeloupe, French West Indies, fish diversity is higher in *Thalassia testudinum* beds near mangroves than in the adjacent coral reefs (Baelde, 1990). Similarly, in Belize, Central America, fish abundance and biomass were highest in a mangrove creek, followed by a seagrass bed and the sand-rubble zone of an adjacent lagoon (Sedberry and Carter, 1993). Arancibia *et al.* (1993) found more than 80 fish species using the mangrove/seagrass habitat; seven species were found only in these areas.

4.6. Saltmarsh and other flora

Saltmarsh plants replace mangroves at their northern limit on the Gulf and Atlantic coasts of North America but the southern limit of the saltmarsh distribution may be set by competition with the mangroves. For example, the common saltmarsh grass *Spartina* cannot survive high salinities and fast sediment accretion. As a result, it grows poorly in areas where mangroves thrive (Kangas and Lugo, 1990). This usually leads to its replacement by mangroves, as in Paranagua Bay, Brazil (Lana *et al.*, 1991).

Though saltmarsh species are generally not common in mangrove habitats, a large number of other non-mangrove plant species may be found coexisting with the mangroves. A floristic survey of the tidal mangrove flora in the Sunderbans, India, documented 1175 angiosperm species in 680 genera and 154 families (Nasakar and Bakshi, 1993). Working in the tropical mangrove forests of the Yucatan Peninsula, Olmsted and Gomez (1996)

found approximately 100 epiphytic species in the families Orchidaceae, Bromeliaceae, Cactaceae, Araceae, Piperaceae and Polypodiaceae scattered through the canopy and on trunks of mangrove trees. The orchid *Brassavola nodosa* is an epiphyte on red mangroves (*Rhizophora mangle*) in Belize, Central America, where it grows anywhere from 1-300 cm above the ground. The largest specimens occur high above the ground where plentiful light enables them to flower continuously through the summer (Murren and Ellison, 1996). Lichens may also be abundant on the bark of the mangroves in some habitats (J.C. Ellison, 1997).

5. MANGROVE-ASSOCIATED FAUNA

5.1. Zooplankton

Diverse communities of zooplankton exist in mangrove habitats and abundances can be extremely high, reaching 10^5 individuals m^{-3} with biomasses up to $623 \text{ mg } m^{-3}$. These numbers are significantly higher than what is often recorded in offshore waters (reviewed by Robertson and Blaber, 1992) and the planktonic organisms may contribute to regional food webs. Such high abundances, however, do not occur in all mangrove environments. On the west coast of India, for example, Goswami (1992) found lower zooplankton biomass in the mangroves than in contiguous estuarine and neritic habitats.

Zooplankton in mangrove waters can be grouped into three size classes. The smallest organisms are the microzooplankton (organisms between 20 and 199 μm). This group includes tintinnids, radiolarians, foraminiferans, ciliates, rotifers, copepod nauplii, barnacle nauplii, and mollusk veligers. Krishnamurthy *et al.* (1995b) found 81 such species in the Pichavaram mangroves of south India. Tintinnids were the dominant microzooplankters with 50 species and densities ranging from 60 to 44,990 individuals m^{-3} . The most important genera were *Tintinnopsis* and *Favella* (Godhantaraman, 1994; Krishnamurthy *et al.*, 1995b). They also found 40 rotifer species in 17 genera. Except for rotifers, whose populations peaked in the premonsoon and monsoon months, the microzooplankters were most abundant in the summer, corresponding with highest phytoplankton abundance.

Copepods are the most abundant group in the mangrove mesoplankton (organisms between 200 μm and 2 mm). In the Pichavaram mangroves of south India, copepod densities reach $80,740$ individuals $\bullet m^{-3}$ (Godhantaraman, 1994); the genera *Acartia* and *Acrocalanus* (Calanoida), *Macrosetella* and *Euterpina* (Harpacticoida) and *Oithona* (Cyclopoida) are the most abundant. In Kenyan mangrove waters, copepods constitute 48.5-92.4% of the zooplankton. Zooplankton counts are high in the creek mouth compared to the inner creek. Abundances peak around May when heavy rains increase nutrient input (Osore, 1992). Species in the cyclopoid genus *Oithona* are particularly abundant in many studies of mangrove plankton. Harpacticoids (e.g., *Pseudodiaptomus* spp.) and calanoids (e.g., *Acartia* spp., *Paracalanus* spp. and *Parvocalanus* spp.) are also important (Ambler *et al.*, 1991). Barnacle nauplii occur in mangrove canals throughout Raby Bay, Australia, but the copepod *Acartia tranteri* is found only in the innermost canals (King and Williamson, 1995).

Dioithona oculata is a particularly interesting member of the copepod assemblage in some mangrove habitats. Individuals congregate to form swarms in light shafts among mangrove prop roots. The swarms maintain their position in currents up to $2 \text{ cm } \bullet \text{ sec}^{-1}$

(Buskey *et al.*, 1996). Buskey *et al.* (1995) showed that the swarms form in response to an endogenous rhythm. They cannot, therefore, be induced to swarm in artificial light shafts created at night.

Copepods and other mesoplanktonic organisms are food for the macrozooplankton (organisms larger than 2 mm). Jellyfish are the most important macrozooplanktonic species. The medusa *Tripedalia cystophora* is attracted to light shafts where non-breeding individuals actively feed on copepods (reproductive males and gravid females do not feed; R.W. Stewart, 1996). Planula larvae of *Cassiopea* species show a strong preference for mangrove substrata, specifically settling and undergoing metamorphosis on submerged, deteriorating mangrove leaves (Hofmann *et al.*, 1996). The larvae are apparently attracted to a soluble protein (molecular weight > 5000 daltons) leaching from the mangrove leaves (Fitt, 1991, Fleck and Fitt, 1999).

Meroplankton (planktonic larval stages of benthic invertebrates) may constitute up to 70% of the zooplankton and span a range the full range of zooplankton sizes. Brachyuran zoeae can be especially abundant. For example, decapod larval densities reached 1000 individuals • m⁻³ in a mangrove area of Costa Rica. These early larval stages are exported from the mangrove areas on outgoing tides; incoming tides bring the older stages back to the habitat (Dittel and Epifanio, 1990).

Bingham (1992) studied larval recruitment of invertebrates (e.g., sponges, oysters, barnacles, bryozoans, ascidians) living epifaunally on *Rhizophora mangle* prop roots in the Indian River Lagoon, Florida (USA). The major factor controlling adult distributions was transport and recruitment of planktonic larvae as influenced by water flow through the habitat. Physical factors also contributed to community structure, but on much larger scales. Farnsworth and Ellison (1996a) reached similar conclusions for *R. mangle* root communities in Belize, Central America. To better understand larval recruitment processes and their importance to the structure and dynamics of mangrove marine communities, Wolanski and Sarsenski (1997) have developed computer models that simulate the dispersal of fish and shrimp larvae through mangrove habitats.

5.2. Sponges and Ascidians

Because they are often surrounded by muddy or sandy sediments, submerged mangroves roots, trunks, and branches are islands of habitat that attract rich epifaunal communities. The epifauna may include a diverse array of invertebrate groups including sponges, hydroids, anemones, polychaetes, bivalves, barnacles, bryozoans, and ascidians. Encrusting sponges and ascidians are particularly important in many environments and may be specially adapted to life there. A number of ascidian and sponge species are largely restricted to mangrove surfaces (Goodbody, 1993, 1994, 1996; Bingham and Young 1991a; de Weerd *et al.*, 1991) and epifaunal species that do occur in other habitats may show distinctly different growth forms when they are attached to mangrove roots (Swearingen and Pawlik, 1998).

As with mangrove bacterial, fungal, and algal communities the invertebrate epifauna can show distinct distributional patterns correlated with desiccation, wave action, temperature and salinity. Rützler (1995) described vertical zonation of sponges on the prop roots of *Rhizophora mangle* in Belize. Differential desiccation tolerance produced the

zonation, with the most resistant species occurring higher on the roots. Farnsworth and Ellison (1996a) found a particularly rich ascidian epifauna on mangroves in leeward areas of another Belizian mangal.

Epifaunal organisms may play important roles in the structure and function of the mangal. Sponges, for example, may be food resources for other invertebrates and fish. Many sponges have anti-predator defenses including siliceous or calcareous spicules and noxious or toxic chemicals (McClintock *et al.*, 1997). However, mangrove species are generally not as well defended chemically as sponges from reef habitats (Pawlik *et al.*, 1995; Dunlap and Pawlik, 1996). Surprisingly, the palatable species also seem to lack any particular structural or nutritional features that would discourage predators (Swearingen and Pawlik, 1998). In light of this vulnerability, the mangrove habitat itself may, to some extent, be a refuge for less protected species. Species here may also rely on faster growth or greater reproductive output to compensate for predation losses (Chanas and Pawlik, 1995). In contrast to the sponges, some of the mangrove ascidians may have unusual chemicals that are potent feeding deterrents (Vervoort *et al.*, 1997).

Mangrove sponges may also lack the allelochemicals that protect them from overgrowth by other species in space-limited coral environments. Bingham and Young (1991b) tested 8 sponges commonly found on submerged roots of *Rhizophora mangle* in the Indian River, Florida, the Florida Keys, and Belize, Central America. None of the sponges appeared to use allelochemicals to reduce settlement or survival of potential competitors. In fact, several epifaunal invertebrate species recruited more heavily in the presence of the sponges.

Despite a seeming lower level of anti-predator and anti-competitor chemicals in mangal than in coral reef communities, epifauna invertebrates in the habitat may still be sources for interesting, and valuable, compounds. *Ecteinascidia turbinata*, for instance, is a colonial ascidian that grows primarily on the submerged prop roots of *Rhizophora mangle* in many areas of the Caribbean. It was recently discovered that *E. turbinata* produces compounds (ecteinascidins, Figure 7) that show strong activity against a variety of carcinomas, melanomas, and lymphomas (Rinehart *et al.*, 1990; Wright *et al.*, 1990, Sakai *et al.*, 1992). This discovery has led to large scale collection of this species for extraction, isolation, purification and testing of the compounds. Depending on the method used, these collections adversely affect the wild populations (in addition to damaging the mangrove trees on which they grow; Pain, 1996). Long distance dispersal of *E. turbinata* appears to depend on rafting of adult colonies; larval dispersal is highly localized. Collection techniques that damage the mangroves or remove large patches of the population, therefore, could have severe consequences of this species (Bingham and Young, 1991a).

The close association of invertebrate epifauna and mangroves may have led to mutualisms between them. For example, sponges and ascidians may protect the mangroves on which they grow. Ellison and Farnsworth (1990, 1992) found that epifaunal

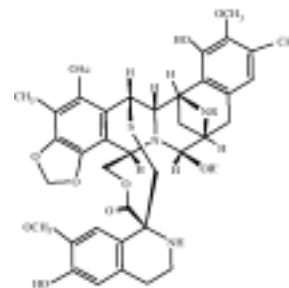


Figure 7. Bioactive compound (ecteinascidin) extracted from the mangrove ascidian *Ecteinascidia turbinata*. The ecteinascidins have shown strong *in vivo* activity against a variety of cancer cells.

sponges and ascidians decreased the amount of damage wood-boring isopods did to the roots of *Rhizophora mangle*. Roots without the sponge/ascidian cover showed significantly more damage and 55% lower growth. In estuarine regions where physical conditions prevented establishment of epifaunal sponges and ascidians, nearly 100% of the *R. mangle* roots were damaged by the isopods.

The invertebrate/mangrove mutualism may also take the form of a symbiotic nutrient exchange. Sponges attached to submerged roots of *Rhizophora mangle* induce the roots to produce fine rootlets that penetrate and grow throughout the sponge tissue. Measurements indicate that the roots obtain dissolved inorganic nitrogen from the sponges. The sponges, in turn, obtain carbon from the roots. Ellison *et al.* (1996) experimentally transplanted sponges to bare *R. mangle* roots in a Belizean mangrove habitat. Within 4 weeks, adventitious rootlets had appeared over the surface of the root. The sponges attached to the roots grew 1.4 – 10 times faster than did control sponges attached to PVC pipes in the same habitat. Miller-Way and Twilley (1999) suggest that nitrogen-fixing bacteria living symbiotically with *Ulosa rutzleri* and *Lissodendoryx isodictyalis* on mangrove roots release significant amounts of NO_3 to surrounding waters.

The epifaunal communities on mangrove roots may show strong fluctuations. In the Florida Keys, USA, *Rhizophora mangle* root communities change dramatically over short time intervals (1-2 months, Figure 8). Physical disturbance from tidal flows, species-specific predation and fragmentation of the dominant sponges produce the variability. The perturbations prevent competitive processes from producing the more stable equilibrium assemblages seen in some other mangrove epifaunal communities (Bingham and Young, 1995).

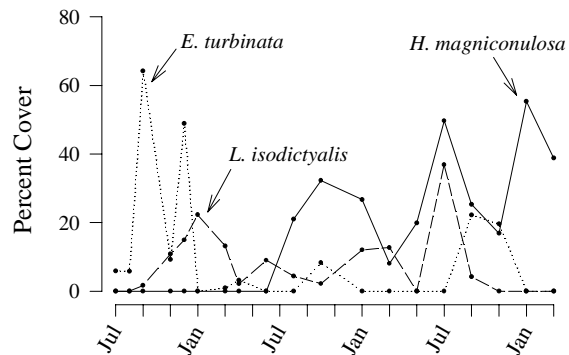


Figure 8. Fluctuations in cover of two epifaunal sponges (*Lissodendoryx isodictyalis* and *Haliclona magniconulosa*) and a colonial ascidian (*Ecteinascidia turbinata*) on submerged *Rhizophora mangle* prop root (Florida Keys, USA). Photographic measurements were made at 2-3 month intervals for 32 months (after Bingham & Young, 1995).

5.3. Epibenthos, infauna, and meiofauna

The muddy or sandy sediments of the mangal may be home to a variety of epibenthic, infaunal, and meiofaunal invertebrates. The composition and importance of these communities varies enormously from habitat to habitat depending on the sediment characteristics of the individual mangal.

Mangrove sediments generally support higher densities of benthic organisms than do adjacent non-vegetated sediments (Edgar, 1990, Sasekumar and Chong, 1998). Sheridan (1997) identified over 300 benthic taxa in red mangrove (*Rhizophora mangle*), seagrass and mud habitats in southern Florida. Densities, which ranged from 22,591 - 52,914 individuals $\cdot \text{m}^{-2}$ were always higher in the red mangrove peat than in the other habitats. The fauna was composed primarily of annelids and tanaids with maximum densities of 31,388 and 35,127 individuals $\cdot \text{m}^{-2}$ respectively (Sheridan, 1997).

The epibenthos may include hydrozoans. For instance, the hydrozoan *Vallentinia gabriellae*, which feeds on a variety of zooplankters, is common in some south Floridan mangals (Rey *et al.*, 1992). Calder (1991) found that hydroids in a Belizean mangal respond to water flow. The hydroid fauna is richer and more diverse in areas exposed to waves and tidal currents than in sheltered, still-water areas of the mangal. Polychaetes are the dominant macrobenthos in mangrove flats at Inhaca Island, Mozambique where their distributions are controlled by sediment grain size, salinity and ground water (Guerreiro *et al.*, 1996). Oligochaetes may also be abundant in shallow mangal waters. Diaz and Erseus (1994) found one oligochaete family, the Limnodriloidinae, entirely restricted to mangrove muds.

The most successful benthic species in the mangal are those that can adapt to the salinity and temperature stresses that are characteristic of these environments (Ferraris *et al.*, 1994). Extreme fluctuations in these physical features may prevent colonization by benthic species. For example, Lana *et al.* (1997) found that benthic infaunal abundance and diversity were significantly lower in mangrove sites than in more seaward zones of Paranagua Bay, Brazil.

Mangrove meiofaunal communities may also include annelids (especially oligochaetes) and crustaceans. However, they are generally dominated by nematodes. As a result, nematodes have been better studied than any other members of the mangrove meiofauna (Olafsson, 1996). In the dry tropical mangroves of northeastern Queensland, nematode abundances may reach 2117 individuals $\cdot \text{cm}^{-2}$ with seasonal fluctuations contributing to variability in the community (Alongi, 1990a). The study of mangrove meiofaunal communities has led to descriptions of several new nematode species. These include *Parapinnanema ritae*, *P. alii* and *P. rhipsoides* from Guadeloupe (Gourbault and Vincx, 1994); *Chromaspirina okemwai*, *Pseudochromadora interdigitatum* and *Eubostrichus africanus* from *Ceriops* sediments along the Belgian coast of the North Sea (Muthumbi *et al.*, 1995); and *Papillonema danieli* and *Papillonema clavatum* from *Ceriops* sediments of Kenya (Verschelde *et al.*, 1995).

The distribution of the nematode fauna has been intensively studied in a temperate mangrove mudflat of southeastern Australia (Nicholas *et al.*, 1991). Approximately 85% of the nematodes occurred in the top layer of the soft mud, but 5-7 species penetrated the deeper anoxic muds down to 10 cm. Abundances were affected by tidal zonation. Nematode biomass was approximately 888 mg dry wt m^{-2} ($\approx 383 \text{ mg C m}^{-2}$) in the low tide zone but was only 19 mg dry wt m^{-2} ($\approx 8 \text{ mg C m}^{-2}$) in the upper tide zone.

Nematode populations may vary with food content, grain size and organic content of the mangrove sediment (Hodda, 1990). The meiofaunal community is undoubtedly part of the detrital food web. Tietjen and Alongi (1990) found a significant correlation between biomass of *Avicennia marina* litter, bacterial abundance, and nematode abundance. The relationship disappears as detritus ages. However, a direct role of nematodes in organic matter cycling could not be demonstrated experimentally. Nor does the meiobenthic community appear to have much direct predator/prey interactions with the epibenthos. Schrijvers *et al.* (1995, 1997) showed this experimentally through exclusions of meiobenthic species from Kenyan *Ceriops tagal* and *Avicennia marina* habitats. There is still much to learn about the role of these less-easily studied members of the mangal community.

5.4. Prawns, shrimp and other crustaceans

5.4.1. Prawns and shrimp

Mangrove habitats and prawn/shrimp populations are tightly linked in many regions. Analyses of commercial prawn catches have repeatedly shown strong correlations between abundance and biomass of prawns and extent of the surrounding mangrove areas (Sasekumar *et al.*, 1992; Kathiresan *et al.*, 1994c; Vance *et al.*, 1996b).

Robertson and Blaber (1992) proposed three explanations for this relationship. First, organic detritus exported directly from the mangroves provides food and habitat for juvenile penaeids in offshore areas (Daniel and Robertson, 1990). Second, the waters in the numerous channels and small creeks of the mangrove receive high levels of terrestrial runoff, rich in nutrients. Export of these nutrients (controlled largely by groundwater flows; Mazda *et al.*, 1990b; Ovalle *et al.*, 1990) contribute to productivity. This productivity, in turn, may support offshore penaeid populations. Third, the mangrove waterways directly serve as nursery grounds for juvenile penaeids that move offshore and enter the commercial fishery as they mature. This hypothesis is strongly supported by surveys of larval, postlarval and juvenile penaeids in nearshore habitats (Vance *et al.*, 1990, 1996b, 1997; Mohan *et al.*, 1997; Primavera, 1998; Rajendran and Kathiresan, 1999a).

Sheridan (1992) found low shrimp abundance among *Rhizophora mangle* prop roots in Rookery Bay, Florida. Only 4% of the collected animals were in the roots, compared with 74% in adjacent seagrass beds. This, however, seems to be unusual, and numbers and biomass of prawns and shrimp are generally higher in mangrove areas than in adjacent nearshore habitats (Chong *et al.*, 1990; Sasekumar *et al.*, 1992). Study of these diverse shrimp communities is revealing new species (Miya, 1991; Bruce, 1991).

In a six-year study, Vance *et al.* (1997) determined the primary factors controlling juvenile prawn abundance in mangroves to be larval supply and postlarval settlement. The young of many shrimp species appear to use the mangal. Juveniles of eight penaeid prawn species (primarily *Metapenaeus monoceras* and *Penaeus indicus*) are common in the Pichavaram mangroves. Catches of the juveniles in core mangrove areas are greater than in open waters (Rajendran, 1997). In Oman, R. Mohan and Siddeek (1996) similarly found abundant postlarval and juvenile shrimp in the detritus-rich, muddy substrates of a mangal they studied. Distributions of the juveniles within the mangal are strongly influenced by salinity; densities are highest at intermediate salinities (R, Mohan *et al.*, 1995).

As the shrimp grow, they may eventually leave the mangal. In the Matang mangroves of Malaysia, Chong *et al.* (1994) measured prawn densities of 4092 individuals $\cdot \text{ha}^{-1}$ in the mangal but only 2668 individuals $\cdot \text{ha}^{-1}$ in the adjacent mudflats. However, biomass was approximately the same in both areas, suggesting that larger individuals move out of the mangal. Using size distribution data, Rajendran and Kathiresan (1999a), concluded that postlarvae of prawns recruit into the Pichavaram mangroves in the postmonsoon period; subadults then leave during the premonsoon and monsoon periods. The annual offshore commercial catch of adult *P. merguensis* is significantly correlated with number of prawn emigrating from the estuary during the wet season (Vance *et al.*, 1997). There is also a strong positive relationship between rainfall and subsequent offshore

commercial catch of adult shrimp (Staples *et al.*, 1995), probably due to flushing from the mangrove habitat as a result of heavy rains.

Although the mangal may be a sink for settlement and early growth of shrimp and prawns, it may also be a source for larvae that are transported to other habitats. Mangrove waters in the Klang Strait of Malaysia may collect 65 billion penaeid prawn larvae before their annual transport and settlement in coastal nursery grounds. Tidal currents and lateral trapping in mangrove-lined channels cause this aggregation (Chong *et al.*, 1996).

There may be a number of benefits for juvenile shrimp and prawns living in mangrove habitats. The habitat is complex and provides a variety of niches within which species can exist. For example, in the mangroves of Muthupet, India, *Penaeus indicus*, *P. merguensis* and *Metapenaeus dobsoni* show clear preference for detritus-rich muddy substrates in which they feed. In contrast, *P. monodon* shows no such preference. Other shrimp feed directly on the mangroves. Cholesterol extracted from *Rhizophora* leaves promotes growth of juvenile *Penaeus indicus* and increases their conversion efficiency (Ramesh and Kathiresan, 1992). However, not all mangrove products are beneficial. *Excoecaria agallocha* latex is toxic to larvae of the freshwater prawn *Macrobrachium lamarrei* (Krishnamoorthy *et al.*, 1995) and to penaeid prawns (Kathiresan and Thangam, 1987).

The mangrove forest, with its small creeks and channels, its hanging roots, and soft substrates may also provide refuge from predators. Prawns in these habitats tend to be most active near high tide and at night (Stoner, 1991; Vance, 1992; Vance and Staples, 1992; Rajendran, 1997). This presumably allows them to forage when food is most accessible and predation danger is lowest.

Some mangrove shrimp may avoid predation by burrowing in the muddy sediments. Primavera and Leбата (1995) found that *Metapenaeus* were particularly active burrowers. *Penaeus monodon* is also a burrower, but burrowing activity is size dependent and increases as the animals grow. Shrimp may also escape predators by migrating with the tides. Vance *et al.* (1996a) observed that juvenile *P. merguensis* are very mobile, moving substantial distances into the mangrove forest at high tide. An extreme example of shrimp migration is the semi-terrestrial *Merguia oligodon*, a species common in some Kenyan mangroves. This species lives among the aerial roots of *Rhizophora mucronata*. It is active at night, grazes on mangrove bark, and climbs mangrove roots and trunks up to 80 cm above the ground (Vannini and Oluoch, 1993). Vance *et al.* (1997) have used a stake-netting method to study distribution and movements of prawn in intertidal mangrove forests. This technique shows promise as a way to provide better information about the shrimp and prawns and their roles within the mangal.

5.4.2. Other Crustaceans

While shrimp and prawns do not generally harm the mangroves, and may actually be beneficial (e.g., through bioturbation of muddy sediments), other crustaceans do significant damage. For example, barnacles can grow abundantly on mangrove roots and pneumatophores (Foster, 1982; Anderson *et al.*, 1988; Bayliss, 1993; Ross and Underwood, 1997). *Balanus amphitrite* and other fouling organisms, for instance, kill 42.5% of the mangrove seedlings in Goa, India (Santhakumaran and Sawant, 1994). Some species of barnacles belonging to the genera *Euraphia*, *Elminius* and *Hexaminus* appear to prefer mangroves over other substrates. The settling barnacle larvae may even show

strong preferences for mangrove species and discriminate among parts of the trees. The barnacle densities are controlled by the physical environment of the mangal (primarily desiccation and temperature). Populations are greater on seaward than on landward areas of the forest. Densities are also greater on lower surfaces than on upper surfaces of trunks and leaves (Ross and Underwood, 1997). In some mangrove areas barnacle numbers are also greater in the mid-intertidal than in the upper or lower intertidal zones (Kathiresan *et al.*, 2000), and the species show marked zonation (Bayliss, 1993), with chthamalids occurring above *Balanus amphitrite*. The recruitment of barnacles, and other sessile invertebrates within the mangal is largely controlled by larval abundance, tidal currents, duration of larval life and density of the adult populations (Bingham, 1992; Farnsworth and Ellison, 1995; Young, 1995). It was at one time thought that the selection by barnacles of their mangrove habitat was so extreme that one species of *Hexaminius* (*H. foliorum*) occurred only on twigs and leaves, while another (*H. popeiana*) was restricted to the bark (Anderson *et al.*, 1988; Ross and Underwood, 1997). Recent studies indicate that phenotypic variation is responsible, and that the leaf-occurring form is comparable morphologically and by DNA to the form on mangrove bark (Ross, 1996; Ross and Pannacciulli, personal communication). This situation can be compared with the changes in form and colour seen in the bivalve *Enigmonia aenigmatica* and the snail *Littoraria pallescens* when inhabiting different parts of the mangrove, trees as noted on page 81.

Burrowing isopods (e.g., *Sphaeroma terebrans* and *S. peruvianum*) also do tremendous damage to mangroves in many regions of the Atlantic, the Caribbean, and the eastern Pacific. Numerous juveniles and adults can be found living inside a single root or stem. Their burrowing can significantly affect root growth and development (Ellison and Farnsworth, 1990; Santhakumari, 1991).

Other crustaceans use mangrove waters temporarily during certain phases of their life history. One of the better known is the Caribbean spiny lobster (*Panulirus argus*), juveniles of which use the mangroves as nursery habitat (Monterrosa, 1991). Like the shrimp and prawns, however, the lobsters migrate out of the mangal as they grow. Adult lobsters remain in the mangal only if their preferred habitat (under coral heads) is unavailable (Acosta and Butler, 1997). Migration to other habitats may reflect a search for better food resources.

5.5. Crabs

Crabs are characteristic members of the invertebrate mangrove fauna and have received much attention. Some indication of the diverse array of mangrove-associated crabs can be found in annotated checklists from India (Sethuramalingam and Ajmal Khan, 1991), Malaysia and Singapore (C.G.S. Tan and Ng, 1994) and Brazil (Vergara-Filho *et al.*, 1997).

Within the complex mangrove environment, crabs fill a variety of niches. For some species, the relationship with mangroves is obligatory; they depend directly on the mangroves for survival (Vergara-Filho *et al.*, 1997). Others simply have ranges that overlap the mangal. The mud crab *Scylla serrata* inhabits seagrass and algal beds in the mangroves of Pichavaram, south India (Chandrasekaran and Natarajan, 1994). Floating leaves in a Costa Rican mangal harbor a unique community dominated by *Uca* crabs (77.8% of all organisms counted; Wehrmann and Dittel, 1990). Perhaps one of the most striking associations is seen with the hermit crab *Clibanarius laevimanus*. Individuals of

this species climb the mangrove roots and rest on them during the entire low water period, forming dense clusters of up to 5,000 individuals (Gherardi *et al.*, 1991; Gherardi and Vannini, 1993). Gherardi *et al.* (1994) have studied size, sex and shell characteristics of this unique mangal species.

Mangrove crabs are morphologically, physiologically, and behaviorally well-adapted to their environment. For example, the semaphore crab, *Heloecius cordiformis*, is active at low tide when it is completely exposed to air. Its branchial chambers are modified for respiration both in the air and under water (Maitland, 1990). A number of other crab species (particularly in the Family Grapsidae) live directly on the mangrove trees. Species in this group generally have a square, flattened carapace, a relative shortening of the dactylus on the walking legs and a lengthening of the propodus (Vannini *et al.*, 1997a). These structural specializations appear to be adaptations for their tree-dwelling existence.

Crabs living in the mangal must adjust to significant temperature and salinity fluctuations. Some, like the grapsid *Metopograpsus messor*, retreat to burrows where temperatures are less variable and consistently lower than the sediment or air temperatures. When it is out of the burrow, *M. messor* uses evaporative cooling to keep its body temperature lower than the surrounding air (Eshky *et al.*, 1995).

Other crabs have adopted a nocturnal lifestyle, possibly to escape high temperatures and/or predators (Micheli *et al.*, 1991). The hermit crabs *Coenobita rugosus* and *Coenobita cavipes* are active 24 hours a day but are most active when they are among the mangrove roots. Barnes (1997) suggests that they do this because wind speeds (and desiccation potential) are lower there. Desiccation can significantly affect ion balances and mangrove crabs are physiologically adapted to resist major changes. In *Ucides cordatus* and *Carcinus maenas* total Na⁺ efflux is markedly reduced during emersion. The reduction in ion and water loss results from decreased urine output (Harris *et al.*, 1993). When *U. cordatus* is placed in low salinity water, active sodium uptake increases 4-5 fold (Harris and Santos, 1993).

Crabs in mangrove habitats show distinct distributional patterns related to substrate characteristics, salinity, degree of tidal inundation, and wave exposure. In the Indian Sunderbans, these conditions produce a vertical zonation of crab species (Chakraborty and Choudhury, 1992, Kathiresan *et al.*, 2000). Machiwa and Hallberg (1995) also found a horizontal zonation of crabs in East Africa. The terrestrial edge of the mangal was occupied by grapsids while mixed associations of ocy podids dominated the open areas of sand and mud.

Different crab species respond differently to disturbance and this affects species distributions. In Kenya, *Sesarma guttatum* prefers shaded habitats and is most common in regions with an established mangrove canopy. In contrast, *Uca urvillei* and *Microphthalmus depressus* prefer clear-cut areas. In the more landward *Avicennia* zone, the species composition of the crab community remains constant whether the vegetation is intact or clear-cut (Ruwa, 1997).

Mangrove crabs can be divided into distinct guilds based on their feeding mode. Some species (e.g., *Uca* and *Macrophthalmus* spp.) are detritivores that extract their food from the sediments while others (e.g., the portunid *Scylla serrata*) are opportunistic scavengers (Micheli *et al.*, 1991). There are also a number of active predators. The swimming portunid *Thalamita crenata* lives on the extreme seaward fringe of the

mangrove swamp where it preys heavily on bivalves and slow-moving crustaceans (Cannicci *et al.*, 1996c). This species is active during high tides, but only when the water is between 10 and 30 cm deep, suggesting that their foraging behavior is controlled by hydrostatic pressure changes associated with tidal flux (Vezzosi *et al.*, 1995).

Epixanthus denatus, which is very abundant in mangrove creeks along the Kenyan coast, is another active predator. It forms dens among the mangrove roots and feeds on almost any slow-moving invertebrate (including other crabs) that comes within a 3-m radius. Their intense predation may be responsible for the climbing behaviour of many potential prey species (Cannicci *et al.*, 1998). Crabs in the mangrove face significant predation risks and may show specific anti-predator adaptations. Diaz *et al.* (1995) suggest that postlarval and juvenile crabs may avoid predation by responding to specific light cues. *Aratus pisonii*, which lives among roots and branches, is attracted to narrow dark rectangles but avoids large dark rectangles. The authors speculate that the narrow rectangles resemble roots that represent refuges while the larger rectangles indicate predators. In contrast, *Chlorodiella longimana*, a subtidal species, moves toward all dark rectangles regardless of their size.

In addition to scavenger and predator guilds, there is a guild of herbivorous mangrove crabs that feed directly on mangrove litter. In Ao Nam Bor, Thailand, up to 82% of the diet of sesarimid crabs consists of mangrove material (Poovachiranon and Tantichodok, 1991). A number of these herbivores show clear feeding preferences. For example, *Sesarma meinertii* generally prefers *Bruguiera gymnorrhiza* to *Avicennia marina* leaves (Micheli *et al.*, 1991). However, Steinke *et al.* (1993a) showed that the age of the litter was more important than its source in determining preference. The crabs chose yellow *B. gymnorrhiza* and *A. marina* leaves over green leaves of either species. *Sesarma messa* and *S. smithii* both prefer decaying leaves to those that are simply senescent, irrespective of leaf species. *Neosarmatium meinerti* does not choose among mangrove species but does, however, strongly prefer fresh leaves. Its heavy, non-selective feeding on mangrove seedlings and propagules could make it a significant threat to afforestation efforts (Dahdouh-Guebas *et al.*, 1997).

It is unclear what factors are responsible for these feeding preferences. Micheli (1993a, b) found that preferences were not affected by tannins, water content, % organics, C:N ratio, or leaf toughness. Many of the herbivorous crabs store the leaves in their burrows for some time. However, the nutritional value of the leaves does not increase during the time they are stored, indicating that the crabs are simply storing the leaves and not gardening them to encourage bacterial or fungal growth (Micheli, 1993a, b). Given that the mangrove leaves, in general, have low nutritional value and the crabs do not have a mechanism to promote bacterial or fungal growth, it may be very important for them to get the maximum food value out of the leaves they eat. This may contribute to their specific preferences.

Although mangrove leaves are not particularly nutritious, they do produce sufficient energy to influence survival, growth and reproduction of the crabs and it seems reasonable to assume that is a sufficient selective force to produce feeding preferences. Survival of two mangrove crabs, *Chiromanthes bidens* and *Parasesarma plicata*, is directly related to litter type. They do best when fed brown *Avicennia marina* leaves, followed by brown *Kandelia candel*, yellow *A. marina*, and finally, yellow *K. candel* (Kwok and Lee, 1995). Mangroves at different sites in Venezuela produce leaves with

different nutritional value. The crabs are smaller in sites where the stunted trees produce leaves of low nutritional value (Conde and Diaz, 1992; Conde *et al.*, 1995).

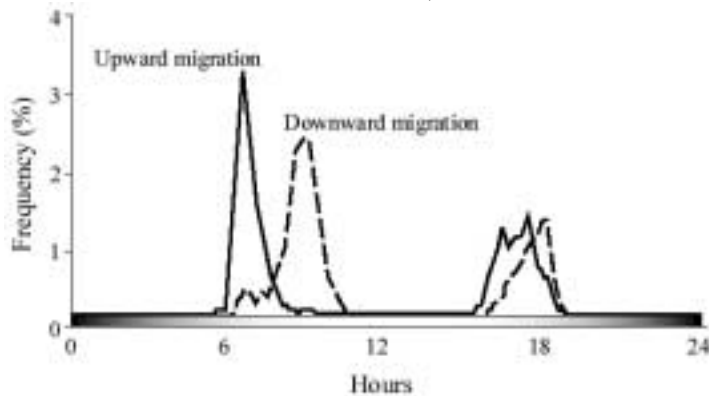


Figure 9. Average daily migration patterns of the crab *Sesarma leptosoma* into and out of the mangrove canopy (after Vannini and Ruwa, 1994).

In the morning, moves up into the canopy to feed on fresh leaves. Increasing temperatures and the danger of desiccation eventually drive the crabs down to the bases of the trees where they spend the hottest hours of the day. In the evening, they return to the canopy for another short feeding period (Figure 9; Vannini and Ruwa, 1994; Vannini *et al.*, 1997b). The crabs tend to return to the same feeding spot each time they visit the canopy and even follow the same path to get there (Figure 10). Cannicci *et al.* (1996b) suggest that site fidelity is important as it takes the crabs near leaf buds where they can find water trapped among the scales. Reduced light delays the migration. It is unclear why migration of this intertidal animal is regulated by light instead of tides (Vannini *et al.*, 1995).

Feeding by crabs hastens composting of mangrove material and contributes to cycling of nutrients through the mangal (Lee, 1998). In the Gazi Bay, Kenya, crabs (along with large snails) process over 18% of the fallen litter (Slim *et al.*, 1997). The large mangrove grapsid *Sesarma meinertii* consumes *Avicennia marina* leaves at a rate of $0.78 \text{ g m}^{-2} \text{ d}^{-1}$, accounting for 43.58% of the leaf-fall in a warm temperate mangrove swamp in southern Africa (Emmerson and McGwynne, 1992).

Digging by crabs, in conjunction with other benthic fauna like nematodes, polychaetes, and mudskippers (Kristensen *et al.*, 1995) can also have a profound effect on

Some of the herbivorous crabs do not simply graze on fallen leaves. Some actively forage in the canopy of the tree. In the mangrove swamps of East Africa, *Sesarma leptosoma* is an active climber that can reach the tops of the tallest trees. It never descends into the water nor venture out on the mud at low tide. This behaviour provides protection from predators (Cannicci *et al.*, 1996a). It spends most of the night among the mangrove roots but, in the

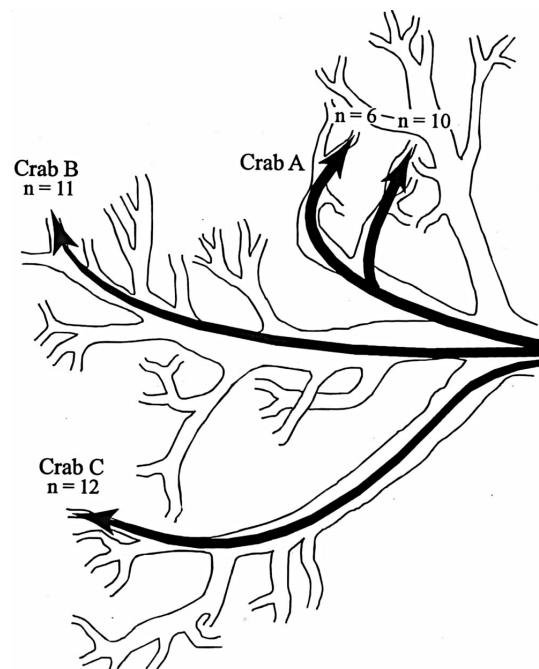


Figure 10. Branch fidelity in the mangrove crab *Sesarma leptosoma*. Arrows indicate movement of three individuals. Individuals B and C always returned to the same branch in the canopy and even followed the same path to get there. Individual A returned to one of 2 branches (after Cannicci *et al.*, 1996b).

nutrient cycling and the physical and chemical environment of the mangal (Lee, 1998). Burrows enhance aeration, facilitate drainage of the soils, and promote nutrient exchange between the sediments and the overlaying tidal waters (Ruwa, 1990). Crab burrows generally have two or more openings and may form extensive labyrinths of interconnected tunnels. Using dye injections and flow measurements, Ridd (1996) estimated that, in a 1 km² area of a North Queensland mangal, 1,000 to 10,000 m³ of water move through crab burrows on each tidal cycle. T.J. Smith *et al.* (1991) removed burrowing crabs from a mangal and observed significant increases in soil sulfide and ammonium levels relative to control sites. These chemical changes led to decreased mangrove growth and reproduction.

5.6. Insects

Insects constitute a significant portion of the fauna in many mangrove communities. They may be permanent residents of the mangal or only transient visitors. In either case, they often play important roles in the ecology of the system and contribute to the unique character of these habitats. Surveys of mangrove insects are revealing complex assemblages of species filling a wide variety of niches. For example, Veenakumari *et al.* (1997) found 276 insect species in the mangals of Andaman and Nicobar Islands of India; 197 of these were herbivores, 43 were parasites and 36 were predators. Similar levels of diversity and abundance have been found in the insect fauna of Thailand's Ranong mangroves (Murphy, 1990a). Many of the insects reported in mangals are only temporary visitors; their ranges included many other habitat types. As a result, they provide linkages between the mangal and other environments (Ananda Rao *et al.*, 1998).

Terrestrial organisms living in mangrove environments are faced with harsh conditions of strong sunlight, high temperatures and desiccation. Many of the insects (and other terrestrial arthropods) avoid these conditions by emerging only at night, or by living entirely within the plants. In the mangals of Belize, wood-boring moths and beetles excavate tunnels through the mangroves. The tunnels then become home to more than 70 other species of ants, spiders, mites, moths, roaches, termites, and scorpions (Rützler and Feller, 1996; Feller and Mathis, 1997). A number of organisms (including isopods, amphipods, myriapods, and spiders in addition to insects) escape high temperatures and desiccation by living in the intertidal portions of the mangal. During periods of high tide, these organisms retreat to air-filled cavities where they remain until they are again exposed by the falling water (Murphy, 1990b).

Herbivorous insects can cause significant damage to the mangroves, attacking leaves and boring through the wood. Seedlings may be particularly vulnerable to attack and are strongly affected by proximity to adult trees. In a Belizean mangal, seedlings growing under the intact adult

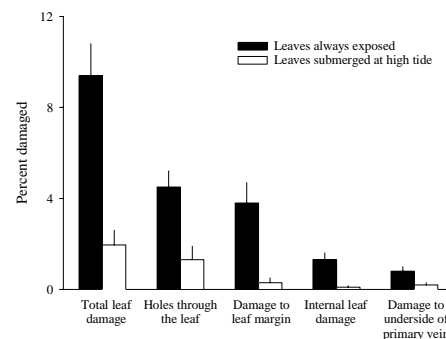


Figure 11. Effect of tidal submergence on *Laguncularia racemosa* leaf damage (Guanacaste Province, Costa Rica). Submergence limits access by terrestrial herbivores and may also cause chemical and structural changes in the foliage. Standard errors are shown. Statistical analysis showed that exposed leaves had significantly more damage in all cases (after Stowe, 1995).

canopy suffered twice as much herbivore damage as seedlings in areas without an established canopy (Farnsworth and Ellison, 1991). Immersion in seawater may help protect the trees. Portions of the mangrove canopy that are submerged by tidal waters suffer significantly less herbivore damage than those that remain exposed (Stowe, 1995; Figure 11).

Recent records of insects in mangrove include 28 species of dragonflies in India (Mitra, 1992), a water strider, *Mesovelia polhemusi* in Belize (Spangler, 1990), an unusual psyllid, *Telmapsylla*, in Florida and Costa Rica (Hodkinson, 1992), and termites, *Nasutitermes nigriceps*, in Jamaica (Clarke and Garraway, 1994). However, some of the more important and best studied mangrove insects are bees, ants, and mosquitoes. Honey bees produce significant quantities of honey from the mangroves of India, Bangladesh, the Caribbean and southwest Florida. The honey is an important food resource for humans in some regions (e.g., Padrón *et al.*, 1993). In India, the dominant bee species (*Apis dorsata*), may travel hundreds of miles to forage in the mangrove forests during periods of peak blooming (March and July). It builds honeycombs on several mangrove species, but prefers *Excoecaria* (Krishnamurthy, 1990). In contrast, the same bee species in southern Vietnam forages on mangrove vegetation primarily during the rainy season and rarely builds combs (Crane *et al.*, 1993).

Twenty-two ant species are known from Brazilian mangrove habitats. *Camponotus* and *Solenopsis* are most common genera (Cortes-Lopes *et al.*, 1996). Clay and Andersen (1996) found 16 ant species in an Australian mangal. Two of these, both in the genus *Polyrhachis*, are apparently restricted to this habitat. In northern Australia, *Polyrhachis sokolova* nests directly in the soft mud of the mangal (Nielsen, 1997). Adams (1994) studied niche partitioning in four ant species common in Panamanian mangroves. These species partition the mangrove canopy in non-overlapping territories that are maintained through a combination of pheromonal signals and tactile displays.

Holes in the mangrove trees (particularly *Avicennia* species) and crab-burrows provide ideal sites for mosquito breeding (Thangam, 1990). Mosquitoes are ubiquitous in mangrove habitats and may act as vectors for diseases of vertebrates. Populations are often dense and species diversity can be high (eighteen species occur in the Pichavaram mangroves of south India alone; Thangam and Kathiresan, 1993b). Predation by fishes may reduce successful mosquito oviposition. Hence, mosquito populations are lower in sites with high fish densities (Ritchie and Laidlaw-Bell, 1994). Regardless of its composition, any mangrove forest that is flooded by < 14% of the highest daily tide can potentially produce the mosquito *Aedes taeniorhynchus* (Ritchie and Addison, 1992). Addison *et al.* (1992) identified *A. taeniorhynchus* oviposition sites and quantified larval production by locating and counting egg shells.

Mangals tend to be reservoirs for a number of pathogenic viruses including Dengue, Haemorrhage Fever, Bakau and Ketapang. Mosquitoes are the most common vectors for these viruses. However, several families of other diptera associated with faecal contamination in mangroves of Singapore and Malay also contribute to the spread of human disease (Murphy, 1990c).

5.7. Mollusks

Mollusks are found throughout most mangrove habitats. They live on and in the muds, firmly attached to the roots, or forage in the canopy. They occupy a number of

niches and contribute to the ecology of the mangal in important ways. The nature of the molluskan community is strongly influenced by physical conditions. For example, in the mangroves of China, Jiang and Li (1995) found that density and biomass of the mollusks (including 52 species) were consistently highest in the high tide zones and decreased with depth. In addition, species abundance increased with salinity. Such a pattern is likely to be found in other mangals. This sensitivity of mollusks to their physical/chemical environment may make them good bioindicators. Skilleter (1996) has used the composition of the molluskan assemblage to assess the health of urban mangrove forests.

The molluskan fauna in mangrove habitats is composed primarily of bivalves and snails and most study has focused on these groups (e.g., Balasubrahmanyam, 1994). Other mollusk groups (e.g., nudibranchs, chitons, scaphopods) are less obvious and have been the subject of only a few studies (e.g., Sigurdsson, 1991). Much of the work with bivalves and snails has concerned individual species and their specific adaptation to the mangrove environment. For example, Dious and Kasinathan (1994) studied the high desiccation,

salinity, and temperatures tolerances of two pulmonate snails, *Cassidula nucleus* and *Melampus ceylonicus*, from a south Indian mangal. Special conditions in the mangal may result in local adaptation. Crow (1996) compared movement of the snail *Bembicium auratum* in mangrove habitats and on rocky shores. Movement patterns in the mangroves were very different (despite similar distributions). This suggests that models developed in rocky intertidal communities may not be directly applicable to mangrove communities.

Color variability may represent a special adaptation to the mangrove environment or possibly a reaction to the complex chemical defenses of the plants. For example, the leaf-inhabiting mangrove snail, *Littoraria pallescens*, has distinct color morphologies that are sometimes associated with other shell differences. The color variation may reflect predation pressures (Cook, 1990; Cook and Kenyon, 1993).

The unique tree-climbing bivalve, *Enigmonia aenigmatica*, which occurs mostly on *Avicennia* and *Sonneratia* also shows color variation. The shells are normally red to deep purple. However, the shells of individuals attached directly to the mangrove leaves are golden yellow. (Sigurdsson and Sundari, 1990). This enigmatic bivalve is one of the gems of the mangal, and belongs to the Anomiidae, of which most species stay cemented to the substratum. It uses its highly mobile foot to reach the desired level in the mangroves and fastens temporarily with transparent byssus threads (Yonge, 1957; Berry, 1975; 1976)

Other bivalves are adapted to the chemical environment of the mangal. Two corbiculids, *Geloina erosa* and *G. expansa*, from Iriomote Island, Japan, occasionally secrete thin organic sheets on the inner shell. Formation of these sheets may be a response to shell dissolution in the acidic mangal environments; the sheets occur only in specimens that have suffered extensive shell damage (Isaji, 1993, 1995).

Frenkiel *et al.* (1996) reported the bivalve *Lucina pectinata* from muddy mangrove sediments. Like most other lucinids inhabiting sulfidic sediments, including also seagrass beds and salt marshes, this species carries endosymbiotic chemoautotrophic sulfur-oxidising bacteria in the gill, and the blood is rich in haemoglobin (see Somero *et al.*, 1989 and Fisher, 1990 and references therein). These bivalves get their organic matter from the bacteria, but the symbiosis requires proximity to both sulfide and oxygen. It has been suggested that in seagrass beds these bivalves might benefit from the proximity to plant

roots carrying oxygen (Fisher & Hand, 1984); a similar relationship could be suggested for mangrove roots.

Some mollusks are critical to the basic ecology of some mangals. For example, the mangrove snail *Thais kioskiformis* plays a central role in maintaining the function and productivity of mangroves in Costa Rica by “cleaning” their root systems of encrusting barnacles (Koch and Wolff, 1996). Ellison and Farnsworth (1992) measured similar effects in the mangals of Belize. Detritivorous snails (e.g., *Terebralia palustris* in Gazi Bay, Kenya) aid nutrient cycling in the mangal by processing mangrove litter (Slim *et al.*, 1997). Bivalves may contribute significantly to the organic biomass in the habitat and may be a link between phytoplankton communities and higher trophic levels (e.g., Ingole *et al.*, 1994; Deekae and Idoniboye-Obu, 1995).

Researchers have collected detailed information on mangrove oysters, largely because they can be valuable food (e.g., Tack *et al.*, 1992; Ruwa and Polk, 1994). Around Tuticorin, India, mangroves provide ideal conditions for production of edible oysters (*Crassostrea madrasensis*) and oyster beds are an important part of the habitat (Rajapandian *et al.*, 1990). Newkirk and Richards (1991) have found that exposing the spat of *Crassostrea rhizophorae* to air increases growth and enhances the yield of marketable oysters. This response may reflect an adaptation to the tidal regime of their mangrove environment.

Teredinids (shipworms) and pholads are specialized bivalves that burrow through wood. Some species within these groups do extensive damage to mangroves by destroying submerged roots and branches. Seven such species (*Bankia campanellata*, *B. carinata*, *Dicyathifer manni*, *Lyrodus pedicellatus* and *Teredo furcifer*, *Martesia striata* and *M. nari*) live in the Pichavaram mangroves of south India (Sivakumar and Kathiresan, 1996). Morton (1991) recently discovered the first mangrove shipworms in Hong Kong (*Lyrodus singaporeana*). A survey for teredinids in the mangroves of Sao Paulo, Brazil revealed four species (*Nausitora fusticula*, *Bankia fimbriatula*, *B. gouldi* and *B. rochi*). Differences in salinity tolerance affect distributions of these species within the mangal (Lopes and Narchi, 1993).

5.8. Fish

Mangroves have a rich and diverse assemblage of fish (Figure 12), some with commercial value. Other fish species are important links in the mangrove food web. Still others are only temporary residents that spend most of their life history elsewhere. Whatever their role, all are important to the character of the mangal.

Extensive studies of the fish community have been made in Alligator Creek, northeastern Queensland, Australia (Robertson and Duke, 1990a, b); in the Embley River estuary (Blaber *et al.*, 1990 a, b; Salini

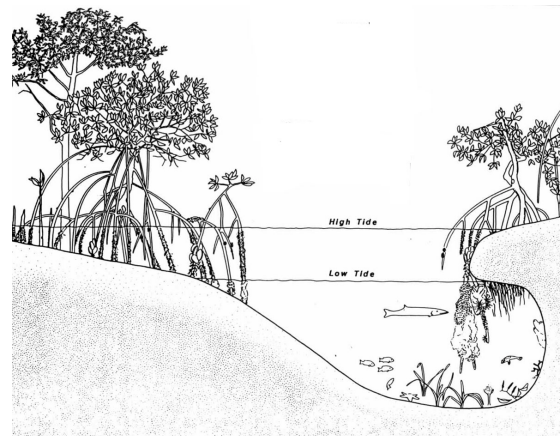


Figure 12. The canopy of *Rhizophora mangle* provides habitat for terrestrial birds and insects. The submerged prop roots provide solid surfaces for attachment of a variety of marine invertebrates. In addition, many fish species use the habitat as a nursery area; the complex tangle of roots provides a refuge from predators (from Rutzler & Feller, 1988).

et al., 1990; Brewer *et al.*, 1991) and the Leanyer Swamp of the Northern Territory; and in the Dampier region of Western Australia (Robertson and Blaber, 1992). The fish fauna is generally very rich; 197 species occur in the mangroves of the Embley River alone. Such high diversity is not restricted to Australian mangals. One hundred and seventeen fish species, in 49 genera, have been recorded in the Matang mangrove waters of Malaysia (Sasekumar *et al.*, 1994; Yap *et al.*, 1994) while Hong and San (1993) reported 260 fish species in the mangroves of Vietnam.

Abundances of the fish can also be very high. In Mexican mangroves, fish biomasses up to 10 g m^{-2} have been recorded (Flores-Verdugo *et al.*, 1990; Arancibia *et al.*, 1993). In Moreton Bay, Australia, the biomass reaches 20 g m^{-2} and ninety-six percent of the biomass (46% percent of the species, 75% of the total fish) is from species important in regional fisheries (Morton, 1990). Robertson and Blaber (1992) measured fish biomasses up to 29 g m^{-2} , with densities up to 161 individuals m^{-2} .

In a Queensland, Australia mangal, sampling suggests that fish regularly move through the habitat with the tidal flows. Density and biomass at high tide were 3.5 individuals m^{-2} and 10.9 g m^{-2} respectively. On the ebb tide, the fish moved to small, shallow creeks where density and biomass reached 31.3 individuals m^{-2} and 29.0 g m^{-2} (Robertson and Duke, 1990a). Fish distributions and abundances may also change on diel or seasonal cycles (Chandrasekaran and Natarajan, 1993). In southwestern Puerto Rico, fish present in the mangal during the day may completely disappear at night (Rooker and Dennis, 1991). Accurately assessing populations of highly mobile species in such a complex environment requires special sampling techniques (Lorenz *et al.*, 1997).

A comparison of catches in various habitats suggests that some species specifically choose to reside in the mangal. For example, the number of fish species in the coastal mangroves of Malaysia (119) exceeds that in all other habitats (inshore waters held 92 species, mudflats held 70 species, and near inshore waters held only 58 species; Chong *et al.*, 1990). A similar result has been found for mangrove habitats in Belize (Sedberry and Carter, 1993). The relative importance of the mangal as habitat, however, may decrease if nearby environments include coral reefs. Acosta (1997) found much higher fish diversity on the reefs of La Parguera, Puerto Rico than in adjacent mangroves.

Fish in mangrove habitats are important predators, consuming amphipods, isopods, shrimp, nematodes, insects, gastropods, other fish, and algae (e.g., Erondy, 1990; Brewer and Warburton, 1992; Williamson *et al.*, 1994; Rooker, 1995; Columbini *et al.*, 1995, 1996). In the Matang mangroves of Malaysia, a suite of fishes feed on shrimp. Croakers (Family Sciaenidae) specialize on penaeid shrimp, consuming about 1.2 kg of shrimp $\text{ha}^{-1} \text{ d}^{-1}$ or about 17% of the total shrimp biomass (Yap *et al.*, 1994). In the Philippines, shrimp predation is significantly higher in bare sand areas than among mangrove pneumatophores (Primavera, 1997).

Feeding activities of mangrove fish can be strongly affected by local conditions. In northeastern Florida Bay, salinity influences feeding behavior of mojarras and gold-spotted killifish. In upstream areas with high salinity variation, the fish eat nutritionally poor algae; in less variable downstream areas, they eat a much better diet of benthic invertebrates. Ley *et al.* (1994) suggested that fish gut content measurements can be a tool to assess environmental conditions and habitat quality. As such, it could be useful in comprehensive monitoring and restoration programs.

Mangals may play a special role as nursery habitat for juvenile fish. The juvenile stages of adults that occur in other habitats (e.g., coral reefs and seagrass beds) may migrate to the refuge on the mangal (Pinto and PUNCHIHEWA, 1996). It is common to find large numbers of larvae and juvenile fish in net samples from mangrove habitats (Dennis, 1992; Tzeng and Wang Yu, 1992; Alvarez-Léon, 1993; Matheson and Gillmore, 1995) and densities of juvenile fish in mangrove habitats are often higher than in adjacent habitats (Robertson and Blaber, 1992). Thollot (1992) found that samples from the mangroves of Southwest Lagoon, New Caledonia held 262 fish species, including the young of 30% of the reef species. Most fish collected in the Lagos Lagoon (Nwadukwe, 1995) and in the mangrove waters of Martinique Island (Louis *et al.*, 1995) were small and sexually immature. In Belize, most of the fish collected from mangrove waters are juveniles of species that live out on the marine reefs as adults (Sedberry and Carter, 1993). Despite this linkage to coral reefs, mangroves also have their own unique fish assemblages. Gill net sampling in a tropical mangrove creek in SW Madagascar produced 60 species of juvenile fish. Only six of those occurred on an adjacent coral reef (Laroche *et al.*, 1997).

Robertson and Blaber (1992) present three explanations for the high density of juvenile fish in mangrove waters. First, mangrove estuaries supply an enormous amount of food appropriate for juvenile fish (Chong *et al.*, 1990). Second, reduced visibility in the turbid mangrove waters may reduce predation by large fish. Third, the structural complexity of the mangroves provides excellent shelter and protection for the juveniles.

There is correlative evidence for the third possibility. In the Solomon Islands, mangrove estuaries clogged with woody debris harbour pomacentrids and some species of Apogonidae and Gobiidae. These groups are largely absent from mangrove estuaries that are clear of the woody material (Blaber and Milton, 1990). Daniel and Robertson (1990) also found a highly significant relationship between amounts of mangrove detritus and fish densities or biomass in mangrove creeks. In Sri Lanka, fishermen increase their catches in lagoons by placing thickets of dead mangrove twigs on the lagoon floor. Netting around these thickets produces much higher catches than in adjacent bare mud areas (Robertson and Blaber, 1992). Experiments with this technique in south India show that *Avicennia* debris works better than *Rhizophora* debris, producing much higher catches (Rajendran, 1997; Rajendran and Kathiresan, 1998). The stilt and prop roots of some mangroves provide a complex environment that would seem to provide an ideal refuge. However, Mullin (1995) found more fish species in the open waters adjacent to *Rhizophora mangle* stands than among the prop roots themselves, but it was unclear why the fish avoided the roots.

While mangroves in general may serve as nursery habitat for many fish species, individual mangals may not. For example, Ley *et al.* (1999) found that mangrove habitats in northeastern Florida Bay did not function as nursery-grounds. The authors suggest that this particular mangrove estuary may be atypical for two reasons: (1) it has no lunar tides and lacks typical tidal circulation, (2) it has little submerged vegetation; and (3) it experiences severe hypersaline conditions. Conditions in this particular environment may be sufficiently stressful to prevent its use by juvenile fish.

Fish living in the mangal must adjust to temporal and spatial variability in physical and chemical conditions, and some species possess specific adaptations to deal with this. For example, the widely distributed hermaphrodite killifish (*Rivulus marmoratus*) is well adapted to mangrove microhabitats (Taylor *et al.*, 1995). Its specializations include an

ability to survive in moist detrital substrates during periods of low water or drought and reproduction by internal self-fertilization (Davis *et al.*, 1995).

Fish without such specific adaptations may respond behaviorally to physical cues that indicate physically or chemically stressful microhabitats. This can lead to distinct distributional patterns (Blaber *et al.*, 1994). For example, Heath *et al.* (1993) demonstrate experimentally that thermal cues affect fish distributions within mangrove ponds. *Cyprinodon* prefers higher temperatures than other fish species tolerate. Temperature differences within the mangal could, therefore, spatially separate fish populations. Fish may also prefer certain areas of the mangal based on the nature of the substrate. Kimani *et al.* (1996) sampled fish populations in an estuarine mangrove bay in Kenya for 12 months. Diversity, density, and biomass were all lower in a silty area than in three other mangrove areas with established seagrass beds.

Hypoxia, which affects plasma osmolality, plasma chloride ion concentration, and hematocrit in fish (Peterson, 1990; Peterson and Gilmore, 1991) can also influence their distributions. For example, juvenile snook (*Centropomus undecimalis*) move toward oxygenated surface waters when deeper waters become anoxic (Peterson and Gilmore, 1991). Habitat degradation can lead to changes in fish distribution. In the Virgin Islands, differences in fish abundance and diversity between degraded and natural mangrove sites are directly related to water quality (Boulon, 1992). The simple installation of culverts creates better water exchange in some mangals, promoting reestablishment of marsh vegetation, and increased fish production (Lin and Beal, 1995).

Mudskippers are a group of unusual amphibious fish (Family Gobiidae: Subfamily Oxudercinae) that are characteristic residents of many mangals. A variety of anatomical, physiological, and behavioral adaptations help them tolerate the stressful mangrove environment (Chew and Ip, 1990; Colombini *et al.*, 1995, 1996; Ikebe and Oishi, 1996, 1997; Ip *et al.*, 1991; Ishimatsu *et al.*, 1999; Ogasawara *et al.*, 1991; reviewed by Clayton, 1993).

Researchers have long believed that one of the primary adaptations of mudskippers is an ability to endure extremely hypoxic conditions. However, recent evidence suggests that this may not be true for all species; many mudskippers are less tolerant of hypoxia than has been assumed. Takeda *et al.* (1999) demonstrated that *Periophthalmodon schlosseri* could recover from post-exercise oxygen debt, but only in air. Furthermore, laboratory experiments demonstrate that *P. schlosseri* may rarely use aquatic gill ventilation at all, apparently preferring aerial respiration (Aguilar *et al.*, in press). A limited capacity for aquatic oxygen uptake has also been proposed for mudskippers in the genus *Periophthalmus*. Aguilar (2000) suggests that *Periophthalmus* spp. lack physiological mechanisms to tolerate hypoxia and instead have a range of adaptive behaviors that allow them to avoid low-oxygen conditions.

A unique behavioral mechanism may enable some species to completely escape hypoxia. A number of mudskippers dig extensive burrows into anoxic mangrove sediments and might be expected to experience extremely hypoxic conditions, particularly during periods of low tide. Ishimatsu *et al.* (1998) found that *Periophthalmodon schlosseri*, for example, creates burrows as deep as 125 cm. However, the burrows have special excavated chambers that hold pockets of air. The *P. schlosseri* fill the pockets by gulping air at the surface, carrying it down to the chamber and releasing it there. The fish, therefore, escape rather than tolerate hypoxia. Such burrowing and air trapping,

particularly where mudskipper populations are dense, may significantly affect oxygenation and chemistry of the mangrove sediments (Kristensen *et al.*, 1995).

5.9. Amphibians and Reptiles

Reptiles, including crocodiles, alligators, lizards, snakes and turtles live in many mangroves. About 35 reptile species are known from the Sunderbans of Bangladesh alone. The most notable ones are saltwater crocodiles (*Crocodylus porosus*), monitor lizards (*Varanus bengalensis*, *V. salvator* and *V. flavascens*), King cobras (*Ophiophagus hannah*), Green Pit vipers (*Vipera trimeresurus*), Rock pythons (*Python molorus*), and the olive Ridley turtles (*Lepidochelys olivacea*, Hussain and Acharya, 1994). In Liberia, Nile crocodiles occur only in the brackish water of mangrove swamps and at river mouths (Kofron, 1992). Indo-Pacific crocodiles *Crocodylus porosus* are abundant in the upper mangrove sections of the Klias River, Sabah, Malaysia (Stuebing *et al.*, 1994).

The amphibian fauna of the Sunderbans mangal includes four genera of frogs (*Rana*, *Bufo*, *Microhyla* and *Rhacophorus*). The ground frog *Rana hexadactyla*, the tree frog *Rhacophorus maculatus*, and the toad *Bufo melanostictus* are particularly common (Gopal and Krishnamurthy, 1993; Hussain and Acharya, 1994). The amphibian fauna has not been well studied in most other mangals.

Human activities that impact mangroves have cascading effects on the reptile and amphibian fauna. There have been drastic declines in the population of crocodiles in the mangals of Liberia (Kofron, 1992) and of both crocodiles and snakes in the mangroves of Bangladesh (Hussain and Acharya, 1994). Habitat loss through human encroachment is a primary cause of the decline. These impacts are likely to continue, and worsen, as human populations expand further into the mangals.

5.10. Birds

Mangroves provide important habitat for landbirds, shorebirds and waterfowl, and they are home to a number of threatened species including spoonbills (*Ajaja ajaja*), large snowy egrets (*Cosmorodius albus*), scarlet ibis (*Eudocimus ruber*), fish hawks (*Pandion haliaetus*), royal terns (*Sterna hirundo*), West Indian whistling-ducks (*Dendrocygna arborea*), and Storm's Storks (Danielsen *et al.*, 1997; Panitz, 1997; Staus, 1998). The birds in the mangal may be permanent residents that forage and nest in the mangroves and the mangrove waters or they can be temporary visitors. Lefebvre *et al.* (1994) measured bird abundances and grouped species according to their diet and the frequency with which they use mangrove habitats. Distributions and abundances of the feeding guild were consistent with the abundance and distribution of their invertebrate prey (Lefebvre and Poulin, 1997).

Lefebvre *et al.* (1992) studied distributions of passerine birds in the mangroves of Venezuela and found that they form highly stable territories. In Singapore, sand pipers, plovers, herons and egrets all regularly use mangrove habitat (Murphy and Sigurdsson, 1990). About 315 species of birds are known from the Sunderbans of Bangladesh. The most common ones are white-bellied sea eagles (*Haliaetus leucogaster*) and Pallas's fish eagles (*Haliaetus leucorhynchus*; Hussain and Acharya, 1994). Alves *et al.* (1997) counted 32 bird species (2 marine species, 18 terrestrial species, and 12 waterfowl) in the mangroves of Jequiama, Brazil.

Migratory birds visiting the mangroves may fly long distances to find food and nesting places there. This may be particularly true in the Neotropics (Parrish and Sherry, 1994; Confer and Holmes, 1995; Lefebvre and Poulin, 1996; Panitz, 1997). Seventy-seven

bird species have been recorded in the Pacific mangroves of Colombia. Forty-three percent of these are permanent residents, 22% are regular visitors and 18% are temporary winter residents (Naranjo, 1997). One migratory species, the black-crowned night heron (*Nycticorax nycticorax*) is an important vector for disease. This mangrove-breeding bird is the principal host for Japanese Encephalitis Virus, which it widely disseminates during its migrations (Murphy and Sigurdsson, 1990).

Some of the resident bird species are highly dependent on mangroves for their survival. The yellow warbler (*Dendroica petechia*) and the mangrove vireo (*Vireo pallens*) are nearly confined to mangroves (Parkes, 1990; Buden, 1992). The mangrove gerygone spends 80% of its time on *Avicennia marina* (Noske, 1996) while *A. germinans* provides important breeding habitat for Florida Prairie Warblers (*Dendroica discolor paludicola*) and Cuban Yellow Warblers (*D. petechia gundlachi*; Prather and Cruz, 1995).

Because of this dependence, disturbances to the mangal may reverberate through the bird populations. This may be particularly true where the bird species show strong site fidelity (Warkentin and Hernandez, 1996). The habitat disturbances may be natural, such as the frequent cyclonic storms that strongly affect myna populations in the Pichavaram mangroves of south India (Nagarajan and Thiyagesan, 1995). More frequently, however, they are caused by human activities.

Mangrove forest destruction and fragmentation, usually due to development, reduce effective habitat and threaten mangrove-dependent species. Bancroft *et al.* (1995) found reduced populations of mangrove cuckoos

(*Coccyzus minor*) in fragmented mangrove areas of Florida, USA (Figure 13). Similarly, the mangrove finch (*Cactospiza heliobates*), once present in six mangrove areas on two of the Galapagos Islands, are now restricted to four mangrove pockets on one island. Habitat destruction has completely eliminated the finches from the other island (Grant and Grant, 1997). Ironically, one potential threat to these populations is the birdwatchers who explore hoping to see the birds in their natural environment (Klein *et al.*, 1995; Ellison and Farnsworth, 1996a).

Protection of the mangrove-dependent birds will require effective management of the entire mangrove habitat. This may be complex and require evaluation of habitat needs on a species by species basis. For example, in Florida Bay, bald eagles (the U.S. national bird) nest almost exclusively in mangrove trees (*Avicennia germinans* and *Rhizophora mangle*). Many of the nest sites are in snags (dead trees) suggesting that a comprehensive eagle management plan will require preservation of both living and dead mangroves (Curnutt and Robertson, 1994).

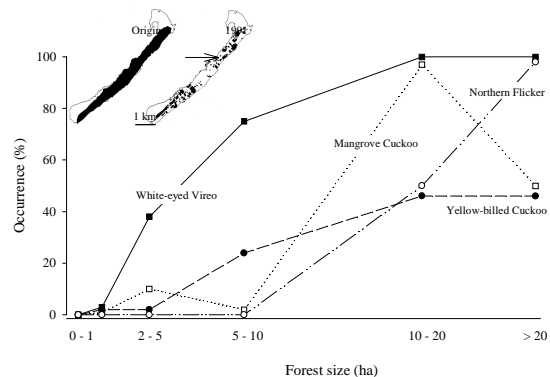


Figure 13. Abundance of mangrove-associated land birds as a function of forest size. Inset shows changes in the mangrove forests of Upper Matecumbe Key (Florida Keys, Florida, USA) from an original 252.2 ha forest to 105 forest fragments totalling only 61.4 ha. Records of 4 bird species show that abundance is strongly affected by forest size (after Bancroft *et al.*, 1995).

5.11. Mammals

A variety of mammals make their homes in the mangal. Their ecology within the mangal and their associations with the mangroves themselves have been little studied and are poorly known. Some of the noteworthy species present include dolphins (*Platanista gangetica*), mangrove monkeys (*Macaca mulatta*) and otters (*Lutra perspicillata*) in India (Gopal and Krishnamurthy, 1993); flying fox (*Pteropus conspicillatus* and *Pteropus alecto*) in northern Australia (Richards, 1990; Loughland, 1998) capuchin (*Cebus apella apella*) in Brazil (Fernandes, 1991). In southeastern Brazil, distributions of some cetacean species can also be related to the distribution of mangroves (Martuscelli *et al.*, 1996). Small clawed otters (Lutrinae) shelter amongst *Acrostichum* ferns during the dry season in the mangroves of Singapore and Malay (Sivasothi and Burhanuddin, 1994).

Thirty-two mammal species once lived in the Sunderban mangals of Bangladesh. Four of these, Javan rhinoceros (*Rhinoceros sondaicus*), wild buffalo (*Bubalus bubalis*), swamp deer (*Cervus duvauceli*) and hog deer (*Axis porcinus*), have gone extinct since the beginning of this century (Hussain and Acharya, 1994). Two additional species, the Royal Bengal Tiger (*Panthera tigris*) and the Chital deer (*Axis axis*), are currently endangered. Studies have shown that the chital deer browses directly on the mangroves. Its feeding damages *Avicennia officinalis*, *Xylocarpus mekongensis*, *Bruguiera sexangula*, and *Aegiceras corniculatum* but has no effect on *Heritiera fomes*, *Excoecaria agallocha* or *Ceriops decandra* (Siddiqi and Hussain, 1994).

Loss of mammalian species in the world's mangrove environments is probably the result of habitat fragmentation. This is particularly true for some of the larger species that have large home ranges. This may largely explain the loss of species from the Sunderbans. Habitat loss, however, can also have a major effect on smaller species. Forsy and Humphrey (1996) studied distribution and movement of an endangered marsh rabbit (*Sylvilagus palustris hefneri*) in the Lower Florida Keys, USA. They found that the rabbits use mangrove tracts as dispersal corridors between marsh habitats. Preservation of this species will require protection of both the marsh and the mangrove corridors. Careful study will be required to implement effective conservation plans for the mammals faced with shrinking, and fragmenting, mangrove habitat.

6. RESPONSES OF MANGROVES AND MANGROVE ECOSYSTEMS TO ENVIRONMENTAL STRESS

6.1. Responses to light

Although mangroves occur in tropical habitats where they are exposed to high light intensities, their photosynthetic rates tend to plateau at relatively low light levels. The trees possess mechanisms to deal with the high sunlight (see section 3.3.2). For example, *Avicennia marina* shows good resistance to high sunlight, hot and dry conditions and is well adapted to arid zones (ElAmry, 1998). However, there is evidence that intense light can damage the mangroves despite these adaptations. For example, Cheeseman *et al.* (1991) demonstrated that rates of photosynthesis drop in mangroves exposed to excessive sunlight. This could explain why *Rhizophora* seedlings establish and sprout most readily under the shady canopy of larger trees (Kathiresan and Ramesh, 1991; Kathiresan, 1999). Kathiresan and Moorthy (1993) also demonstrated that the seedlings grow faster in the shade, use NO₃ more efficiently, and show more efficient photosynthesis.

The negative effects of sunlight may, in some cases, be due to the high doses of UV-B radiation that the mangroves receive (Moorthy, 1995). To date, however, there have been few studies of UV-B and mangroves (Lovelock *et al.*, 1992; S.M. Smith and Snedaker, 1995b). Moorthy (1995) and Moorthy and Kathiresan (1997a) studied mangrove responses to UV-B in the Pichavaram mangroves of south India (total sunlight and UV-B intensities here may exceed 1300 W m^{-2} and 0.31 W m^{-2} respectively). Species in the Rhizophoraceae showed greater UV-B tolerance than did *Avicennia* species or other succulent plants.

To better understand potential effects of global increases in UV-B, Moorthy and Kathiresan (1997b) grew *Rhizophora apiculata* seedlings under the UV-B regimes predicted for 10, 20, 30 and 40% stratospheric ozone depletions. Net photosynthetic rates of seedlings increased 45% under the 10% UV-B treatment (stomatal conductance increased 47%). Raising the UV intensity to the 40% level, however, produced a 59% decrease in net photosynthesis and a 73% increase in intercellular CO_2 concentrations (Moorthy, 1995).

Increasing UV-B exposure also produced biochemical changes. Phenol and flavonoids levels increased with UV-B dose, but anthocyanin concentrations dropped. Small UV-B doses enhanced amino acid and protein levels but the effect was reversed at higher UV-B levels. The UV-B, in general, enhanced saturated fatty acids (maximum increase of 88%) and reduced unsaturated fatty acids (maximum decrease of 26%). Any UV-B exposure also inhibited the activity of nitrate reductase while simultaneously enhancing total tissue nitrate (Moorthy and Kathiresan, 1998). Both growth and biochemical responses indicate that the mangroves are stressed by the high intensity UV-B.

While excessive sunlight can damage mangroves, shading can also have negative effects. Mangrove seedlings under a closed canopy showed lower growth in south Florida (Koch, 1997) and Belizean mangals (Ellison and Farnsworth, 1993). The appearance of gaps in the canopy produced rapid growth of the previously shaded trees. In dense mangrove forests, shaded saplings have lower shoot biomass than those exposed to the sun. The saplings may compensate for this by increasing development of the pneumatophores (Turner *et al.*, 1995).

Shade tolerance differs among mangrove species. Clarke and Allaway (1993) found that shading had no effect on growth or survival of *Avicennia marina*. But, McKee (1995b) noted that shading with brief periods of light exposure increased biomass and growth in *Avicennia germinans* and *Laguncularia racemosa*. The same treatment had little effect on *Rhizophora mangle*. Ellison and Farnsworth (1993) found that *R. mangle* seedlings performed better overall in larger canopy gaps. In *R. mangle*, ontogenetic developments produce changes in light adaptation. Seedlings are apparently adapted for the shaded understory environment while mature trees do better in the sunlit canopy (Farnsworth and Ellison, 1996b).

6.2. Responses to gases

Because of the environment they live in, mangroves may experience episodic, or chronic oxygen stress. The consequences of low oxygen vary among species and appear related to the physiological and morphological adaptations of each (McKee *et al.*, 1996). For example, McKee (1993) found that flooding and anoxia reduced the total biomass of *Avicennia germinans* seedlings 20-40% relative to drained controls. However, under

identical conditions, the biomass of *Rhizophora mangle* seedlings increased 9-24%. The differential tolerance of these species for flooding and low oxygen may partly result from differences in root aeration. *R. mangle* maintains high oxygen concentrations in its roots even under reducing soil conditions; *A. germinans* does not. Skelton and Allaway (1996) showed that a congener (*A. marina*) also does not maintain gas pressures under low-oxygen conditions. Pressures in the aerial roots drop during high tide, probably due to removal of respiratory CO₂ from gas spaces during flooding. As the waters recede on the low tide, a rapid influx of air may take place.

High methane levels can be associated with anoxia in mangrove environments. The methane flux from the sediments is strongly influenced by freshwater loading and nutrient input (Sotomayor *et al.*, 1994; Giani *et al.*, 1996). Fluxes may also vary along tidal gradients being generally low on the landward fringe and high in the seaward transition zone between *Avicennia* and *Rhizophora* communities (e.g., Ye *et al.*, 1997). Mangrove species with pneumatophores may be best equipped to deal with high methane loads. The pneumatophores themselves may be conduits for release of methane gas (Sotomayor *et al.*, 1994). Pneumatophore-bearing species also release more methane through their leaves than do those lacking pneumatophores (Lu *et al.*, 1998).

Predicted global changes in atmospheric carbon dioxide are likely to have strong

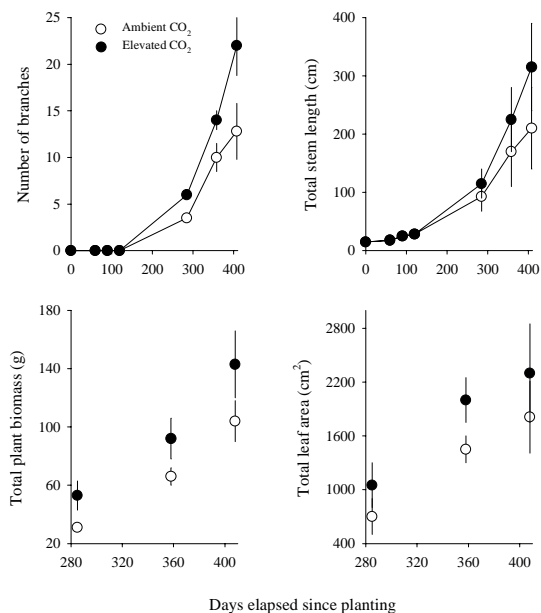


Figure 14. Effects of increased CO₂ on *Rhizophora mangle* growth and morphology. Predicted changes in the global climate could result in significant increases in CO₂ levels. Experimentally doubling the ambient CO₂ levels produced significant increases in number of branches, total stem length, plant biomass, and total leaf area (after Farnsworth *et al.*, 1996).

effects on mangroves. Farnsworth *et al.* (1996) grew *Rhizophora mangle* under double ambient CO₂ for 1 year. Growth rate, net assimilation, and photosynthetic rate all increased significantly. Seedlings in the enhanced CO₂ treatment had greater biomass, longer stems, more branching, and more leaf area than control seedlings (Figure 14). They also became reproductive after only 1 year (2 years sooner than under normal conditions). Ellison (1994) found that, in addition to stimulating productivity, increased CO₂ led to more efficient use of water as a result of reduced stomatal conductance (Ellison, 1994).

The effects of increased CO₂ may vary with other physical and chemical conditions (Ball and Munns, 1992). For instance, *Rhizophora apiculata* and *R. stylosa* both benefit from increased CO₂, but the stimulatory effect is much greater under low salinity conditions (Ball *et al.*, 1997). The effects of increased CO₂ may also differ among habitats and species.

Snedaker and Araújo (1998), for example, studied the effects of a 6 - 34 % increase in CO₂ concentration on four mangrove species in south Florida (*Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*, and *Conocarpus erectus*). Elevated CO₂ reduced stomatal conductance and transpiration and

significantly increased instantaneous transpiration efficiency in all of these species. However, it did not increase net primary productivity in any species and actually reduced the productivity of *Laguncularia racemosa*.

6.3. Responses to wind

Tropical storms (hurricanes and cyclones) cause enormous damage to mangrove forests, particularly in the Caribbean and the Bay of Bengal. The immediate consequence is loss of the mangrove trees themselves. In 1988, for example, a severe cyclone in Bangladesh destroyed 8.5 million trees with a loss of 66.3 million m³ of commercial saw timber (e.g. Mastaller, 1996). Large numbers of trees have similarly been defoliated and destroyed by storms in South Florida, Guadeloupe, Nicaragua, Belize, and Puerto Rico.

Damage to the mangroves may also have indirect consequences. For example, Hurricanes Gilbert and Joan, which both hit the Caribbean in the last quarter of 1988, caused mass mortality of invertebrates growing on the roots of *Rhizophora mangle* (Orihuela *et al.*, 1991). Hurricane Hugo, while passing through the coastal environment of Guadeloupe, French West Indies, killed large numbers of fish, producing changes in the fish community (Bouchon *et al.*, 1991, Imbert *et al.*, 1996).

A far-reaching consequence of mangrove mortality can be serious erosion of the coastal habitat. Hurricane Andrew made landfall in 1992 on the mangrove-fringed coasts of south Florida. Uprooted mangrove vegetation left behind unprotected intertidal and subtidal sediments that were subsequently eroded by currents and waves. (Davis, 1995; Doyle *et al.*, 1995; Swiadek, 1997). In Bangladesh, a mangrove afforestation project was initiated in 1966. A primary goal of the project was to provide a mangrove buffer that would protect the coast from frequent cyclone damage. By 1993, 0.12 million ha had been afforested (Saenger and Siddiqi, 1993).

Some effects of storm damage may not be seen until some time after the event. Often, trees that are broken or severely damaged by the storm later die. T.J. Smith *et al.* (1994) found that mangrove mortality in south Florida continued for many weeks after hurricane Andrew. Many mature trees later died from injuries sustained in the storm. Propagules and seedlings in the habitat were also killed, largely by sedimentation and high porewater sulfides.

Differential species mortality associated with a major storm can change community structure. For example, smaller *Rhizophora mangle* were not greatly affected by Hurricane Andrew whereas large *Laguncularia racemosa* were heavily damaged (McCoy *et al.*, 1996). These differences in survival have produced a shift in species distributions in some areas (Baldwin *et al.*, 1995). A similar shift can be seen with *Avicennia germinans* and *Rhizophora mangle*. Because *A. germinans*, cannot tolerate long periods of pneumatophore submergence, storms and hurricanes in Florida may promote replacement of *A. germinans* by *R. mangle* (Rey *et al.*, 1990a). Even where the regenerated forest is composed of the same species present before the hurricane, different regeneration rates may shift the proportions of those species (Roth, 1992, 1997).

6.4. Responses to coastal changes

Mangroves are tightly bound to the coastal environments in which they occur. Not only are they influenced by chemical and physical conditions in their environment, they

help create those conditions. As a result, perturbations to the system can have cascading long-term effects.

Many changes seen in coastal mangals can be attributed to changes in hydrology. Some of these changes are favorable. For example, in Singapore, increases in the frequency of tidal inundation has created new mangal (comprised of *Avicennia* and *Sonneratia alba*) adjacent to established mangrove stands (Lee *et al.*, 1996). More often, however, hydrological changes result in destruction of mangroves. In Pichavaram, south India, changes in topography and tidal flushing have caused large-scale degradation of mangroves. The mangroves are healthy and diverse where the land is flat. If water flow is reduced, flat areas become shallow basins. The poor flushing and resultant hypersalinity stunt the mangroves or replace them with saltmarsh (*Suaeda* spp.) or barren soil devoid of vegetation. The process can be reversed by simply increasing the free flow of tidal waters (Selvam and Ravichandran, 1998).

In Senegal, decreasing rainfall and increasing evaporation have markedly changed mangrove populations. The changes have been accelerated by altered tidal conditions resulting from the breaching of a protective sand dune (Diop *et al.*, 1997). Riverine mangroves affect the dynamics of tidal currents (Wolanski *et al.*, 1992), producing asymmetrical tidal currents that may be 50% stronger on the ebb than on the flood. Erosion from these flows creates deep channels through the habitat (Medeiros and Kjerfve, 1993). Deforestation changes the tidal asymmetry and leads to changes in channel structure (Wolanski *et al.*, 1992).

Human attempts to modify the physical character of the mangal by erecting hard structures or by dredging can also drastically alter the system. In Florida, a culvert connecting a mangrove marsh to a tidal lagoon was closed in 1979. This led to overflowing and hypersalinity (> 100 ppt) that eliminated the marsh. The culvert was reopened in 1982, but the mangroves did not recover (Rey *et al.*, 1990a, b).

Another potential consequence of flow modification is change in sedimentation patterns (e.g., Q. Zhang *et al.*, 1996). On spring flood tides under normal conditions, about 80% of the sediment transported into the Middle Creek (Cairns, Australia) is trapped by the mangroves. This corresponds to 10-12 kg of sediment m^{-1} on each spring tide and could produce sediment accretions of 0.1 cm y^{-1} (Furukawa *et al.*, 1997). Such levels of sediment trapping can produce major changes to the habitat. Chakraborti (1995) traced the evolutionary history of coastal quaternary deposits on the Bengal Plain of India and found that mangroves were the dominant geomorphic agents in the evolution of tidal shoals and their eventual accretion to the mainland.

Damage to the mangroves strongly affects sediment budgets and promotes coastal erosion (Kamaludin and Woodroffe, 1993). The eroded sediments may then cause further damage the mangroves. For example, Young and Harvey (1996) showed that sediment accretion interferes with root aeration in *Avicennia marina* var. *australasica*. Similarly, movements of sand in mangrove habitats on Portuguese Island, Mozambique have caused high mortality of *Ceriops tagal*. This has changed the mangrove species composition and had significant secondary effects; all crustaceans and mollusks have also disappeared from the mangal (Hatton and Couto, 1992).

Major changes in mangrove distribution and abundance in coastal regions could result from habitat loss associated with rising sea level (Fujimoto and Miyagi, 1990; Woodroffe, 1990; Ellison, 1993; Parkinson *et al.*, 1994). The vulnerability of individual

mangals can be evaluated through annual measurements of soil elevation deficit (elevation change minus sea-level rise). Cahoon and Lynch (1997) suggest that this is a better measure than the more commonly used accretion deficit (accretion minus sea-level rise). Historical patterns of sea level rise in a mangrove environment can be evaluated through measurements of the mangrove trees themselves since the δ^{18} oxygen fraction in the wood is an effective seawater tracer (Ish-Shalom-Gordon *et al.*, 1992).

Ellison and Stoddart (1991) suggested that mangroves are stressed by sea level rises between 9 and 12 cm • 100 y⁻¹ and concluded that faster rates could seriously threaten mangrove ecosystems. This view has been challenged by Snedaker *et al.* (1994) who cite historical records showing mangrove expansion under relative sea level changes nearly twice that great. X. Tan and Zhang (1997) conclude that, given current rate estimates, sea level rises pose no significant threat to most mangrove forests in China. The effects of sea-level rise on any mangrove habitat will be influenced by local wetland type, geomorphic setting, and human activities in the wetland. There is a need for better models predicting effects of sea level and other coastal changes on individual mangals (e.g., Bacon, 1994).

6.5. Responses to tidal gradients and zonation

Zonation can be a structural feature of mangrove forests in some parts of the world (T.J. Smith, 1992; Woodroffe, 1992). However, unlike open coast habitats where zonation patterns are distinct, mangrove distributions are extremely variable and extensive surveys may be necessary to fully document patterns, particularly if diversity is high (Bunt 1996). The “zones” may be obscured by broad overlap in species distributions (e.g., Bunt and Bunt, 1999; Bunt and Stieglitz, 1999; Figure 15) or they may simply be absent in some mangals (Ellison *et al.*, in press). Bunt (1999) has developed methods specifically for evaluating and describing mangrove zonation.

Where zonation does occur, contributing factors may include plant succession, geomorphology, physiological adaptation, propagule size, seed predation and interspecific interactions (e.g., Bunt *et al.*, 1991; Woodroffe, 1992; Ellison and Farnsworth, 1993; Schwamborn and Saint-Paul, 1996). The relative importance of these factors, however, depends on the individual habitat (e.g., McKee, 1995c) and there is disagreement about the general

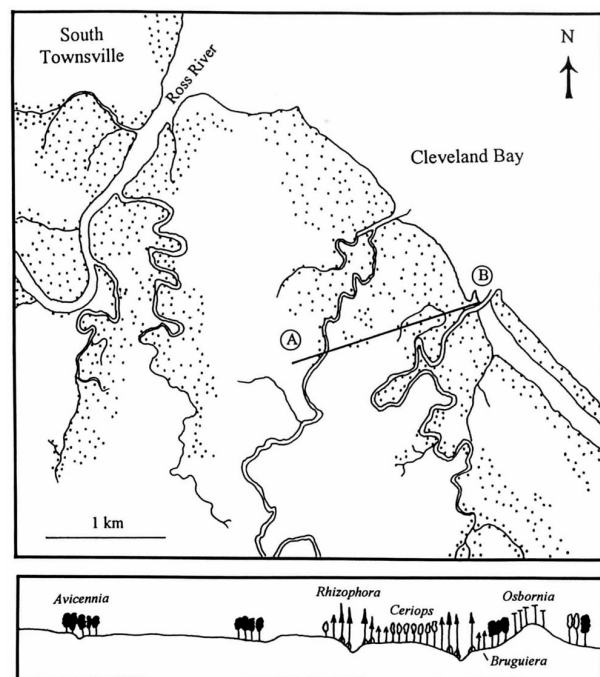


Figure 15. Distribution of mangroves south of Townsville, North Queensland, Australia. Stippled areas of the map represent mangal. Details of transect A-B are shown in the lower panel. The dominant mangrove species (i.e., *Avicennia marina*, *Rhizophora stylosa*, *Ceriops tagal*, *Bruguiera gymnorhiza*, and *Osbornia octodonta*) are represented by different symbols. Note that the mangroves are closely associated with rivers and creeks, resulting in broadly overlapping species distributions (after Macnae, 1967).

importance of some of them. For example, Robertson *et al.* (1991) argue that succession plays a minor role in mangrove zonation and that simple erosion and sedimentation control the distribution of mangroves along the seaward edge of the mangal. The complexity and uniqueness of these communities may make it difficult even to define successional stages (Roth, 1992). The term “old-growth”, for instance, cannot be applied easily to mangrove forests (Lugo, 1997).

One potential cause of mangrove zonation is the differential ability of propagules to establish at different tidal heights. This is directly related to propagule size. It has been suggested that small propagules drift further inland and establish better in shallow water than do large propagules (thus producing a species zonation dependent on propagule size; Kathiresan, 1999). The importance of this process to the creation of mangrove zones has been clearly demonstrated for *Avicennia bicolor* and *Rhizophora racemosa* on the Pacific coast of Costa Rica (Jiménez and Sauter, 1991). However, the more general importance of this process has been contested (T.J. Smith, 1992).

Interspecific differences in tolerance for physiological stress is perhaps the best demonstrated cause of mangrove zonation. However, while physiological responses to physicochemical conditions undoubtedly influence mangrove distributions in some habitats, conclusions must be made cautiously since field measurements do not always support laboratory conclusions (Schwamborn and Saint-Paul, 1996). Despite this limitation, it is clear that mangrove species respond differently to different tidal regimes. For example, in the Indian Sunderbans, a mangrove forest that experiences total diurnal inundation is dominated by *Avicennia marina* and *A. alba* while *Excoecaria agallocha*, *Ceriops decandra* and *Acanthus ilicifolius* dominate sites that are not completely inundated (Saha and Choudhury, 1995). *Nypa fruticans* also seems to prefer sites with low level of tidal inundation (Siddiqi, 1995). Kathiresan *et al.* (1996a) studied growth of *Rhizophora apiculata* seedlings in different tidal zones of a south Indian estuary. Individuals in the low intertidal grew 2.5 times faster and sprouted 4 times as many leaves as individuals in the highest zone. Similar patterns of differential survival and growth have been seen in the mangroves of Qatar (Abdel-Razik, 1991) and New Zealand (Osunkoya and Creese, 1997).

Ellison and Farnsworth (1993) studied survival and growth of *Rhizophora mangle* and *Avicennia germinans* seedlings at tidal heights corresponding to lowest low water (LLW), mean water (MW), and highest high water (HHW). *R. mangle* seedlings survived in the MW (69%) and LLW (56%) treatments; *Avicennia* survived at MW (47%), but not at LLW. Neither species survived at HHW. Seedlings of both species suffered twice as much insect damage in the MW treatment as in the LLW treatment. The combination of insect herbivory and differential flood tolerance may create the zonation of these two species in the Caribbean. Further experimental studies of this nature should help clarify the causes and consequences of zonation in mangrove communities.

6.6. Responses to soil conditions

Soil properties have a major impact on mangrove nutrition and growth. Some of the most important characteristics are siltiness, electrical conductivity, pH, and cation exchange capacity (Kusmana, 1990; V.B. Rao *et al.*, 1992; Pezeshki *et al.*, 1997). The most important factor, however, appears to be nutrient concentrations. Mangals are finely balanced, highly effective nutrient sinks with net imports of dissolved nitrogen,

phosphorus, and silicon. Nutrient fluxes in these environments are closely tied to plant assimilation and microbial mineralization (Alongi, 1996; Middelburg *et al.*, 1996).

Nutrients availability may limit growth and production in many mangals. Varying nutrient concentrations can also change competitive balances and affect species distributions (Chen and Twilley, 1998). As a result, nutrient pulses can create immediate, and impressive, changes in the vegetation. For example, on the southeast coast of India, high nutrient concentrations and low salinity from monsoons produce rapid growth in the mangroves. Seedlings grow 5X as much and produce 4X as many leaves in the post-monsoon season as they do in the dry season (Kathiresan *et al.*, 1996a).

The limiting nutrients may vary with individual mangrove habitats. For example, potassium levels may be important in some regions. *Rhizophora apiculata* seedlings do significantly better in plantation sites with enriched potassium (Kathiresan *et al.*, 1994a). In general, however, mangroves in low-nutrient carbonate soils are limited by phosphorus. What phosphorus is present may be bound with calcium, effectively holding it within the sediments (Silva and Mozeto, 1997). In mesocosm and field experiments with *Rhizophora mangle* seedlings, phosphorus enrichment produced nearly a 7 fold increase in stem elongation rates and a 3 fold increase in leaf area. Nitrogen addition produced no such response (Koch and Snedaker, 1997). Low phosphorus availability similarly limits growth of dwarf *R. mangle* in a Belizean mangal (Feller, 1995) and promotes development of hard, long-lived leaves called sclerophylls. The sclerophylls may be an adaptation to conserve nutrients in these oligotrophic habitats (Feller, 1996). Mangroves may have other mechanisms to hold valuable nutrients. For example, mature photosynthetically active leaves have much higher nitrogen and potassium concentrations than senescent leaves. This is apparently a consequence of nutrients being translocated out of the aging leaves and into other plant parts before the leaves fall (Soto, 1992).

Damage to a mangal may compromise its ability to retain nutrients. For examples, at severely damaged mangrove sites in North Queensland, Kaly *et al.* (1997) measured a significant loss of both nitrogen and phosphorus from the soils. This may have been related to declines in the crab populations and a dramatic decrease in density of burrows. The effects of disturbance will differ from habitat to habitat and will depend on the sediment characteristics and flow regimes of each site. For example, Triwilaida and Intari (1990) found no differences in soil nutrient concentrations between degraded and healthy mangrove stands in the Pedada Strait, Riau.

Sulfides are a characteristic feature of mangrove sediments that influences mangrove distributions and is influenced by their presence. Tidal mixing, bioturbation, and the mangroves themselves (Holmer *et al.*, 1994) control the distributions and concentrations of the sulfides. For example, reoxidation of sulfides is facilitated by roots; soils are often less reduced near the aerial roots of some species. This leads to lower sulfide levels. In a neotropical Florida mangal, the zone dominated by *Rhizophora mangle* (with its numerous aerial prop roots) has moderately reducing soils with low sulfide levels. In contrast, the *Avicennia germinans* zone has strongly reducing soils with high sulfides (McKee, 1993). Surprisingly, this pattern is not repeated in a similar mangal in Brazil. In that location, the *R. mangle* soils are highly reducing with high sulfide concentrations. The sulfide content of the *A. germinans* soil is highly variable as the rhizosphere changes from oxygenated to anoxic conditions (Lacerda *et al.*, 1995). The *Avicennia* soils also contain more exchangeable trace metals (Lacerda *et al.*, 1993).

Reduction of sulfate to sulfide is generally slower in young forests, resulting in higher nutrient levels and lower sulfide toxicity (Alongi *et al.*, 1998). High sulfide levels can damage mangrove seedlings, causing stomatal closure, reduced gas exchange, reduced growth, and high mortality (Youssef and Saenger, 1998). Disturbance can increase rates of sulfate reduction. Clearing of mangrove forests, or simple formation of canopy gaps can change the physical and chemical characteristics of the underlying soils (Ewel *et al.*, 1998a), leading to anaerobiosis and increased sulfide in the sediments (Ibrahim, 1990). Heavy organic input can also increase sulfide production. In Ghana, pyrite (ferric sulfide) accumulates directly in the upper layer of the mangrove soils. The rate of accumulation is directly related to vegetation thickness (Nonaka *et al.*, 1994).

Under normal conditions, sulfides combine with metals in the sediment and precipitate out as metal sulfides. When the metals available for sulfide precipitation are exhausted, H₂S is formed (Kryger and Lee, 1995). Kryger and Lee (1996) found that the H₂S from anaerobic processes accumulates in cable roots of *Avicennia* species as the sediments age. Concentrations of H₂S in the roots may be 30-40 times higher than in the surrounding sediments. The H₂S accumulation can kill the mangroves if their pneumatophores are covered by silt and cannot transport oxygen to the rhizospheres. Because they have aerial roots, *Rhizophora* species can better survive on aged mangrove soils high in H₂S. They may, therefore, be a natural successor to the less-tolerant *Avicennia* species.

6.7. Responses to salinity

Salinity, as controlled by climate, hydrology, topography and tidal flooding, affects the productivity and growth of mangrove forests (Sylla *et al.*, 1996; Twilley and Chen, 1998). It can also strongly influence competitive interactions among species (Ukpong, 1995; Ukpong and Areola, 1995; Cardona and Botero, 1998). The distributions of plant species within the mangal, in many cases, can be explained primarily by salinity gradients (Ukpong, 1994; Ball, 1998).

In general, mangrove vegetation is more luxuriant in lower salinities (Kathiresan *et al.*, 1996a). However, low salinity associated with long periods of flooding contributes to mangrove degradation through reduced cell turgor and decreased respiration (Triwilaida and Intari, 1990). On the Pacific coast of Central America, freshwater availability (largely from rainfall and surface runoff) controls reproductive phenology, growth and mortality of *Avicennia biocolor* (Jiménez, 1990).

Even in mangals with strong riverine input, the combined effects of evaporation and transpiration may remove much of the fresh water entering the system (Simpson *et al.*, 1997). The plants must, therefore, have some salinity tolerance. True mangroves (e.g., *Avicennia* spp. and *Rhizophora* spp.) tolerate higher salinity than do non-mangroves, but tolerance also varies among the true mangroves. For example, *Rhizophora mucronata* seedlings do better in salinities of 30 g l⁻¹, but *R. apiculata* do better at 15 g l⁻¹ (Kathiresan and Thangam, 1990a; Kathiresan *et al.*, 1996b). *Sonneratia alba* grows in waters between 5 and 50 ‰ seawater, but *S. lanceolata* only tolerates salinities up to 5 ‰ seawater (Ball and Pidsley, 1995). Mangrove seedlings require low salinity (S.M. Smith *et al.*, 1996), but their salt tolerance increases as they grow (Bhosale, 1994).

Short periods of high salinity may trigger events in the mangrove life history. For instance, high salinity at the end of dry period, followed by an extended rainy period controls establishment of *Rhizophora* seedlings (Rico-Gray and Palacios-Rios, 1996b). Chronic high salinity, however, is always detrimental to the mangroves. Hypersalinity stunts tree growth in *A. marina* stands (Selvam *et al.*, 1991), reduces biomass in hydroponically grown *Bruguiera gymnorhiza* (Naidoo, 1990), and causes denaturing of terminal buds in *Rhizophora mangle* seedlings (Koch and Snedaker, 1997). Saline interstitial water reduces leaf area, increases leaf sap osmotic pressure, increases the leaf area/weight ratio and decreases total N, K, and P (Medina *et al.*, 1995). Simple salinity fluctuations also have significant negative effects on photosynthesis and growth (Lin and Sternberg, 1993). In Senegal, hypersalinity (from a decade of low rainfall and high evaporation) has caused salt flats to grow into mangrove areas, completely destroying the vegetation (Diop *et al.*, 1997).

Extremely high salt concentrations in the groundwater of tropical salt flats are responsible for the complete absence of macrophytes (including mangroves). There are often very sharp changes in groundwater salt concentrations at the interface between salt flats and mangroves, suggesting that the mangroves are modifying the salinity of the groundwater (Ridd and Sam, 1996). Mathematical models of groundwater flow show that human activity hundreds of kilometers inland can destroy vast mangrove areas by changing groundwater flow and modifying salinity levels (Tack and Polk, 1997).

6.8. Responses to metal pollution

Because of their proximity to population centers and industrialized regions, mangrove habitats have often received inputs of heavy metals and the sediments may show significant metal contamination (Mackey *et al.*, 1992; Larcercda *et al.*, 1993; Rivail *et al.*, 1996; Lacerda, 1998; Tam and Yao, 1998). The mangroves themselves, however, generally have low concentrations of heavy metals. Consequently, they are very poor indicators of trace metal contamination. For example, in Sepetiba Bay, Rio de Janeiro, the sediments contain 99% of the Mn and Cu and almost 100% of the Fe, Zn, Cr, Pb and Cd in the total mangrove ecosystem. The tissues of *Rhizophora mangle* contain less than 1% of the total of these metals (Silva *et al.*, 1990). On the Saudi coast of the Arabian Gulf, there is no correlation between the concentrations of metals in sediments and in the leaves of mangroves living on the contaminated soil (Sadiq and Zaidi, 1994).

The low level of metals in the mangroves themselves may be due to 1) low bioavailability in the mangal sediments 2) exclusion of the metals by the mangroves or 3) physiological adaptations that prevent metal accumulation in the plants. Mangrove roots appear to be barriers that prevent metals from reaching the more sensitive parts of the plant (Tam and Wong, 1997). Oxygen exuded by underground roots forms iron plaques that adhere to the root surfaces and prevent trace metals from entering the root cells. Where the metals do enter, there are apparent mechanisms to keep them from circulating freely through the plant. Heavy metal concentrations in *Rhizophora apiculata* seedlings decrease from root to stem and from stem to leaves (Moorthy and Kathiresan, 1998a).

The chemical and physical environment of the mangal may efficiently trap trace metals in non-bioavailable forms. For example, rapid precipitation of stable metal sulfides under anoxic conditions decreases the bioavailability of trace metals in the mangrove sediments (Di-Toro, 1990; Mackey and Mackay, 1996; Figure 16). All but the most mobile

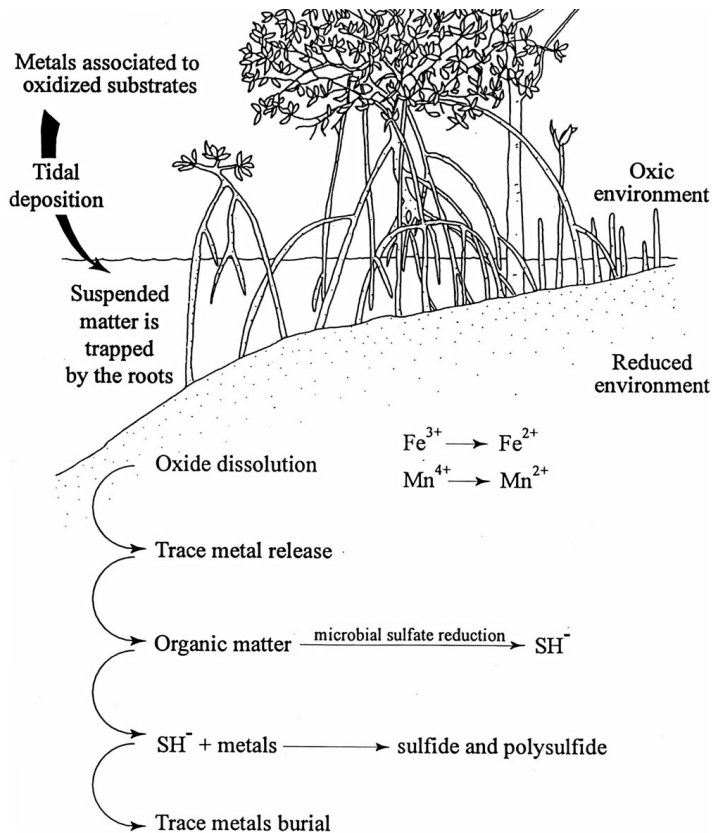


Figure 16. Summary of major metabolic processes involving metals in anoxic mangrove sediments (after

Stigliani, 1995). Tam and Wong (1996a, b) irrigated mangrove soil samples with metal-laden artificial wastewater. They found that the upper centimeter of the soils bound Cu, Cd, Mn and Zn. However, there were also higher concentrations of Mn, Zn and Cd in the water-soluble, exchangeable fraction of the treated sediments than in the untreated, native sediments.

Disturbances may also cause the mangrove soils to lose their metal-binding capacity, resulting in mobilization of the metals. The mangal then shift from a heavy metal sink to a heavy metal source (Lacerda, 1998). Disturbances may be in the form of prolonged dry periods (Clark *et al.*, 1997), changes in the frequency and duration of tidal flooding (Chiu and Chou, 1991) or changes in salinity (Spratt and Hodson, 1994). Often, these disruptions are associated with human activities (Lacerda, 1998).

S. Zheng *et al.* (1997) suggest that mangrove afforestation projects should not be done on Cu or Zn-polluted soils since seedlings secrete organic acids that may increase solubility of the metals. *Rhizophora apiculata* seedlings planted in an area formerly used for tin mining showed high mortality (approximately 47% in the first four years). The mortality, however, was attributed to altered microtopography and soil particle distribution rather than metal contamination (Komiyama *et al.*, 1996).

Metals in mangrove sediments do not appear to strongly affect bacterial populations, even under heavy loads (Tam, 1998). However, if the metals are bioavailable, they may accumulate in the macroinvertebrate fauna. In Yingluo Bay, He *et al.* (1996)

elements (e.g., Mn and Zn) may be in strongly bound fractions. Thus, the mangal may help control trace metal pollution in tropical coastal areas (Lacerda, 1997).

Trace metals may also be bound in organic complexes that show low bioavailability (Clark *et al.*, 1998; Lacerda, 1998). For example, Cr, which does not form sulfide minerals, is immobilized in refractory organic compounds in mangrove sediments (Lacerda *et al.*, 1991). Mercury can be similarly bound. However, it may be bound as the highly toxic dimethyl-mercury. Under oxic conditions, dimethyl-mercury is volatile and unstable; in reducing mangrove sediments, however, it may persist and accumulate (Quevauviller *et al.*, 1992).

While mangrove sediments generally have a high capacity for absorbing and holding trace metals, heavy loads may exceed the

found high Zn and Cd levels in mollusks living in the mangal. Crustaceans had elevated Cu levels and sipunculids concentrated Pb. Meyer *et al.* (1998) similarly found that mangrove oysters (*Crassostrea rhizophorae*) in a northeastern Brazil mangal accumulated mercury and are good biomarkers for mercury contamination. Bioaccumulation of such substances can carry substantial human health risks. Mangrove sediment chemistry and the fate of heavy metals are subjects that merits much more study.

6.9. Responses to organic pollution

Three characteristics have long made mangrove habitats favored sites for sewage dumping: (1) flow through the habitat disperses wastes from a point source over vast areas, (2) the vegetation itself filters nutrients from the water, and (3) the mangrove soil, algae, microbes, and physical processes absorb large amounts of the pollutants (Wong *et al.*, 1995, 1997b).

Nutrients (primarily nitrogen and phosphorus) are often major components of the pollution. Researchers have studied the ability of mangals to absorb nutrients and the effects of the pollutants on the mangal community as a whole. In general, mangrove soils efficiently trap wastewater-borne phosphorus, but are less effective at removing nitrogen (Tam and Wong, 1995). Tam and Wong (1996a, b) experimentally tested the ability of mangrove soils to absorb nutrients when treated with synthetic wastewater. The soils retained both nitrogen and phosphorus. The bulk of these were trapped in the upper 1 cm of the sediment where they could be processed by bacterial communities (Corredor and Morell, 1994).

Wong *et al.* (1995, 1997a) found that two full years of sewage discharge did not adversely affect mangrove growth in the Funtian mangal of China. Nor did sewage affect biomass, density, or community structure of the benthic macrofauna (Yu *et al.*, 1997). Furthermore, wastewater input did not seem to increase litter production or litter decay rates (N.F.Y. Tam *et al.*, 1998).

While these studies suggest that mangroves are tolerant of organic pollution, results should be viewed cautiously since they may not hold in other habitat. The effects of sewage dumping will depend on the quantities of sewage, the duration of dumping, and the unique characteristics of each mangal. Particularly important are the patterns of water flow through the habitat since this will determine flushing rates and residence times of the pollutants (Ridd *et al.*, 1990; Uncles *et al.*, 1990; Wolanski *et al.*, 1990; Wattayakorn *et al.*, 1990).

High levels of organic pollution can contribute to disease, death, and changes in species compositions within the mangal (Tattar *et al.*, 1994). Mandura (1997) found that sewage discharge killed pneumatophores of *Avicennia marina* in the Red Sea. The loss of the pneumatophores decreased surface area for respiration and nutrient uptake and retarded the growth of the trees. The pollution can also have cascading effects on invertebrate populations (e.g., Sanches and Camargo, 1995).

Beyond simple nutrients, organic pollution in mangrove environments may include other anthropogenic chemicals and debris. Mangrove sediments in Cienaga Grande de Santa Marta and Chengue Bay (Colombian Caribbean) contain significant organochlorine pesticide residues. The concentrations of some of these vary seasonally (Espinosa *et al.*, 1995). Large amounts of plastic and non-mangrove wood are present in the mangroves of

Jamaica. The volume of these solid wastes correlates strongly with total rainfall in a nearby metropolitan area (Green and Webber, 1996).

6.10. Responses to oil pollution

Oil pollution from oil or gas exploration, petroleum production and accidental spills severely damages mangrove ecosystems (Mastaller, 1996). Clean-up operations after such calamities are costly and difficult (IUCN, 1993). Oiling of mangroves has a number of significant consequences. One of the most immediate and obvious is defoliation of the trees. The toxicity of the oil may depend on environmental conditions; oil has the greatest effect on survival and growth of *Rhizophora mangle* when the trees are in hot, bright outdoor conditions (Proffitt *et al.*, 1995). Toxicity may also differ among mangrove species. For example, along the coast of Sao Paulo, Brazil, an oil spill caused 25.9% defoliation of *Rhizophora mangle*, 43.4% defoliation of *Laguncularia racemosa*, and 64.5% defoliation of *Avicennia schaueriana* (Lamparelli *et al.*, 1997). Differential mortality of the trees can potentially lead to long-term changes in the community structure.

Oil in a mangrove habitat (whether from a spill or chronic input) can have other less obvious effects on the mangroves. For example, sediments can have significant hydrocarbon pollution long after a spill event, even when there is no evidence of petroleum contamination on the trees or in water samples from surrounding water (Bernard *et al.*, 1995, 1996). Munoz *et al.* (1997) followed the breakdown of Arabian light crude oil in mangrove peat for 8 full years. Sediments contaminated in the Galeta spill in Panama continued to hold oil residue, including the full range of aromatic hydrocarbons, 5 years after the spill (Burns *et al.*, 1994). The authors suggest that it will take at least 20 years for the toxicity to completely disappear.

Grant *et al.* (1993) demonstrated that sediment oil can inhibit establishment and decrease survival of mangrove seedlings for several years. This residual toxicity may interfere with mangrove afforestation efforts (S. Zheng *et al.*, 1997). Dutrieux *et al.* (1990) planted *Sonneratia caseolaris* in soils that had been treated with oil. Many of the plants were killed; the survivors were significantly stunted. The retained oil can also cause mutation. Klekowski *et al.* (1994b, c) found a positive correlation between concentrations of polycyclic aromatic hydrocarbons in mangal sediments, and the frequency of *Rhizophora mangle* carrying chlorophyll-deficient mutations.

The extent of mangrove damage from oil pollution will depend on the kind of oil, and the magnitude and frequency of spilling. For example, fresh oil causes more leaf loss in *Avicennia* seedlings than does aged oil (Martin *et al.*, 1990; Grant *et al.*, 1993). Boer (1996b) measured effects of a mineral oil spill in the Arabian Sea off Fujairah. The mangroves were relatively unaffected and all signs of the spill were nearly gone only 7 months after the spill.

Proffitt and Devlin (1998) tested the effects of sequential oilings on potted *Rhizophora mangle* seedlings, first treating the seedlings with No. 6 fuel oil, followed, 34 months later, by crude oil. They found no evidence of cumulative or synergistic effects, but this conclusion has been challenged because of unnatural laboratory conditions and low statistical power (Ellison, 1999). Given the sensitivity of mangroves to soil conditions, it is essential to study oil effects under conditions that reflect the natural environment as closely as possible. For example, salinity should be held at field levels and realistic oil

concentrations should be used to model chronic exposure of plants in oil-contaminated soil (Ellison, 1999).

The most realistic measure of repeated oil exposure comes from field habitats exposed to natural oiliness. Two large oil spills (the first in 1968 and the second in 1986) have caused large-scale damage to mangrove forests in Panama. In addition to killing trees outright, the oil retained in the sediments caused apparent sublethal effects (Duke *et al.*, 1997). The residual effects of oiling may make the mangroves more vulnerable to future damage. More careful, long-term laboratory experiments under natural conditions are necessary to understand the responses of mangroves to oil and the consequences of oiling.

Oil contamination can damage animals living in the mangal, both in the sediments and on submerged mangrove roots (e.g., Mackey and Hodgkinson, 1996). Five years after the Galeta oil spill in Panama, there was a 60% decrease in the number of isopods on submerged *Rhizophora mangle* prop roots and a 40-50% drop in the number of spiny lobsters (Levings and Garrity, 1994; Levings *et al.*, 1994). Oyster populations dropped 65% along mangrove channels and 99% in mangrove streams. The population decreases are due, in part, to loss of root surface on which to attach (the surface area of submerged roots decreased 38% in the channels and 74% in streams; Garrity *et al.*, 1994).

In addition to killing the mangrove fauna directly, oil can have indirect effects resulting from habitat modification. Oil released during the 1991 Gulf War left a black tar layer in the mangals along the Saudi Gulf. The tar layer created higher than normal temperatures in the soil. The ecological consequences of the higher temperatures, and the effect on epifauna and infauna, are not yet fully known (Boer, 1996a).

The general response of a mangrove forest to oiling can be divided into four phases: 1) immediate effects, 2) structural damage, 3) stabilization and 4) recovery. The third and fourth phases may take many years to occur, if they occur at all. In Brazil, a mangrove area damaged by oil did not begin to recover until approximately 10 years after the event (Lamparelli *et al.*, 1997). Assessing the effects of oil on mangrove environments will require the development of creative methods for measuring impacts and accurate modeling of the physical and chemical events associated with the spill (e.g., Jacobi and Schaeffer Novelli, 1990; Lamparelli *et al.*, 1997). These efforts, however, will only be effective if they are supported by careful monitoring and long-term data sets.

6.11. Responses to pests

A few of the many plants and animals that make their homes in the mangal are serious pests that damage the mangroves, decreasing growth and productivity and, in extreme cases, killing the trees. Some of the harmful species do not directly injure the mangroves. Instead, they cause damage by competing for scarce resources. Allelopathic interactions among mangrove species suggest that interspecific competition is a normal process in the mangal. Toxic leachates from leaf litter of some mangroves (e.g. *Lumnitzera racemosa*, *Ceriops decandra* and *R. apiculata*) inhibit the growth of roots and shoots of *Rhizophora apiculata* and *R. mucronata* seedlings (Kathiresan and Thangam, 1989; Kathiresan *et al.*, 1993).

In general, stressful osmotic conditions that lead to lignification and suberization prevent the development of a luxuriant herbaceous undergrowth in mangrove forests so there is not normally strong competition between mangrove and non-mangrove plants (Schwamborn and Saint-Paul, 1996). However, damage to established stands can open

windows of opportunity for invasive species that may restructure the community (Kangas and Lugo, 1990; Lugo, 1998). The mangrove fern *Acrostichum*, for example, is a weedy pest that causes significant losses to mangrove forestry (Chan, 1996). The pest is currently controlled by application of herbicides, but efforts to control it are being refocused on its responses to shading and salinity (Medina *et al.*, 1990).

Mangroves themselves can become pests when they are introduced to new habitats. At least 6 mangrove species have been introduced to the Hawaiian Islands since the early 1900's. *Rhizophora mangle* has been a particularly successful transplant, but two other species (*Bruguiera gymnorrhiza* and *Conocarpus erectus*) also have self-sustaining populations. The mangroves were planted to help stabilize sediments in coastal mud flats. As invaders, however, the mangroves have had negative effects. In particular, they compete with native plants and modify habitats that are important to Hawaiian birds (including endangered species). They also cause drainage problems in some areas (Allen, 1998).

Other pest organisms damage the mangroves, not by competing with them, but simply by living on their surfaces. For example, the spiders *Tetragnatha nitens* and *Chiracanthium* live on *Rhizophora*. They lay their eggs on the leaves, which induces leaf rolling, chlorosis and wilting. Heavy infestations can kill the trees (Irianto and Suharti, 1994). The semi-parasitic mistletoe, *Phthirusa maritima*, has a more direct effect on the trees. Infections in *Conocarpus erectus* and *Coccoloba uvifera* induce higher transpiration rates, lower CO₂ assimilation rates, and lower water-use efficiency (Orozco *et al.*, 1990).

By far the most extensive and serious damage to mangroves occurs through the feeding activities of herbivorous animals. While most of the damage is done by animals feeding in the canopy, several kinds of crustaceans and mollusks bore directly into submerged mangrove wood and do significant damage. Spaeromatids are generally the most common wood-borers (e.g., Sivakumar, 1992; Huang *et al.*, 1996). Infestations of these isopods are heavier in dead mangrove stumps than in live wood but the stumps and woody debris provide a perennial source of larvae that also attack the living wood (Sivakumar and Kathiresan, 1996). Distributions of these pests are controlled largely by currents and tidal regimes.

Of the animals feeding on the mangrove canopy, insects are undoubtedly the most destructive. Murphy (1990d) described 102 insect herbivores that attack 21 mangrove species in Singapore. Veenakumari *et al.* (1997) listed 197 species of herbivores on the Andaman and Nicobar Islands. Some of the insect herbivores are serious crop pests that simply use mangroves as alternative hosts. Others have apparent preferences for mangroves (e.g., *Mictis* on *Sonneratia*, *Glaucias* on *Lumnitzera*, *Calliphara* on *Excoecaria*, and *Antestiopsis* on *Avicennia*; Murphy, 1990d).

Insect herbivores can completely defoliate mangrove stands. *Rhizophora* leaves that have been attacked by scale insects (*Aspidiotus destructor*) first turn yellow at the site of feeding, then brown and necrotic. In extreme cases, the leaves dry up, drop off, and the entire seedling dies (Kathiresan, 1993). Periodic outbreak populations of the moth *Achaea serva* defoliate large stands of *Excoecaria agallocha* (McKillup and McKillup, 1997). In Singapore, feeding by *Paralebeda* and *Selepa* caterpillars can lead to total loss of shoots in *Excoecaria*; *Trabala krishna* has the same effect on *Sonneratia*. Apical bud destruction may reduce leaf production and change the architecture of the plant (Murphy, 1990d).

Summer feeding by the caterpillar *Nephterix syntaractis* in Hong Kong completely defoliates *Avicennia marina*, severely reducing the reproductive output of the trees (Anderson and Lee, 1995). *Kandelia candel* in the same region may experience a 35% defoliation (Lee, 1991). In Belize, Central America, an outbreak of the lepidopteran *Phocides pigmalion* on *Rhizophora mangle* increases leaf abscission rates and reduces above-ground net primary production by 5-20%. The lost production normally would have been exported to surrounding marine environments (Ellison and Farnsworth, 1996b). The insect defoliator, *Pteroma plagiophleps* (Lepidoptera: Psychidae), has been newly recorded on the Indian west coast (Santhakumaran *et al.*, 1995).

Insect herbivores may show preferences among mangrove hosts. In an Ecuadorian mangal, the bagworm, *Oiketicus kirbyi* removed 80% of the foliage of *Avicennia germinans*, 10% of the *Conocarpus erectus* and < 5% of the *Laguncularia racemosa* (Gara *et al.*, 1990). The susceptibility of mangrove species, and individual mangrove plants, may relate to their physico-chemical characteristics. High leaf toughness, measured as the ratio of protein to fibre, reduces palatability and digestibility (Choong *et al.*, 1992). Tannins also deter herbivores. *Avicennia* species, which have low tannin levels, suffer more herbivore damage than do *Rhizophora* species, which have more tannins (Kathiresan, 1992).

Feeding preferences of the insects may also be influenced by the health of the mangrove. Nutrient enriched trees tend to suffer higher herbivory. Herbivory by *Ecdytolopha* (an endophytic insect that feeds in apical buds) and *Marmara* (which mines stems) on *Rhizophora mangle* increased significantly when the trees were treated with P and NPK. Fertilization with N alone did not increase herbivory (Feller, 1995). Damage from feeding herbivores may also invite further attack. Farnsworth and Ellison (1993) made small holes in the leaves of *R. mangle* and found that the artificial damage increased natural damage from herbivorous insects; in 50 days, the size of the holes had increased 45.1%.

Some herbivores feed specifically on the reproductive tissues and seeds of mangroves. Crabs are particularly important seed predators (Osborne and Smith, 1990; Robertson, 1991; McGuinness, 1997b; Dahdouh-Guebas *et al.*, 1998). However, insects can also attack mangrove seeds. Insect borers appear to impair the growth of *Avicennia marina* propagules, but do not kill them (Robertson *et al.*, 1990). A mite (*Afrocypholaelaps africana*) feeds on mangrove pollen. Unopened flower buds are mite-free, but newly opened flowers are infested by all post-embryonic stages of the mite. Egg-bearing female mites are dispersed among the mangroves by the honeybee *Apis mellifer*. The mite population declines as the mangrove flowering season ends (Seeman and Walter, 1995). It is not clear what affect the mites have on the mangrove population.

6.12. Responses to anthropogenic stress

In recent years, anthropogenic pressures have significantly damaged the world's mangroves, with alarming levels of habitat loss. For example, Ramirez-Garcia *et al.* (1998) estimate a 32% decrease in mangroves in the Santiago River of Mexico in the past 23 years. Aksornkoae (1993) and Raine (1994) report more than a 50% reduction in the mangrove forests of Thailand. Mndeme (1995) reports that the mangrove resources in the Mafia District of Tanzania are in danger of collapse. In the Florida Keys, USA, Strong and Bancroft (1994) report that 15% of the original mangrove forests have been cleared for development; mean forest size has decreased 41%. Approximately 45% of the mangroves

in Indonesia have been heavily impacted by human activities (Choong *et al.*, 1990). Some estimates put global mangrove loss rates at one million ha y⁻¹ (Mohamed, 1996). Such levels of destruction and habitat fragmentation raise concerns about conservation of biodiversity in the mangrove habitats and preservation of the mangals themselves.

Ellison and Farnsworth (1996a) classified anthropogenic disturbances into four types: extraction, pollution, reclamation, and changing climate. These disturbances are listed in the order of their increasing spatial scale, their increasing temporal scales, and the increasing time required for recovery. Research suggests that even relatively low impact human activities can affect the mangrove environment. For instance, boardwalks placed in the mangals around Sydney, Australia to provide access for educational and recreational activities have modified sediment composition and changed benthic invertebrate community structure (Kelaheer *et al.*, 1998a, 1998b). It may require fairly long periods for the mangal to recover from even minor disturbances (Snedaker *et al.*, 1992).

Diversion of freshwater for irrigation and land reclamation has historically been a major cause of wide-scale mangrove destruction (Conde and Alarcón, 1993, Twilley *et al.*, 1998). Throughout the world, mangroves and mangrove products have also been used for timber, fuel, food, clothing, perfume, dyes, tannins, and medicine (Rasolofo, 1997; reviewed by Bandaranayake, 1998). In the past several decades, extensive tracts of mangrove have been converted for aquaculture. Shrimp ponds have become particularly common in many former mangals (Twilley *et al.*, 1993; Primavera 1995; de Graaf and Xuan, 1998). Menasveta (1997) reports that nearly 55% of the mangroves in Thailand were converted to shrimp ponds between 1961 and 1993. Pond culture now surpasses open ocean fishing as the major source of shrimp there. Unfortunately, ponds in many regions are unsustainable and up to 70% of them may be left idle after some period of production (Stevenson, 1997). Because of changes in the sediments caused by pond construction, the abandoned sites are difficult to revegetate with mangroves even after the shrimp farming has ceased (de Graaf and Xuan, 1998).

Intact mangals process heavy organic loads and could help oxidatively process nutrients in shrimp pond effluents (Eguchi *et al.*, 1997; Twilley *et al.*, 1998). Robertson and Phillips (1995) estimated that 2 to 22 hectares of mangrove forest could completely filter excess nitrogen and phosphorus from a one-hectare shrimp pond. The effluents, in turn, could promote growth of the mangroves. A 70% dilution of effluent from a semi-intensive shrimp culturing pond in south India significantly increased growth of mangrove seedlings (Rajendran and Kathiresan, 1996).

In the Mekong Delta of Vietnam, living mangroves actually increase productivity of shrimp aquaculture facilities. Binh *et al.* (1997) collected data suggesting that yields are greater in shrimp ponds with 30-50% mangrove coverage. Farmers who integrate shrimp and mangrove farming may, therefore, realize better economic returns (Hong and San, 1993). P.T. Smith (1996) found that sediments in the shrimp ponds are very similar to those from nearby mangrove habitats, again suggesting that mangrove and shrimp aquaculture should be compatible.

Heavy historical exploitation of mangroves has left many habitats severely damaged. The damage has consequences beyond loss of the trees themselves. For example, because mangroves serve as nursery habitats for many crustaceans and fish, damage can have a direct effect on fishery resources and the lives of those who depend on them (John and Lawson, 1990; Twilley *et al.*, 1991, 1998; Ruitenbeek, 1994; Fouda and

Al-Muharrami, 1995; Primavera, 1998). Recently, community-based approaches to conservation and resource management have been launched with the participation of local people (A.H. Smith and Berkes, 1993; Kairo, 1995; Semesi, 1998). Guidelines for evaluation, restoration, and management of mangrove ecosystems are also being developed (Field, 1996; Siddiqi and Khan, 1996; Ewel *et al.*, 1998b; Gilbert and Janssen, 1998; Kaly and Jones, 1998; Twilley *et al.*, 1998).

Efforts are being made to rebuild damaged mangrove ecosystems in many parts of the world (Semesi, 1992; Chowdhury and Ahmed, 1994; Field, 1998). The programs are called regeneration, reclamation, rehabilitation, or ecodevelopment. Finding adequate supplies of viviparous seedlings for use in such afforestation projects is a challenge and more effective methods are needed. Living seedlings can be cut and the cuttings induced to produce roots and shoots. However, success of the cuttings depends on how they are done (growth and survival depend on where the location and length of the cutting; Ohnishi and Komiyama, 1998). *In vitro* micropropagation methods have been recently developed for *Excoecaria agallocha* (C.S. Rao *et al.*, 1998). These techniques hold promise for mangrove regeneration.

In South Sulawesi, Indonesia, where mangrove removal has produced significant environmental problems, efforts are underway to launch mangrove agroforestry projects. Planting of *Rhizophora mucronata* along the coast is mitigating coastal erosion and preventing flooding (which otherwise damages aquaculture facilities). Controlled harvesting of the mangroves produces income as the product is sold for fuel wood (Weinstock, 1994). Efforts at mangrove agriculture are also underway in the Federated States of Micronesia (Devoe and Cole, 1998). However, there is still much to learn about proper management and sustainable harvesting of mangrove forests. Despite nearly 100 years of careful management, timber yields from the Matang Mangrove Forest Reserve in Malaysia are declining significantly (Gong and Ong, 1995).

6.13. Responses to Global changes

It is expected that increasing concentrations of atmospheric CO₂ and other "greenhouse gases" will bring changes in the global climate. It has been predicted that each decade could bring a 0.3° rise in air temperature and a 6 cm rise in the global sea level (Titus and Narayanan, 1996; Wilkinson, 1996; Gregory and Oerlemans, 1998). Because of their location at the interface between land and sea, mangroves are likely to be one of the first ecosystems to be affected by global changes. Most mangrove habitats will experience increasing temperature, changing hydrologic regimes (*e.g.*, changes in rainfall, evapotranspiration, runoff and salinity), rising sea level and increasing tropical storm magnitude and frequency (R.W. Stewart *et al.*, 1990, Field, 1995; Michener *et al.*, 1997). Davis *et al.* (1994) have developed a framework for assessing risks to mangrove ecosystems in the context of a changing global climate but the seriousness of the effects will be strongly site-specific (Kjerfve and Macintosh, 1997).

Small increases in air temperature may have little direct effect on the mangroves (Field, 1995), but if temperatures exceed 35° C, root structures, seedling establishment and photosynthesis will all be negatively affected. The broader effects of temperature increases may be in modifying larger-scale distribution and community structure, increasing species diversity in higher latitude mangals and promoting spread of mangroves into sub-tropical saltmarsh environments (Ellison, 1994).

Because they are so specialized, and may live so close to their tolerance limits, mangroves are particularly sensitive to minor variation in hydrological or tidal regimes (Blasco *et al.*, 1996). Reduced rainfall and runoff would produce higher salinity and greater seawater-sulfate concentrations. Both would decrease mangrove production (Snedaker, 1995). The most important effects, however, would come from rising sea levels, but responses will vary among locations and will depend on the local rate of the rise and the availability of sediment to support reestablishment of the mangroves (Pernetta 1993; Parkinson *et al.*, 1994; Semeniuk, 1994; Woodroffe, 1995, 1999). For example, in the Caribbean, mangrove seedlings are very sensitive to low sediment availability, suggesting that mangroves will not survive on Caribbean coral islands if sea levels increase as predicted (Ellison, 1996).

Ellison and Farnsworth (1997) studied the response of *Rhizophora mangle* to increased inundation, mimicking the sea-level changes expected in the Caribbean in the next 50-100 years. After 2.5 years of higher water, plants would have significantly lower rates of photosynthesis and growth, be shorter and narrower, have fewer branches and leaves, and more acid-sulfide in their soils. The authors suggested that increased mangrove growth rates predicted for increasing atmospheric CO₂ may be offset by decreased growth resulting from changes in tidal regimes.

Sayed (1995) tested the effects of higher water levels on *Avicennia marina* by flooding potted seedlings. The treatment resulted in stomatal closure, loss of chlorophyll fluorescence, and a slight reduction of leaf water potential. Post-flooding recovery, however, was rapid, suggesting that sea level rises could lead to colonization of supratidal flats by this species (Sayed, 1995). As sea level rises, mangroves, in general, would tend to shift landward. Human encroachment at the landward boundary, however, may make this impossible. Consequently, the width of mangrove systems would be likely to decrease as the sea-level rose (Kjerfve and Macintosh, 1997).

The mangrove-associated fauna would be affected both directly by climatic changes and indirectly by changes in the mangroves. Species that are tolerant of increasing temperatures (e.g., fish, gastropods, mangrove crabs and other crustaceans) may adjust rapidly to the changes. In contrast, soft-bodied animals and bivalve mollusks would be very sensitive to higher temperatures. Desiccation that would accompany increasing temperatures would harm many marine species associated with mangroves (Kjerfve and Macintosh, 1997). For mangrove-dependent species, however, the most serious consequences of a changing climate would likely be the loss of habitat as the global mangrove forests declined.

7. ECOLOGICAL ROLES OF MANGROVE ECOSYSTEMS

7.1. Litter decomposition and nutrient enrichment

Mangrove ecosystems produce large amounts of litter in the form of falling leaves, branches and other debris. Decomposition of the litter contributes to the production of dissolved organic matter (DOM) and the recycling of nutrients both in the mangal and in adjacent habitats. The organic detritus and nutrients could potentially enrich the coastal sea and, ultimately, support fishery resources. The contribution of the mangroves could be particularly important in clear tropical waters where nutrient concentrations are normally low.

The nutrient cycling begins when leaves fall from the mangroves and are subjected to a combination of leaching and microbial degradation (Lee *et al.*, 1990b; Chale, 1993). Leaching alone removes a number of substances and can produce high levels of DOM (Benner *et al.*, 1990b). Potassium is the most thoroughly leached element with up to 95% of the total potassium being removed in a very short time (Steinke *et al.*, 1993b). Carbohydrates also leach quickly during early decomposition. Tannins, in contrast, leach very slowly and the high tannin contents may slow establishment of bacterial populations in the initial period of decomposition. As the tannins are eventually leached, the bacterial populations rapidly increase (Steinke *et al.*, 1990; Rajendran, 1997; Rajendran and Kathiresan, 1999b).

Bacteria and fungi contribute to decomposition of the mangrove material and to the transformation and cycling of nutrients. Fungi are the primary litter invaders, reaching their peak in the early phases of decomposition (Rajendran, 1997). The phylloplane fungi do not attack live leaves; they begin to break the leaf material down only after it has been submerged. There are two major phases of fungal decomposition. Cellulase-producing fungi first attack the leaves between 0 and 21 days after submergence; xylanase producers are active between 28 and 60 days. Pectinase, amylase and protease producers are present throughout decomposition (Singh and Steinke, 1992; Raghukumar *et al.*, 1994a).

Bacterial colonies appear shortly after the litter has been colonized by fungi. The bacteria grow quickly and can reach very high densities. Zhuang and Lin (1993) measured bacterial densities from 2×10^5 to $10 \times 10^5 \cdot \text{g}^{-1}$ on *Kandelia candel* leaves that had decomposed for 2-4 weeks. This was about 100 times higher than densities of actinomycetes and filamentous fungi. The N_2 -fixing azotobacters are one of the important groups in the decomposing litter (Rajendran, 1997) and their activities may increase the nitrogen content of the leaves 2 - 3 times (Wafar *et al.*, 1997; Rajendran, 1997).

Chale (1993) measured a similar rapid nitrogen increase in leaves after six weeks of decomposition and suggested that the litter 1) provides a surface for microbial nitrogen synthesis and 2) acts as a nitrogen reservoir. The C:N ratio of decomposing *Avicennia marina* leaves drops dramatically from approximately 1432 to 28, due primarily to a large increase in their nitrogen content (Mann and Steinke, 1992; Singh and Steinke, 1992). In another study, N.F.Y. Tam *et al.* (1990) saw the C:N ratio in decomposing leaves increase for one week, then decrease, and finally stabilize at approximately 74. They hypothesized that the initial increase resulted from the conversion of particulate and soluble nitrogen in the litter to proteins in bacteria and fungi.

A number of factors can affect the rate of litter decomposition and, therefore, the rates of nutrient cycling. For example, litter decomposition rates vary among mangrove species. *Avicennia* leaves, because they are thinner and have fewer tannins, decompose faster than those of other species (Sivakumar and Kathiresan, 1990; Steinke *et al.*, 1990; Kristensen *et al.*, 1995). *Avicennia* leaves also sink and begin to decompose immediately whereas the leaves of other species (e.g., *Sonneratia* and *Rhizophora*) may float for several days (Wafar *et al.*, 1997). Lu and Lin (1990) found that litter of *Bruguiera sexangula* decomposes quickly. *Aegiceras corniculatum*, in contrast, decomposes slowly (Tam *et al.*, 1990).

Decomposition is influenced by tidal height, rainfall and temperature. In subtropical mangrove forests, mangrove debris decomposes substantially faster in the rainy season (e.g., Woitchik *et al.*, 1997). Mackey and Smail (1996) studied decomposition of

Avicennia marina. They found significantly faster decomposition in lower intertidal zones with greater inundation. They also found an exponential relationship between leaf decomposition rate and latitude with leaves decomposing most quickly at low latitudes. They attributed the pattern to temperature differences, and concluded that seasonality can have important effects on organic cycling and nutrient export from mangrove systems.

Breakdown and decomposition of mangrove litter is accelerated by the feeding activities of invertebrates (Camilleri, 1992). The animals may process large volumes of the litter, contributing significantly to nutrient dynamics. Litter turnover rates have been estimated by measuring rates of leaf decomposition. However, estimates made this way are generally 10-20 times lower than rates calculated from actual measurements of leaf fall and litter standing crop. The difference in the estimates can be attributed to 1) tidal export and 2) the feeding activities of crabs. The

crab feeding may be the more important of these in many regions. For example, in the Ao Nam Bor mangrove forest in Thailand, crabs process about 80% of the litter deposited in the mid-intertidal zone and nearly 100% of the leaves deposited in the high intertidal (Poovachiranon and Tantichodok, 1991). In field experiments, Twilley *et al.* (1997) found that mangrove crabs process the mangrove material very quickly. They removed a full day's accumulation of mangrove leaf litter in only 1 hr. Because the mangrove material is quite refractory, it may need to decompose for some time before it is useful to other invertebrates. Wafar *et al.* (1997) estimated that litter needs to decompose for about two months before it can be used in most detritivores' diets. *In situ* observations verify that mangrove leaves attract shrimp, crabs, and fish (particularly juveniles), but only after several weeks of decomposition (e.g., Rajendran, 1997; Rajendran and Kathiresan, 1999a; Figure 17).

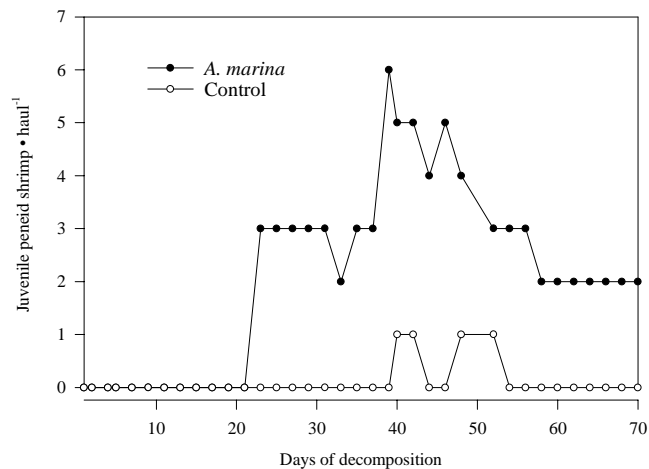


Figure 17. Number of penaeid shrimp associated with decomposing leaves of *Avicennia marina* (in situ litterbag experiment by Rajendran, 1997). Populations increase dramatically, but only after several weeks of decomposition.

7.2. Food webs and energy fluxes

Mangals contribute to complex food webs and important energy transfers. However, it is not clear how, or whether, these processes affect the larger ecosystem. While the living vegetation is a valuable food resource for insects, crustaceans, and some vertebrates, most of the mangrove production is transferred to other trophic levels through litterfall and detrital pathways (Figure 18). Mangrove forests produce organic carbon well in excess of the ecosystem requirements. Duarte and Cebrian (1996) estimate that the excess photosynthetic carbon approaches 40% of net primary production. While some of this organic matter simply accumulates in the sediments, large amounts could potentially

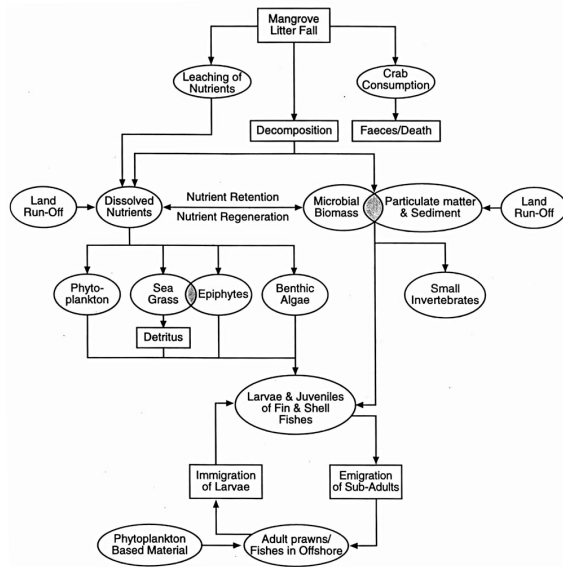


Figure 18. A stylised food web in a mangrove ecosystem. The food web may be highly localized without strong connections to other habitats. The foundations of the web are detritus, microbes, algae and seagrasses.

with stable isotopes also suggest that mangroves do not make major contribution to coastal food webs (Primavera, 1996; Loneragan *et al.*, 1997). In fact, the data suggest that carbon may instead be flowing from oceanic systems into the mangrove habitat (Figure 19). Oceanic carbon contributed up to 86% of the particulate organic carbon (POC) in water samples from a Brazilian mangal (Rezende *et al.*, 1990).

It appears that mangroves, in general, make only a localized contribution to the food web (Fleming *et al.*, 1990; Mohammed and Johnstone, 1995). Sediment meiofauna, for example, feed directly on mangrove detritus. The composition of the meiofaunal community changes during the process of litter decay, suggesting that the community is responding to chemical changes in the leaves (Gee and Somerfield, 1997). The meiofaunal community, though large in some habitats, may largely be a trophic dead end that contributes little to the larger food web (Schrijvers *et al.*, 1998).

The mangroves may have stronger trophic linkages with epibenthic invertebrates and fish living in the mangal and in nearby habitats (e.g., seagrass beds). For example, mangrove detritus contributes to the nutrition of juvenile *Penaeus merguensis* living in tidal creeks. The juveniles feed directly on mangrove detritus, on other small detritivorous invertebrates, and on benthic microalgae growing in the mangal (Newell *et al.*, 1995). Shrimp in mangrove estuaries may also feed heavily on seagrass epiphytes (Loneragan *et al.*, 1997). Invertebrates may also feed on the variety of cyanobacteria and microalgae that live on submerged portions of the mangroves and on leaf litter (e.g., Sheridan, 1991; Farnsworth and Ellison, 1995; Pedroche *et al.*, 1995).

Pinto and Punchihewa (1996) found that syngnathid fish (pipefish) in the Negombo Estuary of Sri Lanka fed primarily on mangrove litter. However, mangroves apparently contribute little of the carbon assimilated by other fishes. This is true despite the movement

be transported offshore (Alongi, 1990b; Robertson *et al.*, 1991, 1992; Lee, 1995). The amount of material exported, however, depends strongly on local conditions and varies enormously among mangals (Twilley *et al.*, 1992).

Material exported from the mangroves could potentially support offshore communities (Marshall, 1994; Robertson and Alongi, 1995; Van Tussenbroek, 1995), but the connections between mangal and adjacent habitats are complex, dynamic, and have been difficult to demonstrate unequivocally (Alongi *et al.*, 1992; Twilley *et al.*, 1992; Hemminga *et al.*, 1995; Alongi, 1998). For instance, Jennerjahn and Ittekkot (1997) found that organic matter in continental sediments in eastern Brazil was very different from that in mangrove environments and concluded the mangrove matter is largely retained and decomposed within the mangal itself. Studies

of a number of fish species between mangrove habitats and nearby seagrass beds (Marguillier *et al.*, 1997).

Mangrove detritus is probably more important as a substrate for microbial activity and nutrient regeneration than it is as a direct food source for detritivores. Wafar *et al.* (1997) analyzed energy and nutrient fluxes between mangroves and estuarine waters and concluded that mangroves contribute significantly to the estuarine carbon budget. However, they contribute little to nitrogen and phosphorus budgets. It is not clear whether any of these substances are exported from the mangal in sufficient quantities to make significant contributions to energy flow and the ecology of the broader ecosystem (Alongi *et al.*, 1992; Alongi, 1998). Mangrove sediments efficiently uptake, retain and recycle nitrogen (Rivera-Monroy *et al.*, 1995). Resident bacteria and benthic algae rapidly assimilate available ammonium and prevent its export (Kristensen *et al.*, 1995; Middelburg *et al.*, 1996). The mangrove environment may, therefore, represent a nutrient and carbon sink rather than a source for adjacent habitats. Careful measurements and creative experimentation will be necessary to clarify the role these habitats play in larger-scale food webs and energy fluxes.

8. CONCLUDING REMARKS

Mangrove ecosystems are receiving increasing attention, but we still lack much basic information about their structure and function. There are still fundamental gaps in our knowledge of the reproductive biology of mangroves, and mangrove evolution is poorly understood. We are still far from understanding energy flow and food web dynamics in mangrove environments and how the mangroves connect with other ecosystems. There is a great need to better understand the effects of environmental change and pollution on mangrove flora and fauna. Animals that are highly dependent on mangroves need additional study, particularly with respect to larval supply and recruitment. Such ecobiological research can be linked to management of mangroves and associated fishery resources (e.g., Bacon and Alleng, 1992; Hudson and Lester, 1994; Fouda and Al-Muharrami, 1995).

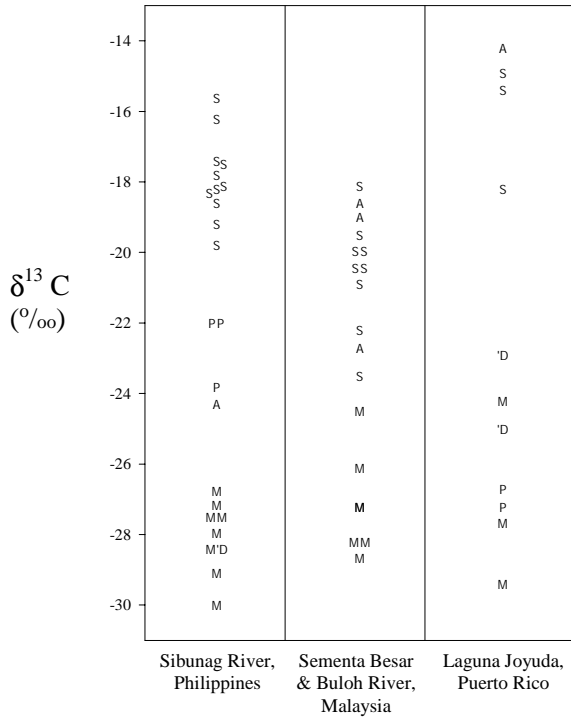


Figure 19. Ratios of stable carbon isotopes in shrimp collected from mangrove habitats in the Philippines (Primavera, 1996), Malaysia (Rodelli *et al.*, 1984), and Puerto Rico (Stoner and Zimmerman, 1988). Shrimp tissue $\delta^{13}\text{C}$ values (S) are much closer to the $\delta^{13}\text{C}$ values of plankton (P) and algae (A) than they are to those of mangrove leaves (M) or detritus (D). This suggests that the shrimp are deriving their carbon primarily from algae and the plankton; the mangrove detrital pathway contributes little to their nutrition (after Primavera, 1996).

Mangrove ecosystems are seriously threatened, mainly by human activities that impact the habitat (Pons and Fiselier, 1991; Fouda and Al-Muharrami, 1995; Farnsworth and Ellison, 1997a; Figure 20). The value of mangroves

has gone unrecognized for many years (Farnsworth, 1998a) and the forests are disappearing in many parts of the world. The full extent of the damage is not yet fully known, but technological advances (e.g., airborne multispectral sensors and satellite imagery) are allowing researchers to map and monitor mangrove habitats (Ibrahim and Hashim; 1990; Gang and Agatsiva, 1992; Lin *et al.*, 1994; Aschbacher *et al.*, 1995; Wei *et al.*, 1995; Long and Skewes, 1996; Green *et al.*, 1997, 1998; N.F.Y. Tam *et al.*, 1997; Blasco *et al.*, 1998; De Jesus and Bina, 1998). The results of such studies are not encouraging; mangrove habitats continue to shrink around the world.

Even where efforts have been made to slow the destruction, remaining forests have a number of problems. In some areas, the health and productivity of the forests have declined significantly. In Indian mangrove ecosystems, 67% of the mangrove plants, 52% of the macroalgae, 10% of the invertebrates and 4% of the vertebrates are endangered (e.g., Ananda Rao *et al.*, 1998). Similar losses have occurred in the mangals of Singapore (Turner *et al.*, 1994) and are likely to be seen in other regions of the world. Mangrove systems require intensive care to save threatened taxa from extinction. The causes of these tragic losses differ from habitat to habitat but are generally tied directly or indirectly to human activities. Individual study is required to determine the most effective remedial measures. Where degraded areas are being revegetated, continued monitoring and thorough assessment must be done to help us understand the recovery process (van Speybroeck, 1992). This knowledge will help us develop strategies to effectively rehabilitate degraded mangrove habitats the world over.

It has long been known that mangrove protect and stabilize coastlines. They are more effective than concrete barriers in reducing erosion, trapping sediments, stabilizing shorelines, and dissipating the energy of breaking waves (Pearce, 1996). We have learned that they are critical nursery habitats for important marine species. Pioneering investigations are now showing that mangroves and their associated fauna can be sources of valuable products like black tea, mosquitocides, gallotannins, microbial fertilizers, antiviral drugs, anti-tumor drugs and UV-screening compounds (Ravi and Kathiresan, 1990; Premanathan *et al.*, 1992; Kathiresan and Pandian, 1991, 1993; Kathiresan, 1995b; Kathiresan *et al.*, 1995a; Ravikumar, 1995; Moorthy and Kathiresan, 1997b; Bandaranayake, 1998; Palaniselvam, 1998; Kathiresan, 2000). Mangroves may be developed as sources of high value commercial products and fishery resources and as sites

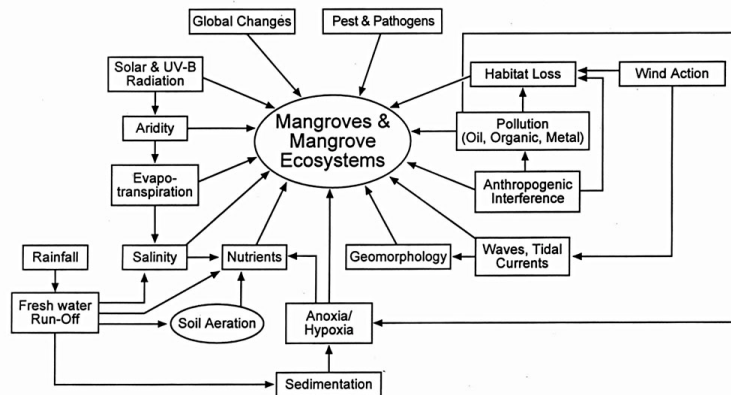


Figure 20. Factors impacting mangroves and ecosystems. These valuable systems are under pressure from a variety of physical, chemical, and biological processes. Many of the stresses on these environments result from human activities.

for a burgeoning ecotourism industry (Thorhaug, 1990; Ruitenbeek, 1994; Barton, 1995). Their unique features may also make them ideal sites for experimental studies of biodiversity and ecosystem function (Osborn and Polsenberg, 1996; Farnsworth, 1998b; Field *et al.*, 1998). All this will require that the resource is understood, carefully managed, and protected (Farnsworth and Ellison, 1997b; Ammour *et al.*, 1999; Figure 21). Involvement of local communities in conservation and education in wise use of our precious mangrove resources will ensure that these unique ecosystems survive and flourish.

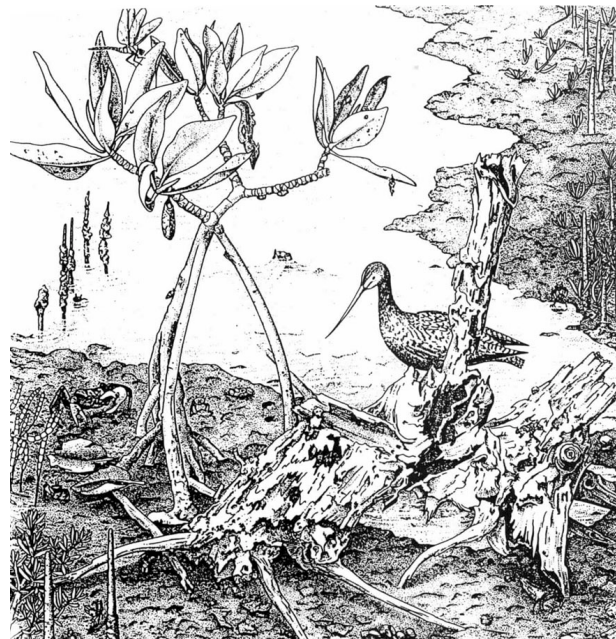


Figure 21. Mangroves are highly dynamic and complex systems that are still poorly understood. Continued study, combined with concerted conservation efforts will be necessary to preserve these fragile and unique environments (from Rutzler & Feller, 1996).

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