COASTAL
WETLANDS

AN INTEGRATED ECOSYSTEM APPROACH

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CHAPTER 22

Paradigm Shifts in Mangrove Biology

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Contents

1. Introduction

Mangroves live at the interface between land and sea in subtropical and tropical latitudes. These woody plants develop as forests and grow best where low wave energy and shelter enable the deposition of fine sediments and subsequent establishment of mangrove propagules. The persistence of warm temperatures is of paramount importance for the existence of mangroves, with roughly 70 species currently occupying a total estimated area of $150,000 \, \text{km}^2$ in low latitudes (down from a global area of $198,000 \, \text{km}^2$ in 1980; Wilkie and Fortuna, 2003). Mangrove forests can attain immense biomass and height, rivaling the size of tropical rain-forests; the standing crop of mangroves is ordinarily greater than other aquatic ecosystems, with equatorial mangrove forests often reaching a dry weight biomass on the order of 300–500 metric tons per hectare (Alongi, 2002).

A number of morphological and ecophysiological adaptations of mangrove trees make them unique, including viviparous embryos, aerial roots, and physiological mechanisms to cope with salt and to maintain water and carbon balance. Living between land and sea, it is not surprising that both terrestrial and aquatic species colonize and live in mangrove trees, soils, and waters nor it is surprising that these tidal forests are a valuable economic and ecological resource. Mangroves are important nursery grounds and breeding sites for fish, birds, mammals, crustaceans, reptiles, and shellfish and are a renewable source of wood and food for many indigenous settlements. They are also accumulation sites for sediment, nutrients, and other elements, including contaminants, and offer some protection against coastal erosion.

The objective of this chapter is to critically examine recent research trends in mangrove biology. The focus here is on some key topics that deviate from established paradigms of the biology and ecology of mangrove forests and their associated food webs. I take this approach simply because the biology of such complex ecosystems cannot be reviewed adequately here, and there exist several recent fine books and comprehensive reviews of mangrove biology and ecology (Ellison and Farnsworth, 2001; Kathiresan and Bingham, 2001; Lacerda, 2002; Saenger, 2002; Kathiresan and Qasim, 2005; Hogarth, 2007).

2. Shifts in Established Paradigms

2.1. Rates of mangrove net primary productivity rival those of other tropical forests

Most initial productivity studies (Golley et al., 1962; see review of Clough, 1992) indicated rates of net mangrove primary production equivalent to salt marshes but less than tropical terrestrial forests and, at best, equal to carbon fixation rates measured in other marine ecosystems (Bunt, 1975). Improvements in technology and methodology, especially over the past decade, have allowed better estimates of tree photosynthesis and respiration and thus more accurate estimates of net primary production of mangrove forests. Not all mangrove forests are productive, as often exemplified by stunted trees at the landward edge or in saline arid regions (Cheeseman, 1994). Estimates of forest net primary production have been problematical, with order–of–magnitude differences in rates based on different methods. Nevertheless, these more recent data indicate that rates of mangrove net primary productivity are greater than previously believed, often rivaling rates of net primary production of tropical terrestrial forests (Komiyama et al., 2008). This is arguably the most critical paradigm shift in mangrove ecology considering that carbon fixed by the trees forms the basis for associated food webs and energy flow.

Five methods are most commonly used to measure net primary production of mangrove forests:

1. Litterfall and incremental growth
2. Harvest

3. Gas exchange
4. Light attenuation/gas exchange
5. Demographic/allometric.

   Litterfall is by far the most common method because it is inexpensive and easy to measure. However, it only measures leaf production and not growth of the remainder of the tree. Harvesting is labor intensive and slow, and such data are usually available only from plantation harvests and like litterfall measurements, account for only aboveground production; most leaf production is unaccounted for. Gas exchange is precise and rapid although subject to the problem (as all methods are) of extrapolating from a small area (usually a few individual trees) to an entire stand, injecting the problem of error. Moreover, relying solely on gas exchange measurements overestimates net production as it does not account for most tree respiration.

   Combining measurements offers the best hope of accounting for production of all, or most, tree parts. Measuring litterfall and incremental growth of the trunk accounts for all aboveground production, but not belowground production. Arguably, one of the best methods currently available is to measure light attenuation. The early efforts (Bunt et al., 1979) provided rapid and relatively easy estimates of potential net primary production but suffered from lack of actual leaf photosynthesis measurements and a number of untested assumptions based on light attenuation models from temperate forests and of the conversion of light absorbed to increases in mass over time. The method relies on relating the amount of light absorbed by the mangrove canopy to the total canopy chlorophyll content. The light attenuation method was subsequently modified, combining measurement of light attenuation with a more robust method of calculation of photon flux density at the bottom of the canopy and empirical measurements of leaf photosynthesis (Gong et al., 1991, 1992; Clough, 1997; Clough et al., 1997). This modified method still relies on measurements of light absorption by the forest canopy to estimate leaf area index, which is the amount of leaf area relative to the amount of ground area. The leaf area index (L) is then used to estimate net canopy photosynthesis (P_N) using the formula, $P_N = A \times d \times L$, where d is the daylength (h) and A is the average rate of photosynthesis per unit leaf area, which is obtained by measurement of CO_2 exchange. Using this modification, Clough et al. (1997) compared their more robust estimates with the earlier light attenuation method. The comparison (Table 1) shows that the original method underestimates the true net production by a factor of 12. This suggests that many measurements using the Bunt et al. (1979) method need to be corrected by this factor, clearly increasing our estimate of mangrove net primary production.

   Comparing the gas exchange, litterfall, and increment growth plus litterfall, the original light attenuation and the modified light attenuation methods illustrate the methodological differences (Table 2) and the difficulty in our ability to settle on an accurate range of net primary production values for mangrove forests. It is clear that litterfall underestimates, and gas exchange measurements alone overestimate, net primary production. But from the remaining data, the modified light attenuation method currently appears to give the most reasonable estimate of total production while litterfall plus incremental growth give reasonable estimates of aboveground

Table 1 Comparison of net primary production (t DW/ha/year) derived from the method described in Bunt et al. (1979) and the modified procedure described in Clough (1997) and Clough et al. (1997)

Measurement set	Light attenuation method	Modified procedure
1	11.0	135
2	13.0	161
3	13.7	165
4	14.3	157
Mean	13.0 ± 1.4	155 ± 13

Measurements were made in a 22-year-old *R. apiculata* forest in peninsular Malaysia.

Table 2 Estimates of net primary production (t DW/ha/year) of *Rhizophora apiculata* forests of various age in peninsular Malaysia using five of the most used procedures

Age	Gas exchange	Litterfall	Litterfall + incremental growth	Light attenuation	Modified light attenuation
5	132	7	19	14	37
10	122	10	34	19	
20	240	10	30	16	65
85		8		21	102

Source: Data from Gong et al. (1984, 1992), Ong et al. (1995), Clough et al. (1997) and Alongi et al. (2004).

production. The modified light attenuation method is most reasonable because it measures total net fixed carbon production and offers the most robust assumptions based on tree physiology and carbon balance.

A number of recent studies have attempted to measure aboveground net primary production using allometry coupled with litterfall or leaf turnover (Coulter et al., 2001; Ross et al., 2001; Sherman et al., 2003). The method employed by Ross et al. (2001) is an adaptation of methods used for grasslands, incorporating detailed allometric measurements of individual trees coupled with observations of leaf demography to measure leaf turnover. Although they were not able to compare their method directly with other procedures, their net production values were at the upper end of the range for similarly sized forests. Coulter et al. (2001) similarly employed analysis of leaf nodes to produce an estimate of new leaf production. Combining leaf production with estimates of the number of inflorescence scars produced by the shedding of leaves and reproductive structures, aboveground production of *Kandelia candel* in Vietnam was estimated at rates comparable to, or greater than, previous values.

Although caution must be applied when considering net primary productivity estimates based on a variety of methods used in disparate settings in forests of different age and living under different environmental conditions, the available data (Table 3) suggest that rates of net primary production are generally rapid compared to other marine primary producers (Gattuso et al., 1998).

Table 3 Estimates of aboveground net primary production (NPP = t DW/ha/year) of mangrove forests in various parts of the world based on different methods

Species	Location	NPP	Method
Rhizophora mangle, *Avicennia germinans,* *Laguncularia racemosa*	USA	46.0	Gas exchange
R. mangle, A. germinans, *L. racemosa*	USA	26.1 (fringe) 8.1 (dwarf)	Demographic/allometric
A. germinans	USA	20.5	Gas exchange
R. mangle	USA	16.9	Gas exchange
R. mangle, A. germinans, *L. racemosa*	USA	22.5	Gas exchange
R. mangle, A. germinans, *L. racemosa*	Puerto Rico	58.4	Gas exchange
R. apiculata	Thailand	63.7[a] (13.1)	Light attenuation
Ceriops decandra	Thailand	48.7[a] (9.7)	Light attenuation
R. apiculata	Malaysia	112.1[a]	Light attenuation
R. apiculata (70 years)	Malaysia	102.2[a] (24.6)	Light attenuation
R. apiculata (18 years)	Malaysia	65.7[a] (14.7)	Light attenuation
R. apiculata (5 years)	Malaysia	36.5[a] (12.8)	Light attenuation
R. mangle (5 years)	Cuba	1.6[b]	Harvest/incremental growth
A. germinans	Cuba	5.9[b]	Harvest/incremental growth
L. racemosa	Cuba	5.4[b]	Harvest/incremental growth
Sonneratia apetala	Bangladesh	12.5[b]	Harvest/incremental growth
S. caseolaris	Bangladesh	26.4[b]	Harvest/incremental growth
A. officinalis	Bangladesh	7.6[b]	Harvest/incremental growth
A. marina	Bangladesh	4.4[b]	Harvest/incremental growth
A. alba	Bangladesh	2.1[b]	Harvest/incremental growth
B. gymnorrhiza	Bangladesh	0.6[b]	Harvest/incremental growth
B. sexangula	Bangladesh	0.1[b]	Harvest/incremental growth
E. agallocha	Bangladesh	4.7[b]	Harvest/incremental growth
X. moluccensis	Bangladesh	0.5[b]	Harvest/incremental growth
Mixed species	Micronesia	4.2[b]	Harvest/incremental growth
R. apiculata, *B. gymnorrhiza*	Malaysia	8.7[b]	Harvest/incremental growth
R. apiculata	Vietnam	4.9[b]	Harvest/incremental growth
R. apiculata	Vietnam	19.0	Incremental growth
R. apiculata	Thailand	15.7	Incremental growth
R. apiculata	Thailand	10.6	Incremental growth
R. apiculata	Vietnam	9.4	Litterfall
R. apiculata	Vietnam	18.7	Litterfall
R. racemosa	Gambia	18.8	Litterfall
A. africana	Gambia	11.6	Litterfall
R. racemosa	Gambia	10.4	Litterfall
R. mucronata	India	14.6	Litterfall
R. apiculata	India	13.6	Litterfall
A. marina	India	6.2	Litterfall
Bruguiera sexangula	China	11.0	Litterfall
Kandelia candel	China	13.3	Litterfall
Kandelia candel	China	24.4	Litterfall/allometric
R. mucronata	Indonesia	23.4	Litterfall/incremental growth
R. apiculata	Thailand	13.5	Light attenuation

(*Continued*)

Table 3   (*Continued*)

Species	Location	NPP	Method
Aegiceras corniculatum	China	11.3	Litterfall
K. candel	Vietnam	5.3	Demographic/allometric
K. candel	Vietnam	13.4	Demographic/allometric
R. stylosa	Australia	40.5[a] (9.6)	Light attenuation
A. marina	Australia	30.6[a] (6.4)	Light attenuation
Mixed *R.mangle, A. germinans, L. racemosa*	Dominican Republic	19.7[c]	Demographic/allometric
Mixed *R.mangle, A. germinans, L. racemosa*	Guadeloupe	21.2 (fringe) 6.2 (dwarf)	Litterfall/incremental growth
R. mangle	Hawaii	29.1	Litterfall/incremental growth
Mixed *Rhizophora* spp.	Australia	29.2	Light attentuation
R. mucronata/A. marina	Sri Lanka	11.0	Litterfall/incremental growth
R. apiculata, B. parviflora	Papua New Guinea	30.5[a] (9.7)	Light attenuation
Nypa fruticans	Papua New Guinea	30.1[a] (9.9)	Light attenuation
A. marina, Sonneratia lanceolata	Papua New Guinea	24.4[a] (6.8)	Light attenuation
R. apiculata, A. marina	Indonesia	104.6	Light attenuation
R. apiculata, A. marina	Indonesia	96.9	Light attenuation
A. officinalis, A. marina	Indonesia	103.2	Light attenuation
C. tagal, R. apiculata	Indonesia	106.1	Light attenuation
C. tagal, R. apiculata	Indonesia	109.4	Light attenuation
R. stylosa, S. alba	Indonesia	63.7	Light attenuation
R. apiculata, K. candel	Indonesia	74.3	Light attenuation
Kandelia candel	Okinawa	36.2	Gas exchange

[a] Estimate using the modified light interception method or original data recalculated using the modified method (see text). Estimates based on the original light interception method are in parentheses.
[b] Assumes an average density of 0.9332 t m^3 (Saenger, 2002).
[c] Sherman et al. (2003).
[d] A correction factor of 4.8 was applied based on the data in Table 2.7 and all data calculated with both light inception methods (all those in above table asterisked[a]). Of $n = 11$ forests, the original method gave a mean NPP estimate of 11.85 t DW/ha/yr and the modified method gave a mean NPP value of 57.08 t DW/ha/year, for an average difference of 4.8. All C values were converted to DW assuming that mangrove wood is 47%C (Saenger, 2002).
Source: Data from Golley et al. (1962), Miller (1972), Hicks and Burns (1975), Lugo et al. (1975), Christensen (1978), Twilley (1985), Putz and Chan (1986), Aksornkoae et al. (1989), Lee (1990), Atmadja and Soerojo (1991), Gong et al. (1991, 1992), Robertson et al. (1991), Amarasinghe and Balasubramaniam (1992), Sukardjo and Yamada (1992), Sukardjo (1995), Day et al. (1996), Ong et al. (1995), Clough et al. (1997, 1999), Clough (1998), Cox and Allen (1999), Alongi and Dixon (2000), Alongi et al. (2000, 2004), Kathiresan (2000), Coulter et al. (2001), Ross et al. (2001), Sherman et al. (2003), Suwa et al. (2006).

    If we accept the data obtained using the modified light attenuation method as the best estimate of net primary productivity of mangroves, the average rate of net primary production is 64 t DW/ha/year. In comparison, the estimates based on incremental growth plus litterfall average to 11 t DW/ha/year. There is considerable range between and within both sets of values, but they both suggest that mangroves are more significant carbon fixers in the tropics than previously thought. Moreover, plotting the data versus latitude (Figure 1) gives a significant negative relationship, indicating that mangrove net primary production declines away from
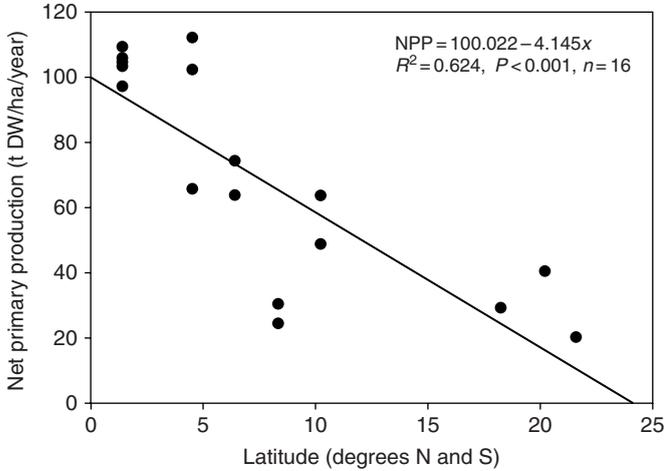
Figure 1 Latitudinal changes in net mangrove primary production measured using a modified light interception method. Data from Gong et al. (1991, 1992), Atmadja and Soerojo (1991), Robertson et al. (1991), Sukardjo (1995), Clough et al. (1997), Clough (1998), Alongi and Dixon (2000), and Alongi et al. (2000, 2004).
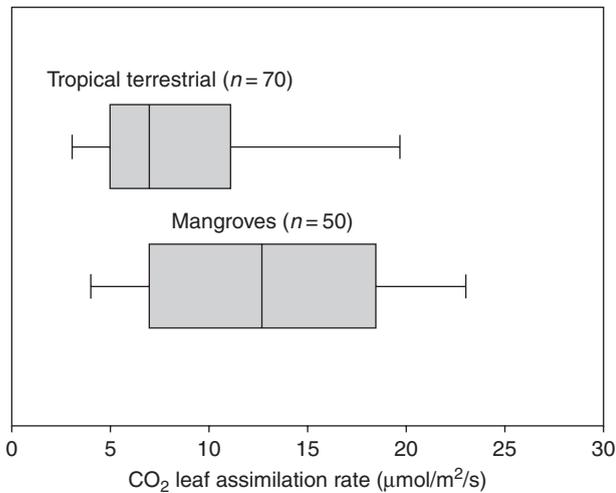
Figure 2 Comparison in CO_2 leaf assimilation rates between various species of mature tropical mangrove and terrestrial trees. Mangrove data from sources listed in Table 3 (plus older references within). Tropical terrestrial tree data from references cited in Figure 2.29 in Turner (2001) plus data in Marenco et al. (2001), Leakey et al. (2003), and Kenzo et al. (2004).

the equator, mirroring the latitudinal decline in mangrove biomass and litterfall (Saenger and Snedaker, 1993).

How do these data compare with productivity data for tropical rain forests? First, we must compare data obtained using identical or very similar methods. A comparison in CO_2 leaf assimilation rates between mangroves and tropical terrestrial trees indicates
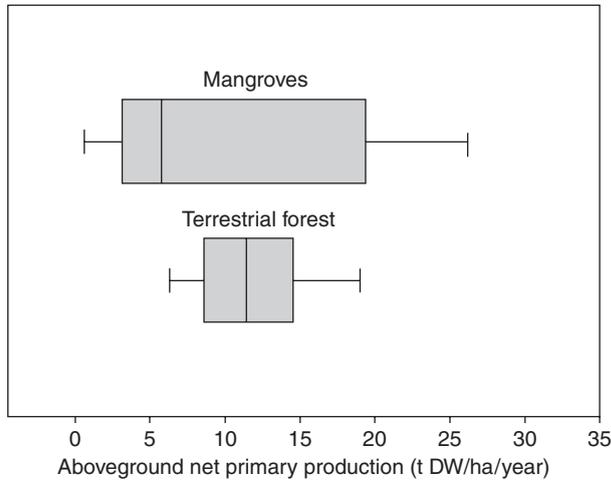
Figure 3 Comparison of above-ground net primary production in mangrove and tropical terrestrial forests based on measurements of biomass increments and litterfall. Vertical line in box denotes median and the boxes encompass the 25 and 75th percentiles and the lower bars denote the 5 and 95th percentiles, respectively. Data from Table 3 and from Clark et al. (2001) and Scurlock and Olson (2002) for terrestrial forests.

great overlap and thus close similarity in rates of leaf photosynthetic rates (Figure 2). Second, the most comprehensive database for both mangroves and tropical terrestrial forests involves measurement of only aboveground biomass accumulation plus litterfall. Comparing the data in Table 3 and the data analyzed by Clark et al. (2001) and Scurlock and Olsen (2002), we find a similar range of productivity estimates (Figure 3). For mangroves, the mean rate of aboveground net primary production is 11.1 t DW/ha/year, with a median value of 8.1 and 25th and 75th percentiles of 4.6 and 19.2, respectively. For terrestrial forests, the mean rate of aboveground NPP is 11.93 t DW/ha/year, with a median value of 11.4 and a 25th percentile of 8.8 and a 75th percentile of 14.4. This similarity suggests that rates of net primary production are equivalent between mangrove and tropical terrestrial forests underscoring similarities in physiological and ecological factors regulating tree production. Rates of belowground production are sorely lacking for all forests. Respiration of roots and woody parts are also badly needed to adjust the photosynthetic rates for an estimate of net carbon fixation.

Like other forests, mangrove stands vary in size and age over time, and therefore vary in rates of production and in the balance between production and respiration. Long-term patterns are important to discern as they reflect a balance between factors promoting and limiting forest growth, but only a few studies have examined the growth dynamics of mangrove forests over time or of stands of known age (Ong et al., 1985; Day et al., 1996; Fromard et al., 1998; Clough et al., 2000; Alongi et al., 2004).

2.2. Mangrove forests appear to be architecturally simple, but factors regulating succession and zonation are complex

Early workers observed conspicuous changes in mangrove forest composition from the water's edge to the highest point of tidal inundation and proposed several

hypotheses to explain these zonation patterns (Watson, 1928; Macnae, 1968). Even into the 1970s and 1980s, attempts were made either to deduce the relative importance of various physical and biological regulatory factors or to categorize forests by type (Lugo and Snedaker, 1974). Although mangrove stands ordinarily have little or no understory of scrubs and ferns and are usually less rich in tree species than other tropical forests, we now understand that their distribution and the factors regulating their floral composition and structure are highly complex (Smith, 1992; Ellison, 2002). On the local scale (e.g., a tidal height gradient or up-estuary gradient), mangrove distribution is regulated by a complex panoply of biotic and environmental factors, including salinity, soil type, degree of anoxia, nutrient availability, physiological tolerances, predation, and competition (Smith, 1992; Ellison, 2002). The interplay of these factors is so complex that it is reasonable to state that generalizations about the mechanisms governing zonation are prohibitive. The reality is that each stand is different, and at the local scale, different sets of factors come into play over different temporal and spatial scales (Bunt, 1996; Ball, 1998). Salinity, for example, may be a crucial regulatory factor in one estuary (or part thereof) but less so in an adjacent estuary.

Processes observed at the local scale can obscure other drivers that are important in structuring mangrove forests over longer scales of space and time. Like other forests, mangrove communities follow a natural succession of stages over time, from an initial pioneering stage of early rapid growth and development through to later maturity, senescence, and death (Fromard et al., 1998; Ward et al., 2006). However, it has been observed that mangrove forests do not always fit neatly into established ecological concepts such as the old-growth or late-successional forest (Lugo, 1997). This apparent paradox is explainable if the role of natural and anthropogenic disturbance is considered, in which the recovery of a forest from a disturbance (such as a hurricane) can "reset the clock" regarding successional stage (Piou et al., 2006). Further, a mosaic of successional stages can coexist within the same stand; tree growth and development can be disrupted by such disparate events as lightning and harvesting. A recent study of the effects of a hurricane on mangrove structural dynamics in south Florida (Ward et al., 2006) showed that forest turnover rates were greater in plots inside the primary hurricane wind field than outside. They showed that mangroves adhere to the same organizing factors as terrestrial forests and to the Twilley et al. (1998) model which predicts that initial differences in stand structure and subsequent seedling and sapling establishment rates would largely control the development of forest structure post-disturbance.

The recruitment of seedlings in mangroves, as in other forests, is controlled by gaps in the canopy created by disturbance (Smith, 1992; Clarke, 2004). Compared with the total pool of species available, the number of species actually colonizing a canopy gap (usually $10-100\,\text{m}^2$) is small. Why? As explained by Clarke (2004), recruitment limitation does not appear to facilitate coexistence; the seeds of local canopy members are much more likely to be successful in colonizing available space than propagules dispersed with distance. This explanation has been supported by more recent evidence of gap dynamics in mangroves of southeast Asia and Africa (Bosire et al., 2006; Iman et al., 2006). In reforested mangrove stands in Kenya, Bosire et al. (2006) found that recruitment into monospecific stands of adult

Sonneratia alba of other species was unsuccessful (100% mortality) suggesting competitive exclusion. Therefore, seed predation by crabs and subsequent competitive exclusion by conspecific canopy dominants play a major role in regulating recruitment in gaps and subsequent forest succession.

To summarize, we can state that *stand composition and structure of mangrove forests are the result of a complex interplay of physiological tolerances and competitive interactions leading to a mosaic of interrupted or arrested succession sequences in response to physical/ chemical gradients and changes in geomorphology* (Alongi, 2008).

2.3. Mangrove tree growth is not constant but related to climate patterns

For decades, growth rings found in mangrove tree species were thought to be anomalous, reflecting variations in the density of wall deposits rather than the result of variations in cambial activity as related to seasonal changes in climate (Chapman, 1975; Tomlinson, 1986). Further research using improved technology has recently discovered genuine growth rings in *Rhizophora apiculata* (Yu et al., 2004), *Rhizophora mangle* (Menezies et al., 2003), and *Xylocarpus mekongensis* (Hancock et al., 2006), in regions with distinct seasons.

Tree ring patterns in *R. apiculata* (Yu et al., 2004) in subtropical China were consistent with trends in annual sea level, salinity, and sea surface temperatures, indicating that the measurement of changes in alpha cellulose δ^{13}C in mangrove rings can be used as a potential indicator of past changes in sea level. In Brazil, *R. mangle* forms annual rings, with the slowest growing trees (1.2 mm/year) showing a close relationship between the number of months with rainfall <50 mm and ring width. The distinctiveness of rings was greater in trees from saline soils compared with those in brackish soils (Menezies et al., 2003). Using a different set of isotopes (^{228}Ra/^{226}Ra), Hancock et al. (2006) were able to measure 3 rings/ year in *X. mekongensis*, matching climate patterns in northern Australia. Like other mangroves, *Rhizophora mucronata* was also thought to lack distinct growth rings, but using high-resolution stable carbon and oxygen isotope ratios, Verheyden et al. (2004, 2005) found an annual cyclicity in the isotope ratios of stem wood that appears to relate best to mean relative humidity and rainfall. Moreover, they found a clear discontinuity in the pattern that may reflect unusually low rainfall during El Niño. Mangrove dendrochronology is still in its infancy, so further studies should shed more light on long-term patterns of tree growth in response to climate change.

2.4. Tree diversity is low, but faunal and microbial diversity can be high

Whether considered from either the generic or species level, the diversity of mangrove tree species within a given area is low compared with other tropical forests (Saenger, 2002). Highest diversity is found in the Indo–Malaysia area of the Indo–west Pacific and the lowest diversity occurs in western Africa (Table 4). While up to approximately 50 species are found in the most diverse

Table 4 Number of genera and species of mangroves among the six biogeographical provinces (Adapted from Alongi, 2002)

Province	Genera	Species
West America	8	12
East America	7	11
West Africa	6	8
East Africa	11	11
Indo–Malaysia	22	51
Australasia	21	47

mangrove areas, tropical rainforests may contain up to several hundred tree species (Clark et al., 2001).

And while some invertebrate phyla are similarly species poor (e.g., nematodes and other benthic meiofauna; Alongi, 1989), recent evidence suggests much greater species richness among fungi, bacteria, protists, viruses, and other phyla (Kathiresan and Bingham, 2001). An adequate inventory of microbes in mangrove forests has not yet been developed, but new species are continually being found throughout the world, especially as microbial techniques and methods improve. With technological advances, it is reasonable to expect the true number of bacterial species to eventually number in the thousands. Even on a small piece of leaf litter, a rich variety of microbes exist. For instance, 12 species of flagellates, 2 species of sarcodines, 17 species of ciliates, and 2 species of suctorids were discovered on a single mangrove leaf in India, in addition to several species of nematodes, diatoms, and copepod nauplii (Padma et al., 2003). Like the bacteria, it is likely that the true number of species of other microbiota is far higher. Similarly, fungal diversity is high, especially on rotting vegetation. On *Rhizophora* leaves in a Panamanian forest, over 183 different morphological types of fungi were discovered, with over 60 types on *Avicennia* leaves and 106 types on *Laguncularia* leaves (Gilbert et al., 2002). As of 2003, a total of 625 species of terrestrial, freshwater, and marine fungi have been reported from mangroves worldwide, including 278 ascomycetes, 277 mitosporic fungi, 30 basidiomycetes, and 14 oomycetes (Schmit and Shearer, 2003). Different fungal species are often found in different parts of the forest. Diversity of fungi was higher in woody litter than on leaves, with 78 taxa found on the floor of two Indian mangrove forests (Ananda and Sridhar, 2004).

As in other ecosystems, species diversity declines as individual body size increases. Most aquatic invertebrate groups consist of a few to <50 species within a given forest area (Alongi and Sasekumar, 1992) with highest diversity most often found among the crustaceans (Kathiresan and Bingham, 2001). Insects and birds, although most are only temporary visitors, are highly diverse with species numbers often exceeding 300 within a single mangrove estuary. Fish are the most diverse among vertebrate phyla with species numbers usually ranging from 100 to 250 per estuary (Robertson and Blaber, 1992). In a southeast Asian mangrove estuary, a maximum of 260 fish species was recorded (Hong and San, 1993). Such wide ranges of species numbers are a reflection of variable environmental conditions. There are also biogeographical differences. For instance, east Africa has a reduced

mangrove crab richness (about 35 species) compared with southeast Asia (>100 species; Gillikin and Schubart, 2004), mirroring the diversity differences between the regions in mangrove flora. At the local scale, metazoan diversity is, on average, higher on the tree (encrusting or epibiont assemblages) or on the forest floor surface and in tidal waters than within the forest floor (Alongi, 1989).

2.5. Arboreal communities are important in food webs, exhibiting predatory, symbiotic, and mutualistic relations

Like other forests, the fauna and flora inhabiting the mangrove canopy are important in structuring food webs and in influencing the species composition of mangroves, but this was not recognized until quite recently (Ellison and Farnsworth, 2001; Kathiresan and Bingham, 2001). Insects ordinarily consume mangrove material equivalent to only approximately 5% of net primary production (Robertson, 1991), but recent findings point to the importance of insects in affecting the establishment and growth of seedlings (Minchinton and Dalby-Ball, 2001; Burrows, 2003; Sousa et al., 2003) and as pollinators (Ellison and Farnsworth, 2001). In a series of field and shadehouse experiments, Sousa et al. (2003) found that the rate of insect attack varied as a function of intraspecific variation in propagule size and tree species, with *Avicennia* suffering 90% damage compared with 33% for *Laguncularia* and 20.5% for *Rhizophora*, respectively. These species differences were partly explained by differences in chemical composition of propagules. Major defoliation has been reported in mature forests from Hong Kong, Colombia, Costa Rica, Ecuador, Indonesia, India, Bangladesh, and Thailand (see references in Saenger, 2002) and, although rare, illustrates the potential for insect herbivory to greatly affect tree mortality.

Birds and mammals either temporarily or permanently reside in mangrove forests, using the forest as shelter and to find food. The work of Lefebvre (Lefebvre et al., 1992, 1994; Lefebvre and Poulin, 1996, 1997) has established the importance of mangroves as a home for many species of birds, with some forests containing up to 315 species and feeding extensively on invertebrates on the trees, on the forest floor, and in tidal water. In Brazilian mangroves, Martinez (2004) found that sympatric Scarlet Ibis (*Eudocimus ruber*) and Yellow-Crowned Night Heron (*Nyctanassa violacea*) fed mainly on ocypodid crabs in significantly greater proportion relative to their abundance.

Prey segregation plays a role in sustaining such numerous species of birds in mangroves, with prey size usually being the prime factor. Birds may exhibit comparatively restricted feeding niches given the high availability of prey within the forest. However, it is more likely that mangroves have a more significant impact on the life cycles of many bird species than vice versa; mangrove habitat destruction and fragmentation has been shown to reduce population of mangrove-dependent birds (Grant and Grant, 1997).

Predation has been somewhat over-emphasized at the expense of other important trophic relationships. For instance, epiphytes growing on mangrove trees and tree parts also have a role to play in the biology of mangrove forests (Ellison and

Farnsworth, 2001). Epiphytic orchids, bromeliads, mistletoes, and ferns are less common and of lower diversity than in upland forests but can affect the physiology of mangroves (Orozco et al., 1990) and exhibit mutualism with insects, especially ants, which provide nutrients to the epiphytes in return for shelter (Rico-Gray et al., 1989).

Many epibionts do not interact directly with the trees but many fouling communities interact both indirectly and directly. In Belize, Ellison and her colleagues (Ellison and Farnsworth, 1990; Ellison et al., 1996) found that sponges living on roots precluded colonization of and damage to the roots by isopods and facilitated nitrogen uptake by the roots. When present, sponges induced the formation of fine roots that absorbed ammonium produced by the sponge fouling communities. Such mutualistic relationships likely evolved as a result of mangrove forests and their associated biota inhabiting an oligotrophic environment.

2.6. Plant–Microbe–Soil Relations are tightly linked and help conserve scarce nutrients

It is now recognized that the high rates of photosynthesis and primary productivity of many mangrove forests depend on not only unique and highly evolved physiological mechanisms (Ball, 1988) but also highly evolved and energetically efficient interrelationships among soil nutrient pools, microbes, and trees (Alongi, 2005). Such close linkages are necessary in tropical habitats, as available nutrient pools (e.g., nitrate) are small and microbial growth is rapid, in the face of coping with a harsh, waterlogged environment. However, owing to the physical nature of soil, there is more inferential data than direct evidence of the complexity and nature of these interrelationships.

As for other vascular plants, bacteria, fungi, and other microflora alter the microenvironment around mangrove roots via their metabolic activities, transforming and releasing nutrients, and modifying soil chemistry. These microbes depend on the leakage of nutrients from roots as a source of energy. Thus, the relationship is mutualistic, as both trees and microbes share the need for limiting nutrients. Indeed, both bacterial transformation of nutrients and subsequent tree growth are often rapid, as reflected in nutrient use efficiencies of mangroves equal to or higher than those of other tropical trees (Alongi et al., 2005).

Mangrove–microbe relations have been most closely observed within the rhizosphere where highly specialized groups of bacteria and fungi coexist within the root matrix (Sengupta and Chaudhuri, 2004; Ravikumar et al., 2004; Kothamasi et al., 2006). In mangroves lining the lower reaches of the Ganges, rates of nitrogen-fixing activity and numbers of bacterial colonies are related to forest age, with richer and more active colonies in the rhizosphere of early successional mangroves and lower microbial activity in mature mangrove stands (Sengupta and Chaudhuri, 2004). When the roots of seedlings and saplings of 16 mangrove species were inoculated with cultured nitrogen-fixing bacteria, root biomass nearly doubled, leaf area increased by 270%, and shoot biomass increased by nearly 30% compared with control plants (Ravikumar et al., 2004). Also in Indian mangroves,

Kothamasi et al. (2006) found arbuscular mycorrhizal fungi in the aerenchymatous cortex of several mangrove species, suggesting that the plants may be providing the fungus with oxygen; phosphate-solubilizing bacteria were also abundant suggesting that these bacteria mobilize insoluble phosphates for the plants. Other workers have also recently found that bacterial colonies reside within the aerenchyma, including methogens (Purvaja et al., 2004). Other nutrient elements may also be made available to mangroves via bacterial activities, as indicated by observations of active bacterial iron and manganese reduction in close association with mangrove roots (Kristensen et al., 2000; Alongi et al., 2005; Kristensen and Alongi, 2006).

Mangrove trees alter the soil environment, and this affects the growth and survival of individual functional types of aerobic and anaerobic bacteria. It has been known for decades that translocation of oxygen to the roots serves as a means of oxidizing potentially toxic metabolites, such as sulfides. However, it has only recently been shown that these activities shift the competitive balance for substrates from favoring sulfate reducers to favoring iron- and manganese-reducing bacteria, thus increasing availability of soluble Fe and Mn required for plant growth. Highly evolved and energetically efficient plant–soil–microbe relations are a major factor in explaining why mangroves can be highly productive in a typically harsh environment.

2.7. Crabs are keystone species influencing function and structure in many, but not all, mangrove forests

Recognition of the importance of crabs in mangroves emerged from research conducted in Australia in the 1980s, resulting in a paradigm shift as to how mangroves link to adjacent coastal habitats. The established view based on research conducted earlier in the Caribbean was that, like their salt marsh counterparts, mangroves export large quantities of detritus to the adjacent coastal zone, subsidizing coastal food webs and the flow of energy and nutrients (Odum and Heald, 1975; Lee, 1999; Alongi, 2002). Studies in tropical Australia (and confirmed in other tropical mangroves worldwide) found that grapsid crabs, especially sesarmids, consume a significant fraction of leaf litter lying on the forest floor (Robertson, 1986), thus reducing the detritus subsidy to the adjacent coastal zone.

Grapsid and ocypodid crabs are the most important organisms influencing the structure and function of many tropical mangrove forests, after bacteria and the trees (Lee, 1998, 1999; Kristensen, 2008). Through their life activities, they exert extraordinary influence on a wide variety of mangrove processes. Through their consumption of mangrove leaf litter, they significantly reduce the amount of detritus available for export, thus enhancing retention and recycling of nutrients and organic matter internally; their wastes can support coprophagous organisms further ensuring conservation of materials within the forest, and their selective consumption of mangrove propagules affects forest structure by reducing the recruitment and relative abundance of tree species whose propagules are preferentially consumed. Bioturbation by crabs also results in changes in soil texture and chemistry, surface topography, degree of anoxia, and abundance of meiofauna while stimulating microbial

production. The presence of crab burrows enhances the flow of tidal water through the forest floor, speeding up the flow of water and associated dissolved and particulate material between forest and adjacent waterway (Ridd, 1996).

Crabs, however, are not keystone species in all mangrove ecosystems. In temperate Australian mangrove-salt marsh systems and in some Caribbean mangroves, crabs play only a minor role in litter decomposition and in structuring forests and, in fact, often avoid eating mangrove leaves and seeds (Smith et al., 1989; Saintilan et al., 2000; Guest et al., 2004, 2006). Why crabs are important in some forests but not others is unclear, but it may be due to different combinations of crab and mangrove species between locations.

Recent work has focused on clarifying the trophic role of crabs, especially positive feedback loops and interactions with trees and other flora and fauna in relation to food availability (Ashton, 2002; Kristensen and Alongi, 2006), and their reproductive and life history strategies in relation to tree composition and environmental factors (Lee and Kwok, 2002; Koch et al., 2005; Moser et al., 2005). In mesocosm experiments, Kristensen and Alongi (2006) found that the presence of the fiddler crab, *Uca vocans*, stimulated the growth and development of *Avicennia marina* saplings but depressed the abundance and productivity of microalgal mats at the soil surface. The association between the saplings and the crabs also greatly influenced the pathways of microbial decomposition (Table 5), with sulfate reduction being more important than iron reduction in the presence of crabs and saplings. Fiddler crabs and tree roots thus appear to have complementary effects on sediment microbial processes.

Sesarmid crab biology and productivity may be related to forest type, and forest type may be linked to crab activities. In field experiments excluding crabs, Smith et al. (1991) found that the absence of crabs increased the concentration of ammonium and sulfide in soils, but reduced plant stipule and propagule production. The presence of crabs therefore facilitates plant growth by aerating the soil to limit the buildup of toxic metabolites. The presence of tree species may also influence crab productivity. In experiments in the Mai Po marshes in Hong Kong, Lee and Kwok (2002) found faster reproductive rates and higher sesarmid crab productivity in a *K. candel* stand as opposed to an adjacent *A. marina* forest. These differences

Table 5 Rates of sulfate and iron (Fe III) reduction in microcosm sediments in various treatments with and without fiddler crabs and *Avicennia marina* saplings

Depth integrated rates	$-C+P$	$-C-P$	$+C+P$	$+C-P$
Total C production	80 ± 22	90 ± 12	56 ± 18	38 ± 7
Sulfate reduction	50 ± 18 (63%)	63 ± 28 (70%)	21 ± 7 (37%)	24 ± 5 (62%)
Iron reduction	19 ± 4 (23%)	16 ± 6 (18%)	24 ± 5 (44%)	14 ± 2 (36%)

Rates are given as mmol $C/m^2/day$ ($\pm SD$). Values in parentheses indicate the percentage contribution of sulfate and iron reduction to total carbon production. $-C$, crabs absent; $+C$, crabs present; $-P$, saplings absent; $+P$, saplings present (Adapted from Kristensen and Alongi, 2006).

may be due to other factors, such as differences in tidal height, but modification of the soil and/or differences in food availability may play an important role. Regardless of the mechanisms involved, positive interactions between trees, crabs, and microbes make ecological sense in that the overall stability of mangrove ecosystems is enhanced.

2.8. Algae, not just detritus, are a significant food resource

The pioneering work of Odum and Heald (1975) in south Florida in the late 1960s established the paradigm that detritus-based food chains were the primary mode by which mangroves support nearshore secondary production. This initial paradigm was modified in the early 1980s to include alternative energy and carbon sources for consumers (Odum et al., 1982), but much of the idea that mangroves are linked to coastal secondary production and energy flow rested, until very recently, on carbon fixed by mangroves.

Recent work indicates that various types of algae are a preferred food for many organisms, including those ordinarily classified as detritivores and that herbivory and omnivory are more common than previously believed (Ellison and Farnsworth, 2001; Bouillon et al., 2008). Grapsid crabs are often voracious consumers of mangrove detritus and leaves, but the nutritional rationale for ingesting such material has been a mystery, as mangrove material is high in tannin and $C:N$ content. Even aged leaves that have undergone microbial enrichment do not possess enough sustenance, especially labile nitrogenous compounds, to maintain crab nutrition. How do crabs sustain themselves? The answer is that grapsid crabs consume other foods in order to sustain a balanced diet. In field experiments, Skov and Hartnoll (2002) observed that crabs fed mostly on sediment, with <10% of the time spent on eating leaves. These observations suggest that crabs forage on bacteria, protists, fungi, and other small organisms from the sediment surface and within their burrows. Indeed, ocypodid crabs have high assimilation efficiencies for bacteria and are efficient consumers of benthic microalgae (France, 1998; Kristensen and Alongi, 2006). Grapsid crabs may behave similarly. Recent evidence using fatty acid markers suggests that grapsid crabs consume fungi and bacteria in addition to mangrove litter, whereas ocypodid crabs consume mostly benthic microalgae (Meziane et al., 2006); both groups supplement their diets with other foods.

The use of stable isotopes established that zooplankton (Bouillon et al., 2000; Werry and Lee, 2005; Schwamborn et al., 2006), polychaetes (Hsieh et al., 2002), fish (Melville and Connolly, 2004), and a variety of other macroinvertebrates (Bouillon et al., 2002) consume and often utilize various algal foods in order to sustain their nutrition. Studies conducted in southeast India have found that benthic invertebrates rely almost entirely on benthic microalgae (Bouillon et al., 2000, 2002, 2004, 2008). However, southeast Indian mangrove estuaries are the exemplar of coastal habitats subjected to a wide variety of pollutants, especially organic wastes from heavily populated catchments (Sudhakar and Venkateswarlu, 1989) and so may be atypical of other mangroves. With such high organic loading, Indian estuaries have very high rates of primary production (Monbet, 1992), thus the

diets of the animals in these habitats reflect the high availability of algal foods, such as benthic microalgae and phytoplankton.

On the trees, the arboreal fauna is known to readily feed on various organisms growing epiphytically on stems, branches, fallen timber, and pneumatophores (Kathiresan and Bingham, 2001). Terrestrial and semiterrestrial gastropods, mites, crustaceans and insects, as well as nematodes, copepods, and other estuarine biota colonize vertical wood structures in mangrove forests and use both sessile and planktonic algae for food (Alongi and Sasekumar, 1992; Nagelkerken et al., 2008). Even pneumatophores are sites of intense biological and trophic activity involving highly diverse and abundant metazoan and algal communities (Proches and Marshall, 2002). Regardless of physical niche, it makes nutritional sense for secondary consumers to feed on a variety of foods of higher nutritional quality in addition to mangrove detritus.

2.9. Mangroves are an important link to fisheries

Mangroves have long been considered important nursery grounds for finfish and shellfish (Macnae, 1968). This paradigm, however, is still controversial because it has rarely, if ever, been empirically tested. There is little direct evidence of a positive relationship between mangrove area and fisheries yield (Faunce and Serafy, 2006). One reason for this lack of empiricism is the fact that most species utilize mangroves for only part of their life cycle and for only part of the time in synchrony with the tides, using other habitats, such as adjacent seagrass beds and coral reefs, when mangroves are inaccessible (Sheaves, 2005). These biological connections between mangroves, seagrass beds, intertidal flats, and coral reefs have been considered by Sheaves (2005) as an "interconnected habitat mosaic," in which the connectivity of these different habitats must be considered when establishing the nature of mangrove–fisheries linkages. This idea is a more realistic and pragmatic consideration of the problem than the simplistic views (and studies) offered in the past and is supported by more recent analyses of the available data for shrimp (Lee, 2004) and for all fisheries, including finfish (Saintilan, 2004; Manson et al., 2005).

The analysis of shrimp yield and mangrove data by Lee (2004) involved the use of principal components analysis rather than use of regression analysis as various independent variables are usually autocorrelated. Using data on mangrove area, tidal amplitude, rainfall, temperature, human population density, length of coastline, relative mangrove abundance, and marine shrimp catch, the analysis showed that shrimp yield is strongly correlated with tidal amplitude, suggesting that shrimp catch is influenced by the amount of intertidal area available and not just the area of mangroves. And while the length of coastline was a strong correlate, it is likely that this relationship reflects the simple fact that a longer (and larger) coastline would result in a larger shrimp catch. It does not necessarily mean that the presence of mangroves per se is the cause of greater shrimp yields. There was no significant relationship between shrimp catch and relative mangrove area. This analysis points to the idea offered by Sheaves (2005) for fish that the connectivity of adjacent habitats needs to be considered as shrimp do not utilize only mangroves as habitat

throughout their life cycle. Dietary evidence supports this view as stable isotope studies have shown that the proportion of mangrove matter used as food for shrimp declines further offshore. While shrimp proximal to mangroves are fairly mangrove food–dependent, offshore shrimp utilize mainly phytoplankton and, to a lesser extent, benthic microalgae (Chong et al., 2001). So, mangroves are important for a part of the life cycle of shrimp, but shrimp are not wholly dependent on mangrove forests and their waterways.

Mangroves appear to be linked to fisheries catch in three principle ways: as a refuge from predators, as a source for food, and as shelter from environmental disturbance (Robertson and Blaber, 1992; Manson et al., 2005). Several studies have identified correlations between mangroves and fisheries, but as Manson et al. (2005) point out, correlative information does not shed light on causal relationships. Part of the problem from a statistical viewpoint is that some species are estuarine residents, spending their entire lives within the mangroves, whereas others spend only crucial juvenile stages in the estuaries, while some species are stragglers, moving into and out of the estuaries and having no clear dependence on mangroves. These various life styles and consequent relationships of fish and shrimp with mangroves are too subtle to be captured statistically. A diverse array of fish and invertebrate species clearly use mangrove habitats for a variety of reasons, for different periods of time, and at different life history stages. At present, it is difficult to separate the value of mangrove attributes from estuarine attributes more generally, as the exact nature of fisheries use of mangroves is not clearly understood (Manson et al., 2005).

Empirical evidence of the importance of mangroves to fisheries species lies in studies that have considered the effect of changes in mangrove habitat on faunal abundance and diversity. Manson et al. (2005) cited studies that found (1) a loss of densities and diversity of fauna commensurate with the loss of mangrove forest, (2) a decline in faunal richness and abundance with physical disturbance, and (3) a net gain in faunal numbers and species diversity with an increase in mangrove forest. Thus, the global decline in mangrove forest area (Wilkie and Fortuna, 2003) has likely resulted in a loss of faunal (and floral) biodiversity and yield of fisheries species.

2.10. Mangroves are chemically diverse and a good source of natural products

Mangroves, like other tropical vascular plants, possess a number of chemical defense mechanisms against potential herbivores. Chemical metabolites derived from mangroves have been used traditionally by indigenous people for centuries but, until recently, the chemistry of these natural products has remained poorly defined (Bandaranayake, 2002). We now know that most mangrove species produce a plethora of natural products, such as antioxidants and terpenoids, to modulate physiological activities, including membrane permeability to salt and other solutes (Oku et al., 2003; Parida et al., 2004; Vijayavel et al., 2006) in addition to providing chemical defense.

Aliphatic alcohols and acids, amino acids, alkaloids, carbohydrates, lignins, polysaccharides, carotenoids, hydrocarbons, fatty acids, lipids, pheromones,

Table 6 Individual natural products discovered from mangroves and their uses

Mangrove species	Chemical	Real and Potential Use
Acanthus ilicifolius	Stigmasterol	Hypercholestrolemic properties
	2–Benzoxazoline	Nerve depressant, muscle relaxant
Bruguiera sexangula	Brugine	Antitumor activity
B. conjugata	Brugierol	Antibacterial, insecticidal activity
Heritiera littoralis	Vallapianin	Ichthyotoxin
Aegiceras corniculatum	Embelin, 5-O-methy embelin	Ichthyotoxin, antifungal
Excoecaria agallocha	Excoecarin	Ichthyotoxin
Rhizophora mucronata	Rhizophorine	Insecticidal, control diabetes, astringent
Sonneratia acida	2-nitro-4-(2′–nitroethenyl) phenol	Antihemorrhaging agent
Xylocarpus moluccenis, X. granatum	Xyloccensin 1 and 2	Antimalarial

Source: Bandaranayake (2002).

phorbol esters, phenolics, steroids, troterpenes, tannins and other terpenes, and related compounds have been isolated from various parts of mangroves. Extracts from mangroves and associated biota have proven activity against human, animal, and plant pathogens although the number of studies has, until very recently, been limited. Nearly all species of mangroves possess some chemical agents that have some human use (Bandaranayake, 2002; Table 6).

Mangroves are a rich source of toxins, such as rotenoids, alkaloids, and terpenoids, which can be developed as repellants or agrochemicals. These toxins, if properly developed and purified, may prove useful for the treatment of diseases. A good example is the drug sodium stiboggluconate, derived from *Acanthus ilicifolius*, and used to treat infections of *Leishmania donovani* (Kapil et al., 1994). Useful metabolites have also been discovered from mangrove–associated biota, such as fungi (Chen et al., 2003; Wu et al., 2005). In addition, it has been proposed that hydrocarbon–degrading bacteria should be batch cultured and used to biologically degrade oil spills (Brito et al., 2006). Clearly, the chemistry and potential benefits of natural products derived from mangrove tissues has just begun to be adequately explored.

3. Conclusions

Mangrove forests have often been viewed as tropical counterparts to salt marshes, with analogous roles in the ecology of coastal food webs and energy flow. Often underappreciated, even by scientists, a picture is gradually emerging of a highly dynamic and complex ecosystem that (while similar in some respects to salt

marshes) is unique. Mangroves are not simple systems whose main function is to support and supplement coastal food webs but are highly productive forests with complex physiological and growth processes (especially in relation to climate patterns), high species diversity of biota, highly evolved plant–soil and arboreal animal–plant relations, and high chemical diversity. They are indeed important to fisheries, including species important to adjacent tidal flats, seagrass meadows, and coral reefs, making these tidal forests of considerable ecological and economic importance, disproportionate to their dwindling area worldwide.

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