

---

# 13 Biodiversity and Ecosystem Processes in Tropical Estuaries: Perspectives of Mangrove Ecosystems

---

ROBERT R. TWILLEY, SAMUEL C. SNEDAKER,  
ALEJANDRO YÁÑEZ-ARANCIBIA AND ERNESTO MEDINA

## 13.1 INTRODUCTION

The major form of vegetation that supports the biodiversity of tropical estuarine ecosystems consists of intertidal forested wetlands known as mangroves. Mangroves form a small portion of the world's forested landscape, but cover  $240 \times 10^3 \text{ km}^2$  of sheltered subtropical and tropical coastlines (Lugo *et al.* 1990; Twilley *et al.* 1992). This vegetation dominates the intertidal zone of tropical river deltas, lagoons and estuarine coastal systems that have significant inputs of terrigenous sediments (allochthonous materials), and it can also colonize the shoreline of carbonate platforms that are developed from calcareous sedimentary processes (with little or no influence from terrestrial runoff) (Thom 1982; Woodroffe 1992). In each of these geomorphologically distinct regional landscapes, local variations in topography and hydrology also result in the development of distinct ecological types of mangroves such as riverine, fringe, basin and dwarf forests (Lugo and Snedaker 1974). The combination of different geomorphological settings, each with a variety of ecological types, results in a diversity of mangrove ecosystems, each with specific characteristics of structure and function (Twilley 1988, 1995). Although there are relatively few species of trees (54 true species, Tomlinson 1986) in mangrove ecosystems, the biodiversity components of these ecosystems are unique because they include structural niches and refugia for numerous faunal and microbial species. In addition, the locations of these forested wetlands at the land-sea interface form interdependent assemblages that link the nearshore marine environment with inland terrestrial landscapes (Macnae 1968; Chapman 1976;



Odum *et al.* 1982; Tomlinson 1986; Gilmore and Snedaker 1993; Twilley *et al.* 1993).

The mosaic of mangrove habitats provides a variety of biodiversity components that are important to the function and environmental quality of tropical estuarine ecosystems. The dominant ecological function of mangroves is the maintenance of nearshore marine habitats and the concomitant provision of food and refugia to a variety of organisms at different trophic levels (Odum and Heald 1972; Thayer *et al.* 1987; Yáñez-Arancibia *et al.* 1988, 1993; Rojas *et al.* 1992; Sasekumar *et al.* 1992). In addition, mangroves play a major role in maintaining water quality and shoreline stability by controlling nutrient and sediment distributions in estuarine waters (Walsh 1967; Nixon *et al.* 1984; Twilley 1988; Alongi *et al.* 1992). Coastal forested wetlands are unique in that tides allow for an exchange of water, nutrients, sediment and organisms between intertidal and coastal regions of tropical estuaries. In addition, rivers link the runoff of sediments and nutrients from upland watersheds to the productivity and biogeochemistry of tropical estuaries. The multiple functions of mangrove ecosystems result in the extremely high primary and secondary productivity of tropical estuaries.

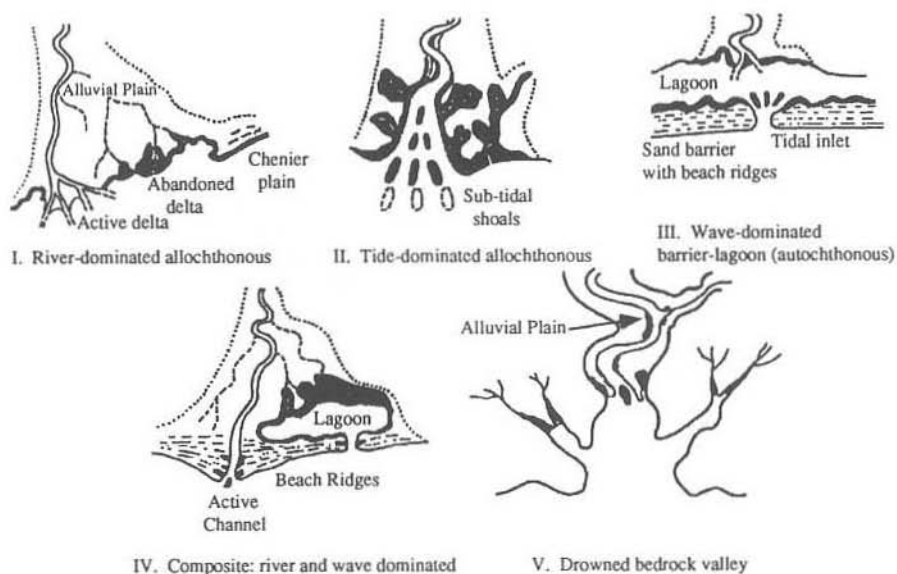
This chapter will summarize information that links the biodiversity components of mangrove habitats with the functional ecology of tropical estuarine ecosystems. Although the understanding of the functional ecology of mangroves is fairly limited, there are some examples that describe the influence of specific guilds on ecological properties of mangrove ecosystems. We will present an overview of the biodiversity of mangroves using ecological classifications of landscape mosaics, and including the traditional analysis based on species diversity. Although regions of estuaries are considered depauperate in species number, these areas have always been described as one of the most productive regions of the biosphere. Information on biodiversity and ecosystem function will be presented, along with examples of the vulnerability of these coastal systems to change. Change will include land-use alterations within both the estuary and its watershed, together with projections of climate change in tropical coastal areas.

### 13.2 BIODIVERSITY OF MANGROVES

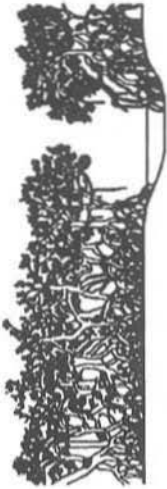
Biodiversity is usually defined at three levels, i.e. species, populations and ecosystems (Ray and McCormick 1992). The term "biodiversity components" has been recommended as an ecological reference to these several hierarchical levels, and the idea is particularly appropriate to describe tropical estuarine ecosystems (Yáñez-Arancibia *et al.* 1994). Biodiversity components of tropical estuaries can refer to the high diversity of species,

life histories, habitats and links in food webs, or the diverse pathways of energy flow and nutrient cycles that couple terrestrial and marine ecosystems at the land-sea interface. In addition, coastal geomorphological landforms and geophysical processes represent diverse components that effectively modulate the properties of estuarine ecosystems. These fluctuating environmental conditions of estuaries result in diverse spatial and temporal patterns of habitat utilization by organisms. This is especially true in mangrove ecosystems, since they are open systems interacting with a high diversity of functional landscapes, such as borders with terrigenous freshwater, coastal ocean water, the atmosphere and the sediment-water interface. Macnae (1968) used the term "mangal" to specify the properties of the mangrove ecosystem within the coastal landscape, in contrast to "mangrove" which is restricted to the characteristic spermatophyte in the intertidal zone. This distinct term to describe the properties of mangrove ecosystems, while seldom used in mangrove ecology, emphasizes the need to integrate the diverse physical, chemical and biological characteristics of tropical coastal ecosystems.

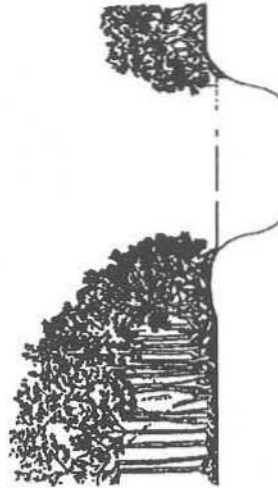
The diverse landforms of coastal regions can be considered as a biodiversity component of mangrove ecosystems (Figure 13.1). These regions can be classified into distinct geomorphological units that describe the influence of



**Figure 13.1** Five basic classes of geomorphological settings that influence the distribution of mangroves in the intertidal zone. Redrawn from Thom (1982)



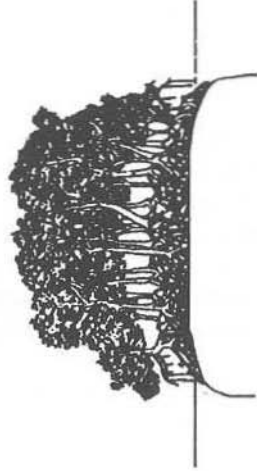
1.- Basin forest



2.- Riverine forest



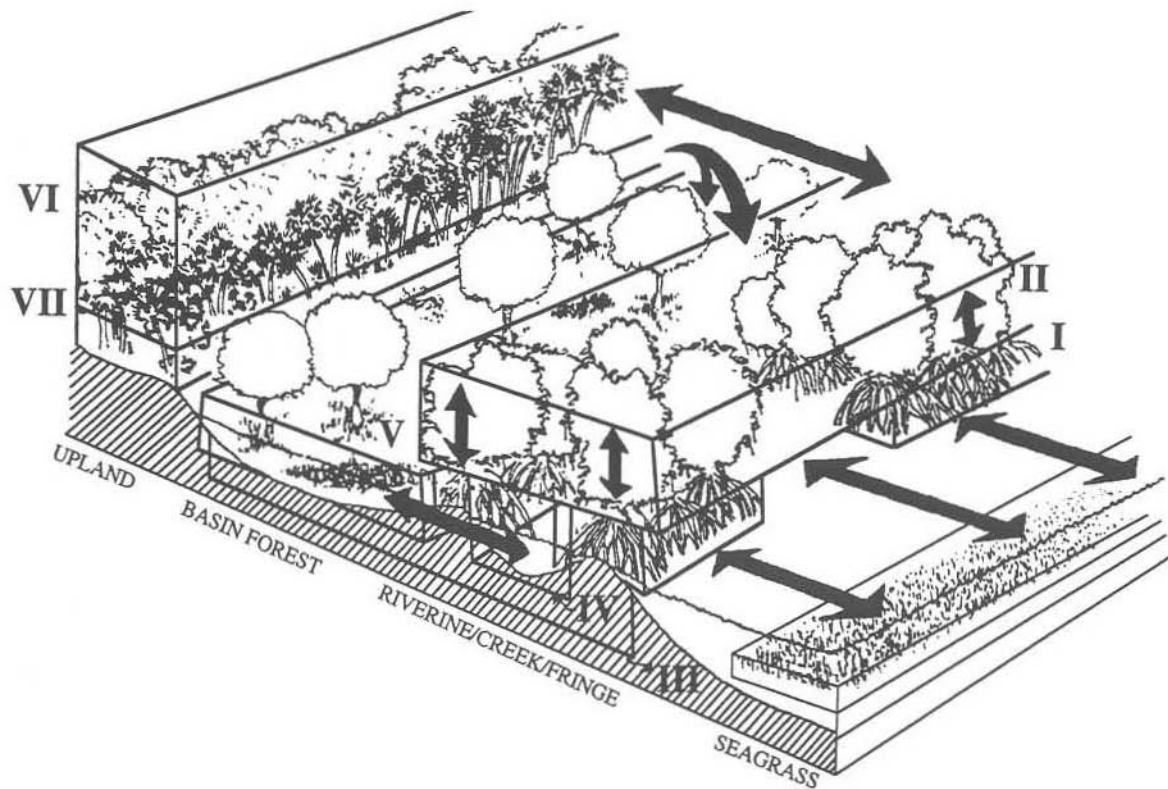
3.- Fringe forest



4.- Overwash forest



5.- Dwarf forest

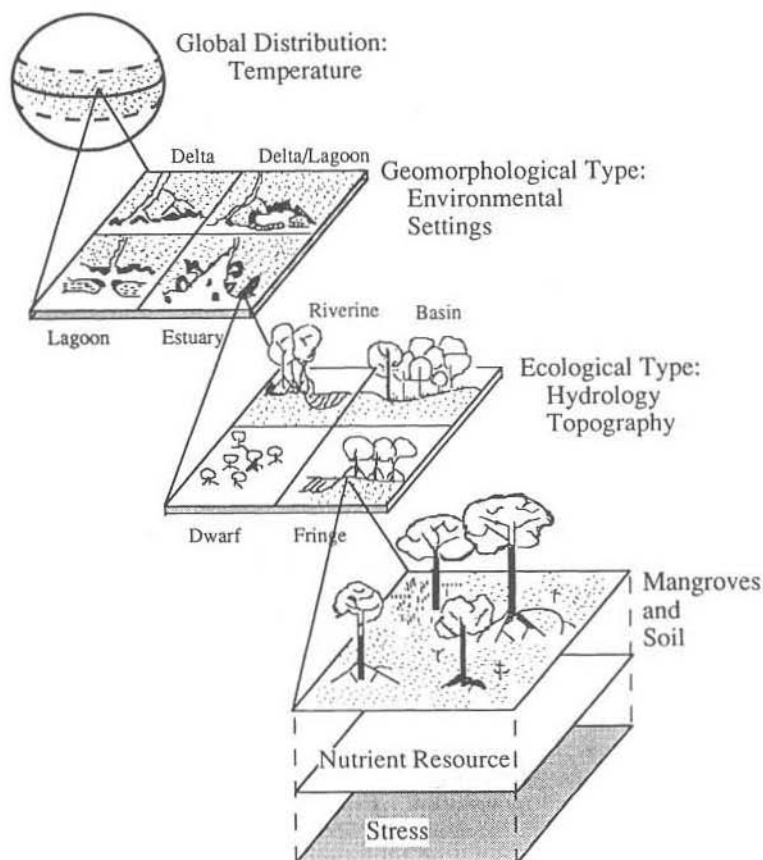


**Figure 13.2** Ecological types of mangroves (Lugo and Snedaker 1974) and the spatial distribution of these ecological types within the intertidal zone (from Gilmore and Snedaker 1993, reprinted by permission of John Wiley and Sons, Inc.). The arrows and roman numerals are used to define the location and movement of seven specific spatial guilds by principal habitat association in mangroves as described by Gilmore and Snedaker 1993 – I. Sublittoral/Littoral; II. Arboreal Canopy; III. Benthic and Infauna Community; IV. Tidal Creek and Ditch Community; V. Basin Community; VI. Upland Arboreal Community; VII. Upland Terrestrial Community

geophysical processes on the ecological characteristics of mangroves (Thom 1982). Mangroves occur within five basic groups of coastal environments depending on a combination of geophysical energies including the relative influences of rainfall, river discharge, tidal amplitude, turbidity and wave power (Figure 13.1). These five environmental settings are all influenced by inputs of terrigenous materials, while mangroves also occur on carbonate platforms where environmental settings are dominated by calcareous sedimentary processes and nutrient-poor conditions (Woodroffe 1992). The structure and function of these carbonate platform communities provide an interesting contrast to those mangroves influenced more by terrigenous materials.

The microtopographic factors of a region determine many of the hydrologic and chemical conditions of soil that control the patterns of forest physiognomy and zonation. In addition, tidal flooding frequency of the intertidal zone can influence the distribution of propagules and species (Rabinowitz 1978), although the influence of this mechanism ("tidal sorting") on forest structure has been recently questioned (Smith 1992). Lugo and Snedaker (1974) used the local patterns of mangrove structure in the south Florida and Caribbean regions to classify mangroves into riverine, fringe, basin, hammock and dwarf forests (Figure 13.2). This ecological classification of mangroves is also influenced by biological factors such as predation on propagules (e.g. crabs), differential resource utilization by seedlings, and physiological tolerance of trees that determine the patterns in physiognomy and zonation of mangrove trees (Davis 1940; Ball 1980; Lugo 1980; Snedaker 1982; Smith 1992). These two types of classification systems, geomorphological (Figure 13.1) and ecological (Figure 13.2), represent different levels of organization of the coastal landscape. Together they can be used to integrate the different scales of environmental factors that control the attributes of forest structure (Figure 13.3).

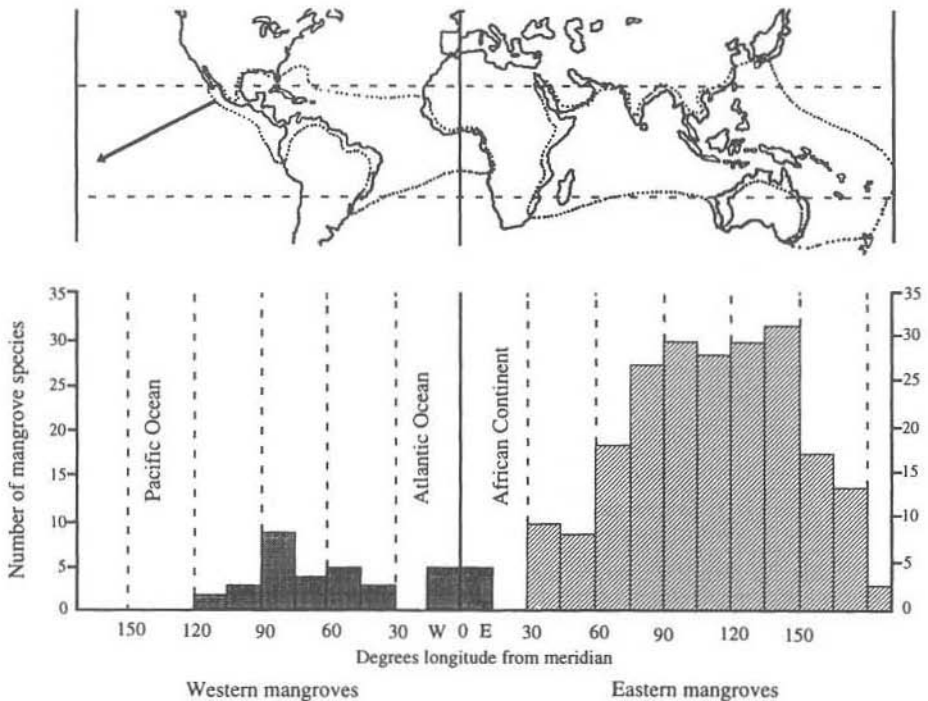
The species richness of trees is another biodiversity component of mangrove ecosystems (Figure 13.4). The environmental settings and biological factors described above not only influence the formation of different geomorphological and ecological types of mangrove forests, but they may also control species richness (Smith 1992). It is clear that within a continental area, changes in rainfall, temperature and tidal range may be important to the diversity of mangrove trees (Smith and Duke 1987). However, there are biogeographic factors that have resulted in an unbalanced global distribution of species richness (Tomlinson 1986). The diversity of mangrove tree species in the western hemisphere (11 species) is less compared with the eastern hemisphere (over 30 species) (Figure 13.4). This also results in much more complex zonation patterns along the intertidal zone of Old World continents as compared with the simpler patterns in the neotropics (such as those in Watson, 1928, compared with Davis, 1940;



**Figure 13.3** Hierarchical classification system to describe diverse patterns of mangrove structure and function based on global, geomorphological (regional) and ecological (local) factors that control the concentration of nutrient resources and stressors in soil

see Chapman 1976). At present, general conceptual models have improved to explain the development of zonation and forest structure within specific continental regions (Smith 1992; Gilmore and Snedaker 1993), but the development of specific ecological models to project change in species richness and ecological types of mangroves in response to land-use or global-climate changes is still limited by a lack of understanding of the manifold routes of coastal forest development (Twilley 1995).

Mangrove ecosystems support a variety of marine and estuarine food webs involving an extraordinarily large number of animal species (Macnae 1968; Odum and Heald 1972; Yáñez-Arancibia *et al.* 1988; Robertson and



**Figure 13.4** Generalized global distribution of mangroves including approximate limits of all species (upper panel) and histogram showing approximate number of species of mangroves per 15° of longitude (lower panel). (from Tomlinson 1986, reprinted with the permission of Cambridge University Press)

Duke 1990). The export of particulate organic matter (POM) supports food webs originating with particulate feeders, whereas the sometime larger export of soluble (dissolved) organic matter (DOM) forms the basis of the nearshore heterotrophic microorganism food web (Odum 1971; Alongi 1988; Snedaker 1989; Robertson *et al.* 1992). Many of the species of finfish and invertebrates that utilize the mangrove habitat and its organic resources are also components of offshore areas, a phenomenon that suggests intricate patterns of diel and seasonal migrations (cf. Thayer *et al.* 1987; Yáñez-Arancibia *et al.* 1988; Sasekumar *et al.* 1992). In addition to the marine estuarine food webs and associated species, there are a relatively large number and variety of animals, that range from terrestrial insects to birds, that live in and/or feed directly on mangrove vegetation. These include sessile organisms such as oysters and tunicates, arboreal feeders such as foliovores and frugivores, and ground-level seed predators. In consideration of the entire resident and casual faunal population in south Florida



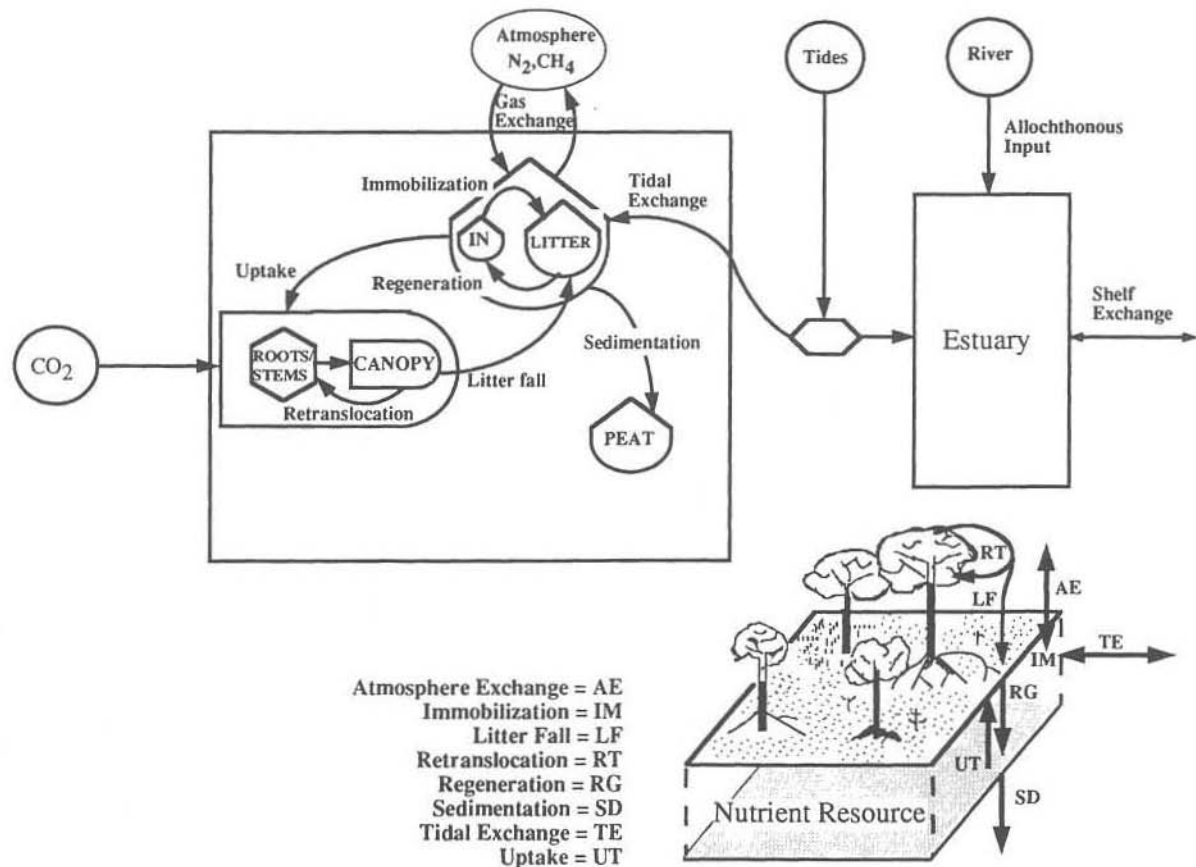
mangroves, Gilmore and Snedaker (1993) were able to recognize four distinct spatial guilds that may have well over an estimated 200 species, many of which are as yet uncataloged. In addition, Simberloff and Wilson (1969) documented over 200 species of insects in mangroves in the Florida Keys. For reference, the Florida mangroves consist of only three major tree species and one minor species of vascular plants. Based on these considerations, one can conclude that the low species richness of mangroves in Florida supports a disproportionately rich diversity of animals, the dimensions of which are only now being documented. This same conclusion can be applied to other parts of the Caribbean (Ruetzler and Feller 1988; Bacon 1990; Feller 1993). Even though there is a global difference in species richness of mangrove trees between the east and west hemispheres, there does not seem to be a corresponding contrast in the functional diversity of the associated fauna. One exception is that Robertson and Blaber (1992) suggested that species richness of fish communities in the tropical Atlantic Ocean region was less than in the Indo-Pacific areas.

### 13.3 FOREST STRUCTURE AND ECOSYSTEM FUNCTION

#### 13.3.1 Mangrove-specific effects on nutrient dynamics

Litter produced in the canopy of mangrove forests influences the cycling of inorganic nutrients on the forest floor, and the outwelling of organic matter to adjacent coastal waters (Figure 13.5) (Odum and Heald 1972; Twilley *et al.* 1986). Thus the dynamics of mangrove litter, including productivity, decomposition and export, influence the nutrient and organic matter budgets of mangrove ecosystems (Twilley 1988). Mangroves are forested ecosystems, and many of the ecological functions of nutrient cycling described for terrestrial forests may also occur in these intertidal forests. The amount of litter produced and the quality of that litter, as represented by C:N ratios and concentrations of lignin and polyphenols, contributes to the nutrient dynamics of forested ecosystems (Aber and Melillo 1982; Melillo *et al.* 1982). Thus, nitrogen cycling in the forest canopy is coupled to the nutrient dynamics in forest soils, and these are influenced by the species-specific nutritional ecology of the trees. Studies to test the presence of these feedback mechanisms will give insights into the ecological significance of tree biodiversity to the litter and nutrient dynamics of mangrove ecosystems.

The accumulation of leaf litter on the forest floor of mangrove ecosystems can be an important site for nutrient immobilization during decomposition (Figure 13.5; see also Section 13.3.2) (Twilley *et al.* 1986). The concentration of nitrogen in leaf litter usually increases during decomposition on the forest floor (Heald 1969; Rice and Tenore 1981; Twilley *et al.* 1986; Day *et al.*



**Figure 13.5** Fluxes of organic matter and nutrients in a mangrove ecosystem, including exchange with the estuary (IN=inorganic nutrients). A diagram of a mangrove forest with soil nutrient resources is also presented to describe the spatial linkages in these ecological processes

1987). If this increase of nitrogen is proportionately greater than the loss of leaf mass during decomposition, then there will be a net input of nitrogen to mangrove soil. The source of this nitrogen may be absorption and adsorption processes by bacterial and fungal communities (Fell and Master 1973; Rice and Tenore 1981; Rice 1982), and nitrogen fixation (Gotto and Taylor 1976; Zuberer and Silver 1978; Potts 1979; Gotto *et al.* 1981; van der Valk and Attiwill 1984). Twilley *et al.* (1986) found that this process of nitrogen immobilization was more significant in decomposing *Rhizophora mangle* leaf litter than in leaf litter of *Avicennia germinans* in a basin mangrove forest. The enrichment of decomposing litter with new nitrogen is apparently a function of demand for this substrate by microorganisms colonizing the detritus. Leaf litter with high C:N ratios ( $>30$ ) usually has a higher potential for nitrogen immobilization since nitrogen concentrations are low relative to carbon, requiring high demand by microorganisms. C:N ratios of *Rhizophora* litter are usually double the levels in *Avicennia* litter, and accordingly there is a lower decomposition rate and higher nitrogen immobilization in forests dominated by *Rhizophora* trees (Twilley *et al.* 1986).

The C:N ratios of leaf litter are linked to recycling processes in the canopy whereby nutrients are reabsorbed or retranslocated prior to leaf fall (Figure 13.5) (Ryan and Bormann 1982; Vitousek 1982). Steyer (1988) found that retranslocation of *Rhizophora* was higher than that of *Avicennia*, contributing to the higher C:N ratio of leaf litter in the former genus. This indicates that more nitrogen may be recycled in the canopy of a mangrove forest dominated by *Rhizophora* compared with *Avicennia*. Higher recycling of nutrients in the canopy could improve nutrient use efficiency and thus result in less demand for nitrogen uptake by the tree. In the *Rhizophora* forest, nitrogen immobilization in leaf litter during decomposition as result of the higher C:N ratio will result in less remineralization on the forest floor, compared with *Avicennia* forest where nitrogen regeneration occurs during litter decomposition. Higher nitrogen remineralization in litter of *Avicennia* would supply the higher demand for nitrogen in the canopy of this genus. Experimental tests are needed to demonstrate if there exist cause and effect linkages in nutrient recycling due to the relative dominance by *Rhizophora* and *Avicennia* in a mangrove forest. However, these ideas suggest that shifts in the species composition of mangrove forests could contribute to different patterns of nitrogen dynamics between the canopy and soils of mangrove ecosystems.

### 13.3.2 Ecological type and litter dynamics

Productivity of mangroves, both primary and secondary, is usually associated with the concepts of outwelling in estuarine ecosystems (Twilley 1988). One reason for this may be related to the greater tidal amplitude, as

in Ecuador or Australia, and by higher runoff in some tropical deltaic systems, as in Mexico, Brazil or Venezuela, used to study mangrove export compared with temperate intertidal wetlands. The productivity of mangroves may be strongly related to the ecological type of mangrove (see discussion in Section 13.2), since processes may be specific to riverine, fringe or basin mangroves according to their respective hydrologic characteristics (Twilley 1988, 1995). This conclusion is based mainly on organic matter exchange in mangroves, although there are indications that nutrient recycling may also vary along a continuum in hydrology.

In mangroves, the residence time of litter on the forest floor is largely controlled by tidal flooding frequency. Trends for litter productivity and export suggest that as geophysical energy increases, the exchange of organic matter between mangroves and adjacent estuarine waters also increases. The average rate of carbon export from mangroves is about  $210 \text{ gC m}^{-2} \text{ year}^{-1}$ , with a range from 1.86 to  $401 \text{ gC m}^{-2} \text{ year}^{-1}$  (based on 10 estimates in the literature; Twilley *et al.* 1992). Total organic carbon (TOC) export from infrequently flooded basin mangroves in southwest Florida is  $64 \text{ gC m}^{-2} \text{ year}^{-1}$ , and nearly 75% of this material is dissolved organic carbon (DOC) (Twilley 1985). Particulate detritus export from fringe mangroves in south Florida was estimated at  $186 \text{ gC m}^{-2} \text{ year}^{-1}$  (Heald 1971), compared with  $420 \text{ gC m}^{-2} \text{ year}^{-1}$  for a riverine mangrove forest in Australia (Boto and Bunt 1981). Estimates of average tidal amplitude in these three forests types are 0.08 m, 0.5 m and 3 m, respectively. Rates of organic carbon export from basin mangroves are dependent on the volume of tidal water inundating the forest each month, and accordingly export rates are seasonal in response to the seasonal fluctuation in sea level. Rainfall events may also increase organic carbon export from mangroves (Twilley 1985), especially DOC. Accordingly, as tidal amplitude increases, the magnitude of organic material exchanged at the boundary of the forests increases (Twilley 1985).

Geophysical processes alone do not control the fate of leaf litter in mangrove ecosystems. Litter productivity in a riverine forest in Ecuador is similar to that in a riverine forest in south Florida at about  $10 \text{ Mg ha}^{-1} \text{ year}^{-1}$ . Leaf litter turnover rates in the two sites were different by factor of 10, which fits the model discussed above, since the tidal amplitude in Ecuador is 3–4 m compared to  $<1 \text{ m}$  in Florida. Yet observations in the mangroves in Ecuador suggest that most of the leaf litter on the forest floor is harvested by the mangrove crab, *Ucides occidentalis*, and transported to sediment burrows rather than exported out to the estuary (Twilley *et al.* 1990). The influence of mangrove crabs on litter dynamics has been described in other mangrove ecosystems with high geophysical energies and rates of litter turnover  $>5 \text{ year}^{-1}$  (Malley 1978; Leh and Sasekumar 1985; Robertson and Daniel 1989; see Section 13.4.1). Thus, the patterns of leaf litter export from mangroves are not restricted to just geophysical forcings

such as tides; in some locations there are important biological factors that influence litter dynamics. In these examples, high rates of litter turnover do not reflect the coupling of mangroves to coastal waters, but the conservation of organic matter within the forest. This demonstrates the complex nature of the relative importance of geophysical processes and biodiversity on the ecological functions of mangrove ecosystems.

### 13.4 MANGROVE FAUNAL GUILDS AND ECOSYSTEM FUNCTION

Animal species co-occurring in mangrove forests can be separated into guilds characterized by the utilization of available resources (Ray and McCormick 1992). Faunal guilds described in this section are basically resident species that exploit the habitat with different intensity in space and time, in contrast to the nekton guilds discussed below (Section 13.6). The utilization and exploitation of the mangrove habitat by faunal guilds, both resident and migratory, can contribute to the structure and function of mangrove ecosystems. The loss of faunal guilds, described below, may influence the ecological properties of mangrove ecosystems.

#### 13.4.1 Crabs

Crabs are one of the most important animal groups contributing to the high biodiversity in mangrove ecosystems. Moreover, it is not only their high species diversity but also their functional role that make crabs a fundamental component in the ecological diversity of mangrove ecosystems. Crabs play a central role in the structure and energy flow of these coastal forested wetlands (Micheli *et al.* 1991) as well as influencing the structure (Warren and Underwood 1986) and chemistry (Smith *et al.* 1991) of mangrove soils. These roles are accomplished by predation on mangrove seedlings (Smith 1987; Smith *et al.* 1989), facilitating litter decomposition (Robertson and Daniel 1989), and formation and transfer of detritus to predator food chains (Malley 1978; Jones 1984; Camilleri 1992).

There are about 4500 species of crabs, and they are the largest part of the decapoda. Six of the 30 families of the Brachyura are present in mangrove ecosystems (Mictyridae, Grapsidae, Geocarcinidae, Portunidae, Ocypodidae, Xanthidae), which include an estimated 127 species (Jones 1984). Eighteen of 19 genera occur within the Ocypodidae and comprise at least 80 species. In general, the mangrove crab fauna is dominated by representatives of two families, the Ocypodidae and Grapsidae, and each family by one genus, *Uca* and *Sesarma*, respectively. Furthermore, within the Grapsidae the genus *Sesarma* accounts for over 60 species of crabs predominantly associated with

mangroves (Jones 1984). For example, the Indo Malayan region provides the richest zone with 30 species of *Sesarma*, then east Africa (9–16), followed by Australasia (8–14) and tropical America (3–5).

Although the high diversity of crabs and its potential effect on the productivity of mangrove forests has long been recognized (Macnae 1968; Malley 1978), there is little quantitative data on community structure, population dynamics and the ecological interactions between crabs and mangrove litter production. For example, Macnae (1968) correlated the scarcity of leaf litter in Malaysian mangroves with crab consumption, while Malley (1978) and Leh and Sasekumar (1985) provided evidence through gut content analyses that mangrove leaf litter was consumed by Sesarminae crabs, *Chiromanthes* spp. (Lee 1989). This pattern of litter consumption has also been observed in the majority of the genera *Cardisoma*, *Goniopsis*, *Ucides* and *Aratus* (Jones 1984). Since crab densities in mangrove forest can be high, crabs may play an important role in leaf litter decomposition and transport to adjacent estuarine waters. Indeed, studies in Malaysia, Jamaica, South Africa, Kenya, India and Puerto Rico show that the crab density may be as high as 63 individuals per m<sup>2</sup> (Jones 1984).

The crab community can have significant effects on pathways of energy and carbon flow within the forest, the quantities of organic material available for export from forest, and the cycling of nitrogen to support forest primary production (Robertson 1991; Robertson *et al.* 1992). Malley (1978) found that the contents of the proventriculus and rectum of the sesarmid crab *Chiromanthes onychophorum*, a common crab species in mangroves in Malaysia, consisted of more than 95% mangrove leaf material by volume. The first quantitative estimates of litter consumption by crabs was between 22 and 42% of the daily leaf fall (mean 28%) depending on the time of year (Robertson 1986). These rates showed that leaf-burying crabs were a major link between primary and secondary production within mangrove forests in northeastern Australia. Emmerson and McGwynne (1992) found that leaf litter was the major component in the diet of the crab *Sesarma meinerti*, a dominant species in the mangroves of south Africa, and estimated that 44% of *Avicennia marina* leaf fall was consumed by this species. Leh and Sasekumar (1985) calculated that in Malaysia two sesarmids, *Chiromanthes onychophorum* and *Chiromanthes eumolupe*, could remove ~9% of the annual leaf fall from mid-intertidal *Rhizophora* forests and up to 20–30% of leaf fall in high intertidal forests. Similarly, Robertson and Daniel (1989) reported that sesarmids removed 71% and 79% of the total annual litter fall from the forest floor in mangrove forest dominated by *Ceriops tagal* and *Bruguiera exaristata*, respectively. Yet only 33% was removed in an *Avicennia marina*-dominated forest.

Leaf processing by crabs can also be responsible for litter turnover rates that are >75 times higher than the rate of microbial decay. Micheli *et al.*

(1991) found that crab leaf removal ( $14 \text{ g m}^{-2} \text{ day}^{-1}$ ) was much greater than any previous measurement of litterfall in mangrove environments. Lee (1990) estimated that 40% of particulate organic matter produced by the mangrove *Kandelia candel* and the reed *Phragmites communis* was consumed by crabs. He emphasized that since tidal inundation in this mangrove forest was infrequent, crab consumption may be enhanced by the long residence times of organic matter on the forest floor. Lee (1989) also observed that crabs from the genus *Chiromantes* were capable of consuming >57% of the litter production by the mangrove *Kandelia candel* in a tidal shrimp pond. However, Emmerson and McGwynne (1992) stressed that the feeding behavior and feeding rate for each crab species should be known accurately in order to minimize overestimates of litter processing.

Camilleri (1992) demonstrated that crabs, among other invertebrates, break down whole senescent mangrove leaves lying on the mud, thus providing particulate organic matter (POM) for at least 38 species of detritivores and forming a primary link in the marine food web inside the mangrove forest at Myora Springs on Stradbroke Island, Australia. He showed that 12 species of leaf shredders manufactured small detrital particles from mangrove leaves that are consumed by at least 38 other species of invertebrates. Therefore, leaf fall from mangrove trees provided food for about 50 species of invertebrates in the mangrove forest. Camilleri (1992) listed five reasons why species that shred whole leaves into small particles are significant in mangrove ecosystem: (1) they prevent mangrove leaf material from being washed out of the forest; (2) they make POM available as a food source to detritivores which feed on fine POM; (3) they regulate the size of POM in the environment; (4) they stimulate the colonization of POM by microfauna and microorganisms making nutrient available to trees; (5) they simplify the structure and chemical composition of detrital particles and that can facilitate degradation by microbial organisms.

In addition to the impact crabs have on organic matter export and decomposition, they may also affect forest structure and species composition along the intertidal zone by consumption of mangrove propagules (Smith 1987, 1988; Smith *et al.* 1989; Osborne and Smith 1990). Caging experiments in northern Queensland, Australia, showed that *Avicennia marina* propagules can survive and grow when they are protected from crabs (Smith 1987). Crabs consumed 100% of the post-dispersal propagules of mangroves in Australia mangrove forests, especially of the genus *Avicennia*. In both Malaysia and Australia grassid crabs composed >95% of the predators on propagules (Smith 1992). As seed predators, grassid crabs can control where some mangrove species become established in the forest, as shown in southeast Asia, North and Central America, and Australia (Smith *et al.* 1989). Based on these studies, Smith (1992) proposed that predation on

propagules can influence succession in north Queensland mangrove forests in Australia. Recent studies in Africa (Micheli *et al.* 1991) also showed that propagule consumption can have an impact on species distribution.

On a global scale, Smith (1992) reviewed current data on propagule consumption by crabs in the New and Old Worlds. He pointed out that in Queensland, Sesarmids remove up to 80% of annual leaf fall (Robertson and Daniel 1989) and 75% of the propagules (Smith 1987) from the forest floor, whereas in Florida and Panama crabs have been indicated as minor consumers of forest primary production (Smith *et al.* 1989). These differences among continents suggest that the effects of invertebrate biodiversity on ecological function is not consistent globally, since crabs do not play an important role in the structure and function of mangroves in Florida. However, recent studies in Ecuador (Twilley *et al.* 1993) showed that mangrove crabs, *Ucides occidentalis*, can influence the fate of leaf litter in the Churute Ecological Preserve.

Smith *et al.* (1991) have proposed that sesarmid crabs represent keystone species since they exert a major influence on mangrove ecosystem functions. For example, they found that sesarmid crabs have an impact on soil ammonium and sulfide levels, and as a consequence on forest productivity and reproductive status. This effect on nutrient cycling has also been reported in high intertidal forests in other mangrove forests in Australia, where between 11 and 64% of nitrogen requirements for forest primary production is recycled through litter processed by crabs (Lee 1989). Along with evidence by others demonstrating the effect of crabs on carbon cycling and forest structure (e.g. Robertson 1986; Robertson and Daniel 1989), Smith *et al.* (1991) concluded that crabs occupy a keystone position in Australian mangrove forests. Given the lack of extensive data on crab communities (Michelli *et al.* 1991), it is not clear if indeed crabs are also keystone guilds regulating forest development and productivity in other mangrove ecosystems. Yet current data strongly suggest that crabs play an important role in maintaining a high biodiversity that is linked to significant ecological functions in mangrove ecosystems (Camilleri 1992).

#### 13.4.2 Insects

The ecology of insects in mangrove ecosystems is poorly understood, including inadequate records of their distribution and few studies of their ecological function. One of the more thorough treatments of the subject is by Feller (1993), which includes examples of unpublished records of insects in mangroves of Belize, and summaries of leading hypotheses describing the role of herbivory in mangrove ecosystems. In her own work, Feller tested the importance of soil resource availability on the pattern of herbivory in oligotrophic dwarf mangrove forests on an island in Belize.



The occurrence of insects in mangrove forests may be higher than previously considered (Ruetzler and Feller 1988; Feller 1993). A thorough inventory of insects on small mangrove islands in the Florida keys uncovered 200 species (Simberloff and Wilson 1969). In Belize, the hollow twigs of *R. mangle* host more than 70 species of insects, including at least 20 species of ants (Lynch, unpublished data, from Feller 1993), while Farnsworth and Ellison (1991, 1993) have identified more than 60 species of folivores feeding on *Rhizophora* and *Avicennia*. The research effort in Belize has uncovered many undescribed species of xylophagous insects (half of the 35 species are new) and shore flies (many of the 50 total species were previously undocumented). Insects habitats are diverse in mangroves, including not only the leaf surface of the canopy, where inventories of species are more common, but also in less obvious sites within twigs, trunks and prop roots of the trees. In general, studies of herbivory of these and other diverse insect guilds have found that they can influence ecological processes such as root branching that enhances tree support (Simberloff *et al.* 1978), girdling of branches and trunks that causes formation of forest gaps (Feller, 1993, and unpublished material discussed), premature leaf abscission that changes nutrient recycling in the forest canopy (Onuf *et al.* 1977), and predation on mangrove seedlings (Rabinowitz 1977; Robertson *et al.* 1990). However, for each study promoting a causal mechanism of herbivory to an ecological function in mangroves, there is a study that contradicts the effect (e.g. Johnstone 1981; Lacerda *et al.* 1986; Ellison and Farnsworth 1990, 1992). In addition, there are also accounts that insects are a minor component in the ecology of mangroves (Janzen 1974; Huffaker *et al.* 1984; Tomlinson 1986). It is not presently clear how changes in the biodiversity of insects can influence the function of mangrove ecosystems; however, it is evident that more ecological studies of these guilds are needed to define their role in particularly oligotrophic mangrove ecosystems.

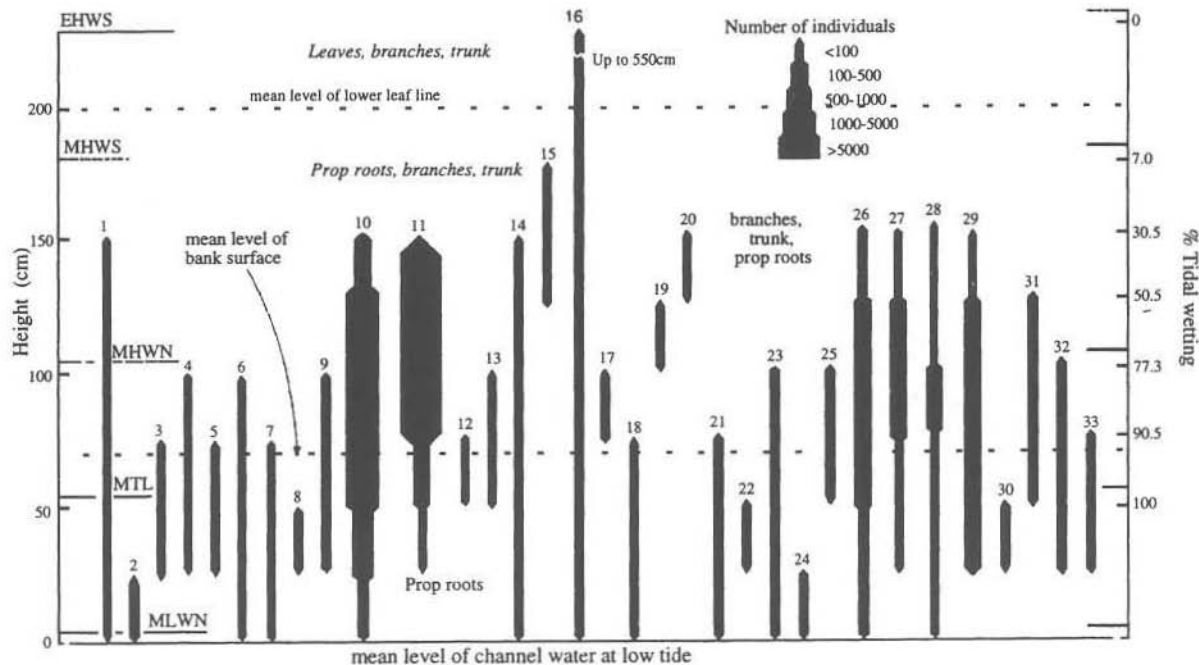
Mangrove rookeries (bird nesting sites) are enriched in nitrogen and phosphorous which stimulate the productivity of mangroves by a factor of 1.4. The density and diversity of herbivores is greater on mangrove island rookeries compared with proximal islands that lack nutrient enrichment (Onuf *et al.* 1977). The increased herbivory by several folivorous caterpillars and scolytid beetles on mangrove rookeries apparently maintained a constant standing crop, despite the increased rate of production. The enhanced growth rate of several herbivores and other fauna on the nutrient-enriched islands suggests that resource utilization may limit population size on the control (unenriched) islands. However, the control sites were of different size and distance from the mainland, confusing the linkage of nutrient enrichment to specific ecological processes. Other studies have found little enhancement of herbivory with increased levels of nutrients in either mangrove soil or leaves (Robertson and Duke 1987; Farnsworth and Ellison 1991; Feller 1993).

although responses in herbivory may differ among benign and stressed environments, particularly related to hydroperiod (Feller 1993).

One of the largest scale manipulations of mangrove ecosystems was an experimental study of eight small mangrove islands in Florida Bay specifically to test biogeographic hypotheses of landscape richness (Simberloff and Wilson 1969; Simberloff 1976a). Mangrove islands of different size (264–1263 m<sup>2</sup>) and distance from source populations (2–432 m) were defaunated by fumigation with methyl bromide, and repeated censuses of animal species were used to determine immigration and extinction processes. Censuses were retaken on islands reduced in area of habitation to test the factors that control equilibration processes on these islands. The studies showed that biodiversity of animals was directly controlled by the size of the island, and the studies allowed for direct determination of extinction rates. Simberloff (1978) also summarized from these studies that community structures in these environments were not deterministic, but were largely controlled by the physical environment together with individual adaptations. While Heatwole and Levins (1972) attempted to relate the results of these mangrove island studies to interactions of trophic structure following disturbance, Simberloff (1976b) concluded that the significance of trophic interactions to the biodiversity of this ecosystem remains unproven. These studies do demonstrate the importance of island size and location (fragmentation relative to source materials) to the resiliency of biodiversity following disturbance in mangrove ecosystems. However, other tests have not demonstrated any relation in levels of herbivory to these dimensions of mangrove islands (Beever *et al.* 1979; Farnsworth and Ellison 1991). Studies with similar approaches are needed to link these patterns in species richness to specific ecosystem processes of mangroves.

### 13.4.3 Benthos and epibionts

One of the more comprehensive descriptions of the biodiversity (Alongi and Sasekumar 1992) and ecological function (Alongi *et al.* 1992; Robertson *et al.* 1992) of benthic communities is published in a book by Robertson and Alongi (1992) that describes the ecology of mangroves in Australia and surrounding regions. The meio- and macro-faunal diversity of the benthos are better documented than microbial communities (see Section 13.5), as represented by more than 100 species of macrofauna in some mangrove sites such as Thailand (Nateewathana and Tantichodok 1984), northwest Australia (Wells 1983) and southern Africa (Day 1975) (as reported in Alongi and Sasekumar 1992). Microhabitat diversity in the intertidal zone of mangroves is frequently cited as an important factor in the diversity of benthic communities (Figure 13.6), as has been found in temperate zones (Frith *et al.* 1976). In addition, the increased habitat diversity afforded by



**Figure 13.6** Vertical zonation and abundance of epibenthos on *Rhizophora apiculata* trees, Phuket Island (Taken from Alongi and Sasekumar 1992 as modified from Frith *et al.* 1976). Species codes: 1, Sea anemone sp.A; 2, Sea anemone sp.B; 3, *Nemertine* sp.A; 4, *Lepidonotus kumari*; 5, *Petrolisthes* sp.; 6, *Cibanarius padavensis*; 7, *Diogenes avarus*; 8, *Leipocten sordidulum*; 9, *Tylodiplax tetra-tylophora*; 10, *Balanus amphitrite*; 11, *Chthamalus withersii*; 12, *Ligia* sp.; 13, *Sphaeroma walkeri*; 14, *Nerita birmanica*; 15, *Littorina carinifera*; 16, *Littorina scabra*; 17, *Assiminea brevicula*; 18, *Cerithidea cingulata*; 19, *Cerithidea obtusa*; 20, *C. breve*; 21, *C. patulum*; 22, *Capulus* sp.; 23, *Murex capucinus*; 24, *Nassarius jacksonianus*; 25, *Onchidium* sp.; 26, *Brachidontes rostratus*; 27, *Isognomon ephip- pium*; 28, *Enigmonia aenigmatica*; 29, *Saccostrea cucullata*; 30, *Diplodonta globosa*; 31, *Teredo* sp.; 32, *Xylophaga* sp.; 33, *Trapezium sublaevigatum*

the unique architecture of mangrove trees, such as prop roots and pneumatophores, may facilitate biodiversity in the tropical intertidal zone. However, chemical leachates from mangrove trees, especially tannins from the genus *Rhizophora*, may reduce the density and diversity of benthic communities. Alongi (1987a) demonstrated that the density of meio-fauna was negatively correlated with concentrations of soluble tannins in mangrove sediments. In addition, laboratory feeding experiments have shown that population dynamics of meio-fauna may differ when fed detritus of *Avicennia* compared with *Rhizophora*, apparently owing to higher concentrations of tannin in the latter genus (Alongi 1987b). Infaunal communities can also be regulated by tannin concentration (Giddins *et al.* 1986; Neilson *et al.* 1986). However, other studies by Tietjen and Alongi (1990) present evidence that the negative effects of tannins may be reduced with higher nitrogen concentrations of mangrove detritus. It is evident however that there may be important linkages in the chemical ecology of specific mangrove tree species to the biodiversity and ecological function of benthic communities.

There is an increasing knowledge of nutrient fluxes (Figure 13.5) within mangrove forests and surrounding areas of tropical coastal ecosystems (see reviews by Alongi 1989, 1990). However, the functional ecology of benthos relative to the biogeochemistry of these ecosystems is not clear. Specifically, the role of benthic faunal guilds in the exchange of nutrients across the sediment-water interface is poorly understood, while this ecological function has been described in temperate estuaries. There may be some interesting linkages in the species-specific chemistry of mangrove sediments, benthos density and diversity, and nutrient cycling properties of mangrove ecosystems.

Sponges, tunicates and a variety of other forms of epibionts on prop roots of mangroves are highly diverse (Sutherland 1980; Ruetzler and Feller 1988; Ellison and Farnsworth 1992), especially along mangrove shorelines with little terrigenous input. The diversity and biomass of these communities and associated ecological functions may be limited to specific geomorphological types that are protected from turbid waters. The ecology of these communities has been dominated by studies of species distribution and population dynamics, although there are a few studies on ecosystem function. For example, the growth rates of prop roots can be reduced by root-boring isopods (Perry 1988; Ellison and Farnsworth 1990, 1992); however, sponges and ascidians that colonize prop roots prevent the invasion of these isopods and enhance root productivity (Ellison and Farnsworth 1990). There is evidence that epibionts on prop roots may be a source of nutrition for higher-level predators as well as influencing various processes in mangrove fringe forests. These processes of nutrient regeneration associated with sponge communities that colonize aerial root systems of mangroves have

received comparatively little attention, but they may influence the productivity of fringe mangrove forests, as well as enhance the exchange of nutrients with coastal waters (Ellison *et al.* 1996; R. Twilley and T. Miller-Way, unpublished data for 1993–1995 in Belize). The specific contribution of these productive and diverse epibiont communities in predominately carbonate environments may demonstrate an important linkage between biodiversity and ecosystem function.

### 13.5 MICROBIAL PROCESSES AND ECOSYSTEM FUNCTION

The biodiversity of microbial communities in mangrove ecosystems is poorly documented, but the biomass and metabolism of this guild is well established for tropical intertidal environments (Fell and Master 1980; Newell *et al.* 1987; Alongi 1988, 1989; Alongi and Sasekumar 1992). The microbial ecology of mangrove sediments and its influence on ecological processes, particularly decomposition, has been related to the chemical diversity of mangrove leaf litter (Benner and Hodson 1985; Benner *et al.* 1986; Benner *et al.* 1990a,b). As discussed above for meio-fauna, chemical compounds such as tannins may influence the population dynamics of microbial communities on specific leaf litter. This, in turn, influences the fate of organic matter and nutrients on the forest floor of mangrove ecosystems. Most of the research relating the chemical ecology of mangroves with specific ecological processes has been done with *Rhizophora*, while there may be other interesting comparisons among the different mangrove tree species. A potentially important area of study is the effect of species richness of trees on the chemical ecology of mangrove litter and soils, and how this can influence the ecosystem functions of mangrove forests.

Nitrogenase activity has been observed on decomposing leaves and root surfaces (prop roots and pneumatophores) and in sediment. This enzyme makes an important contribution to the nitrogen budget in mangrove systems (Kimball and Teas 1975; Gotto and Taylor 1976; Zuberer and Silver 1978; Potts 1979; Gotto *et al.* 1981). Results from studies of mangrove sediments in south Florida indicate the nitrogen fixation rates range from 0.4 to 3.2 g N m<sup>-2</sup> year<sup>-1</sup> (Kimball and Teas 1975; Zuberer and Silver 1978). These studies have shown that decomposing mangrove leaves are sites of particularly high rates of fixation, and thus account for some of the nitrogen immobilization in leaf litter (Gotto *et al.* 1981; van der Valk and Attiwill 1984). For example, Gotto *et al.* (1981) found that nitrogen fixation in *Avicennia* leaves was nearly twice that in *Rhizophora* leaves. Thus, the contribution of this ecological process to the fertility of mangrove ecosystems may depend on the nutrient status of litter among different types of mangrove ecosystems, as discussed above. Whereas mangrove forests also fix and store

carbon in wood and organic-rich sediments, the total carbon sequestration in tropical coastal ecosystems is unknown, but may represent a potentially important sink of carbon in tropical coastal ecosystems (Twilley *et al.* 1992).

The colonization of microbial communities on leaf litter can influence the exchange of nutrients at the boundary of mangrove ecosystems. Rivera-Monroy *et al.* (1995) observed that there was a net uptake of ammonium and nitrate during tidal exchange in a flume constructed in a fringe forest in Terminos Lagoon, Mexico. Organic nitrogen was exported from this flume to the estuary at rates equal to the uptake of inorganic nitrogen. Thus this mangrove zone functioned as a transformer of inorganic nitrogen to organic detritus, which is similar to processes observed in salt marsh ecosystems. Based on these flume studies of nutrient exchange, nitrate uptake was assumed to be denitrified to gaseous form, representing a sink of nitrogen from the system. However, studies with nitrogen-15 labeled nitrate showed that very little of the amended nutrient was transformed to nitrogen gas (Rivera-Monroy *et al.* 1995; Rivera-Monroy and Twilley 1996). In addition, nearly all of the enriched ammonium N-15 could be accounted for in sediments; thus no coupled denitrification occurs in these wetland soils. Loss of nitrogen via denitrification was low, apparently due to the high nitrogen demand in decomposing leaf litter on the forest floor (Rivera-Monroy *et al.* 1995; Rivera-Monroy and Twilley 1996). These studies further indicate the significance of the quality of leaf litter to nitrogen cycles in mangrove forests (Figure 13.5), as has been observed in other forest ecosystems (see Section 13.3).

### 13.6 NEKTON BIODIVERSITY AND MANGROVE FOOD WEBS

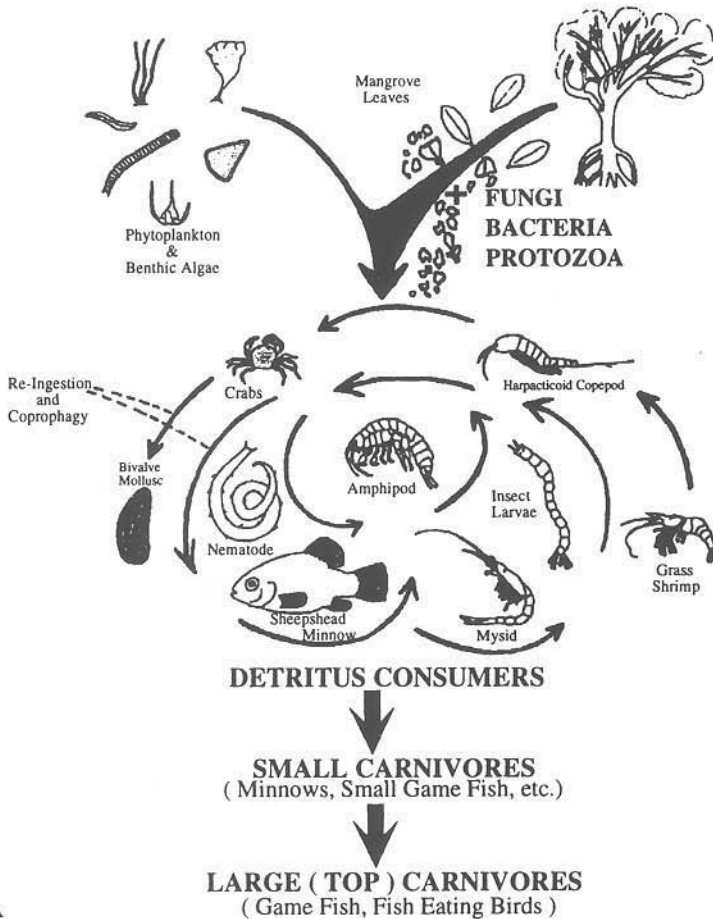
Nekton (free-swimming organisms) food webs represent faunal guilds that utilize mangrove habitats for food and protection at different stages of their life cycle. Most of these organisms are migratory (while there may be some residents), and the ephemeral nature of the periods when these organisms utilize mangrove habitats contributes to the poor understanding of their ecology. Robertson and Blaber (1992) reviewed the results of four mangrove fish community studies in northern Australia where species richness varied from 38 to 197 species. In the neotropics, extensive surveys of the composition and ecology of mangrove nekton have found 26–114 species of fish (from Table 9 in Robertson and Blaber, 1992). Tropical estuarine fishes in mangrove ecosystems, as secondary consumers, can be important in energy and nutrient flow in several ways. They can be stores of nutrients and energy, control rates and magnitude of energy flow through grazing of food sources, and move energy and nutrients across ecosystem boundaries (Yáñez-Arancibia 1985; Robertson and Duke 1990).

The structural and ecological functions of mangroves sustain nearshore marine habitats and provide food and refugia to a variety of organisms at different trophic levels (Odum and Heald 1972; Thayer *et al.* 1987; Yáñez-Arancibia *et al.* 1988, 1993; Robertson and Duke 1990; Rojas *et al.* 1992; Sasekumar *et al.* 1992). This is clearly reflected in the description of nekton food webs in mangroves (Figure 13.7). The complexity of food sources found in fish stomachs documents changes in food diversity and fish preferences as fish grow. Often the diet of a single species comprise more than 20 different (or diverse) food types in mangrove areas. The whole trophic structure does not comprise specific trophic levels, as fish eat food from a diversity of sources in the mangrove ecosystem (Figure 13.7). In summary, the general characteristics of feeding relationships among "mangrove-related fishes" are: (1) flexibility of feeding in time and space; (2) sharing of the common pool of most abundant food resources among a diverse pool of species; (3) the taking of food from different levels of the food web by each species; (4) the changing of the diet with growth, food diversity, and locality within the estuary; (5) the use of both the pelagic and benthic pathways by a given species.

One of the key questions about mangrove ecology is the significance of these habitats to the dependence of marine organisms on estuaries during the juvenile or adult stages of their life cycle (Robertson *et al.* 1992; Yáñez-Arancibia *et al.* 1994). The seasonal pulse of primary production along with temporal variation in physical constraints (e.g. temperature and salinity) provide a unique set of conditions for estuarine-dependent life cycles (Rojas *et al.* 1992). Three primary types of migration have been documented: diel, seasonal and ontogenetic. Rooker and Dennis (1991) report both diel and seasonal migrations at a mangrove key near Puerto Rico, suggesting that diel movements are primarily the result of feeding habits, while seasonal migrations "may be related to changes in environmental parameters (i.e. salinity, temperature, turbidity) that alter habitat characteristics, or to aspects of life-history (e.g. reproduction, recruitment) (Williams and Sale 1981; Williams 1983)". More often reported are migrations due to ontogenetic causes (Odum *et al.* 1982; Ogden and Gladfelter 1983; Gilmore and Snedaker 1993). Ontogenetic migrants generally spend their juvenile stage in the relative protection of the mangrove habitat, and subsequently move offshore as they grow too large to effectively utilize the mangrove structure as shelter (Odum *et al.* 1982; Ogden and Gladfelter 1983). For the most part, however, very little detail is known about the life-history characteristics of many of these multi-habitat fishes, especially the larval phase (Voss *et al.* 1969).

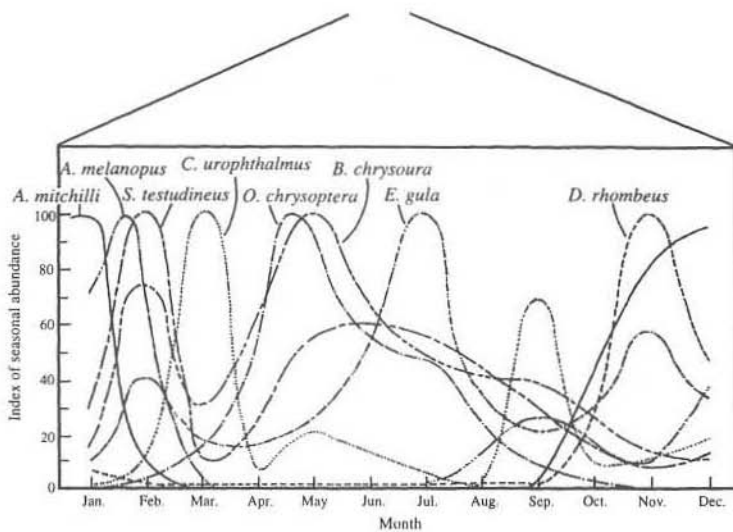
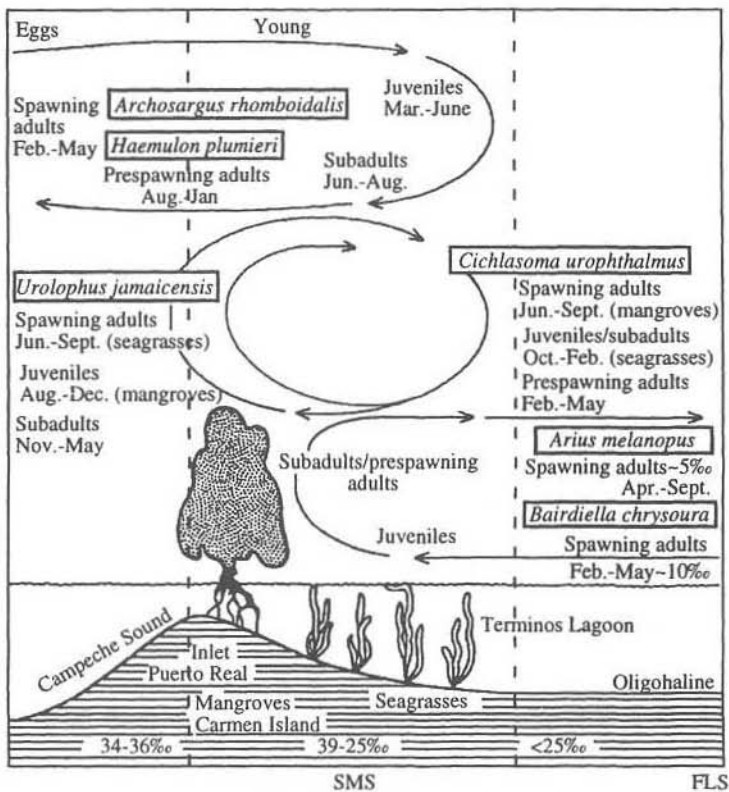
The sequential pulsing of primary production by planktonic and macrophyte communities, coupled with seasonal export of mangrove detritus, suggest that the delivery of organic matter sustains high estuarine secondary

production and species diversity of estuarine-dependent consumers (Figure 13.8) (Rojas *et al.* 1992; Yáñez-Arancibia *et al.* 1994). The seasonal coupling of primary and secondary production in mangrove ecosystems, along with variation in environmental conditions, shows how the functional assemblages of fish use tropical lagoon habitats in time and space to reduce the effect of competition and predation. Assemblages of macroconsumers within functional groups play an important ecological role by coupling life-history strategies with the environmental gradients within the estuary (Figure 13.8). In Figure 13.8 we can see the two main mangrove habitats, fringe (SMS) and riverine (FLS), where the same fish population assemblages utilize the habitats in a sequential manner from one season to the next. This diversity in behavior suggests that the lag in fluctuations of total biomass through the year, as is common in high-latitude estuaries, is a consequence of the









migratory lives of associated fishes (Odum *et al.* 1982; Ogden and Gladfelter 1983). Difficulty in sampling fringing and overwash mangrove habitats may account for some of this lack of knowledge; in particular, mangrove prop roots hinder movement of both researchers and equipment, while the often turbid waters associated with the prop root environment obstruct visual censuring techniques (Thayer *et al.* 1987; Rooker and Dennis 1991; Sedberry and Carter 1993).

Fish that migrate between mangroves and coral reefs are typically reef-associated species. There are several reasons for coral reef fish to migrate to the mangroves. The mangrove habitat is generally recognized to act as a nursery for the juvenile stage of many coral reef fish species (Odum *et al.* 1982; Ogden and Gladfelter 1983; Gilmore and Snedaker 1993; Sedberry and Carter 1993). There are indications that this is not the case for sites in the southwest Pacific (Quinn and Kojis 1985; Blaber and Milton 1990). Mangrove detritus (leaves, branches, etc.) is the base of an extensive food web comprised of dissolved and particulate organic matter, as well as an associated microorganism community (Figure 13.7; Odum and Heald 1972). This detrital-based food source is highly accessible and nutritious for young fish. In addition, the mangrove prop root structure offers physical protection from predatory fishes (Odum *et al.* 1982; Ogden and Gladfelter 1983), while the turbidity of nearshore waters often hinders visual predators (Thayer *et al.* 1987; Rooker and Dennis 1991; Sedberry and Carter 1993). Conversely, larger piscivorous fish often find the mangrove habitat an excellent feeding ground, as the mangrove habitat boasts a greater number of fish as well as overall biomass than surrounding habitats in some areas (Thayer *et al.* 1987; Blaber and Milton 1990; Sedberry and Carter 1993). In the Caribbean region, typical migratory piscivorous fishes are redfish, tarpon and snook (Ogden and Gladfelter 1983).

The fragmentation of mangrove-dominated landscapes is believed to create the same types of problems for migratory organisms that are associated with the fragmentation of upland forests, yet there has been little, if any, research on this topic. There is no documentation concerning diel or seasonal migration patterns of resident species within mangroves, or how such species might be affected by the impact of fragmentation. For instance, seagrass and adjacent mangrove habitats are used by many species of

---

**Figure 13.8** (*and opposite*) Life histories and habitat utilization of six selected dominant fish species including marine-estuarine spawners, estuarine spawners and freshwater-estuarine spawners in Terminos Lagoon, Mexico. The fish migrate using SMS and FLS habitats (see bottom of upper panel) for the highest periods of productivity for feeding, spawning or nursery grounds (upper panel). The seasonal abundance of fish species in the SMS habitats (lower panel). (from Yáñez-Arancibia *et al.* 1988, represented by permission of Academic Press)

nekton and are generally characterized by high fish abundance and diversity. From Yáñez-Arancibia *et al.* (1993) it is clear that the utilization of the two interacting habitats by fishes is spatially distinct, but linked by the life-cycles of organisms (Figure 13.8). They found that there is a strong correlation between the life-history patterns of migratory fish and the pattern of primary production, using the two habitats sequentially in a time period. The fragmentation of mangrove-seagrass landscapes will probably reduce ecosystem complexity and nekton diversity. It has been speculated that one of the consequences in loss of mangrove area and/or increased fragmentation will be reduction in population numbers (and this may be important for commercial species) or outright local extinctions of certain species. However, as recently reviewed by Robertson and Blaber (1992), there is no empirical evidence that such a consequence will occur.

### 13.7 VULNERABILITY OF BIODIVERSITY IN TROPICAL ESTUARIES

#### 13.7.1 Land-use change

A 1991 workshop on the status of mangroves of Southeast Asian coastlines (Sasekumar 1993) reported that the region has lost large areas of mangroves in the Philippines (80%), Thailand (50%), Indonesia (50%) and Malaysia (32%). This pattern is likely to continue as greater demands are placed on forest and fishery resources, along with land-use changes along coastlines and in upland watersheds; the result will necessarily cause a change in the ecological characteristics of tropical estuaries. Many of the species guilds and biodiversity components described above are sensitive to changes in physical conditions (salinity, turbidity), chemical balances (eutrophication) and biological changes (exotic species).

Indirect loss of mangrove biodiversity components has resulted from human alterations of upland watersheds causing redirection of freshwater (dams and canals), and deterioration of water quality from input of toxic materials (heavy metals, oil spills, pesticides) and nutrients to rivers and coastal waters. Regional-scale changes in freshwater surface inflow into mangrove areas are associated with reduction in secondary productivity of tropical estuarine ecosystems due to degradation of habitat and water-quality of those ecosystems. Changes in species composition of mangrove communities alters the quality of leaf litter, resulting in different rates of decomposition and an altered quality of organic matter export (POC vs. DOC) to the adjacent estuary (Boto and Bunt 1981; Twilley 1985, 1988; Snedaker 1989). Species substitution along zones of edaphic conditions is limited in mangroves due to narrow species-specific tolerances (Rabinowitz

1978; Lugo 1980; Snedaker 1982); therefore, eliminating a given species may alter specific types of refugia available to consumers (e.g. species with prop roots vs. those with pneumatophores).

River (and surface runoff) diversions that deprive tropical coastal deltas of freshwater and silt result in losses of mangrove species diversity and organic production, and alter the terrestrial and aquatic food webs that mangrove ecosystems support. Freshwater diversion of the Indus River to agriculture in Sind Province over the last several hundred years has reduced the once species-rich Indus River delta to a sparse community dominated by *Avicennia marina*; it is also responsible for causing significant erosion of the sea front due to sediment starvation and the silting-in of the abandoned spill rivers (Snedaker 1984a,b). A similar phenomenon has been observed in southwestern Bangladesh following natural changes in distributary rivers of the Ganges and the construction of the Farakka barrage that reduced the dry season flow of freshwater into the mangrove-dominated western Sundarbans. Freshwater starvation, both natural and man-caused, has had negative impacts on the rich vertebrate fauna (e.g. arboreal primates, deer, gaviel, large cats) of the Ganges River delta (Hendricks 1975; Das and Siddiqi 1985). In the delta region of the Magdalena river, redirection of freshwater has resulted in the loss of about 50% (21 778 ha) of mangroves in the Santa Marta lagoon (Ciénaga Grande) (Botero 1990). The loss of mangroves and decline in water quality are associated with the loss of fishery resources in this region. These case studies demonstrate the sensitive nature of mangrove ecosystems to changes in freshwater diversion, particularly in dry coastal climates. They represent examples where reductions in the various biodiversity components change the function of tropical estuarine ecosystems.

The coupling of mangroves to coastal waters is considered to be the most important link in sustaining commercial and recreational fisheries that are associated with estuaries and related nearshore marine habitats. Utilization of mangrove as forest plantations promotes sustainable use of this valuable resource for forest products such as timber, fuelwood, tannins, pulpwood and charcoal (see Watson 1928; Saenger *et al.* 1983), albeit only, until recently, in the Old World tropics (Snedaker 1986). Recent forms of direct exploitation include the destruction of biodiversity components of mangrove forests by land uses such as aquaculture (shrimp ponds), agriculture (rice and salt ponds), urban development and forest clear-felling for economic gain and other purposes (*vide* Pannier 1979). The so-called "soil reclamation" projects in Africa, as well as in parts of Asia (cf. Ponnampuruma 1984), for agriculture (and aquaculture) have reduced regional levels of coastal productivity owing to loss of mangrove habitats. In many instances the conversion of organic-rich, pyritic mangrove soils leads to the formation of acid sulfate soils that are extremely difficult to further reclaim

or to make support the original diversity of the landscape (cf. Dost 1973; Moorman and Pons 1975).

### 13.7.2 Global climate change

Tropical estuarine ecosystems are also vulnerable to changes in coastal environments due to the global perturbations resulting from increased greenhouse gases in the atmosphere. Mangroves occur at the interface between land and sea, and therefore are very sensitive to changes in sea-level. CO<sub>2</sub> and other greenhouse gases may double by the year 2050 as compared with the amounts present at the start of the industrial revolution, warming the earth's surface between 2 and 4°C. If the average temperature increases by 3°C by 2050 and remains constant thereafter, the sea level will probably rise approximately 1 m by 2100 (50–91 cm per 100 years); a global warming of 6°C by 2100 could result in a sea level rise of 2.3 m (>100 cm per 100 years; Intergovernmental Panel on Climate Change 1990). These figures represent an increase over present rates of sea level rise, and are important relative to the rise in sea-level rates observed during the late-Holocene phase (Scholl *et al.* 1969; Parkinson 1989; Wanless *et al.* 1994).

There is much controversy over the threshold level of sea-level rise that mangroves can tolerate. Scholl and Stuiver (1967) and Parkinson (1989) have demonstrated that mangrove peat production and accumulation rates were unable to keep pace with a rising sea-level of 27 cm per 100 years, and mangrove colonization was maximum during periods when sea-level rates decreased to 4 cm per 100 years (Scholl 1964a,b). Ellison and Stoddart (1991) reviewed Holocene stratigraphic records and sea-level change for a number of sites worldwide and emphasized that mangroves in low islands can only keep up with a sea-level rise of up to 8–9 cm per 100 years, and rates of 12 cm per 100 years will collapse these systems. However, Woodroffe (1990) showed that mangroves in Belize and Jamaica, characterized by autochthonous sediment, have persisted for 6000 years. He suggests that mangroves may be able to keep pace with rates of sea-level rise of 50–80 cm per 100 years for short periods. In addition, mangroves in Key West, Florida, have expanded both seaward and landward in the last 56 years in spite of a rise in sea level equivalent to about 23 cm per 100 years (Maul and Martin 1993; Snedaker *et al.* 1994).

Changes in the species richness of mangroves during horizontal migration inland in response to changing sealevel will depend on the species-specific responses of mangroves to increased inundation and erosion (Clarke and Hannon 1970; McMillan 1971; Ellison and Farnsworth 1993; McKee 1993), and effects of propagule size to tidal sorting along the intertidal zone (Rabinowitz 1978; Jiménez and Sauter 1991). Both of these factors indicate that the depth of tidal inundation will be a primary factor in regulating the

species zonation with rise in sea level. Most studies summarize that *Rhizophora* is more tolerant of low oxygen availability caused by tidal inundation and waterlogging than *Avicennia*. If no inland barriers are behind mangroves, mangroves would migrate inland facing a rising sea level. Assuming other ecological factors keep relatively constant, *Rhizophora*, with larger propagule size and higher tolerance to inundation, will invade and dominate the higher zone previously occupied by *Avicennia* and *Laguncularia*. *Avicennia* and *Laguncularia* will retreat to newly formed saline, shallow intertidal areas, and the fringe mangroves, basically consisting of *Rhizophora*, will eventually disappear (Snedaker 1993). Bacon (1994) argues that most predictions of how wetlands in the Caribbean will respond to rise in sea level are too simplistic because they do not account for the site-specific responses of wetlands to changes in hydrology.

Temperature is the basic climatic factor governing the northern and southern limits of mangrove distribution. The responses of mangrove forest to decreasing temperature are reductions in species richness (Tomlinson 1986), forest structure (Lugo and Patterson-Zucca 1977), forest height (Cintrón *et al.* 1985) and biomass (Twilley *et al.* 1992; Saenger and Snedaker 1993). Although mean air or water temperature show some correlation with mangrove distribution in the world (Chapman 1977; Tomlinson 1986; Clough 1992), extreme temperature may be the principal controlling factor. In this regard, it has been suggested that the frequency, duration and/or severity of freezing temperature is a prime factor governing the distribution and abundance of mangroves in the northern Gulf of Mexico (Sherrod *et al.* 1986). *Avicennia germinans* and *Laguncularia racemosa* appear to be more tolerant to freezing temperature in the neotropics than *Rhizophora* (McMillan 1975; Lugo and Patterson-Zucca 1977; Sherrod and McMillan 1981; McMillan and Sherrod 1986; Sherrod *et al.* 1986; Olmsted *et al.* 1993). The greater resprouting ability of *Avicennia* and *Laguncularia* results in greater recovery from freeze damage (Sherrod and McMillan 1985; Snedaker *et al.* 1992; Olmsted *et al.* 1993). The different tolerance to low temperature among individual mangrove species is usually inferred from their natural distribution and morphological adaptation. However, genetic diversity has been demonstrated to influence the tolerance of mangroves to chilling (McMillan 1975; Markley *et al.* 1982; Sherrod and McMillan 1985; McMillan and Sherrod 1986; Sherrod *et al.* 1986). For example, analysis of isozyme patterning in *Avicennia germinans* revealed a divergence of phosphoglucose mutase and phosphoglucose isomerase among the Gulf of Mexico-Caribbean populations (McMillan 1986).

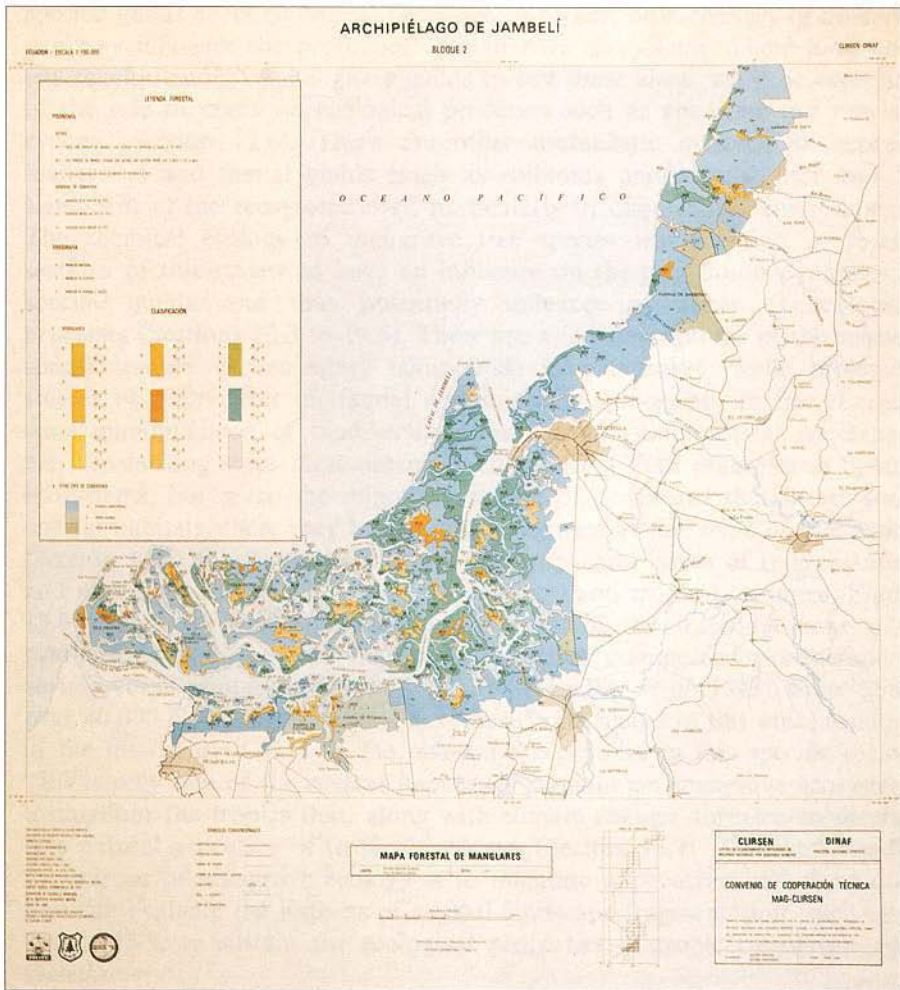
Several studies indicate that the frequency and intensity of tropical storms and hurricanes are likely to increase under warm climate conditions (deSilva 1986; Emanuel 1987; Hobgood and Cerveny 1988). Since mangroves are distributed in latitudes where the frequency of hurricanes is high, it is

important to understand how tropical storms and hurricanes affect forest development. (i.e. forest structure, species composition, etc.) and community dynamics, including biodiversity, in mangrove ecosystems. Yet this type of information is very limited, and restricted to a few areas in tropical and subtropical latitudes. For example, studies in Florida (Davis 1940; Eglar 1952; Craighead and Gilbert 1962; Alexander 1967), Puerto Rico (Wadsworth 1959; Glynn *et al.* 1964), Mauritius (Sauer 1962) and British Honduras (Vermeer 1963; Stoddart 1969) describe the effects of hurricanes on defoliation and tree mortality, but most of the information lacks quantitative assessments of the damage. Recent studies in Nicaragua (Roth 1992) and Florida (Smith *et al.* 1994) have provided a more quantitative evaluation of the effects of hurricanes on mangrove forests. High density of seedlings and fast recovery of mangroves in Isla del Venado, Nicaragua, suggest that they are not threatened as a community from hurricane damage. Ogden (1992) pointed out that mangrove forests in Florida will be able to recover following Hurricane Andrew, but Smith *et al.* (1994) were more cautious based on the dynamic role that soil status (e.g. redox and sulfide concentrations) can have in controlling tree growth and development.

### 13.8 SUMMARY

Mangroves may be one of the most well-investigated habitats among tropical ecosystems, particularly when you consider all the botanical, zoological and ecological studies. The unique adaptations of plants and animals that inhabit the tropical intertidal zone have always captured the interest of scientists (Tomlinson 1986). In addition, these coastal forested wetlands have long been linked to the sustainability of commercially important fisheries (Macnae 1974). Given this extensive pool of information, it should be appropriate to summarize the linkages between changes in biodiversity and ecosystem function in tropical estuaries. Our inability to integrate these two properties of mangrove ecosystems may indicate the inadequate approach used to study these interactions in mangrove ecology. Linking biodiversity and ecosystem function requires pluralistic investigations of different ecological scales, since an emergent property of the ecosystem must be interpreted relative to changes in specific biodiversity components. These approaches to ecological studies need to be the products of appropriate questions focusing on biodiversity and ecosystem function, whereas much of the information on mangrove ecology has lacked clear testing of specific hypotheses. Nixon (1980) criticized the lack of hypothesis testing in approaches to study the ecology of marsh ecosystems, and this same analysis may be appropriate for mangrove ecology. In our review, we have relied on examples of how





**Figure 13.9** Photointerpretation of land use in the southern coastal province of El Oro, Ecuador, based on SPOT image of 1987. Dark blue represents shrimp ponds and lighter blue estuarine waters, while different heights of mangroves are presented in green, brown and grey

specific guilds effect ecological processes to project how changes in biodiversity may influence the properties of mangrove ecosystems. There have been few manipulations of mangrove guilds to test these ideas, with the exception of the role of crabs on ecological processes such as zonation and nutrient cycling (Section 13.4). There are other mutualistic interactions between mangroves and faunal guilds (such as epibionts and insects) that may be significant at the ecosystem level, particularly in oligotrophic environments. The chemical ecology of mangrove tree species was mention in several sections of this review to have an influence on the population dynamics of specific guilds, and thus potentially influence a variety of ecological processes (Sections 13.3 to 13.5). There are a few descriptions of the species-specific nature of secondary compounds in mangroves, while ecological studies of their effect on faunal and microbial processes are few. Larger-scale manipulations of biodiversity components within coastal watersheds are also lacking since these are more complicated than examples in upland ecosystems, but given the migratory nature of organisms that utilize these coastal habitats, there may be significant linkages at this scale of interaction (Section 13.6). This void in information complicates issues of fragmentation and minimum conservation size of mangroves and tropical estuaries. Figure 13.9 shows the landscape-scale modification of the intertidal zone of a southern coastal province in Ecuador for the commercial production of shrimp (1988 photograph from CLIRSEN; Twilley *et al.* 1993). Since 1981, over 40 000 ha of shrimp ponds have been constructed in this area, resulting in the loss of over 40% of the mangrove ecosystem in this specific region. This is only one of the several impacts of humans on mangrove ecosystems throughout the tropics that, along with climate change, threaten to deteriorate natural processes of tropical estuaries (Section 13.7). The challenge for the science of mangrove ecology is to integrate approaches and techniques that can evaluate the impacts of coastal landscape fragmentation, such as in Figure 13.9, to sustain the ecological properties of tropical estuarine ecosystems.

## ACKNOWLEDGEMENTS

This study was supported in part by grants R806079010 and CR 820667 from the United States Environmental Protection Agency and the US National Biological Survey cooperative agreement 14-16-0009-89-963. This chapter is the product of a workshop at the University of Southwestern Louisiana in Lafayette, supported by the Scientific Committee on Oceanographic Research. The authors gratefully acknowledge the diligent collaboration of Victor Rivera-Monroy, Ronghua Chen and Alfred Holmes. Claudia Munoz provided invaluable assistance in editing the manuscript and preparing illustrations for final preparation.

## REFERENCES

- Aber, J.D. and Melillo, J.M. (1982) Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. *Can. J. Bot.* **60**: 2263–2269.
- Alexander, T.R. (1967) Effect of hurricane Betsy on the southeastern Everglades. *Q. J. Fla. Acad. Sci.* **30**: 10–24.
- Alongi, D.M. (1987a) Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. *Mar. Biol.* **95**: 447–458.
- Alongi, D.M. (1987b) The influence of mangrove-derived tannins on intertidal meiobenthos in tropical estuaries. *Oecologia* **71**: 537–540.
- Alongi, D.M. (1988) Bacterial productivity and microbial biomass in tropical mangrove sediments. *Microbiol. Ecol.* **15**: 59–79.
- Alongi, D.M. (1989) The role of softbottom benthic communities in tropical mangrove and coral reef ecosystems. *Rev. Aquat. Sci.* **1**: 243–280.
- Alongi, D.M. (1990) The ecology of tropical softbottom benthic ecosystems. *Oceanogr. Mar. Biol. Annu. Rev.* **28**: 381–496.
- Alongi, D.M. and Sasekumar, A. (1992) Benthic communities. In: Robertson, A.I. and Alongi, D.M. (Eds): *Tropical Mangrove Ecosystems*. American Geophysical Union, Washington, DC, pp. 137–171.
- Alongi, D.M., Boto, K.G. and Robertson, A.I. (1992) Nitrogen and phosphorus cycles. In: Robertson, A.I. and Alongi, D.M. (Eds): *Tropical Mangrove Ecosystems*. American Geophysical Union, Washington, DC, pp. 251–292.
- Bacon, P.R. (1990) The ecology and management of swamp forests in the Guianas and Caribbean region. In: Lugo, A.E., Brinson, M. and Brown, S. (Eds): *Forested Wetlands. Ecosystems of the World 15*. Elsevier Press, Amsterdam, pp. 213–250.
- Bacon, P.R. (1994) Template for evaluation of impacts of sea level rise on Caribbean coastal wetlands. *Ecol. Eng.* **3**: 171–186.
- Ball, M.C. (1980) Patterns of secondary succession in a mangrove forest in south Florida. *Oecologia* **44**: 226–235.
- Beever III, J.W., Simberloff, D. and King, L.L. (1979) Herbivory and predation by the mangrove tree crab *Aratus pisonii*. *Oecologia* **43**: 317–328.
- Benner, R. and Hodson, R.E. (1985) Microbial degradation of the leachable and lignocellulosic components of leaves and wood from *Rhizophora mangle* in a tropical mangrove swamp. *Mar. Ecol. Prog. Ser.* **23**: 221–230.
- Benner, R., Peele, E.R. and Hodson, R.E. (1986) Microbial utilization of dissolved organic matter from leaves of the red mangrove, *Rhizophora mangle*, in the Fresh Creek Estuary, Bahamas. *Estuarine, Coastal Shelf Sci.* **23**: 607–619.
- Benner, R., Weliky, K. and Hedges, J. I. (1990a) Early diagenesis of mangrove leaves in a tropical estuary: molecular-level analyses of neutral sugars and lignin-derived phenols. *Geochim. Cosmochim. Acta* **54**: 1991–2001.
- Benner, R., Hatcher, P.G. and Hedges, J.I. (1990b) Early diagenesis of mangrove leaves in a tropical estuary: bulk chemical characterization using solid-state <sup>13</sup>C NMR and elemental analyses. *Geochim. Cosmochim. Acta* **54**: 2003–2013.
- Blaber, S.J.M. and Milton, D.A. (1990) Species composition, community structure and zoogeography of fishes of mangrove estuaries in the Solomon Islands. *Mar. Biol.* **105**: 259–267.
- Botero, L. (1990) Massive mangrove mortality on the Caribbean coast of Colombia. *Vida Silvestre Neotrop.* **2**: 77–78.

- Boto, K.G. and Bunt, J.S. (1981) Tidal export of particulate organic matter from a Northern Australian mangrove system. *Estuarine, Coastal Shelf Sci.* **13**: 247-255.
- Camilleri, J.C. (1992) Leaf-litter processing by invertebrates in a mangrove forest in Queensland. *Mar. Biol.* **114**: 139-145.
- Chapman, V.J. (1976) *Mangrove Vegetation*. J. Cramer, Vaduz, Germany.
- Chapman, V.J. (1977) Introduction. In: Chapman, V.J. (Ed.): *Ecosystem of the World. 1. Wet Coastal Ecosystem*. Elsevier, Amsterdam, pp. 1-29.
- Cintrón, G., Lugo, A.E. and Martínez, R. (1985) Structural and functional properties of mangrove forests. In D'Arcy, W.G. and Correa, M.D. (Eds): *The Botany and Natural History of Panamá*. Missouri Botanical Garden, Saint Louis, MO, pp. 53-66.
- Clarke, L.D. and Hannon, N.J. (1970) The mangrove swamp and salt-marsh communities of the Sydney District. III. Plant growth in relation to salinity and waterlogging. *J. Ecol.* **58**: 351-369.
- Clough, B.F. (1992) Primary productivity and growth of mangrove forest. In: Robertson, A.I. and Alongi, D.M. (Eds): *Tropical Mangrove Ecosystems*. Vol. 41. American Geophysical Union, Washington, DC, pp. 225-249.
- Craighead, F.C. and Gilbert, V.C. (1962) The effects of Hurricane Donna on the vegetation of southern Florida. *Q. J. Fla. Acad. Sci.* **25**: 1-28.
- Das, S. and Siddiqi, N.A. (1985) The mangroves and mangrove forests of Bangladesh. *Mangrove Silviculture Division Bulletin No. 2*, 142 pp.
- Davis, J.H., Jr. (1940) The ecology and geologic role of mangroves in Florida. *Bull. Am. Assoc. Pet. Geol.* **26**: 307-425.
- Day, J.H. (1975) The mangrove fauna of the Mozambique estuary, Mozambique. In Walsh, G.E., Snedaker, S.C. and Teas, H.J. (Eds): *Proceedings of the International Symposium on the Biology and Management of Mangroves*. Institute of Food and Agricultural Sciences, University of Florida, FL, pp. 415-430.
- Day, J., Conner, W., Ley-Lou, F., Day, R. and Machado, A. (1987) The productivity and composition of mangrove forests, Laguna de Términos, Mexico. *Aquat. Bot.* **27**: 267-284.
- DeSylva, D.P. (1986) Increased storms and estuarine salinity and other ecological impacts of the "Greenhouse effect". In: Titus, J.G. (Ed): *Effects of Changes in Stratospheric Ozone and Global Climate*. Vol. 4. US Environmental Protection Agency, Washington, DC, pp. 153-164.
- Dost, H. (1973) *Acid Sulfate Soils*. International Institute for Land Reclamation and Improvement, Publication No. 575, Vols. I and II. Wageningen, 701 pp.
- Egler, F.E. (1952) Southeast saline Everglades vegetation, Florida, and its management. *Vegetatio* **III**: 213-265.
- Ellison, A.M. and Farnsworth, E.J. (1990) The ecology of Belizean mangrove-root fouling communities. I. Epibenthic fauna are barriers to isopod attack of red mangrove roots. *J. Exp. Mar. Biol. Ecol.* **142**: 91-104.
- Ellison, A.M. and Farnsworth, E.J. (1992) The ecology of Belizean mangrove-root fouling communities: Patterns of epibiont distribution and abundance, and effects on root growth. *Hydrobiologia* **20**: 1-12.
- Ellison, A.M. and Farnsworth, E.J. (1993) Seedling survivorship, growth, and response to disturbance in Belizean mangal. *Am. J. Bot.* **80**: 1137-1145.
- Ellison, J.C. and Stoddart, D.R. (1991) Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. *J. Coastal Res.* **7**: 151-165.

- Emanuel, K.A. (1987) The dependence of hurricane intensity on climate. *Nature* **326**: 483–485.
- Emmerson, W.D. and McGwynne, L.E. (1992) Feeding and assimilation of mangrove leaves by the crab *Sesarma meinertide* in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. *J. Exp. Mar. Biol. Ecol.* **157**: 41–53.
- Ellison, A.M., Farnsworth, E.J. and Twilley, R.R. (1996) Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangal. *Ecology* **77**.
- Farnsworth, E.J. and Ellison, A.M. (1991) Patterns of herbivory in Belizean mangrove swamps. *Biotropica* **23**: 555–567.
- Farnsworth, E.J. and Ellison, A.M. (1993) Dynamics of herbivory in Belizean mangal. *J. Trop. Ecol.* **9**: 435–453.
- Fell, J.W. and Master, I.M. (1973) Fungi associated with the degradation of mangrove (*Rhizophora mangle* L.) leaves in south Florida. In: Stevenson, L.H. and Colwell, R.R. (Eds): *Estuarine Microbial Ecology*. University of South Carolina Press, SC, pp. 455–465.
- Fell, J.W. and Master, I.M. (1980) The association and potential role of fungi in mangrove detrital systems. *Bot. Mar.* **23**: 257–263.
- Feller, I.C. (1993) Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove. Ph.D. Dissertation, Georgetown University.
- Frith, D.W., Tantanasiwong, R. and Bhatia, O. (1976) Zonation of macrofauna on a mangrove shore, Phuket Island. *Phuket Mar. Biol. Cent. Res. Bull.* **10**: 37.
- Giddins, R.L., Lucas, J.S., Neilson, M.J. and Richards, G.N. (1986) Feeding ecology of the mangrove crab *Neosarmatium smithi* (Crustacea: Decapoda: Sesarmidae). *Mar. Ecol. Prog. Ser.* **33**: 147–155.
- Gilmore, R.G. and Snedaker, S.C. (1993) Mangrove forests. In: Martin, W.H., Boyce, S. and Echternacht, K. (Eds): *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities*. Wiley, New York, pp. 165–198.
- Glynn, P.W., Almodovar, L.R. and Gonzalez, J.G. (1964) Effects of hurricane Edith on marine life in La Parguera, Puerto Rico. *Caribb. J. Sci.* **4**: 335–345.
- Gotto, J.W. and Taylor, B.F. (1976) N<sub>2</sub> fixation associated with decaying leaves of the red mangrove (*Rhizophora mangle*). *Appl. Environ. Microbiol.* **31**: 781–783.
- Gotto, J.W., Tabita, F.R. and Baalen, C.V. (1981) Nitrogen fixation in intertidal environments of the Texas Gulf Coast. *Estuarine Coastal Shelf Sci.* **12**: 231–235.
- Heald, E.J. (1969) The production of organic detritus in a south Florida estuary. Ph.D. Dissertation, University of Miami.
- Heald, E.J. (1971) The production of organic detritus in a south Florida estuary. *Univ. Miami Sea Grant Tech. Bull.* **6**: 110.
- Heatwole, H. and Levins, R. (1972) Trophic structure stability and faunal change during recolonization. *Ecology* **53**: 531–534.
- Hendricks, H. (1975) The status of the tiger *Panthera tigris* (Linne 1758) in the Sundarbans mangrove forest (Bay of Bengal). *Saingetierkundliche Mitteilungen* **23**: 161–199.
- Hobgood, J.S. and Cerveny, R.S. (1988) Iced-age hurricanes and tropical storms. *Nature* **333**: 243–245.
- Huffaker, C.B., Dahlsten, D.L., Janzen, D.H. and Kennedy, G.G. (1984) Insect influences in the regulation of plant populations and communities. In: Huffaker, C.B. and Rabb, R.L. (Eds): *Ecological Entomology*. Wiley, New York, pp. 659–695.

- Intergovernmental Panel on Climate Change (1990) Potential impacts of climate change. Report from Working Group II to IPCC. World Meteorological Organization, Geneva.
- Janzen, D.H. (1974) Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6: 69–103.
- Jiménez, J.A. and Sauter, K. (1991) Structure and dynamics of mangrove forests along a flooding gradient. *Estuaries* 14: 49–56.
- Johnstone, I.M. (1981) Consumption of leaves by herbivores in mixed mangrove stands. *Biotropica* 13: 252–259.
- Jones, D.A. (1984) Crabs of the mangal ecosystem. In: Por, F.D. and Dor, I. (Eds): *Hydrobiology of the Mangal*. Junk, The Hague, pp. 89–110.
- Kimball, M.C. and Teas, H.J. (1975) Nitrogen fixation in mangrove areas of southern Florida. In: Walsh, G., Snedaker, S. and Teas, H. (Eds): *Proceedings of the International Symposium on the Biology and Management of Mangroves*. Institute of Food and Agricultural Sciences, University of Florida, FL, pp. 654–660.
- Lacerda, L.D. de, José, D.V., Rezende, C.E. de, Francisco, M.D.F. and Martins, J.C. (1986) Leaf chemical characteristics affecting herbivory in a New World mangrove forest. *Biotropica* 18: 350–355.
- Lee, S.Y. (1989) The importance of sesarminae crabs *Chiromanthes* spp. and inundation frequency on mangrove (*Kandelia candel* (L.) Druce) leaf litter turnover in a Hong Kong tidal shrimp pond. *J. Exp. Mar. Biol. Ecol.* 131: 23–43.
- Lee, S.Y. (1990) Net aerial primary productivity, litter production and decomposition of the reed *Phragmites communis* in a nature reserve in Hong Kong: Management implications. *Mar. Ecol. Prog. Ser.* 66: 161–173.
- Leh, C.M.U. and Sasekumar, A. (1985) The food of sesarimid crabs in Malaysian mangrove forests. *Malay Nat. J.* 39: 135–145.
- Lugo, A.E. (1980). Mangrove ecosystems: Successional or steady-state? *Biotropica* 12: 65–72.
- Lugo, A.E. and Patterson-Zucca, C. (1977) The impact of low temperature stress on mangrove structure and growth. *Trop. Ecol.* 18: 149–161.
- Lugo, A.E. and Snedaker, S.C. (1974) The ecology of mangroves. *Annu. Rev. Ecol. Syst.* 5: 39–64.
- Lugo, A.E., Brown, S. and Brinson, M.M. (1990) Concepts in wetland ecology. In: Lugo, A.E., Brinson, M. and Brown, S. (Eds): *Ecosystems of the World. 15. Forested Wetlands*. Elsevier, Amsterdam, pp. 53–85.
- Macnae, W. (1968) A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *Adv. Mar. Biol.* 6: 73–270.
- Macnae, W. (1974) Mangrove forests and fisheries. FAO/UNDP Indian Ocean Programme, IOFC/DEV/7434.
- Malley, D.F. (1978) Degradation of mangrove leaf litter by the tropical sesarimid crab *Chiromanthes onychophorum*. *Mar. Biol.* 49: 377–386.
- Markley, J.L., McMillan, C. and Thompson, G.A. (1982) Latitudinal differentiation in response to chilling temperatures among populations of three mangroves, *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle* from the western tropical Atlantic and Pacific Panama. *Can. J. Bot.* 60: 2704–2715.
- Maul, G.A. and Martin, D.M. (1993) Sea level rise at Key West, Florida, 1846–1992: America's longest instrument record? *Geophys. Res. Lett.* 20: 1955–1958.
- McKee, K.L. (1993) Determinants of mangrove species distribution in neotropical forests: Biotic and abiotic factors affecting seedling survival and growth. Ph.D. Dissertation, Louisiana State University.

- McMillan, C. (1971) Environmental factors affecting seedling establishment of the black mangrove on the central Texas coast. *Ecology* **52**: 927-930.
- McMillan, C. (1975) Adaptative differentiation to chilling in mangrove populations. In: Walsh, G.E., Snedaker, S.C. and Teas, H.J. (Eds): *Proceedings of the International Symposium on Biology and Management of Mangroves*. Vol. I. Institute of Food and Agricultural Sciences, University of Florida, FL, pp. 62-70.
- McMillan, C. (1986) Isozyme patterns among populations of black mangrove, *Avicennia germinans*, from the Gulf of Mexico-Caribbean and Pacific Panama. *Contrib. Mar. Sci.* **29**: 17-25.
- McMillan, C. and Sherrod, C.L. (1986) The chilling tolerance of black mangrove, *Avicennia germinans*, from the Gulf of Mexico coast of Texas, Louisiana and Florida. *Contrib. Mar. Sci.* **29**: 9-16.
- Melillo, J.M., Aber, J.D. and Muratore, J.F. (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**: 621-626.
- Micheli, F., Gherardi, F. and Vannini, M. (1991) Feeding and burrowing ecology of two east African mangrove crabs. *Mar. Biol.* **111**: 247-254.
- Moorman, F.R. and Pons, L.J. (1975) Characteristics of mangrove soils in relation to their agricultural land use and potential. In: Walsh, G., Snedaker, S. and Teas, H. (Eds): *Proceedings of the International Symposium on the Biology and Management of Mangroves*. Institute of Food and Agricultural Sciences, University of Florida, FL, pp. 529-547.
- Nateewathana, A. and Tantichodok, P. (1984) Species composition, density and biomass of microfauna of a mangrove forest at Ko Yao Yai, southern Thailand. In: Soepadmo, E., Rao, A.N. and MacIntosh, D.J. (Eds): *Proceedings of the Asian Symposium on Mangrove Environments: Research and Management*. University of Malaya and UNESCO, Kuala Lumpur, pp. 258-285.
- Neilson, M.J., Giddins, R.L. and Richards, G.N. (1986) Effects of tannins on the palatability of mangrove leaves to the tropical sesarmid crab *Neosarmatium smithi*. *Mar. Ecol. Prog. Ser.* **34**: 185-187.
- Newell, S.Y., Miller, J.D. and Fell, J.W. 1987. Rapid and pervasive occupation of fallen mangrove leaves by a marine zoosporic fungus. *Appl. Environ. Microbiol.* **53**: 2464-2469.
- Nixon, S.W. (1980) Between coastal marshes and coastal waters - a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In Hamilton, P. and MacDonald, K.B. (Eds): *Estuarine and Wetland Processes with Emphasis on Modeling*. Plenum Press, New York.
- Nixon, S.W., Furnas, B.N., Lee, V., Marshall, N., Jin-Eong, O., Chee-Hoong, W., Wooi-Khooon, G. and Sasekumar, A. (1984) The role of mangroves in the carbon and nutrient dynamics of Malaysia estuaries. In: Soepadmo, E., Rao, A.N. and Macintosh, D.J. (Eds): *Proceedings of the Asian Symposium on Mangrove Environments: Research and Management*. University of Malaya and UNESCO, Kuala Lumpur, pp. 496-513.
- Odum, W.E. (1971) Pathways of energy flow in a south Florida estuary. *Univ. Miami Sea Grant Bull.* **7**: 162.
- Odum, W.E. and Heald, E.J. (1972) Trophic analysis of an estuarine mangrove community. *Bull. Mar. Sci.* **22**: 671-738.
- Odum, W.E., McIvor, C.C. and Smith, T.J. (1982) *The Ecology of the Mangroves of South Florida: A Community Profile*. Fish and Wildlife Service/Office of Biological Services, Washington, DC, FWS/OBS-81/24, 144 pp.

- Ogden, J.C. (1992) The impact of Hurricane Andrew on the ecosystems of south Florida. *Conserv. Biol.* **6**: 488-491.
- Ogden, J.C. and Gladfelter, E.H. (1983) Coral reefs, seagrass beds and mangroves: Their interaction in the coastal zones of the Caribbean. *UNESCO Rep. Mar. Sci.* **23**: 133.
- Olmsted, I., Dunevitz, H. and Platt, W.J. (1993) Effects of freezes on tropical trees in Everglades National Park, Florida, USA. *Trop. Ecol.* **34**: 17-34.
- Olsen, D.A., Dammann, A.E., Hess, J.F., Sylvester, J.R. and Untema, J.A. (1973) The ecology of fishes in two mangrove lagoons in the US Virgin Islands. Report of the Puerto Rico International Underseas Laboratory, 42 pp.
- Onuf, C., Teal, J. and Valiela, I. (1977) The interactions of nutrients, plant growth, and herbivory in a mangrove ecosystem. *Ecology* **58**: 514-526.
- Osborne, K. and Smith, T.J. (1990) Differential predation on mangrove propagules in open and closed canopy forest habitats. *Vegetatio* **89**: 1-6.
- Pannier, F. (1979) Mangrove impacted by human-induced disturbance: A case study of the Orinoco Delta mangrove ecosystem. *Environ. Manage.* **3**: 205-216.
- Parkinson, R.W. (1989) Decelerating holocene sea-level rise and its influence on southwest Florida coastal evolution: A transgressive/regressive stratigraphy. *J. Sediment. Petrol.* **59**: 960-972.
- Perry, D.M. (1988) Effects of associated fauna on growth and productivity in the red mangrove. *Ecology* **69**: 1064-1075.
- Ponnamperuma, F.N. (1984) Mangrove swamps in south and southeast Asia as potential rice lands. In: Soepadmo, E., Rao, A.N. and McIntosh, D.J. (Eds): *Proceedings Asian Mangrove Symposium*. Percetakan Ardyas Sdn. Bhd., Kuala Lumpur, pp. 672-683.
- Potts, M. (1979) Nitrogen fixation (acetylene reduction) associated with communities of heterocystous and non-heterocystous blue-green algae on mangrove forests of Sinai. *Oecologia* **39**: 359-373.
- Quinn, N.J. and Kojis, B.J. (1985) Does the presence of coral reefs in proximity to a tropical estuary affect the estuarine fish assemblage. *Proc. 5th Int. Coral Reef Congr.* **5**: 445-450.
- Rabinowitz, D. (1977) Effects of mangrove borer, *Pecilips rhizophorae*, on propagules of *Rhizophora harrisonii*. *Fla. Entomol.* **60**: 129-134.
- Rabinowitz, D. (1978) Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. *J. Biogeogr.* **5**: 113-133.
- Ray, G.C. and McCormick, M.G. (1992) Functional coastal-marine biodiversity. *Transactions of 57th North American Wildlife and Natural Resource Conference*, pp. 384-397.
- Rice, D.L. (1982) The detritus nitrogen problem: New observations and perspectives from organic geochemistry. *Mar. Ecol. Prog. Ser.* **9**: 153-162.
- Rice, D.L. and Tenore, K.R. (1981) Dynamics of carbon and nitrogen during the decomposition of detritus derived from estuarine macrophytes. *Estuarine, Coastal Shelf Sci.* **13**: 681-690.
- Rivera-Monroy, V.H. and Twilley, R.R. (1996) The relative importance of nitrogen immobilization and denitrification in mangrove forests of Terminos Lagoon, Mexico. *Limnol. Oceanogr.* **41**: 284-296.
- Rivera-Monroy, V.H., Day, J.W., Twilley, R.R., Vera-Herrera, F. and Coronado-Molina, C. (1995) Flux of nitrogen and sediment in a fringe mangrove forest in Terminos Lagoon, Mexico. *Estuarine, Coastal Shelf Sci.* **40**: 139-160.



- Robertson, A.I. (1986) Leaf-burying crabs: Their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. *J. Exp. Mar. Biol. Ecol.* **102**: 237–248.
- Robertson, A.I. (1991) Plant-animal interactions and the structure and function of mangrove forest ecosystems. *Aust. J. Ecol.* **16**: 433–443.
- Robertson, A.I. and Duke, N.C. (1987) Insect herbivory on mangrove leaves in North Queensland. *Australian Journal of Ecology* **12**: 1–7.
- Robertson, A.I. and Daniel, P.A. (1989) The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia* **78**: 191–198.
- Robertson, A.I. and Alongi, D.M. (1992) *Tropical mangrove ecosystems*. American Geophysical Union, Washington, DC, 329 pp.
- Robertson, A.I. and Duke, N.C. (1990) Mangrove fish-communities in tropical Queensland, Australia: Spatial and temporal patterns in densities, biomass and community structure. *Mar. Biol.* **104**: 369–379.
- Robertson, A.I. and Blaber, S.J.M. (1992) Plankton, epibenthos and fish communities. In: Robertson, A.I. and Alongi, D.M. (Eds): *Tropical Mangrove Ecosystems*. American Geophysical Union, Washington, DC, pp. 173–224.
- Robertson, A.I., Giddins, R.L. and Smith, T.J. (1990) Seed predation by insects in tropical mangrove forests: Extent and effects on seed viability and growth of seedlings. *Oecologia* **83**: 213–219.
- Robertson, A.I., Alongi, D.M. and Boto, K.G. (1992) Food chains and carbon fluxes. In: Robertson, A.I. and Alongi, D.M. (Eds): *Tropical Mangrove Ecosystems*. American Geophysical Union, Washington, DC, pp. 293–326.
- Rojas, J.L., Yáñez-Arancibia, A., Day, J.W. and Vera-Herrera, F. (1992) Estuary primary producers: Laguna de Terminos – a case study. In: Seeliger, U. (Ed): *Coastal Plant Communities of Latin America*. Academic Press, New York, Chap. 10, pp. 141–154.
- Rooker, J.R. and Dennis, G.D. (1991) Diel, lunar, and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bull. Mar. Sci.* **49**: 684–698.
- Roth, L.C. (1992) Hurricanes and mangrove regeneration: Effects of hurricane Juan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. *Biotropica* **24**: 375–384.
- Ruetzler, K. and Feller, C. (1988) Mangrove swamp communities. *Oceanus* **30**: 16–24.
- Ryan, D.R. and Bormann, F.H. (1982) Nutrient resorption in northern hardwood forests. *BioScience* **32**: 29–32.
- Saenger, P. and Snedaker, S.C. (1993) Pantropical trends in mangroves above-ground biomass and annual litterfall. *Oecologia* **96**: 293–299.
- Saenger, P., Hegerl, E.J. and Davie, J.D.S. (1983) *Global Status of Mangrove Ecosystems*. Commission on Ecology Paper No. 3, International Union for the Conservation of Nature (IUCN), p. 88.
- Sasekumar, A. (1993) Asean-Australia marine science project: Living coastal resources. *Proceedings of a Workshop on Mangrove Fisheries and Connections*. Australian International Development Assistance Bureau (AIDAB), Brisbane.
- Sasekumar, A., Chong, V.C., Leh, M.U. and Du Cruz, R. (1992) Mangroves as habitat for fish and prawns. In: Jaccarini, V. and Martens, E. (Eds): *The Ecology of Mangroves and Related Habitats. Development in Hydrobiology 80*. Kluwer, Boston, MA, pp. 195–207.
- Sauer, J.D. (1962) Effects of recent tropical cyclones on the coastal vegetation of Mauritius. *J. Ecol.* **50**: 275–290.

- Scholl, D.W. (1964a) Recent sedimentary record in mangrove swamps and rise in sea level over the southwestern coast of Florida: Part I. *Mar. Geol.* **1**: 344–366.
- Scholl, D.W. (1964b) Recent sedimentary record in mangrove swamps and rise in sea level over the southwestern coast of Florida: Part II. *Mar. Geol.* **2**: 343–364.
- Scholl, D.W. and Stuiver, M. (1967) Recent submergence of southern Florida: A comparison with adjacent coasts and other eustatic data. *Geol. Soc. Am. Bull.* **78**: 437–454.
- Scholl, D.W., Craighead, F.C. and Stuiver, M. (1969) Florida submergence curve revised – its relation to coastal sedimentation rates. *Science* **163**: 562–564.
- Sedberry, G.R. and Carter, J. (1993) The fish community of a shallow tropical lagoon in Belize, Central America. *Estuaries* **16**: 198–215.
- Sherrod, C.L. and McMillan, C. (1981) Black mangrove, *Avicennia germinans*, in Texas: Past and present distribution. *Contrib. Mar. Sci.* **24**: 115–131.
- Sherrod, C.L. and McMillan, C. (1985) The distribution history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contrib. Mar. Sci.* **28**: 129–140.
- Sherrod, C.L., Hockaday, D.L. and McMillan, C. (1986) Survival of red mangrove, *Rhizophora mangle*, on the Gulf of Mexico coast of Texas. *Contrib. Mar. Sci.* **29**: 27–36.
- Simberloff, D.S. (1976a) Species turnover and equilibrium island biogeography. *Science* **194**: 572–578.
- Simberloff, D.S. (1976b) Trophic structure determination and equilibrium in an arthropod community. *Ecology* **57**: 395–398.
- Simberloff, D.S. (1978) Using island biogeographic distributions to determine if colonization is stochastic. *Am. Nat.* **112**: 713–726.
- Simberloff, D.S. and Wilson, E.O. (1969) Experimental zoogeography of islands: The colonization of empty islands. *Ecology* **50**: 278–295.
- Simberloff, D.S., Brown, B.J. and Lowrie, S. (1978) Isopod and insect root borers may benefit Florida mangroves. *Science* **201**: 630–632.
- Smith, T.J. (1987) Seed predation in relation to tree dominance and distribution in mangrove forests. *Ecology* **68**: 266–273.
- Smith, T.J. (1988) Differential distribution between subspecies of the mangrove *Cerriops tagal*: Competitive interactions along a salinity gradient. *Aquat. Bot.* **32**: 79–89.
- Smith, T.J. (1992) Forest structure. In: Robertson, A.I. and Alongi, D.M. (Eds): *Tropical Mangrove Ecosystems*. American Geophysical Union, Washington, DC, pp. 101–136.
- Smith, T.J. and Duke, N.C. (1987) Physical determinants of inter estuary variation in mangrove species richness around the tropical coastline of Australia. *J. Biogeogr.* **14**: 9–19.
- Smith, T.J., Chan, H-T., McIvor, C.C. and Robblee, M.B. (1989). Comparisons of seed predation in tropical, tidal forests on three continents. *Ecology* **70**: 146–151.
- Smith, T.J., Boto, K.G., Frusher, S.D. and Giddins, R.L. (1991) Keystone species and mangrove forest dynamics: The influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal Shelf Sci.* **33**: 419–432.
- Smith, T.J., Robblee, M.B., Wanless, H.R. and Doyle, T.W. (1994) Mangroves, hurricanes, and lightning strikes. *BioScience* **44**: 256–262.
- Snedaker, S. (1982) Mangrove species zonation: Why? In Sen, D. and Rajpurohit, K. (Eds): *Tasks for Vegetation Science. Vol. 2*. Junk, The Hague, pp. 111–125.

- Snedaker, S.C. (1984a) The mangroves of Asia and Oceania: Status and research planning. In: Soepadmo, E., Rao, A.N. and McIntosh, D.J. (Eds): *Proceedings of the Asian Symposium on Mangrove Environments: Research and Management*. University of Malaya and UNESCO, Kuala Lumpur, pp. 5–15.
- Snedaker, S.C. (1984b) Mangroves: A summary of knowledge with emphasis on Pakistan. In: Haq, B.U. and Milliman, J.D. (Eds): *Marine Geology and Oceanography of Arabian Sea and Coastal Pakistan*. Van Nostrand Reinhold, New York, pp. 255–262.
- Snedaker, S.C. (1986) Traditional uses of South American mangrove resources and the socio-economic effect of ecosystem changes. In: Kunstadter, P., Bird, E.C.F. and Sabhasri, S. (Eds): *Proceedings, Workshop on Man in the Mangroves*. United Nations University, Tokyo, pp. 104–112.
- Snedaker, S.C. (1989) Overview of ecology of mangroves and information needs for Florida Bay. *Bull. Mar. Sci.* **44**: 341–347.
- Snedaker, S.C. (1993) Impact on mangroves. In: Maul, G.A. (Ed): *Climate Change in the Intra-Americas Sea*. Edward Arnold, Kent, pp. 282–305.
- Snedaker, S.C., Brown, M.S., Lahmann, E.J. and Araujo, R.J. (1992) Recovery of a mixed-species mangrove forest in South Florida following canopy removal. *J. Coastal Res.* **8**: 919–925.
- Snedaker, S.C., Meeder, J.F., Ross, M.S. and Ford, R.G. (1994) Discussion of Joanna C. Ellison and David R. Stoddart. Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. *J. Coastal Res.* **7**: 151–165; (1991) *J. Coastal Res.* **10**: 497–498.
- Steyer, G. (1988) Litter dynamics and nitrogen retranslocation in three types of mangrove forests in Rookery Bay, Florida. M.S. Thesis, University of Southwestern Louisiana.
- Stoddart, D.R. (1969) Post-hurricane changes on the British Honduras reefs and cays: Resurvey of 1965. *Atoll Res. Bull.* **131**: 1–242.
- Sutherland, J.P. (1980) Dynamics of the epibenthic community on roots of the mangrove *Rhizophora mangle*, at Bahia de Buche, Venezuela. *Mar. Biol.* **58**: 75–84.
- Thayer, G.W., Colby, D.R. and Hettler, W.F. (1987) Utilization of red mangrove prop root habitat by fishes in south Florida. *Mar. Ecol. Prog. Ser.* **35**: 25–38.
- Thom, B.G. (1982) Mangrove ecology: A geomorphological perspective. In: Clough, B.F. (Ed.): *Mangrove Ecosystems in Australia*. Australian National University Press, Canberra, pp. 3–17.
- Tietjen, J.H. and Alongi, D.M. (1990) Population growth and effects of nematodes on nutrient regeneration and bacteria associated with mangrove detritus from northeastern Queensland (Australia). *Mar. Ecol. Prog. Ser.* **68**: 169–180.
- Tomlinson, P.B. (1986) *The Botany of Mangroves*. Cambridge University Press, New York.
- Twilley, R.R. (1985) The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. *Estuarine, Coastal Shefl Sci.* **20**: 553–557.
- Twilley, R.R. (1988) Coupling of mangroves to the productivity of estuarine and coastal waters. In: Jansson, B.O. (Ed.): *Coastal-Offshore Ecosystem Interactions*. Springer, Berlin, Germany pp. 155–180.
- Twilley, R.R. (1995) Properties of mangrove ecosystems related to the energy signature of coastal environments. In: Hall, C. (Ed.): *Maximum Power*. University of Colorado Press, Niwot, Colorado, pp. 43–62.
- Twilley, R.R., Lugo, A.E. and Patterson-Zucca, C. (1986) Production, standing crop,

- and decomposition of litter in basin mangrove forests in southwest Florida. *Ecology* **67**: 670–683.
- Twilley, R.R., Zimmerman, R., Solórzano, L., Rivera-Monroy, V., Boderó, A., Zambrano, R., Pozo, M., García, V., Lóor, K., García, R., Cárdenas, W., Gaibor, N., Espinoza, J. and Lynch, J. (1990) The importance of mangroves in sustaining fisheries and controlling water quality in coastal ecosystems. Final Report, US Agency for International Development, Program in Science and Technology Cooperation, Washington, DC.
- Twilley, R.R., Chen, R.H. and Hargis, T. (1992) Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water, Air Soil Poll.* **64**: 265–288.
- Twilley, R.R., Boderó, A. and Robadue, D. (1993) Mangrove ecosystem biodiversity and conservation: Case study of mangrove resources in Ecuador. In: Potter, C.S., Cohen, J.I. and Janczewski, D. (Eds): *Perspectives on Biodiversity: Case Studies of Genetic Resource Conservation and Development*. AAAS Press, Washington, DC, pp. 105–127.
- Van der Valk, A.G. and Attiwill, P.M. (1984) Acetylene reduction in an *Avicennia marina* community in southern Australia. *Aust. J. Bot.* **32**: 157–164.
- Vermeer, D.E. (1963) Effects of Hurricane Hattie, 1961, on the cays of British Honduras. *Z. Geomorphol.* **7**: 332–354.
- Vitousek, P.M. (1982) Nutrient cycling and nutrient use efficiency. *Am. Nat.* **119**: 553–572.
- Voss, G.L., Bayer, F.M., Robins, C.R., Gomon, M. and La Roe, E.T. (1969) A report to the National Park Service, Department of the Interior, on the marine ecology of the Biscayne National Monument. Institute of Marine and Atmospheric Sciences, University of Miami, FL.
- Wadsworth, F.H. (1959) Growth and regeneration of white mangrove in Puerto Rico. *Caribb. For.* **20**: 59–69.
- Walsh, G.E. (1967) An ecological study of a Hawaiian mangrove swamp. In: Lauff, G.H. (Ed.): *Estuaries*. AAAS Press, Washington, DC, pp. 420–431.
- Wanless, H.R., Parkinson, R.W. and Tedesco, L.P. (1994) Sea level control on stability of Everglades wetlands. In: Davis, S.M. and Ogden, J.C. (Eds): *Everglades. The Ecosystem and its Restoration*. St. Lucie Press, Delray Beach, Florida, pp. 199–223.
- Warren, J.H. and Underwood, A.J. (1986) Effects of burrowing crabs on the topography of mangrove swamps in New South Wales. *J. Exp. Mar. Biol. Ecol.* **102**: 223–235.
- Watson, J.G. (1928) Mangrove forests of the Malay Peninsula. *Malay. For. Rec.* **6**: 1–275.
- Wells, F.E. (1983) An analysis of marine invertebrate distributions in a mangrove swamp in northwestern Australia. *Bull. Mar. Sci.* **33**: 736–744.
- Williams, D. (1983) Daily, monthly, and yearly variability in recruitment of coral reef fishes. *Mar. Ecol. Prog. Ser.* **10**: 231–237.
- Williams, D. and Sale, P.F. (1981) Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral reef habitats within “One Tree Lagoon”, Great Barrier Reef. *Mar. Biol.* **65**: 245–253.
- Woodroffe, C.D. (1990) The impact of sea-level rise on mangrove shoreline. *Prog. Phys. Geogr.* **14**: 483–502.
- Woodroffe, C.D. (1992) Mangrove sediments and geomorphology. In: Robertson, A.I. and Alongi, D.M. (Eds): *Tropical Mangrove Ecosystems*. American Geophysical Union, Washington, DC, pp 7–41.

- Yáñez-Arancibia, A. (1985) *Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration*. UNAM Press, Mexico DF.
- Yáñez-Arancibia, A., Lara-Domínguez, A.L., Rojas-Galaviz, J.L., Sánchez-Gil, P., Day, J.W. and Madden, C.J. (1988) Seasonal biomass and diversity of estuarine fishes coupled with tropical habitat heterogeneity (southern Gulf of Mexico). *J. Fish. Biol.* **33** (Suppl. A): 191–200.
- Yáñez-Arancibia, A., Lara-Domínguez, A.L. and Day, J.W. (1993) Interactions between mangrove and seagrass habitats mediated by estuarine nekton assemblages: Coupling of primary and secondary production. *Hydrobiologia* **264**: 1–12.
- Yáñez-Arancibia, A., Sánchez-Gil, P. and Lara-Domínguez, A.L. (1994) Functional groups, seasonality, and biodiversity in Terminos Lagoon a tropical estuary, Mexico. In *Proceedings, International Workshop on Ecosystem Function of Marine Biodiversity in Estuaries, Lagoons and Near-shore Coastal Ecosystems*, 9 pp.
- Zuberer, D.A., and Silver, W.S. (1978) Biological nitrogen fixation (acetylene reduction) associated with Florida mangroves. *Appl. Environ. Microbiol.* **35**: 567–575.