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Different kinds of mangrove forests provide different goods and services

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Abstract. The goods and services that mangrove forests provide to society are widely understood but may be too generally stated to serve as useful guidelines in decision-making. Understanding the differences between fringe, riverine, and basin forests may help to focus these guidelines and to determine the best use of a particular forest. Fringe mangroves are important primarily for shoreline protection. Riverine forests, which are likely to be the most productive of the three types of forests, are particularly important to animal and plant productivity, perhaps because of high

nutrient concentrations associated with sediment trapping. Basin forests serve as nutrient sinks for both natural and anthropogenically enhanced ecosystem processes and are often important sources of wood products. Exploitation of a forest for one particular reason may make it incapable of providing other goods and services.

Key words. Mangrove forests, flood protection, nutrients, wastewater recycling, timber harvesting, shrimp ponds.

INTRODUCTION

Mangrove forests are widely recognized as providing a wide variety of goods and services to people, including protection from floods, provision of a variety of plant and animal products, sediment trapping, and nutrient uptake and transformation (FAO, 1994). Destruction of these forests continues, however, in spite of this understanding of their importance. Although these wetlands are abundant along many protected shorelines around the world, the life-sustaining but still poorly documented benefits they can provide, such as support to offshore fisheries, are likely to be diminishing.

The lack of a direct, easily observed relationship between a mangrove forest and the benefits it provides (and sometimes the lack of sufficient research to document it) may be one reason for continued exploitation, and often loss, of these wetlands. Another reason may be the generality that cloaks many discussions of the importance of these wetlands. In fact, not all mangrove forests provide all the goods

and services attributed to them. There are significant differences in the characteristics of mangrove habitats, not only between continents and regions but within individual stands of mangroves as well. Using a simple rationale for classifying a given mangrove stand may assist land-use managers in determining its likely value to society and subsequently in using it more wisely. The purpose of this paper is to develop a simple functional classification of mangrove forests and to identify which goods and services are likely to derive from which kinds of forests.

DIFFERENCES WITHIN AND AMONG MANGROVE FORESTS

Efforts to understand mangrove forests focused for many years on the significance to tree species distributions of spatial differences in soil water characteristics (Macnae, 1968), short-term differences in propagule dispersal and survival (Rabinowitz, 1978; Smith, 1987), competition among species (Clarke & Hannon, 1971), and geomorphological history or characterization of estuaries (Thom, Wright &

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Coleman, 1975). Some studies have de-emphasized tree species zonation because of the large number of exceptions to simple patterns (e.g. West, 1977). High and low intertidal zones are likely to differ as a result of gradients in frequency of inundation, soil porewater salinity, and soil waterlogging, that are usually interrelated and often difficult to predict in the absence of information about both regional hydrology and animal activity. No consistent pattern or cause of mangrove zonation has yet to be derived (Smith, 1992).

Two systems that may be particularly useful to land managers have been proposed for classifying mangrove forests. Six different kinds of mangrove forests are commonly distinguished in the Neotropics, where many are underlain by a carbonate limestone base: overwash, fringe, riverine, basin, scrub, and hammock (Lugo & Snedaker, 1974; Cintrón, Lugo & Martínez, 1986). A more general system has been proposed for Old World mangroves, which are more likely to develop on accreting sediments deposited by rivers and tides (Woodroffe, 1992). This system distinguishes three extremes, based on dominant physical processes: river-dominated, tide-dominated, and interior mangrove forests. Intermediate kinds of forests, including the six New World types, can be located within this framework (Fig. 1a).

In this paper, we adopt a hybrid of these systems, combining the familiarity of Lugo & Snedaker's terms with the flexibility of Woodroffe's system. We refer to tide-dominated mangroves as fringe mangroves, river-dominated mangroves as riverine mangroves, and interior mangroves as basin mangroves (Fig. 1b). Basin mangroves are likely to contain the most variation within a region, including low and high intertidal zones as well as small forests far inland, fed only occasionally by storm tides. Others have used the same system already for more local descriptions (e.g. Florida: Odum & McIvor, 1990). We suggest that this framework can be used to define the extremes among mangrove forests within any region without having to determine how fringe mangrove forests (for instance) in one part of the world are related to fringe mangrove forests in another.

The three extremes are easily described. Fringe mangroves receive the brunt of the tides, which are often full-strength seawater. Prop roots, buttresses, and pneumatophores are common among trees in this part of a forest. Riverine mangroves are flooded by river water as well as by tides, so that salinity is moderate.

Trees in this zone are likely to be among the most productive in a forest (Twilley, Lugo & Patterson-Zucca, 1986). Basin mangroves generally cover large areas behind fringe and riverine mangroves, and only occasionally do tides inundate an entire basin forest. Soil salinity may be very high at higher elevations where evapotranspiration causes salts to accumulate. In small forests that are frequently flooded, or where rainfall is high and/or groundwater flow is substantial, a basin mangrove forest can be of moderate or even low salinity (e.g. Cintrón *et al.*, 1978; Semeniuk, 1983; Ewel *et al.*, 1998a). Clearly, there may be substantial differences in hydrology, nutrient cycling, and productivity between these three types of forests (Twilley, 1995). Productivity (generally measured by litterfall alone in these forests) is closely related to water turnover, with riverine > fringe > basin (Pool, Lugo & Snedaker, 1975), because higher turnover is likely to mean: (i) an increased supply of nutrients, silts, and clays; (ii) less accumulation of toxic substances in porewater; and (iii) greater aeration of the soil matrix.

Distinct boundaries between the three hydrogeomorphic types of mangrove forest in the same stand may be difficult to define. Some characteristics of each, such as inundation time and porewater salinity, may vary from region to region, and there is likely to be no single measure that enables one kind of forest to be unambiguously assigned to one zone or another. Nevertheless, recognizing these broad groupings should assist in formulating generalizations that may be particularly helpful in establishing appropriate management policies (e.g. Bacon, 1994).

GOODS AND SERVICES PROVIDED BY MANGROVE FORESTS

In this paper, we consider a range of goods and services provided by mangrove forests (Table 1). Some, such as sediment trapping, nutrient processing, and providing food and habitat for animals, are essential for preserving ecosystem integrity and regional biodiversity. Others are not obtained without considerable human intervention, such as harvesting mangrove trees. The magnitude and quality of each of these goods and services are likely to vary among the three hydrogeomorphic zones, and no zone can be designated as 'most' or 'least' important overall.

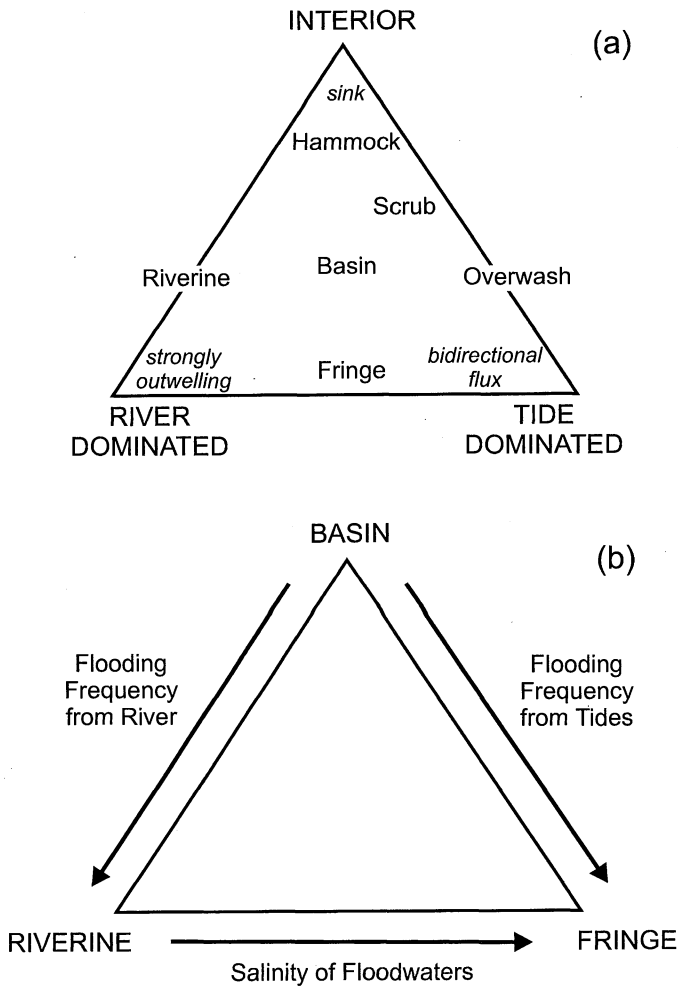


Fig. 1. (a) The relationships among three functional types of mangrove forests (river-dominated, tide-dominated, and interior), dominant physical processes (in italics), and six types of mangrove forests described for the Neotropics (Woodroffe, 1992). (b) Proposed relationship among three functional types of mangrove swamps that can be distinguished within any given region (original).

Sediment trapping

Entire mangrove forests can trap and retain sediments generated in the uplands by virtue of their position in the landscape (Lynch *et al.*, 1989; Parkinson, DeLaune & White, 1994). Riverine forests are likely to be particularly important in this respect, because river waters usually carry a heavier sediment load than ocean tides. Sediments deposited in fringe forests can be riverine in origin, however, having been recirculated within the nearshore waters (Wolanski, Mazda & Ridd,

1992). Basin swamps also trap sediments, receiving the finest particles that are carried past riverine and fringe forests by floods and tides. They may also trap sediments deposited by runoff from uplands along the landward edge of the swamp.

Simply leaving mangrove forests intact avails society of the service of sediment trapping, because removal of the forest, particularly along the banks of fringe and riverine mangrove forests, opens up vulnerable soils to erosion and offshore sediment deposition. Mangrove forests can also be exploited for this service

Table 1. Relative importance of different types of mangrove forests in providing goods and services. 1 = most important

Role	Riverine	Basin	Fringe
Trap sediments	1	2	3
Process nutrients and organic matter			
Provide a source of detritus to nearshore waters	1	3	2
Serve as a sink for nutrients and carbon			
C, N	2	1	3
P	1	3	2
Improve water quality	2	1	3
Provide food and habitat for animals	1	3	2
Provide aesthetically pleasing environments	1	3	2
Protect shorelines	2	3	1
Provide plant products	2	1	3

when excess sediments generated by anthropogenic activities such as road construction and upland forest clearing are prevented from washing out to offshore seagrass beds and coral reefs. Riverine forests are most important in this respect, but basin forests often perform this service also, as well as narrow fringe forests that directly abut against uplands (Nixon *et al.*, 1984). The ability of mangrove forests to receive sediments is limited, however, because trees are killed when lenticels on pneumatophores, prop roots, and young stems are buried. The second largest cause of mangrove loss on the Pacific island of Pohnpei, Federated States of Micronesia, over a 10-year period, was road construction, due to both clearing the road bed and the death of adjacent and downstream trees from excess sedimentation (W. Raynor, The Nature Conservancy, pers. comm.).

The prospect of sea level rise brings a new dimension to the importance of sediment trapping. It is possible that thoughtful manipulation of sediment delivery to a mangrove forest could ensure continued existence of the forest even in the face of rising tides. An understanding of the balance between sediment accretion and compaction as well as of potential vegetation and hydrodynamic changes due to associated climate change would also be required, however.

Processing of organic matter and nutrients

The exchanges of nutrients and detritus between mangroves and near-shore waters in areas of different geomorphology and hydrodynamics are widely accepted as important but complex and difficult to quantify (Boto & Bunt, 1981; Twilley, 1985; Gong &

Ong, 1990; Wattayakorn, Wolanski & Kjerfve, 1990). Measurements of the net flux of different forms of nutrients and organic matter are required in order to understand the role and relative importance of mangrove forests to biogeochemistry and productivity of coastal waters (Boto & Wellington, 1988; Rivera-Monroy *et al.*, 1995). As observed for salt marshes, there may be a net flux of inorganic nutrients into mangroves from coastal waters and a net export of organic nutrients associated with particulate and dissolved organic matter export (Twilley *et al.*, 1997). Even though there are still few studies of these processes, highlighting important differences between fringe, riverine, and basin mangroves may transcend much of this complexity.

Organic matter export

Estimates of carbon export to offshore waters range across two orders of magnitude; the average rate is about $210 \text{ gC m}^{-2} \text{ yr}^{-1}$, with greatest export values coming from fringe mangroves (Table 2). In Rookery Bay, Florida, for instance, fringe mangrove forests export twice as much organic matter per hectare as basin forests (but taking the area of each type of wetland into account results in equal loading rates of detritus between them; Twilley, 1982). The presence of crabs that consume litter (28–79% of annual leaf fall; Robertson, 1986, 1988; Robertson & Daniel, 1989; Twilley *et al.*, 1997) may increase the tightness of nutrient cycles in the mangrove forest and decrease the amount of outwelling, particularly from interior portions of basin forests and especially in Old World sites, where crabs are more common (Jones, 1984). High productivity and relatively short residence times

Table 2. Export of organic carbon from mangrove forests (after Twilley *et al.*, 1992).

Swamp type	Export (gC m ⁻² yr ⁻¹)	Location	Reference
Fringe	2	Hong Kong	Lee (1989)
Basin	64	Florida, USA	Twilley (1985)
Basin	91	Florida, USA	Lugo & Snedaker (1974)
Swamp*	110	New Zealand	Woodroffe (1985)
Fringe	186	Florida, USA	Heald (1969)
Fringe	292	Florida, USA	Odum & Heald (1972)
Swamp*	340	Hinchinbrook, Australia	Robertson (1986)
Fringe	401	Puerto Rica, USA	Golley, Odum & Wilson (1962)
Swamp*	420	Hinchinbrook, Australia	Boto & Bunt (1981)
Average	210		

* Because flux measurements were made at the mouth of a tidal creek, exchange represents the combined export from both fringe and basin mangroves and therefore the entire swamp.

of litter in riverine and fringe mangroves, both associated with higher frequency of inundation, make them particularly important, except where basin zones are much larger.

Nutrient sink

Basin mangrove forests may rank lower in organic matter export because of lower flooding frequency, but they may have higher rates of organic matter and nutrient accumulation. Soil redox potential is a particularly important measure of the soil environment for determining characteristics of nutrient cycles because of its control over oxidation states of P, N, S, Mn, Fe, and many other elements. It should be lowest where hydroperiods are longest, although the presence of pneumatophores and prop roots (McKee, Mendelssohn & Hester, 1988) and the absence of strong differences in water turnover rates between the zones (Ewel *et al.*, 1998a) may mitigate this. Basin mangrove forests are more likely to serve as a sink for inorganic N because of the likelihood of denitrification in an anaerobic environment, but in fact both denitrification and nitrogen fixation rates in mangrove swamps are slow (e.g. Rivera-Monroy & Twilley, 1996). Denitrification can be significant, even in a fringe mangrove forest, under sewage enrichment, however (Corredor & Morell, 1994). Formation of H₂S and CH₄ should be particularly common in basin mangrove forests, but oxygen transport via prop roots (e.g. McKee *et al.*, 1988) may slow the formation and release of these gases.

Water quality improvement

The service of nutrient processing has often been exploited for water quality improvement. Mangrove forests, like wetlands in general around the world, often inadvertently receive untreated wastewater of both human and animal origin. Basin mangrove forests may be particularly useful for transforming nutrients, particularly N, and immobilizing microbes and chemicals such as pesticides (Clough, Boto & Attiwill, 1983). Denitrification effectively removed nitrate from a heavy wastewater load in a Puerto Rican basin mangrove forest, for instance (Corredor & Morell, 1994). However, the full implications of disposal of wastewater into mangrove forests are seldom considered. To safeguard human health, effluent should be retained in an area free from contact with humans or commonly eaten fish and shellfish, i.e. as far back in a basin forest as possible. Although increased productivity of an ecosystem was once considered as a useful by-product of this kind of enrichment, the changes in a habitat that can follow such dramatic changes in ecosystem function, both on-site and downstream, are now regarded as potentially harmful (Ewel, 1997). Nevertheless, when the expense of constructing a wastewater treatment plant is considered, wetlands are still commonly selected as receiving areas for effluent.

Retrofitting mangrove forests for wastewater treatment is preferable to destruction, and wastewater disposal may even be considered as a tool in mangrove restoration. Directing secondarily treated wastewater

through a complex of coastal ecosystems on a Caribbean island resulted in both 'mangrove rejuvenation' and increased use by water birds and other wildlife (Bacon & Morgan, 1996). Although care must still be taken to meet acceptable public health standards, the 'constructed wetland' model used widely now in the USA (Ewel, 1997) may be appropriate for coastal wetlands in many tropical countries.

Animal habitat

Mangrove forests support animal populations both within the forest and in offshore areas. Some of these animals spend only part of their life cycle in mangrove forests, either during a particular stage of their maturation or as migrants (Yáñez-Arancibia *et al.*, 1988; Yáñez-Arancibia, Lara-Domínguez & Day, 1993). Where mangroves are a dominant source of carbon, they are important to estuarine consumers (Rodelli *et al.*, 1984). Crabs are among the characteristic invertebrate fauna of mangrove forests that are particularly important in human food chains. Densities of crabs are especially likely to be highest on unvegetated mudbanks adjacent to mangroves, with lower numbers along fringe mangroves; their densities are often low inside mangrove forests, however, perhaps because of low food quality as a result of high concentrations of tannins (Alongi & Sasekumar, 1992). There, they are more common at high intertidal locations than at lower zones, perhaps because feeding times are longer (McIvor & Smith, 1995).

Some species of crabs process detritus, as described earlier, and some feed on propagules (and thereby directly affect forest structure; Smith, 1987). They are clearly important in maintaining ecosystem processes in mangrove forests, and many provide food, both directly and indirectly, to people. Culturing mangrove crabs (specifically *Scylla serrata* (Forsk.)) has been proposed, but this would have to be done without clearing the forest or impeding water flows in order to maintain suitable habitat. Crab production might be increased by augmenting food supply, such as with kitchen scraps, but because mangrove crabs are territorial and can be cannibalistic (T. J. Smith III, US Geological Survey, Biological Resources Division, pers. comm.), this is not likely to be sustainable on a commercial scale.

Juvenile shrimp (e.g. penaeid prawns) are also important components of the invertebrate fauna. Shrimp are more common in fringe and riverine mangroves as well as in more frequently inundated

portions of basin mangroves (Robertson & Blaber, 1992). Conflicting data indicate that shrimp obtain carbon from plankton and possibly epiphytic algae rather than from mangroves (Primavera, 1996) and that mangrove-derived carbon fuels bacteria production that is subsequently found in higher trophic levels (Cifuentes *et al.*, 1996). It is possible that the roles of mangrove detritus and *in situ* primary productivity in supporting higher trophic levels vary among different types of estuary.

The use of land where mangrove forests once grew to culture shrimp (prawns) has a long tradition in Asia. Mariculture and shrimp farming expanded more recently into Ecuador, where, by the late 1980s, there were more shrimp produced than anywhere else in the world (Twilley, Bodero & Robadue, 1993). The intensity of use ranges from trapping shrimp within mangrove forests and holding them there until harvest, usually for a lunar cycle, to more intense systems where mangrove trees coexist with pond and shrimp, as in the traditional 'tambak' of Indonesia. Much more intensive culture techniques have been introduced recently, primarily in basin mangroves, where mangrove trees are totally cleared and ponds are dug to a depth of 1–2 m. Much of this started in the Philippines, initially for the culture of milkfish (*Chanos chanos* Forsskal.). The system depended on the natural fertility of the ponds, which decreased in productivity very quickly, and required the clearing and construction of new ponds in a system of shifting aquaculture. Most of the mangroves in the Philippines had been degraded when shrimp culture (*Penaeus monodon* Fabricius) took hold. By the early 1990s, 50% of the mangrove forests in Thailand (Spalding, Blasco & Field, 1997) and 21% of the mangroves in Ecuador (CLIRSEN, 1992) had been lost, mostly due to construction of shrimp ponds.

Overall, approximately 24% of shrimp ponds in Thailand have been abandoned because of diseases (which have also affected ponds in India, the Philippines, Taiwan, and Indonesia) (Stevenson & Burbridge, 1997). Also, many mangrove soils, particularly in the Old World tropics, are potentially acid sulphate soils, and sulphuric acid will form (reducing water pH to around 3) if the soil is oxidized (as when water circulation begins after the ponds are built). This can be overcome by heavy liming and extensive flushing (which is not only expensive but reduces water quality in the neighbouring estuary). Mangrove forests are still being used because mangrove land is grossly undervalued and often belongs to the state. There is thus an urgent need to establish the real

value of mangrove land not only in economic terms but also in terms of its ecological and sociological value.

There is no clear explanation for the high densities of fish that have been reported in and around mangrove forests, although they are often associated with *Rhizophora* forests, where well-developed prop roots may provide safety from predation (Robertson & Blaber, 1992). Habitat availability for juvenile and adult fish is likely to be greater in fringe and riverine forests, as well as in those portions of basin forests where tidal channels provide access.

Many higher vertebrates also use mangrove forests. Few amphibians are found in mangroves (although, for example, ranid frogs occur in mangroves in SE Asia and the Philippines), but several reptiles, including crocodiles, snakes, and lizards, use mangrove forests (Macnae, 1968; Hutchings & Recher, 1983). Some sea turtles feed on mangrove roots and leaves and appear to use mangrove estuaries as nursery areas (Odum, McIvor & Smith, 1982).

Large numbers of birds use mangroves for feeding and/or nesting in many parts of the world. For example, 181 species are reported from Florida mangroves, but very few are heavily dependent on these forests alone. Those most closely associated with mangrove forests feed primarily in the canopy and are especially common in fringe and riverine forests (Odum *et al.*, 1982). Fringe and riverine mangroves are especially important to migrating birds (Ogden, 1994). More than 200 species of birds have also been reported from Australian mangrove forests, including some endemic species (e.g. the mangrove heron, *Butorides striatus* (L.)) (Hutchings & Recher, 1983).

Many mammals also use mangrove forests, most of them in addition to other terrestrial or aquatic ecosystems. There are a few endemic mammal species in mangroves, e.g. a crab-eating rat (*Xeromys myoides* Thomas) in Australia (Hutchings & Recher, 1983), the leaf monkey (*Presbytis cristatus* (Raffles)) in Malaysia, and the proboscis monkey (*Nasalis larvatus* (Wurmb.)) in Borneo (Macnae, 1968). Mangroves are particularly important to a few large mammals, such as large cats (e.g. the Royal Bengal tiger, *Panthera tigris* Linnaeus, in the Sundarbans, between India and Bangladesh), as well as a variety of deer and otters (Odum *et al.*, 1982; Dugan, 1993; FAO, 1994).

Aesthetically pleasing environment

Large, undisturbed stands of mangrove forests are attractive to tourists (Hamilton & Snedaker, 1984).

Boardwalks and canoe trails, particularly along stately riverine corridors and the edges of fringe mangrove forests, provide an opportunity for obtaining income from otherwise undeveloped land as well as for educating laypeople on the functions and values of wetlands.

Healthy stands of fringe and riverine mangroves, however, are not always appreciated. In the USA, the State of Florida recently passed legislation that permits homeowners to prune mangroves along the shoreline to allow an unobstructed view, in spite of the fact that one of the most common species, *Rhizophora mangle* L., does not retain the ability to regenerate after cutting (Gill & Tomlinson, 1969; Snedaker *et al.*, 1992). The 'Ding' Darling National Wildlife Refuge, also in Florida, cuts 'windows' in the stands of mangroves that grow up along dikes to allow easier viewing of wildlife, particularly alligators and wading birds that use the ditches on the other side.

Protection from floods

Protection of human infrastructure from storm surges, tidal waves, and floods is one of the most widely touted services provided by wetlands. This is because (1) the boundaries of a wetland indicate the extent of normal flooding and therefore the zone where human development should cease, and (2) wetland vegetation decreases the rate at which water passes over land, slowing the destructive force of floodwaters as they approach the uplands. Like many other ecosystem services, in spite of the general recognition it receives, the value of shoreline protection (or flood protection in general) provided by a wetland lies in the cost that society does not have to pay until that service is lost (Goulder & Kennedy, 1997).

Mangroves develop only along low-energy or protected coasts, where sediments are retained and mangrove seedlings can become established. Only where high energy events such as major storm surges and tidal waves are episodic are mangrove forests likely to be important in protecting human structures. In such places, fringe mangrove forests are believed to be particularly important, but this is a difficult hypothesis to prove, and anecdotal evidence is not always convincing (Clough, 1993). Perhaps the most widely cited observation is Fosberg's (1971) suggestion that the loss of more than 100,000 lives in Bangladesh in 1970 following a hurricane and tidal wave might have been reduced had large areas of mangroves not been replaced by rice paddies. Other anecdotes are

accumulating. Erosion along a coastal road behind mangroves on St. John, US Virgin Islands, after a hurricane in fall 1995 was least where the mangroves were thickest (T.J. Smith III, pers. comm.). Loss of mangroves following diversion of a river on the Pacific island of Kosrae, Federated States of Micronesia, has been correlated with increased wear on the coastal road and nearby structures by storm tides (K.C. Ewel and R. R. Twilley, pers. obs.). Instances in which storm surges have affected vegetation on the landward side of mangrove forests while mangrove remained unscathed (e.g. Steers, 1977) do not prove that the disturbed area would have suffered further destruction had the mangroves not been there. In the absence of more definitive data, however, it seems apparent that zoning regulations that protect a wetland to its landward limit, recognized as the normal upper limit of flooding, should enable it in turn to protect homes, roads, and other infrastructure from flood damage.

Pacific Islanders in the western Carolines recognize the importance of the characteristically drooping branches along the edge of fringe mangrove forests for breaking the force of storm tides (K.C. Ewel, pers. obs.). The roots of mangrove trees in both fringe and riverine forests play an important role in binding surface soils tightly (e.g. Scoffin, 1970). Both fringe and riverine mangroves are therefore particularly important for preventing shorelines from eroding, thereby not only affording shoreline protection but protecting offshore seagrass beds and coral reefs from sediment deposition as well.

Basin mangrove forests may assist in protection from episodic floods as well, both by reducing water velocity and by adding flood storage capacity behind fringe and riverine forests. The amount of forest necessary for adequate protection in a particular area depends on the geomorphology of an individual shoreline as well as on the frequency and magnitude of possible storms.

Plant products

An impressive diversity of plant products is harvested from mangrove trees, including tannins, honey, medicinal products, and thatch (Hamilton & Snedaker, 1984). Some of these can be obtained with little impact on the forest; harvesting for firewood and timber probably has the greatest effect.

Net primary productivity of mangrove forests, as measured by litterfall, is often high relative to upland forests at the same latitude (Saenger & Snedaker, 1993),

but tree growth rates vary considerably from site to site, generally decreasing with latitude (Twilley *et al.*, 1996). Mangrove forests appear to be most productive where there is no distinct dry season, and biomass can exceed 250 Mg/ha (Ong *et al.*, 1979), reaching 350–400 Mg/ha in protected areas of Malaysia (Putz & Chan, 1986). The best growth of mangrove trees is generally believed to occur in riverine forests, where floods deposit sediments periodically (e.g. Lacerda *et al.*, 1993; Hussain, 1995), but harvesting is often most common in basin forests where large monospecific stands and less frequent flooding may make extraction more economical.

Different species of mangrove timber have different physical properties (FAO, 1994) but there is no information on how variations within and among species may be related to the physical forces that affect different kinds of forests. Some species, like *Avicennia*, are widespread ecologically; they are very soft and have little commercial use. *Rhizophora*, which is also found in a variety of different environments and often in extensive, almost monospecific stands, has many uses and is the most widely exploited commercial genus. The wood is very hard and dense but tends to split very readily. It is not suitable for furniture but is often used for firewood and charcoal and is ideal for conversion to rayon. It is also often used for poles and, because it is extremely resistant to rot under anaerobic conditions, is very suitable as piling material. A number of less widely spread genera like *Xylocarpus* and *Heritiera* are found primarily in basin or riverine mangrove forests; they are excellent furniture grade timber but are seldom exploited for that purpose because they tend to occur in low numbers. *Xylocarpus* is used extensively in Micronesia for carving.

In most of the tropics, mangrove timber has traditionally been used mainly as fuelwood (either directly as firewood or after conversion to charcoal), as fishing stakes, and as building materials (pilings, poles, and timber for buildings and boats). Here, mangrove use is not a matter of choice but rather of survival, and intensity of use depends on ease of access and population pressures.

Commercial production is common primarily in Asia, where large stands of *Rhizophora* are harvested for poles (including pilings), charcoal and, more recently, woodchips (for conversion into rayon). Where the net productivity of mangroves is high, it is possible to harvest timber on a sustainable basis. A simple rule of thumb—clearfelling small patches and thinning around 15 years and again around 20 years—was developed

in the early part of this century in Malaysia by British foresters (Watson, 1928). The classic success case is in the Matang Mangrove Forest in Malaysia where *Rhizophora apiculata* BL. has been harvested sustainably (annual coupe of about 1000 ha) since the early part of this century (Ong, 1995). Here the timber is used as poles for piling as well as for the production of charcoal (for export). Yet, in the same country, pristine mangroves (e.g. the mangrove forest of the Rajang Delta in Sarawak) have been badly degraded as a result of harvesting for woodchips (annual coupe of about 600 ha). This operation started in the late 1960s and ran out of mangrove timber after about 25 years. A minimum girth system of management was practiced but appears to have failed. A similar operation in the neighbouring State of Sabah was closed down earlier.

The mangrove woodchip industry is now very active in some of the best mangrove forests (in Kalimantan, Sumatra and Irian Jaya) in Indonesia, where it operates almost unnoticed in remote, sparsely populated, or unpopulated areas, where some of the world's best pristine mangrove forests (*Rhizophora*-dominated) have been targeted. These operations generally last for about 25 years and then are moved to another site. It is not known if the Indonesian operations can be sustained as they are presently run, but a sustained-yield management system has not been implemented elsewhere (Ong, 1995).

MAKING DECISIONS BASED ON GOODS AND SERVICES

The usefulness of mangrove forests can be attributed to both the diversity among forests and the diversity of goods and services that they supply. A synopsis of the relative importance of fringe, riverine, and basin mangrove forests indicates that all three may be considered critical in at least one respect (Table 1). Riverine forests, with their nutrient inflows and moderate salinities are important interfaces between the more expansive basin forests and the fresh and salt water inflows. Basin forests, on the other hand, with their more restricted water flows, are often the sites of greatest human activity. Fringe mangrove forests, subject to the greatest water movement and consistently high salinity, are critical as a protective barrier for the rest of the forest and, occasionally, for human structures as well.

Understanding the importance and best use of

different parts of a forest may help in formulating management policies that enable the continued supply of essential goods and services. For instance, a basin forest from which crabs are harvested should not be used for wastewater treatment, and timber harvest should be restricted or even prohibited in riverine and fringe forests, which are more subject to erosion than basin forests. All three kinds of forests can be aesthetically pleasing and are important in production of animals and nutrient processing, although in very different ways.

Exploiting a mangrove forest for one product or service can reduce its ability to provide others. Timber harvest, water quality improvement, and shrimp ponds are all concentrated in basin forests, where they are likely to reduce a forest's potential for creating an aesthetically pleasing environment, change the nature of its nutrient cycles, and alter habitat for animal populations. However, with regional planning it should be possible to determine where conflicting goods and services could be obtained from different zones within the same forest, perhaps as mitigation for preserving a similar forest in an area where habitat value or recreation benefits may be higher. For instance, some of the concern about unregulated growth of shrimp ponds centres around the loss of water quality in neighbouring coastal ecosystems. Distributing effluent from shrimp ponds into nearby basin mangrove forests would not only limit negative impacts on water quality in coastal ecosystems (Robertson & Phillips, 1995), but it could also increase mangrove tree growth rates, thereby reducing intensity of harvesting in more pristine stands.

We do not yet understand all the consequences of disturbances to mangrove forests. For instance, does removal of large volumes of timber from basin mangrove forests lead to sediment compaction as dead roots decay, in turn leading to lower redox levels and changes in habitat value for both plants and animals? Lower redox but no apparent subsequent changes in species composition in small basin-zone gaps in high-rainfall forests have been recorded (Ewel *et al.*, 1998b), and these effects might be accentuated in more arid regions. Lower redox values could also increase release of N_2 , H_2S , and perhaps CH_4 to the atmosphere to the extent that they affect regional or even global climate. However, we cannot yet define acceptable limits that can be used to formulate management policies in different parts of the world.

Acknowledging and understanding the diversity that exists within mangrove forests should provide a broader

perspective for judging all the implications of the uses of this important form of wetland. Aggregating this diversity around simplifying concepts such as the distinctions among fringe, riverine, and basin zones in mangrove forests may assist local natural resource managers in restricting uses of these wetlands to the kind of forest where they are most likely to be tolerated and even sustained. Boundaries among these zones may be difficult to define, and particular zones in one area may not be directly comparable to the same zone in another area. A conservative approach, until more definitive guidelines can be obtained, may be to define Best Management Practices that limit potentially destructive management practices, such as harvesting, within the first 50 or 100 m (or some multiple of the normal tidal range) of a fringe or riverine forest. Being able to restrict development by means of easily understood guidelines may be the first step not only toward reducing the loss of mangrove forests in a region but also to reducing the rate of loss of their goods and services.

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REFERENCES

- Alongi, D.M. & Sasekumar, A. (1992) Benthic communities. *Tropical mangrove ecosystems: coastal and estuarine studies 41* (ed. by A.I. Robertson & D.M. Alongi) pp. 137–171. American Geophysical Union, Washington DC.
- Bacon, P.R. (1994) Template for evaluation of impacts of sea level rise on Caribbean coastal wetlands. *Ecol. Eng.* **3**, 171–186.
- Bacon, P.R. & Morgan, A.C. (1996) Integrating wetland restoration with wastewater treatment in a Caribbean coastal environment (abstract). *INTECOL's V International Wetlands Conference, Perth, Western Australia*.
- Boto, K.G. & Bunt, J.S. (1981) Tidal export of particulate organic matter from a northern Australian mangrove system. *Estuarine Coast Shelf Sci.* **13**, 247–255.
- Boto, K.G. & Wellington, J.T. (1988) Seasonal variations in concentrations and fluxes of dissolved organic and inorganic materials in a tropical, tidally-dominated, mangrove waterway. *Mar. Ecol. Progr. Ser.* **50**, 151–160.
- Cifuentes, L.A., Coffin, R.B., Solarzano, L., Cardenas, W., Espinosa, J. & Twilley, R.R. (1996) Isotopic and elemental variations of carbon and nitrogen in a mangrove estuary. *Estuarine Coast Shelf Sci.* **43**, 781–800.
- Cintrón, G., Lugo, A.E., Pool, D.J. & Morris, G. (1978) Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica*, **10**, 110–121.
- Cintrón, G., Lugo, A.E. & Martínez, R. (1986) Structural and functional properties of mangrove forest. *The botany and natural history of Panama: La botánica e historia natural de Panama* (ed. by W.G. D'Arcy, and M.D. Correa), pp. 53–66. Monogr. Syst. Bot. 10, Missouri Bot. Gardens, St. Louis MO, USA.
- Clarke, L.D. & Hannon, N.J. (1971) The mangrove swamp and salt marsh communities of the Sydney district. IV. The significance of species interaction. *J. Ecol.* **59**, 535–553.
- CLIRSEN (1992) *Estudio multitemporal de manglares, camaronerías y áreas salinas, mediante información de sensores remotos*. Centro de levantamientos integrados de recursos naturales por sensores remotos. Memoria Técnica. Quito, Ecuador.
- Clough, B.F. (1993) The status and value of mangrove forests in Indonesia, Malaysia and Thailand: Summary. *The economic and environmental values of mangrove forests and their present state of conservation in the South-east Asia/Pacific Region* (ed. by B. F. Clough) pp. 1–10. ITTO/ISME/JIAM Project PD71/89 Rev. 1.
- Clough, B.F., Boto, K.G. & Attiwill, P.M. (1983) Mangroves and sewage: a re-evaluation. *Tasks for vegetation science* **8** (ed. by H. J. Teas), pp. 151–161. Dr W. Junk, The Hague.
- Corredor, J.E. & Morell, J.M. (1994) Nitrate depuration of secondary sewage effluents in mangrove sediments. *Estuaries*, **17**, 295–300.
- Dugan, P. (ed) (1993) *Wetlands in danger*, 187pp. Oxford University Press, New York.
- Ewel, K.C. (1997) Water quality improvement by wetlands. *Ecosystem services* (ed. by G. Daily), pp. 329–344. Island Press, Washington DC.
- Ewel, K.C., Bourgeois, J.A., Cole, T.G. & Zheng, S. (1998a) Variation in environmental characteristics and vegetation in high-rainfall mangrove swamps in Kosrae, Micronesia. *Global Ecol. Biogeogr. Letts*, **7**, 49–56.
- Ewel, K.C., Zheng S., Pinzón, Z. & Bourgeois, J. A. (1998b) Environmental effects of canopy gap formation in high-rainfall mangrove swamps. *Biotropica*, in press.
- FAO (1994) *Mangrove forest management guidelines*, 319 pp. Rome.
- Fosberg, F.R. (1971) Mangroves versus tidal waves. *Biol. Conserv.* **4**, 38–39.
- Gill, A.M. & Tomlinson, P.B. (1969) Studies on the growth of red mangrove (*Rhizophora mangle* L.). I. Habit and general morphology. *Biotropica*, **1**, 1–9.
- Golley, F.B., Odum, H.T. & Wilson, R.F. (1962) The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology*, **43**, 9–19.
- Gong, W.K. & Ong, J.E. (1990) Plant biomass and nutrient flux in a managed mangrove forest in Malaysia. *Estuarine Coast Shelf Sci.* **31**, 519–530.

- Goulder, L.H. & Kennedy, D. (1997) Valuing ecosystem services: philosophical bases and empirical methods. *Nature's services. Societal dependence on natural ecosystems* (ed. by G. Daily), pp. 23–47. Island Press, Washington.
- Hamilton, L.S. & Snedaker, S.C. (1984) *Handbook for mangrove area management*, 123 pp. East-West Center, Honolulu HI, USA.
- Heald, E.J. (1969) *The production of organic detritus in a south Florida estuary*, 110 pp. Ph.D. thesis, University of Miami.
- Hussain, M.Z. (1995) Silviculture of mangroves. *Unasylva*, **46**, 1003–1009.
- Hutchings, P.A. & Recher, H.F. (1983) The faunal communities of Australian mangroves. *Biology and ecology of mangroves* (ed. by H.J. Teas), pp. 103–110, Dr W. Junk, The Hague.
- Jones, D.A. (1984) Crabs of the mangal ecosystem. *Hydrobiology of the mangal* (ed. by F. D. Por and I. Dor) pp. 89–109, Dr. W. Junk, The Hague.
- Lacerda, L.D., Conde, J.E., Alarcon, C., Alvarez-León, R., Bacon, P.R., D'Croz, L., Kjerfve, B., Polaina, J. & Vannucci, M. (1993) Mangrove ecosystems of Latin America and the Caribbean: a summary. *Conservation and sustainable utilization of mangrove forests in Latin America and Africa regions. Part I. Latin America* (ed. by L. D. Laderda), pp. 1–42. ITTO/ISME Project PD114/90(F).
- Lee, S.Y. (1989) Litter production and turnover of the mangrove *Kandelia candel* (L.) Druce in a Hong Kong tidal pond. *Estuarine Coast Shelf Sci.* **29**, 75–87.
- Lugo, A.E. & Snedaker, S.C. (1974) The ecology of mangroves. *Ann. Rev. Ecol. Syst.* **5**, 39–64.
- Lynch, J.C., Meriwether, J.R., McKee, B.A., Vera-Herrera, F. & Twilley, R.R. (1989) Recent accretion in mangrove ecosystems based on ^{137}Cs and ^{210}Pb . *Estuaries*, **12**, 284–299.
- 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.
- McIvor, C.C. & Smith, T.J. III (1995) Differences in the crab fauna of mangrove areas at a southwest Florida and a northeast Australia location: implications for leaf litter processing. *Estuaries*, **18**, 591–597.
- McKee, K.L., Mendelsohn, I.A. & Hester, M.W. (1988) Re-examination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *Am. J. Bot.* **75**, 1352–1339.
- Nixon, S.W., Furnas, B.N., Lee, V., Marshall, N., Ong, J.-E., Wong, C.-H., Gong, W.-K. & Sasekumar, A. (1984) The role of mangroves in the carbon and nutrient dynamics of Malaysia estuaries. *Proceedings of the Asian mangrove environments: research and management* (ed. by E. Soepadmo, A.N. Rao, and D.J. MacIntosh), pp. 534–544. University of Malaya and UNESCO, Kuala Lumpur.
- Odum, W.E. & Heald, E.J. (1972) Trophic analyses of an estuarine mangrove community. *Bull. Mar. Sci.* **22**, 671–738.
- Odum, W.E. & McIvor, C.C. (1990) Mangroves. *Ecosystems of Florida* (ed. by R.L. Myers and J.J. Ewel), pp. 517–548. University Presses of Florida, Gainesville.
- Odum, W.E., McIvor, C.C. & Smith, T.J. III (1982) *The ecology of the mangroves of south Florida: a community profile*, 144 pp. US Dept. Int., Biol. Serv. Progr., FWS/OBS-81/24.
- Ogden, J.C. (1994) A comparison of wading bird nesting colony dynamics (1931–1946 and 1974–1989) as an indication of ecosystem conditions in the southern Everglades. *Everglades—the ecosystem and its restoration* (ed. by S. M. Davis and J. C. Ogden), pp. 533–571. St. Lucie Press, Delray Beach FL, USA.
- Ong, J.E. (1995) The ecology of mangrove conservation and management. *Hydrobiologia*, **295**, 343–351.
- Ong, J.E., Gong, W.K., Wong, C.H. & Dhanarajan (1979) Productivity of a managed mangrove forest in West Malaysia (Abstract). *Intl. Conf. Trends Appl. Biol. SE Asia*, USM Penang, Malaysia.
- Parkinson, R.W., DeLaune, R.D. & White, J.R. (1994) Holocene sea-level rise and the fate of mangrove forests within the wider Caribbean region. *J. Coastal Res.* **10**, 1077–1086.
- Pool, D.J., Lugo, A.E. & Snedaker, S.C. (1975) Litter production in mangrove forests of southern Florida and Puerto Rico. *Proceedings of the International Symposium on Biology and Management of Mangroves* (ed. by G. E. Walsh, S. C. Snedaker and H. J. Teas) pp. 213–237. Inst. Food Agric. Sci., Univ. Fla., Gainesville.
- Primavera, J.H. (1996) Stable carbon and nitrogen isotope ratios of penaeid juveniles and primary producers in a riverine mangrove in Guimaras, Philippines. *Bull. Mar. Sci.* **58**, 675–683.
- Putz, F.E. & Chan, H.T. (1986) Tree growth, dynamics and productivity in a mature mangrove forest in Malaysia. *For. Ecol. Mgmt.* **17**, 211–230.
- 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.
- Rivera-Monroy, V.H. & Twilley, R.R. (1996) The relative role of denitrification and immobilization in the fate of inorganic nitrogen in mangrove sediments. *Limnol. Oceanogr.* **41**, 284–296.
- Rivera-Monroy, V.H., Day, J.W., Twilley, R.R., Vera-Herrera, F. & Coronado-Molina, C. (1995) Flux of nitrogen and sediment in a fringe mangrove forest in Terminos Lagoon, Mexico. *Estuarine Coast 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 north eastern Australia. *J. Exp. Mar. Biol. Ecol.* **102**, 237–248.
- Robertson, A.I. (1988) Decomposition of mangrove leaf litter in tropical Australia. *J. Exper. Mar. Biol. Ecol.* **116**, 235–247.
- Robertson, A.I. & Blaber, S.J.M. (1992) Plankton,

- epibenthos and fish communities. *Tropical mangrove ecosystems: coastal and estuarine studies 41* (ed. by A. I. Robertson and D. M. Alongi) pp. 173–224. American Geophysical Union, Washington DC.
- Robertson, A.I. & 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. & Phillips, M.J. (1995) Mangroves as filters of shrimp pond effluent: predictions and biogeochemical research needs. *Hydrobiologia*, **295**, 311–321.
- Rodelli, M.R., Gearing, J.N., Gearing, P.J., Marshall, N. & Sasekumar, A. (1984) Stable isotope ratio as a tracer of mangrove carbon in Malaysian ecosystems. *Oecologia*, **61**, 326–333.
- Saenger, P. & Snedaker, S.C. (1993) Pantropical trends in mangrove above-ground biomass and annual litterfall. *Oecologia*, **96**, 293–299.
- Scoffin, T.P. (1970) The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *J. sedim. Petrol.* **40**, 249–273.
- Semeniuk, V. (1983) Mangrove distribution in northwestern Australia in relationship to regional and local freshwater seepage. *Vegetatio*, **53**, 11–31.
- Smith, T.J. III (1987) Seed predation in relation to tree dominance and distribution in mangrove forests. *Ecology*, **68**, 266–273.
- Smith, T.J. III (1992) Forest structure. *Tropical mangrove ecosystems: coastal and estuarine studies 41* (ed. by A.I. Robertson and D.M. Alongi) pp. 101–136. American Geophysical Union, Washington DC.
- Snedaker, S.C., Brown, M.S., Lahmann, E.J. & Araujo, R.J. (1992) Recovery of a mixed-species mangrove forest in South Florida following canopy removal. *J. Coastal Res.* **8**, 919–925.
- Spalding, M., Blasco, F. & Field, C. (eds) (1997) *World mangrove atlas*, 178 pp. ISME, Okinawa, Japan.
- Stevenson, N.J. & Burbridge, P.R. (1997) Abandoned shrimp ponds: options for mangrove rehabilitation. *Intercoast Network*, March 1997, 13–14, 16.
- Steers, J.A. (1977) Physiography. *Wet coastal ecosystems. Ecosystems of the world I* (ed. by V.J. Chapman), pp. 31–60. Elsevier, New York.
- Thom, B.G., Wright, L.D. & Coleman, J.M. (1975) Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf-Ord River, Western Australia. *J. Ecol.* **63**, 203–232.
- Twilley, R.R. (1982) *Litter dynamics and organic carbon exchange in black mangrove (Avicennia germinans) basin forests in a southwest Florida estuary*, 262 pp. Ph.D. thesis., University of Florida.
- Twilley, R.R. (1985) The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. *Estuarine Coast Shelf Sci.* **20**, 554–557.
- Twilley, R.R. (1995) Properties of mangrove ecosystems related to the energy signature of coastal environments. *Maximum power: the ideas and applications of H. T. Odum* (ed. by C. A. S. Hall) pp. 43–62. University Press of Colorado, Niwot CO.
- Twilley, R.R. (1998) Mangrove wetlands. *Southern forested wetlands: ecology and management* (ed. by M. Messina and W.H. Conner), pp. 445–473. CRC Press, Boca Raton, Florida, USA.
- Twilley, R., Lugo, A.E. & Patterson-Zucca, C. (1986) Litter production and turnover in basin mangrove forests in southwest Florida. *Ecology*, **67**, 670–683.
- Twilley, R.R., Chen, R.H. & Hargis, T. (1992) Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water, Air Soil Polln.* **64**, 265–288.
- Twilley, R.R., Boderó, A. & Robadue, D. (1993) Mangrove ecosystem biodiversity and conservation in Ecuador. *Perspectives on biodiversity: case studies of genetic resource conservation and development* (ed. by C.S. Potter, J.I. Cohen and D. Janczewski), pp. 105–127. AAAS, Washington DC.
- Twilley, R.R., Snedaker, S.C., Yáñez-Arancibia, A. & Medina, E. (1996) Biodiversity and ecosystem processes in tropical estuaries: perspectives from mangrove ecosystems. *Biodiversity and ecosystem functions: a global perspective* (ed. by H. Mooney, H. Cushman and E. Medina) pp. 327–370. Wiley, New York.
- Twilley, R.R., Pozo, M., Garcia, V.H., Rivera-Monroy, V.H., Zambrano, R. & Boderó, A. (1997) Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador. *Oecologia*, **111**, 109–122.
- Watson, J.G. (1928) *Mangrove forests of the Malay Peninsula*. Malay For. Rec. No. 6. Fraser & Neave, Singapore. 275 p.
- Wattayakorn, G., Wolanski, E. & Kjerfve, B. (1990) Mixing, trapping and outwelling in the Klong Jgao mangrove swamp, Thailand. *Estuarine Coast Shelf Sci.* **31**, 667–688.
- West, R.C. (1977) Tidal salt-marsh and mangal formations of Middle and South America. *Wet coastal ecosystems. Ecosystems of the world I* (ed. by V.J. Chapman), pp. 193–213. Elsevier, New York.
- Wolanski, E., Mazda, Y. & Ridd, P. (1992) Mangrove hydrodynamics. *Tropical mangrove ecosystems: coastal and estuarine studies 41* (ed. by A.I. Robertson & D.M. Alongi) pp. 43–62. American Geophysical Union, Washington DC.
- Woodroffe, C. (1992) Mangrove sediments and geomorphology. *Tropical mangrove ecosystems: coastal and estuarine studies 41* (eds. by A.I. Robertson and D.M. Alongi) pp. 7–41. American Geophysical Union, Washington DC.
- Yáñez-Arancibia, A., Lara-Domínguez, A.L., Rojas-Galaviz, J.L., Sánchez-Gil, P., Day, J.W. & 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. & 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.